Relative performance of eelgrass genotypes shifts during an extreme warming event: disentangling the roles of multiple traits

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ABSTRACT: Extreme climatic events can lead to rapid yet long-term ecosystem alteration, especially when such events impact foundation species. The response and recovery of these foundation species will depend on the diversity and plasticity of traits within these species. However, it is often unknown which traits determine foundation species′ performance under average compared to extreme climatic conditions. Eelgrass *Zostera marina* is a marine foundation species distributed along coastlines throughout the northern hemisphere, on which a unique community of fishes and invertebrates depends. We assessed the performance (i.e. productivity) of 36 genotypes of *Z. marina* across winter and summer seasons, during one average year (2013) and one year in which summertime temperatures were 2.5°C above average (2014). We used structural equation modeling to relate trait data to variation in performance of genotypes across environmental conditions. Genotypes with the highest productivity during winter were predicted by traits related to light capture (leaf length and photosynthetic efficiency). During the extremely warm summer, genotypes with the lowest winter shoot densities, the longest summer leaves, and the lowest sensitivity to high light (least photoinhibited) achieved the highest productivity. Because traits related to high winter performance differed from traits related to high summer performance, genotype performance rank order shifted through time. By directly linking functional trait differences to performance, our results demonstrate how genotypic composition could be shifted by an extreme climatic event and how genetic diversity may contribute to population resilience in the face of a changing climate.

KEY WORDS: Extreme climatic events · Ocean warming · Functional traits · Genotype performance · *Zostera marina*

1. INTRODUCTION

Anthropogenic climate change is escalating extreme climatic events such as persistent droughts, high-intensity storms, and heat waves (Luterbacher et al. 2004, Schar et al. 2004, Coumou & Rahmstorf 2012). The resilience of species facing extreme climatic events depends not only on the severity of change, but also on the diversity of functional traits within a population, the heritability or plasticity in those traits, and the connectivity between populations (Bernhardt & Leslie 2013). Extreme conditions can select against genotypes within a population that are either intolerant of, or unable to acclimate (Chevin et al. 2010, Hoffmann & Sgro 2011). However, the occurrence of extreme climatic events also creates

increased variability in environmental conditions that could promote or maintain diversity by creating fluctuating selection (Chesson 2000, Shurin et al. 2010), select for highly plastic 'generalist' phenotypes (Moran 1992), and potentially counteract directional selection by changing climatic means (Adler et al. 2006).

In ecosystems dominated by a sessile and long-lived foundation species, functional trait diversity and trait plasticity at the genotypic level will likely play key roles in determining ecosystem-wide response to extreme climatic events. Genotypic diversity in foundation species influences many facets of ecosystem and community processes (Crutsinger et al. 2006, Johnson et al. 2006, Bangert et al. 2008, Hughes & Stachowicz 2009). Some evidence shows that intraspecific trait complementarity underlies this diversity effect (Vavrek et al. 1996, Albert et al. 2011, Hughes & Stachowicz 2011, Abbott et al. 2017), but links to specific traits have yet to be identified in most cases. Therefore, to better understand how foundation species will respond to extreme climatic events, it is essential to quantify the diversity in functional traits across genotypes within populations and relate these traits to genotype performance. However, the link between traits and performance is complicated and can be the result of a network of direct and indirect effects, as well as interactions between genetically determined traits, acclimation, and environmental conditions. Thus far, simple approaches have had limited success in identifying how changing climate interacts with trait assemblages to determine performance.

The temperate seagrass *Zostera marina* is a foundation species that forms vast intertidal and shallow subtidal meadows throughout the northern hemisphere (Moore & Short 2006). *Zostera marina* experiences temporal fluctuations in key environmental parameters such as light, temperature, nutrients, and salinity on both short time scales (i.e. daily and tidal fluctuations) and longer time scales (i.e. seasonal and interannual variation). Genotypes of *Z. marina* vary in their physiological and morphological responses to changes in these environmental parameters (Ehlers et al. 2008, Tomas et al. 2011, Salo et al. 2015, Reynolds et al. 2016). Difference in genotype response (genotype−environment interaction) is thought to underlie the diversity effect observed where *Z. marina* plots with greater numbers of genotypes are more resilient to disturbance from extreme warming events, algal blooms, and geese grazing (Hughes & Stachowicz 2004, 2011, Reusch et al. 2005). Similarly, functional trait diver-

sity determines the outcome of interactions among eelgrass genotypes (Abbott & Stachowicz 2016) and promotes ecosystem functioning (Abbott et al. 2017). However, the link between specific traits and trade-offs in genotype performance across different environmental conditions is unclear, limiting our ability to predict population responses based on standing trait diversity.

Here, we measured growth and functional traits of 36 genotypes of *Z. marina* in a common garden setting for 2 yr (2013−2014) during both the winter and summer seasons. We determined if genotype performance rank order, quantified in terms of above-ground productivity (leaf area production per day), was consistent across seasons and years that varied in both temperature and light regimes. In particular, we were interested in how the extreme ocean warming event in the northern Pacific Ocean during summer 2014 (known as The Blob) (Bond et al. 2015) could have contributed to unusual patterns in productivity among genotypes. We used structural equation modeling (SEM) as a first attempt to assess which traits might explain variation in plant response to changing environmental conditions, across winter and summer seasons and during an extreme ocean warming event.

2. MATERIALS AND METHODS

2.1. Field collection and propagation in common garden

During May 2012, eelgrass (*Zostera marina*) ramets were collected along 40 m transects from 3 tidal heights at 5 sites within Bodega Harbor, Bodega Bay, CA, USA (see Abbott et al. 2018 for details and GPS coordinates of collection locations). We identified 219 unique genotypes using 11 microsatellite markers previously designed for *Z. marina* (Abbott et al. 2018). From the original 219 genotypes, we selected 36 genotypes to propagate in common garden conditions; these genotypes represented individuals from all tidal heights and sites, included both close genetic relatives and distantly related individuals, and were subsequently demonstrated to cover a broad range of trait space across 17 different traits (see Abbott et al. 2018). Leaves and rhizomes of each individual were trimmed (to 30 cm and 3 cm, respectively) and then each ramet was planted in homogenized sediment collected from Bodega Harbor in 3.79 l plastic flowerpots. All potted individuals were kept in a single outdoor tank at the Bodega Marine Laboratory, Bodega

Bay, CA, USA. The common garden was provided with a constant flow-through supply of seawater, sand filtered to 30 µm. Genotypes were grown for 1 yr to allow new side shoots to develop within the common garden environment. We rotated the pots once a week to reduce any position effects created by light or flow gradients within the tank. We logged seawater temperature every 15 min using an Onset HOBO Light and Temperature Pendant. We used the sea surface irradiance (photosynthetically active radiation, PAR) data from the Bodega Ocean Observing Node (boon.ucdavis.edu/) and extrapolated these continuous measurements using an extinction coefficient obtained by measuring average daily irradiance during August 2013 at a 30 cm depth in the common garden using a Li-COR Spherical Quantum Sensor (K. Dubois unpubl. data). We measured water column nitrate levels within the common garden by taking 3 water samples during each of the 2014 time points (winter 2014: 19−21 and 24−25 February; summer 2014: 25−29 August). These water samples were analyzed for total nitrates using a LACHAT FIA 8000 series autoanalyzer (method number 31-107-04-1-E).

2.2. Productivity and morphology measurements

We measured productivity and morphology on all 36 genotypes by selecting 5 clonal shoots (sub replicates) per pot for trait determination. We used the 'hole punch' method (see Dennison 1987) to non-destructively determine the leaf growth rates of all leaves on each shoot measured. We calculated productivity as the new leaf area (length elongation multiplied by leaf width) divided by the number of days since initial hole punch (5−14 d). We consider leaf productivity a good proxy for plant-level performance because it is positively correlated with net photosynthesis, metabolic carbon balance, and biomass change (Dennison 1987), and declines in response to a range of stressors such as light limitation (Dennison 1987), high temperatures (Hammer et al. 2018), anoxia and sulfide toxicity (Terrados et al. 1999, Holmer & Bondgaard 2001), and nutrient limitation (Short 1987).

We also measured shoot- and clonal-level traits for each genotype including shoot length, width, number of leaves per shoot, and shoot density. We considered shoot density a genotype-specific trait because after an initial increase, all genotypes reached a stable density that lasted for at least 1 yr (see Fig. S2B,C in the Supplement at www.int-res.com/articles/suppl/m615p067_supp.pdf). Thus, we

could not measure asexual reproduction under these common garden conditions because there was no net change in shoot density once this stable density was reached. We were also unable to assess sexual reproduction (i.e. seed production) as flowering shoots were removed to prevent the introduction of new genotypes into the common garden. Productivity and morphology measurements were taken at 4 time points: winter 2013 (19−27 December 2012), summer 2013 (18−27 September 2013), winter 2014 (19−21 and 24−25 February 2014), and summer 2014 (25−29 August 2014). Additionally, we acquired productivity data from a separate planting of these 36 genotypes in an adjacent mesocosm during July 2014 (Abbott et al. 2018).

2.3. Chlorophyll fluorescence measurements

We measured pulse amplitude modulation (PAM) chlorophyll fluorescence using a diving PAM (Walz, Germany) during winter 2014 and summer 2014. We measured fluorescence on the same 5 shoots for each of the 36 genotypes used to obtain productivity and morphology measurements. The order of genotypes being measured was randomized each day, and measurements were taken between 09:00 h and 14:00 h to minimize the effect of diurnal cycles in photosynthesis. We completed measurements on all genotypes over 5 consecutive days. To take fluorescence measurements, we placed a 4 mm diameter leaf clip on the outer surface of the third leaf, 20 cm from the base of the shoot. We gently cleaned the leaves of epiphytes using tissues prior to placing the leaf clip for 30 min of dark acclimation. Maximal yield of photochemical energy conversion was determined (F_v/F_m, i.e. the proportion of photons absorbed into the photosystem) and a rapid light curve (RLC) was performed immediately after to assess light adaptation (see Ralph & Gademann 2005). For the RLC, actinic light from the diving PAM was applied in 8 incremental steps from 0 to 1400 µmol photons m^{-2} s^{-1}, and the resulting yield measurements were converted to relative electron transport rates (rETR) using the equation:

$$rETR = Yield \times PAR \times 0.5 \times AF \qquad (1)$$

where AF is the absorption factor of the leaf (a reasonable estimate of AF = 0.55 was used; see Cummings & Zimmerman 2003, Durako 2007), and 0.5 assumes that photons absorbed are equally distributed between photosystems I and II (Genty et al. 1989).

Data were fit to a double exponential decay function (Ralph & Gademann 2005):

$$\text{rETR} = P_s(1 - e^{-(\alpha E_d/P_s)}) \, e^{-(\beta E_d/P_s)} \qquad (2)$$

where P_s is the scaling factor that defines the maximum potential rETR and E_d is the irradiance (PAR) for any given step within an RLC. We determined the light-harvesting efficiency (α, the initial slope of the curve) and a metric for photoinhibition (β, the declining slope of the curve). From curve coefficients, we calculated maximum relative electron transport rate (rETR$_{\text{MAX}}$, the asymptote of the curve — a measure of the photosystem's capacity to use absorbed light), E_k (minimum saturating irradiance), and E_m (minimum irradiance for onset of photoinhibition) (Ralph & Gademann 2005). Curve fitting and parameter calculations were done in R (version 3.0.2, www.R-project.org)

2.4. Data analyses

First, we used our data to describe seasonal and interannual variation in environmental parameters and productivity. Differences among environmental parameters across seasons were evaluated using a 1-way ANOVA using daily averages for each day that trait measurements were taken for the following: temperature, maximum irradiance (I_{max}), hours of saturating irradiance (H_{sat}, based on ETR values calculated above), and water column nitrate. In order to assess how productivity in the common garden varied through time, we compared the average productivity of all genotypes combined across all 4 time points using repeated-measures ANOVA. We also compared variation in common garden-level average productivity, morphology, and photosynthetic parameters between winter and summer 2014 using a paired t-test. We tested for correlations between the average productivity in the common garden at 5 different time points (including the fifth time point from Abbott et al. 2018) and 3 environmental parameters: temperature, I_{max}, and H_{sat}.

Next, we assessed how the productivity of individual genotypes varied over time and in response to environmental changes. For each time point, we averaged the 5 shoot-level productivity measurements (sub-replicates) to estimate mean productivity for each genotype. We then assessed whether genotype rank order for productivity was consistent across seasons using Kendall's rank correlation.

Within 2014, we observed strong differences among genotype rank productivity in summer compared

to winter (see 'Results'). We used observed-variable structural equation modeling (SEM) to investigate how differences in morphological and photosynthetic traits contributed to this variation. First, we selected 5 traits out of the 11 measured that we hypothesized to have the greatest influence on productivity and were least redundant in terms of quantifying genotype physiology (see Table S1 in the Supplement for justification). We then averaged the 5 shoot-level measurements (sub-replicates) to obtain one trait value for each genotype during each season: winter and summer 2014. We standardized trait data into z-scores to allow for comparisons of traits with different units of measurement. We then confirmed that data were multivariate normal using the Mardia's multivariate normality test from the R package 'MVN' (Korkmaz et al. 2014). We started with a meta-SEM that incorporated all 5 traits at each time point (see 'Results'), and then through an exploratory model-building process attained more parsimonious models by consecutively removing insignificant paths until all remaining paths were significant. We then explored additional paths suggested by the model's modification indices, which identify potential missing correlations based on global estimation of the model. For the nested candidate models that fit the data, we used Akaike's information criterion (AIC) (Mitchell 1992, Preacher 2006, Grace et al. 2010) and knowledge of *Z. marina* physiology from the literature to select the most likely model (Table S1 in the Supplement). We confirmed that the residuals of the selected model were multivariate normal. SEM was performed in the R package 'lavaan' (Rosseel 2012). All data analyses were performed in R (version 3.0.2, www.R-project.org).

3. RESULTS

3.1. Seasonal trends in common-garden-level productivity and environmental parameters

Average productivity of all 36 genotypes combined during summer 2014 was almost double that of the prior 3 seasons, which differed little from each other ($p < 0.001$, $F_{3,102} = 40.58$; post hoc Tukey, $p < 0.001$; Fig. 1A). This large spike in summer 2014 productivity coincided with summer seawater temperatures that were 2.5°C warmer than at the other 3 time points ($p < 0.001$, $F_{3,45} = 185$; post hoc Tukey, $p < 0.001$; Fig. 1B) and over 3 standard deviations higher than average summer seawater temperature recorded at the site over the previous 27 yr (see Fig. S1 in
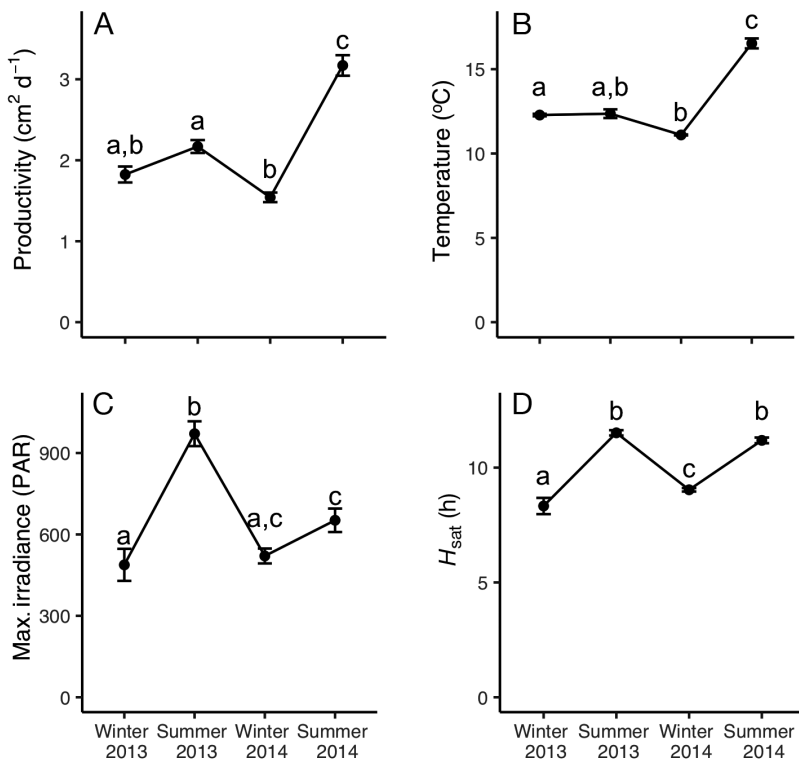
Fig. 1. (A) Average productivity for all 36 genotypes of eelgrass *Zostera marina* was significantly higher in the summer of 2014, as was (B) average seawater temperature. (C) Average maximum irradiance (I_{max}) varied across time points but not predictably by season. (D) Photoperiod (H_{sat}: hours of saturating irradiance) varied by season but was not significantly different between summers. Letters indicate statistically similar groups. N = 36

icantly lower than during the winter 2014 time point, 9.64 ± 0.44 and 12.17 ± 0.22 µM, respectively (p = 0.002, t = 7.37, df = 3.951), contrary to what would be expected if nitrate differences among seasons led to productivity differences.

Most morphological traits averaged across all genotypes (shoot width, leaf count, and shoot density) did not change significantly between time points, although overall, shoots were longer in the summer than in the winter (Table 1). PAM fluorometry measurements revealed physiological changes consistent with acclimation to higher light conditions in the summer, including increased maximum electron transport rate within photosystem II ($rETR_{max}$) and photosynthetic efficiency (α, represented as the rising slope of the RLC). Dark acclimated yield (a measure of the photosystems' ability to harvest electrons that is sensitive to environmental stressors) decreased from winter 2014 to summer 2014 (Table 1). Other PAM measurements did not change between winter and summer 2014 time points (Table 1).
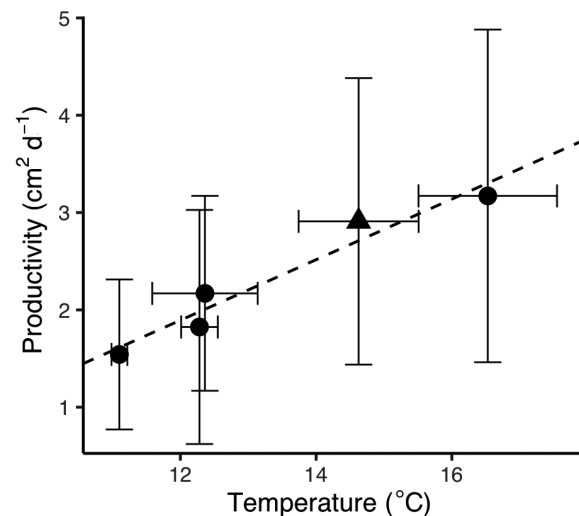
the Supplement). There was a strong positive relationship between average productivity of the 36 genotypes in common garden and seawater temperature (p = 0.009, R^2 = 0.94), at least for temperatures ranging from 11°C to 17°C (Fig. 2).

In contrast, although other environmental parameters such as H_{sat} and I_{max} varied across seasons (Fig. 1C,D), this variation was uncorrelated with the average productivity of the genotypes (p = 0.119, R^2 = 0.781 and p = 0.456, R^2 = 0.44, respectively; see Fig. S3 in the Supplement). H_{sat} varied by season (i.e. 3 h longer in the summer than winter) but was not significantly different between the summers (p < 0.001, $F_{3,48}$ = 64.61; post hoc Tukey, summer comparison: p = 0.68; Fig. 1D), even though the 2 summers differed considerably in productivity. Average maximum irradiance did not differ between winters, but was significantly lower during summer 2014, when productivity was highest (p < 0.001, $F_{3,49}$ = 20.89; post hoc Tukey, winter comparison: p = 0.937, summer comparison: p < 0.001; Fig. 1C). Average water column nitrate during summer 2014 was signif-

Fig. 2. Temperature is significantly correlated with the average productivity of the 36 *Zostera marina* genotypes (p = 0.009, R^2 = 0.94). Circles denote measurements taken from common garden plants; triangles are data taken from all 36 genotypes in a separate experiment (Abbott et al. 2018) during July of 2014. Error bars are ±1 SD, showing considerable variation among genotypes

Table 1. Paired *t*-test comparison of trait values during winter and summer 2014 averaged across all 36 genotypes. Data are means ± SD. Significant results are highlighted in **bold**

Parameter	Season		p
	Winter (n = 36)	Summer (n = 36)	
Productivity (cm^2 d^{-1})	1.51 ± 0.46	3.17 ± 1.04	**<0.001**
Shoot length (cm)	60.59 ± 13.63	96.96 ± 11.92	**<0.001**
Shoot width (cm)	6.29 ± 0.77	6.49 ± 0.78	0.28
Leaf count	3.28 ± 0.39	3.12 ± 0.33	0.07
Shoot density (shoots m^{-2})	518 ± 336	561 ± 337	0.33
Dark acclimated yield (%)	0.75 ± 0.21	0.72 ± 0.04	**<0.001**
Photosynthetic efficiency (α)	0.21 ± 0.04	0.23 ± 0.05	**0.02**
Photoinhibition (β)	0.009 ± 0.004	0.009 ± 0.005	0.99
Maximum electron transport rate ($rETR_{max}$, µmol electrons m^{-2} s^{-1})	4.12 ± 0.45	4.68 ± 0.60	**<0.001**
Saturating irradiance (E_k, µmol photons m^{-2} s^{-1})	57.73 ± 9.43	58.47 ± 11.07	0.76
Downwelling irradiance (E_m, µmol photons m^{-2} s^{-1})	356.15 ± 140.01	317.22 ± 121.79	0.21

3.2. Rank order of genotype productivity across seasons

Despite increased productivity when averaged across all genotypes during summer 2014, individual genotypes varied considerably in their response to elevated temperatures such that productivity of individual genotypes under increased temperatures was not predicted by productivity at cooler temperatures. Ranked order of performance (productivity) among genotypes in summer 2014 was uncorrelated with genotype rank during the previous season (p = 0.525, τ = 0.08; Fig. 3C). In contrast, rank order was very consistent across summers and winters between the other 3 time points, which did not differ much in

mean temperature. Genotypes with the highest productivity in summer 2013 also ranked the highest in productivity during winter 2013 and winter 2014 (p < 0.001, τ = 0.41 and p = 0.011, τ = 0.30, respectively; Fig. 3A,B).

3.3. Explaining variation among genotypes in response to unusual warming

SEM revealed traits predictive of individual genotype productivity and how trait variation resulted in shifts in rank order of genotype performance between winter and summer 2014. The best fitting model included the following predictor variables: shoot length, shoot density, photosynthetic efficiency (α), and summer photoinhibition (β) (Table 2, Fig. 4). The model better explains variation among genotype productivity during the summer (54%) than during the winter (32%). During winter 2014, genotypes with greater photosynthetic efficiency (α) and greater shoot length achieved the highest productivity. In contrast, during summer 2014, the genotypes with the lowest winter shoot densities, greater summer shoot length, and least sensitivity to summer photoinhibition (β) achieved the highest productivity.

The SEM did not find a direct relationship between winter productivity and summer productivity, and indirect pathways between these were both positive and negative. For example, genotypes with greater
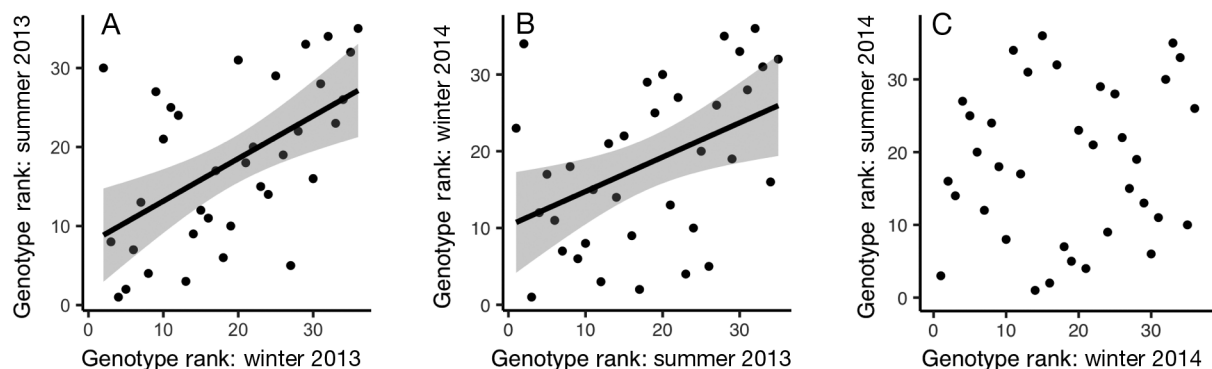

Fig. 3. Kendall's rank correlations for 36 *Zostera marina* genotypes ranked by average productivity between 4 consecutive time points: (A) winter 2013–summer 2013 (p < 0.001, τ = 0.41), (B) summer 2013–winter 2014 (p = 0.011, τ = 0.30), and (C) winter 2014–summer 2014 (p = 0.525, τ = 0.07). Shaded regions denote 95% confidence intervals. Data shown in C are the same productivity data used in structural equation modeling (see Fig. 4). N = 36

Table 2. Candidate path models (see Fig. 4A for meta-model). Model 7 was selected as the final model (**bold**) and is drawn in Fig. 4B. Models 4−7 are all similar and all fit the data. Model fit was determined using a chi-squared test of model fit, Fit (p); p-values greater than 0.05 denote good model fit. Models that fit the data were compared using Akaike's information criterion (AIC)

Model	Description	χ^2	DF	Fit (p)	AIC
1	Full meta-model: includes all traits (Fig. 4A)	60.4	35	0.005	N/A
2	Removed cross season correlations between shoot length, photoinhibition, and maximum electron transport rate	62.5	38	0.007	N/A
3	Removed maximum electron transport rate completely, and link between winter productivity and summer photosynthetic efficiency	41.9	26	0.025	N/A
4	Added links: winter shoot density to summer productivity, summer shoot length to summer shoot density, and summer shoot length to summer photoinhibition	25.3	21	0.234	564.27
5	Removed non-significant link between summer shoot length and summer shoot density	27.3	22	0.199	564.28
6	Removed non-significant link between summer shoot density and summer productivity	27.0	21	0.168	566.05
7	Added significant link between summer photosynthetic efficiency and summer photoinhibition	**24.0**	**22**	**0.345**	**561.01**

winter productivity had longer summer shoots, which had a direct positive effect on summer productivity and an indirect negative effect on summer productivity mediated by increasing susceptibility to summer photoinhibition. Thus, the SEM results are consistent with our finding that rank order in genotype productivity was uncorrelated across these seasons (Fig. 3C).

We also found links between traits across seasons that influenced productivity. Winter productivity was increased by greater winter photosynthetic efficiency (α) and shoot length during this light-limited period. Winter and summer α were positively correlated, indicating a likely genetic component to the trait. However, summer α did not directly affect summer productivity; instead summer β indirectly increased productivity by decreasing susceptibility to summer photoinhibition (β). In turn, summer β decreased summer productivity. Additionally, traits in one season could directly affect production in another: winter shoot density directly and negatively affected summer productivity.

4. DISCUSSION

Although temperature was strongly positively correlated with mean eelgrass productivity across seasons and years (Fig. 2), this did not result from uniform increases in productivity of all genotypes with temperature (Fig. 3). There was a clear shuffling of genotype productivity rank that was associated with the anomalously warm summer of 2014 (Fig. 1). For

several reasons it seems likely that temperature (rather than light) was responsible for the changes in the rank order of genotype productivity that we observed across seasons in 2014. First, there was a positive correlation in the rank order of genotype productivity between winter 2013 and summer 2013 (Fig. 3), which had similar mean temperatures, but different light levels (Fig. 1). Second, in a separate study, we found that experimentally mimicking the summer 2014 warming event differentially affected shoot production among *Zostera marina* genotypes (Reynolds et al. 2016). Thus, our results suggest that extreme events can shift genotypic productivity rank order, and to the extent that productivity differences translate to relative abundances of clonal plants in the field (Pan & Price 2001), influence genotypic composition and ecosystem function.

Differences in the morphological and photosynthetic traits appear to underlie the variable response of genotypes through time (Fig. 4). Our analysis provides evidence that the same traits can have different effects on productivity across seasons, due to both direct and indirect linkages between traits and production that are revealed by SEM. Below, we detail several pathways that may contribute to the positive correlation in growth among genotypes in some years (winter−summer 2013) and lack of correlation in others (winter−summer 2014).

First, in winter, when light conditions are lowest, genotypes with high photosynthetic efficiency (i.e. large α) or longer shoots (i.e. more photosynthetic tissue) had the greatest productivity (Fig. 4B). Winter genotypes with high productivity had longer summer

Winter 2014   Summer 2014
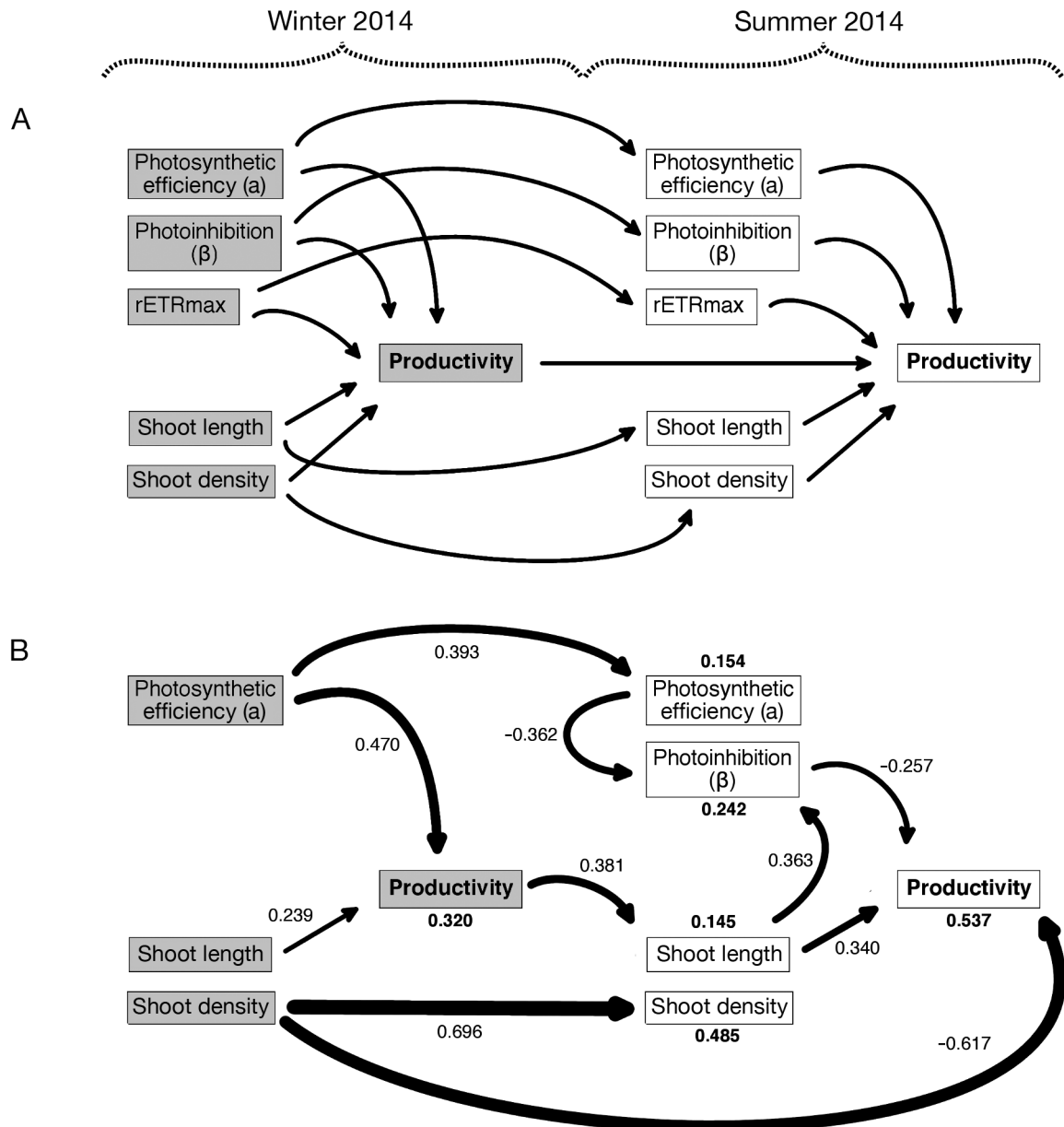
A

B

Fig. 4. Path diagrams of (A) the theoretical meta-model and (B) the selected model. The selected model (B) demonstrates that traits related to productivity differ between time points and that changes in relative productivity among *Zostera marina* genotypes during summer 2014 were primarily driven by a legacy effect of winter shoot density. Gray shaded variables are winter 2014 measurements; unshaded variables are summer 2014 measurements. In the selected model (B), all paths are significant. Coefficients of determination are shown in bold by the endogenous variables: winter productivity, summer productivity, summer shoot density, summer shoot length, summer photosynthetic efficiency, and summer photoinhibition. Path regression coefficients are standardized. Arrow widths in (B) are proportional to the value of the path regression coefficients. N = 72

leaves, which led to both a direct increase and an indirect decrease in summer productivity. Genotypes with long summer leaves were the most sensitive to high light conditions, expressed as higher photoinhibition (i.e. large β), which decreased summer productivity (Fig. 4B). Summer shoot length could result in increased photoinhibition if longer leaves

were older and thus less efficient or more damaged from grazing or epiphytes (Alcoverro et al. 1998, Ralph et al. 2005). The positive relationship between shoot length and photoinhibition could be strengthened by stressful, high temperatures because enzyme processes that reduce photoinhibition are damaged when seagrass experiences temperature

stress (Campbell et al. 2006, Lee et al. 2007). This would counteract positive relationships between shoot length and productivity, decoupling genotype rank order between the winter and summer of 2014 (Fig. 3C). Consistent with this, in the cooler year of 2013, there was a positive correlation between summer and winter productivity, suggesting that in the absence of temperature stress, the direct positive effect of shoot length (Fig. S8 in the Supplement) outweighs the indirect negative effect of photoinhibition.

A second pathway within our SEM highlights how genetically determined traits can cause legacy effects that can produce an unfit phenotype in future contexts. Shoot density is a genotype-specific trait that remained stable after genotypes reach individual carrying capacity after 1 yr in common garden (Fig. S2 in the Supplement), and winter shoot density has a negative effect on summer productivity. It is possible that this negative legacy effect of winter shoot density on productivity during an extremely hot summer is due to genotypic differences in stored carbohydrates, which buffer seagrass production under seasonal stress (Zimmerman et al. 1995, Alcoverro et al. 2001, Govers et al. 2015). Overwintering in high-density ramets decreases stored carbohydrates and survival by increasing winter respiratory demand (Vermaat & Verhagen 1996, Alcoverro et al. 2001). If relative differences in carbohydrate stores are persistent, genotypes with high shoot density during the winter could have fewer stored carbohydrates to maintain relative productivity during a period of extremely high temperatures.

Alternatively, winter and summer shoot densities are highly correlated, and it is possible that high summer shoot densities could decrease productivity via self-shading (Dennison 1987, Vermaat & Verhagen 1996, Ralph et al. 2007). However, we found evidence that photoinhibition at the base of the plant negatively affected summer productivity (Fig. 4), suggesting that even beneath the canopy light was not limiting. Furthermore, differences in light levels as a function of shoot density were modest: using light extinction coefficients measured in the common garden for the densest genotype ($k = 0.29$) and adjacent clear water ($k = 0.79$), we found that across all genotypes, the number of hours of saturating irradiance was greater than 10 and differed by only about 10% within versus outside the eelgrass canopy. Consequently, our data do not support summer self-shading as a mechanism linking summer shoot density and productivity in our mesocosms. Regardless of how winter density is mechanistically linked to sum-

mer productivity, shoot density was not related to winter productivity but did negatively influence summer productivity, predominantly driving the change of genotype rank during summer 2014.

While the 2 pathways described above link photo-physiological and morphological traits to shifts in genotype relative performance through negative correlations, other pathways simultaneously reveal robust positive correlations through time. For example, photosynthetic efficiency (α) ultimately has a positive effect on productivity in both seasons, but the mechanism by which the trait acts in each season differs. During the summer, the positive effect of photosynthetic efficiency (α) was achieved by reducing the impact of photoinhibition (β) on productivity. Under high light conditions, the fraction of excitation energy that can be used in photochemistry becomes less, allowing excess energy to cause greater photodamage in the photosystem II (PSII) and greater photoinhibition (Lambers et al. 2008). Consequently, genotypes that are more efficient at light capture could be less likely to accumulate damage to PS II, as seen in the negative path connecting summer photosynthetic efficiency to summer photoinhibition. In the winter, under low-light conditions, high photosynthetic efficiency (α) directly increases productivity by allowing for better light harvesting. Thus, genotypes characterized by higher photosynthetic efficiency are predicted to perform better in both seasons, but for different reasons. However, under the warmer summer conditions of 2014, simultaneous positive and negative correlations between traits and performance result in the lack of correlated genotype performance through time, and demonstrate how a suite of functional traits is required to tease apart the complex mechanisms underlying changing genotype performance across seasons and years.

As foundation species are critical to ecosystem functioning, understanding the links between traits and performance of foundation species can have broad, ecosystem-level implications. Additionally, the importance of facilitative interactions from foundation species should become increasingly important as environmental stress increases (Bruno et al. 2003, Anthelme et al. 2014), and will be essential for maintenance of associated species diversity when these species are limited in their ability to adapt or acclimate (Michalet et al. 2006, Bulleri et al. 2016). Idiosyncratic differences in community response to extreme warming events have been linked to differences among species in their functional traits (reviewed in Brotherton & Joyce 2015). In eelgrass, intraspecific trait diversity enhances biomass accu-

mulation and invertebrate grazer abundance (Abbott et al. 2017), influences the outcome of intraspecific interactions (Abbott & Stachowicz 2016), and likely underlies the observed relationship between genotypic diversity and ecosystem functioning (Hughes & Stachowicz 2004, 2011, Reusch et al. 2005, Duffy et al. 2015). Beyond eelgrass, decreased variability in photophysiological traits and genetic diversity of kelp was associated with population decline after an extreme warming event (Wernberg et al. 2018), suggesting that links between trait diversity and the maintenance of foundation species' biomass and functioning may be widespread. Our results demonstrate that variability in response to changing environmental conditions (such as seasonal fluctuations or extreme climatic events) can only be understood as the result of multiple physiological and morphological processes (Kraft et al. 2015), and that the net effect of these processes is context dependent. Clarifying the suites of traits that drive individuals' responses to a changing environment, as well as describing the distribution of functional trait variation within and among populations, should improve predictions of which populations are most vulnerable to extreme events.

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