Form-function relationships in a marine foundation species depend on scale: a shoot to global perspective from a distributed ecological experiment

Running page head: Global form-function relationships in eelgrass

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Abstract

Form-function relationships in plants underlie their ecosystem roles in supporting higher trophic levels through primary production, detrital pathways, and habitat provision. For widespread, phenotypically-variable plants, productivity may differ not only across abiotic conditions, but also from distinct morphological or demographic traits. A single foundation species, eelgrass (*Zostera marina*), typically dominates north temperate seagrass meadows, which we studied across 14 sites spanning 32-61° N latitude and two ocean basins. Body size varied by nearly two orders of magnitude through this range, and was largest at mid-latitudes and in the Pacific Ocean. At the global scale, neither latitude, site-level environmental conditions, nor body size helped predict productivity (relative growth rate 1-2% d^{-1} at most sites), suggesting a remarkable capacity of *Z. marina* to achieve similar productivity in summer. Furthermore, among a suite of stressors applied within sites, only ambient leaf damage reduced productivity; grazer reduction and nutrient addition had no effect on eelgrass size or growth. Scale-dependence was evident in different allometric relationships within and across sites for productivity and for modules (leaf count) relative to size. *Z. marina* provides a range of ecosystem functions related to both body size (habitat provision, water flow) and growth rates (food, carbon dynamics). Our observed decoupling of body size and maximum production suggests that geographic variation in these ecosystem functions may be independent, with a future need to resolve how local adaptation or plasticity of body size might actually enable more consistent peak productivity across disparate environmental conditions.

Key words: seagrass productivity, allometry, multiple stressors

Introduction

Because they underlie habitat provision and food web support, plant form and function provide critical linkages from species to ecosystem processes. Plant traits differ reliably among taxa (Kattge et al. 2011), yet may also be modified by the plant's experience of its local environment. Thus ecologists have framed their understanding of form and function in two ways. First, traits of a particular species could differ across contexts due to variability in bottom-up limitation or top-down control; these constitute external constraints (Fig. 1). Second, different allocation among traits may inherently follow plant size, as plants balance size-specific demands for support, transport and resource acquisition. Optimal branching patterns predict 3/4-power scaling relationships of photosynthetic area with size (Niklas and Enquist 2001), a pattern that has recently been extended from seed plants to kelps (large marine macrophytes; Starko and Martone 2016). Thus, as an internal constraint, plant productivity (relative growth rate) declines with body size (Enquist et al. 1999; Fig. 1). Metabolic scaling relationships are expected to hold best for adult plants growing as monocultures under optimal conditions (generally across species varying by orders of magnitude in body size), whereas productivity reduced by external constraints clearly applies when conditions are not optimal, and comparisons often involve a single species in different contexts. Consequently, challenges emerge in any simultaneous consideration of internal vs. external factors influencing form-function relationships (Brown et al. 2004, Tilman et al. 2004). Here we examine plant form and function in the context of a distributed experimental manipulation of resources and consumers affecting a marine Angiosperm (eelgrass, *Zostera marina* L.). This plant typically occurs in monocultures forming meadows, occupies a broad geographic range from ~30-70°N in both Atlantic and Pacific Ocean basins, and spans two orders of magnitude in local adult body size. These attributes make it an excellent candidate for joint consideration of trophic dynamics, resources and conditions, and body size as drivers of plant productivity, while the distributed experiment enables scaling from shoot (within-site) to global scales (across-site).

Distributed experiments provide a test of general ecological concepts across contexts, where methodological approaches remain constant and therefore do not interfere with examining context-dependence (Borer et al. 2014a). Recent distributed experiments have demonstrated that consumers accelerate decomposition in streams (Boyero et al. 2011) and grasslands (Wall et al. 2008) and promote coexistence in grasslands (Borer et al. 2014b), while grassland production appears generally constrained by multiple nutrient limitation (Fay et al. 2015). Latitude underlies a portion of the context-dependence in results, perhaps through differences in thermal conditions or length of growing season. Similarly for altitude, in neighbor-removal experiments established at multiple sites along elevation gradients, competitive interactions among plants characterized low-elevation results, and these interactions became more facilitative under stressful high-elevation conditions (Callaway et al. 2002). Notwithstanding these distributed experimental tests of top-down, bottom-up, and within-trophic level control, terrestrial grassland annual production at a global scale is linked strongly to the amount and seasonality of precipitation (Knapp and Smith 2001, Guo et al. 2012, Gang et al. 2015).

This brief compilation of terrestrial grassland studies, especially those with multi-site or large-scale considerations, already highlights several reasons why marine grasslands might function quite differently: 1) water is never limiting within the low intertidal and subtidal zones occupied by *Z. marina*; 2) *Z. marina* reaches high cover in meadows as the sole Angiosperm present, rather than being one of a functionally-diverse set of plants as in terrestrial grasslands; 3) annual production cannot be measured through changes in live or dead standing biomass of *Z.*

marina, due to rapid turnover of leaves – each lasting less than a growing season – followed by remineralization or export; 4) *Z. marina* can harbor dense epiphytic cover, which is targeted for consumption by mesograzers (small crustaceans and gastropods), such that eelgrass shoots receive little direct herbivory (with some notable exceptions); and 5) nutrient addition often favors competing microalgae – that is, eutrophication has been a global driver of the loss of seagrass meadows (Orth et al. 2006).

Perhaps because spatial variability in water resources is irrelevant, *Z. marina* provides exceptionally strong evidence of a latitudinal gradient in annual productivity (Olesen et al. 2015). These data come from the rate of leaf production by individuals (productivity), not from production per area, which is affected by spatial variation in cover unrelated to latitude (Clausen et al. 2014). Possible mechanisms include thermal constraints or short growing seasons that limit productivity at high latitudes. This latitudinal pattern in annual production is recapitulated in *Spartina alterniflora* (across ~17° latitude), a salt marsh grass that, like eelgrass, defines its habitat type (Kirwan et al. 2009), but perhaps not in giant kelp (*Macrocystis pyrifera*) whose growth responds to photoperiod at higher latitudes but nutrient availability at lower latitudes (Graham et al. 2007). With global patterns of annual productivity in eelgrass meadows well established, we focus instead on the productivity of plants under optimal conditions in summer, when rates of leaf turnover are typically most rapid. Because of targeting this maximum productivity, distinct predictions at the global scale emerge from internal and external constraints (Fig. 1), the former predicting a decline in productivity with body size, and the latter predicting that body size or productivity differs by site-level environmental conditions. Additionally, range edges may include conditions that compromise peak performance, and since we are targeting a single grassland species, a unimodal latitudinal pattern in form and function could emerge.

Layered within this global perspective, our distributed experiment modified top-down and bottom-up factors in ways that could alleviate some potential constraints on productivity (Fig. 1). Key responses by epiphytes have already been published from this distributed experiment, showing that epiphytes increased by 30% when crustacean mesograzers were reduced but did not respond to water-column fertilization (Duffy et al. 2015). As we address the eelgrass response in this paper, we predict a negative effect of increased epiphyte load (due to competition; Neckles et al. 1993) and a positive effect of fertilizer where eelgrass beds tend to be nutrient-limited (Duarte 1990). At the same time, shoots experiencing direct damage could also contribute to within-site variability in productivity as an immediate response to reduced leaf area (Ruesink et al. 2012). Finally, much of the variability in shoot size within sites arises ontogenetically, such that productivity may decline with body size due to accumulation of non-productive tissue and self-shading (Pommerening and Muszta 2016). The negative relationship between productivity and body size is thus expected both across sites from metabolic scaling considerations for adult plants, and within sites from ontogenetic scaling (Fig. 1C). Nevertheless, as in the across-site case detailed above, distinct predictions about within-site patterns of productivity can be made with respect to body size and experimentally-manipulated environmental conditions.

We measured form and function traits of *Z. marina* at 14 sites spanning its wide biogeographic range, where we experimentally established mesograzer deterrent and fertilizer treatments in a factorial design. The above-ground morphology of *Z. marina* consists of several leaves, all essentially rectangles of the same width, bundled together at the base by a sheath (Fig. 1B). This morphology lends itself to several simple metrics of plant size based on measuring the length of each leaf, the sheath width and length (Echevarría-Heras et al. 2013). Leaf extension derives from a leaf-punching method, tracked as these holes move away from the basal meristem, and this absolute growth rate is used to calculate productivity (RGR, relative growth rate) as daily leaf extension relative to the summed length of all standing leaves (Dennison 1990, Herbert and Fourqurean 2009). We developed our predictions specifically for this marine plant, considering its peak summer productivity in monocultures across a variety of local environmental conditions and for ecotypes that differ dramatically in body size and allocation (e.g., Keddy 1987, Backman 1991, Short and Short 2003, Clausen et al. 2014, Fig. 1).

1) At the global scale, summer productivity could vary with A) body size, following metabolic scaling rules (internal), or B) latitude (external), declining in response to lower temperatures towards the pole, or increasing if lower-latitude populations experience stressful high temperatures or shorter photoperiod relative to higher-latitude sites. Overall, these countervailing factors could generate a mid-range peak in productivity.

2) At the local scale, productivity is expected to decline with A) body size (internal), but additionally be sensitive to B) increased epiphytes, C) limited nutrients, and D) leaf tissue loss (external).

Methods

We measured eelgrass growth at 14 sites within the *Zostera* Experimental Network in 2011 (Fig. 2A, Supplementary Material Appendix 1 Table A1). These sites are distributed throughout the range of *Z. marina*, including both Atlantic and Pacific coastlines and from 32° to 61°N. Sites were selected where perennial *Z. marina* spanned an alongshore distance of at least 100 m, and they ranged in cover of *Z. marina* from 17 to 93% (mean 67%; Supplementary Material Appendix 1 Table A2). More northerly sites were generally sampled later in the summer coincident with anticipated peak biomass (Clausen et al. 2014; Supplementary Material Appendix 1 Table A1).

Experimental design

At each site, an identical factorial experimental design was carried out to manipulate nutrients and mesograzers over a four-week period. Both nutrients and mesograzer deterrent were applied using slow-release methods in the water column, and the fully-factorial design resulted in four treatment groups (n=10 plots per treatment; Duffy et al. [2015]). Plots were triangular in shape, 50 cm on a side, and separated by ~2 m within a continuous area of *Z. marina*.

Eelgrass shoots were marked for growth during the third week of the experiment. Near the top of the leaf sheath, a puncture was made with a sharp wire or syringe in each of several shoots in each of the 40 plots per site (Dennison 1990). These marks on growing leaves diverged from the mark on the non-growing outer sheath as younger leaves grew from the basal meristem (= new leaf extension; Fig. 1B). After 6-16 days, the shoots were collected and one to three shoots per plot were measured for sheath length and width and the length of each leaf, distinguishing new leaf extension from distal portions above each leaf's mark that were originally present (Fig. 1B). (At one site (San Diego), the distance between each shoot base and the original mark in the leaf sheath was used as a surrogate for sheath length.) Body size was determined as the sum of all leaf lengths (from meristem to distal tip), multiplied by sheath width; this should index above-ground biomass since only leaves project above the sediment, and they are flat and can be assumed rectangular (Echevarría-Heras et al. 2013). Allometric relationships among traits were examined for maximum length (=canopy height), number of leaves, sheath width, and sheath length, with this last trait serving a unique role as it remained intact even when leaves were damaged or some abscised. Absolute growth rate (AGR) is daily leaf extension, considering all growing leaves (Fig. 1B). Relative growth rate (RGR) is the percentage of the total shoot that consists of each day's new growth (Herbert and Fourqurean 2009). The duration between marking and collecting differed across sites but these differences did not bias daily growth calculations (Supplementary Material Appendix 1 Table A1, A3).

Measurements from each shoot were further used to describe "leaf condition" along a spectrum from damaged to intact. This index was based only on the original leaf material above the sheath and not on new growth between marking and collecting (Fig. 1B). Once the total length of original leaf material was standardized to sheath length, larger values indicated more leaf material remaining above the sheath, and smaller values were associated with loss of whole or distal parts of leaves.

Within each plot, we determined epiphyte load as in Duffy et al. (2015). Epiphytes and associated material were gently scraped from one shoot per plot and chlorophyll-*a* (μg) was extracted for spectrophotometric analysis to estimate microalgal biomass. Chl-*a* was then divided by shoot dry mass to obtain epiphyte load per unit leaf biomass. Leaf nitrogen content was measured in the youngest leaf from three shoots per plot, including those measured for growth, which were dried and pooled for nutrient analysis on a CHN analyzer (Thermo Fisher Scientific Inc., Waltham, MA; Duffy et al. 2015).

Global variation in eelgrass size and productivity

Biogeographic patterns were tested for size and growth traits of *Z. marina* based on site-level means. We included latitude as a first- and second-order predictor, as well as ocean (Atlantic including Baltic Sea, or Pacific) to account for distinct evolutionary lineages of *Z. marina* (Olsen et al. 2004). While latitude and ocean may explain global traits statistically, they do not provide underlying mechanisms for variability. Limiting factors for plants span general categories of light, temperature, moisture (i.e., salinity in aquatic environments), and nutrients (Fig. 1C). Diversity (i.e., genotypic) promotes seagrass population growth, resistance and resilience to perturbations (Procaccini et al. 2007, Hughes and Stachowicz 2011). To test for these global-scale predictors, we took a model comparison approach to evaluate shoot size (sheath length) and RGR in relation to all possible subsets of nine abiotic and biotic variables that were both available at all sites and appeared in the published literature as potentially influential (Fig. 1C). These nine predictors were: minimum water depth, tidal amplitude, photoperiod, epiphyte load, total macrophyte cover, salinity, water temperature, % nitrogen in unfertilized leaf tissue, and *Z. marina* genotypic richness (Supplementary Material Appendix 1 Table A1-A3). All but the first two were specific to the time of study. All predictors were normalized (mean=0 and SD=1) so that model results show standardized coefficients. We compared all possible combinations of predictor variables and a null model with an intercept but no predictors. Interactions among predictors were not possible to include due to the high number of predictors relative to global sample size. The models were compared by Akaike's Information Criterion, adjusted for small sample size (AICc), which penalizes more complex models (Burnham and Anderson 2002), using the *dredge* function in the Multimodel Inference package in R (MuMIn; Barton 2015, R Core Team 2015).

Allometric relationships were determined for RGR as a function of $\log_{10}$(body size), motivated by metabolic scaling laws, and for leaf extension (AGR) relative to sheath length, which has precedent for eelgrass (Gaeckle et al. 2006). Allometry among plant traits was also examined for sheath width, maximum length, and number of leaves vs. sheath length. Allometric relationships are typically tested by reduced (standard) major axis regression on log-transformed values (Smith 2009), which we implemented in the *lmodel2* package in R (Legendre 2015). Each trait relationship was described by a slope and 95% confidence interval at each site, and also across sites based on site means. We considered allometric relationships to differ across scales if the 95% confidence intervals did not overlap.

Eelgrass size and productivity in the distributed experiment

Eelgrass was analyzed with respect to initial treatments of the distributed experiment (mesograzer deterrent and water-column fertilizer), as well as with respect to continuous variables representing nutrient conditions, epiphyte load, and shoot damage. Analyses were carried out for response variables of sheath length (size) and absolute growth rate. In the latter case, sheath length was included as a covariate because leaves from larger shoots extend faster (i.e., Fig. 3B). Sheath length and AGR were evaluated with deterrent, nutrients, and their interaction as fixed effects. Site and plot within site were random effects in linear mixed effects models. Analyses were performed in the *nlme* package in R (Pinheiro et al. 2016, R Core Team 2015), and we set an α-level of 0.05.

AGR was also modeled as a function of three continuous variables that are potential stressors to eelgrass: epiphyte load, nutrient limitation, and leaf damage. As in our analyses of deterrent and nutrient treatments, sheath length was included as a covariate. Epiphyte load was based on the plot-level measurement of epiphyte load (chl-*a* μg per gDW *Z. marina*). Nitrogen content of leaf tissue in each plot provided an index of nutrient limitation (cf. Duarte 1990). Leaf condition, which we calculated as the length of all original leaves per sheath length for each shoot (Fig. 1B), by definition reaches higher values in shoots with less damage. With sheath length in the denominator of leaf condition, some values of leaf condition appeared biologically unrealistic given typical numbers of leaves and their maximum length. Further, underestimates of sheath length could introduce artificial positive relationships between leaf condition and absolute growth. Thus, we censored shoots with leaf condition > 16 (Supplementary Material Appendix 4 Figure A2), a threshold that we set by considering it unlikely that shoots would retain more than four fully-extended leaves, especially as this referred only to leaf material present at the time of marking and still present at collection. This threshold reduced total shoot number from 856 to 704 and removed one site altogether (San Diego, consistent with underestimates of sheath length at that site). Because of our focus on within-site variability in epiphytes, nutrients, and damage, all of which had continuous distributions, we carried out separate multiple regressions using data at each site, then combined across sites using a meta-analytic approach. The multiple regressions generated mean effect sizes and standard errors for each predictor (sheath length, epiphyte load, leaf nitrogen content, and leaf condition) at each site; plot was included as a random effect at sites with more than one shoot measured per plot. Then we used the site-specific ratios of mean effect size to standard error as samples in a calculation of global mean and 95% confidence interval for each predictor variable.

Data deposition

Data are archived through the Biological and Chemical Oceanography Data Management Office (http://www.bco-dmo.org/project/472215; Duffy et al. 2014) and in DataDryad (doi:10.5061/dryad.r417d; Ruesink et al. 2017).

Results

Global variation in eelgrass size and productivity

We expected summer productivity to vary with latitude in either linear or quadratic relationship, but *Z. marina* RGR across 14 sites did not (Fig. 2C). Biogeographic patterns did, however, emerge for body size. Based on total leaf area, sheath length and canopy height, eelgrass shoots were largest in the middle of the latitudinal range (~42-50ºN) and larger at sites in the Pacific than Atlantic Ocean (Fig. 2B, Supplementary Material Appendix 2 Table A4).

In our more extensive comparison of models containing up to nine mechanistic predictors, none predicted site-level variation in sheath length well; the top model was the null model, with some support for size increasing with genotypic richness or leaf nitrogen content (Table 1). Relative growth rate was positively related to epiphyte load in all of the top four models, with the null model (ranked fifth) more than 2 AICc units away from the top model (Table 1). However, this across-site pattern was sensitive to a single site (Washington) with highest epiphyte load and RGR (Supplementary Material Appendix 1 Table A1, A3).

The relationship of productivity to body size, which we expected to emerge under internal constraints, showed distinct within- and across-site patterns. RGR declined with size within sites but did not change with size across sites (Fig. 3A, Supplementary Material Appendix 3 Table A5). Absolute growth rate increased with sheath length both within and across sites (Fig.

3B). This relationship was isometric across sites but within many sites showed positive allometry.

One other allometric comparison showed distinct within- and across-site patterns: number of leaves increased with sheath length at some sites, but did not differ by sheath length across sites (Fig. 4C). Sheath width increased slower than length (negative allometry) whereas canopy height was isometric with sheath length, but both relationships were similar within and across sites (Fig. 4A, B, Supplementary Material Appendix 3 Table A5; this supplement also documents a linear mixed-effects approach in which results align with reduced major axis regression).

Eelgrass size and productivity in the distributed experiment

The nutrient and food web manipulations imposed at each site had little overall consequence for eelgrass form and function. Neither deterrent, nutrients, nor their interaction had a significant effect on size (sheath length) or growth (daily leaf extension, standardized to sheath length; Table 2). Further, when epiphyte load and leaf nitrogen content were considered as continuous predictors across plots within sites, neither affected leaf extension (Fig. 5). However, growth increased significantly with leaf condition at an approximately one-to-one rate (Fig. 5). That is, each additional length of original leaf material per sheath length led to a similar additional amount of leaf extension d^{-1}; site-level coefficients for leaf condition averaged 1.45 (Supplementary Material Appendix 4 Table A7). Leaf condition is reduced by partial or entire loss of leaves, and such damage does not immediately change sheath length but reduces size-corrected growth.

Discussion

Internal constraints on plant architecture and productivity result in robust allometric relationships across taxa (Enquist et al. 1999, Niklas and Enquist 2001, Starko and Martone 2016). Across diverse seagrass species, allometry informs life history strategy and functional role. Larger species have lower productivity and lower frequencies of module initiation (leaves, branches), whereas smaller species have rapid rhizome extension and a vegetative colonization strategy (Duarte 1991). A unique aspect of our study was its attention to a single species exhibiting dramatic phenotypic variation (Fig. 1), studied biogeographically under peak local growing conditions. At this within-species view, an expected negative size-productivity relationship was not evident across sites (Fig. 3A). Possibly, *Z. marina* can achieve rapid productivity (RGR 1-2% d^{-1}) regardless of size due to its growth form in an aquatic environment, since it need not build up non-photosynthetic biomass (support structures) or self-shading leaves, and instead rapidly turns over its photosynthetic biomass. As a result, it also limits the build-up of epiphytes that are potential competitors. Some of the features that make *Z. marina* especially suited to a comparison of internal and external constraints on form-function relationships may also decouple size and productivity.

When form-function relationships are scale-dependent, different controls on trait expression must dominate across scales, while scale-dependence may also emerge statistically when different traits do not share the same degree of within- and across-site variability. In our data, both RGR and module (leaf) number were more variable within than across sites relative to body size (Fig. 3A, 4C). Thus, although different ecotypes converged on similar rates of biomass (and module) turnover in summer, ontogenetic development did not recapitulate the form-function variability observed across sites. Indeed, the accumulation of leaves in larger shoots within sites (Fig. 4C) helps to reconcile two otherwise opposing trends at this smaller scale, because larger shoots grow in total area faster than in sheath length: positive allometry for leaf extension relative to sheath length (Fig. 3B), but negative allometry for RGR relative to total leaf area (Fig. 3A). Going forward, it may be possible to link scale-dependence to plant growth form, for instance, consistent allometric relationships within and across sites for plants altering photosynthetic area through leaf number rather than size, or developing support structures ontogenetically.

Although internal constraints are germane to our study, focused on a single species under peak growing conditions, other distributed experiments have revealed a general role for external constraints on community-level responses. For instance, in multi-species grasslands, resource levels, diversity, and biomass (which accumulates during the growing season) show complex relationships (Grace et al. 2016), and consumers and resources interactively determine plant species coexistence (Borer et al. 2014b). In *Z. marina*, we found many traits to be unexpectedly robust to both across-site environmental variation (Table 1) and within-site manipulation of top-down and bottom-up drivers (Table 2, Fig. 5). We also found no latitudinal pattern in summer RGR (Fig. 2B), despite latitudinal declines in annual productivity of *Z. marina* (Olesen et al. 2015). How can a single species grow equally well under such different thermal, salinity, and resource levels? One possible explanation at the across-site scale comes from local adaptation, which generates locally-tuned traits, just as ecotypes of trees (*Pinus sylvestris*) from different latitudes have different optimal temperatures for growth (Rehfeldt et al. 2002). Additionally, what might make growth and form insensitive to experimental treatments? Seagrass systems contain two functionally-distinct groups of primary producers (seagrass, epiphytes), with epiphytes being the target of experimental treatments (Duffy et al. 2015). More generally, nutrients may either alleviate nutrient limitation or interfere with standing biomass or growth through proliferation of algal competitors (Hughes et al. 2004, Moksnes et al. 2008, Cabaço et al. 2013, Östman et al. 2016). Unfertilized shoots exceeded the threshold for nutrient limitation (1.8% nitrogen; Duarte 1990) at most sites (Supplementary Material Appendix 1 Table A2), which may have precluded any overall positive fertilizer effect. We can also draw on evidence from a few sites suggesting why an indirect effect (mediated through epiphytes) could be weak overall. Negative effects of epiphytes were evident in Virginia after two months of mesograzer exclusion (Reynolds et al. 2014), and in Sweden when fertilized, due to macroalgal blooms rather than epiphytic microalgae (unpublished data). In contrast, experimental removal of heavy epiphyte loads at Washington did not improve eelgrass RGR, which was already relatively rapid (Ruesink 2016). Overall, then, the diversity of direct and indirect pathways potentially linking plant responses to experimental treatments could obscure any general pattern, especially among just 14 sites in the present study.

Internal constraints predict negative size-productivity relationships from metabolic scaling, and external constraints predict that both growth and size could be limited in concert (Fig. 1). Such internal and external constraints have also been proposed as mechanisms for shrinking body size of many species under anthropogenic climate change (Sheridan and Bickford 2011) and for latitudinal patterns of body size (Blackburn et al. 1999). However, the scheme in Figure 1 was insufficient to capture all the form-function patterns in our distributed experiment, particularly because we did not predict a mid-range peak in body size or larger shoots at Pacific than Atlantic sites, independent of summer RGR (Fig. 2). These biogeographic patterns in size appear distinct from other taxa, despite the variety of body size patterns reported (e.g. Mousseau 1997, Meiri and Dayan 2003). Figure 1 also needs modifying for modular organisms to incorporate an external constraint from leaf damage (Fig. 5). Body size reduction (removing photosynthetic leaf area) immediately slowed growth (Fig. 5; positive size-productivity relationship, rather than the negative size-productivity relationship proposed in Fig. 1). The result here contrasts with some other studies of simulated or actual grazing that augments seagrass productivity or rate of branching (Valentine et al. 1997, Cebrian et al. 1998) in a manner similar to compensatory growth documented in terrestrial grasslands (McNaughton et al. 1983). Because water is a dense fluid, water motion can transport sloughed leaves of *Z. marina* away from their site of production, thus preventing build-up of litter that is part of the mechanism of compensatory growth in terrestrial grasslands. Both modifications of Figure 1 would benefit from data regarding allocation among photosynthetic tissues, since leaf area increases with either new shoots or larger leaves. The relationships here between size and productivity are at the level of ramets and could be different for genets. Similarly, compensatory growth may be more evident in shoot counts than in RGR, since shoot removal can be compensated by accelerated clonal production of shoots (Ruesink et al. 2012).

In the framework of ecological traits, body size may act as either a response trait, such that size characterizes particular environmental conditions, or as an effect trait driving productivity (Suding et al. 2008, Fig. 1C). A further aspect of size acting as an effect trait in foundation species arises when plant architecture shapes the modification of abiotic conditions and the suitability as habitat for other species. Because of the isometry of leaf extension (AGR) and canopy height relative to sheath length across sites (Fig. 4A, B), sheath length can serve as a reliable indicator of services deriving from other traits. However, the particular trait relationships documented in this distributed experiment mean that services related to architecture (habitat, flow reduction; Fonseca et al. 1982, Heck et al. 2003) may differ more than those related to RGR, such as summer carbon dynamics or detrital provisioning. For *Z. marina*, our results open up a new challenge to resolve the contributions of phenotypic plasticity and genetic adaptation underlying ecotypes, especially enabling convergent RGR across a wide range of environmental conditions in summer. Genetically based trait variation in *Z. marina* is well-established (Hughes et al. 2009, Winters et al. 2011), and local adaptation seems likely (Boström et al. 2004, Salo et al. 2014), but shoots are also able to remodel in response to changes in environmental conditions such as light, temperature, water motion, and disturbance (Ruesink et al. 2012, Eriander 2017). More broadly, our study points to the value of tracking variability in traits within species, in the context of an ongoing challenge to meld ecological perspectives emphasizing internal and external constraints. This melding is improved by setting up competing hypotheses at particular scales, while rich testing grounds exist in emerging trait databases – if collated with environmental data – and distributed studies.

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Supplementary material (Appendix oik.XXXXX at <www.oikosjournal.org/readers/appendix>).

Appendix 1-4.

Table 1. Standardized coefficients for top models relating eelgrass (*Zostera marina*) biometrics to nine predictor variables. Coefficients are provided for variables that appear in each model, with models ranked by AICc, and accordingly from model with most to least weight. Models with weight <0.02 are not shown.

Tidal amplitude	Total macrophyte cover	Photoperiod	Minimum depth	Epiphyte load	Genotypic richness	%N	Salinity	Temperature	AICc	Model wt
Response variable = Sheath length (mm), Intercept =156.3										
									176.0	0.108
					48.77				176.3	0.089
						45.74			176.7	0.073
	38.60								177.5	0.050
					43.92	40.47			178.0	0.039
31.03									178.1	0.036
								-30.72	178.2	0.036
					54.12			-38.27	178.3	0.034
				27.69					178.4	0.032
			-18.95						178.9	0.025
							16.55		179.0	0.024
		13.92							179.0	0.023
29.61					47.90				179.1	0.022
Response variable = Relative growth rate (% d^{-1}), Intercept = 1.651										
				0.279					21.8	0.131
				0.356	-0.214				22.0	0.121
			0.205	0.360					22.5	0.095
				0.240			-0.169		23.3	0.062
									23.9	0.045
							-0.225		23.9	0.045
	-0.103			0.296					24.9	0.027
			0.150	0.398	-0.166				25.0	0.027

Table 2. Results of linear mixed-effects models examining size and growth of eelgrass (*Zostera marina*) at 14 sites in summer 2011, with respect to experimental treatments of crustacean mesograzer deterrent and water column nutrient addition. Sheath length was included as a covariate of daily leaf extension, e.g. Fig. 2B. Total samples = 856. Bold is significant at α=0.05.

Response variable	Sheath length		Daily leaf extension per shoot	
	Effect size	SE	Effect size	SE
Intercept	**157.0**	**30.1**	**21.61**	**6.76**
Sheath length	--	--	**0.17**	**0.01**
Deterrent (D)	-1.55	3.74	-3.01	1.59
Nutrients (N)	-0.52	2.30	-1.59	1.28
D x N	0.35	3.22	1.93	1.80

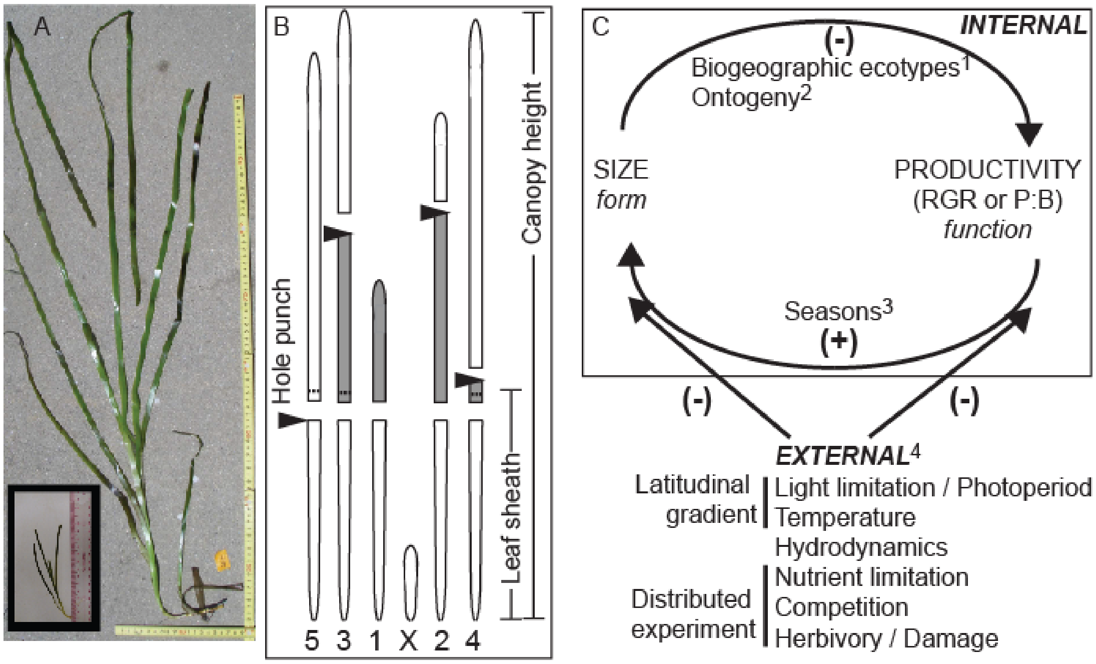

Figure 1. Eelgrass (*Zostera marina*) (A) ecotypes, (B) schematic representation of form and function traits, and (C) internal and external controls on form and function. Larger shoot was collected from Southern Japan (JS), smaller shoot from Virginia (VA), shown at same scale. The traits in panel (B) are shown for one eelgrass shoot with five intact leaves, separated in order from the enclosing leaf sheath. Grey represents leaf extension between marking and collecting. Distal leaf material in white is greater when shoots retain more intact leaves, used to calculate leaf condition. Superscripts in panel (C) refer to supporting citations: [1]Enquist et al. 1999, [2]Pommerening and Muszta 2016, [3]Gaeckle et al. 2006, [4]Koch et al. 2001, Lee et al. 2007, Yang et al. 2013. RGR = relative growth rate; P:B = production per biomass

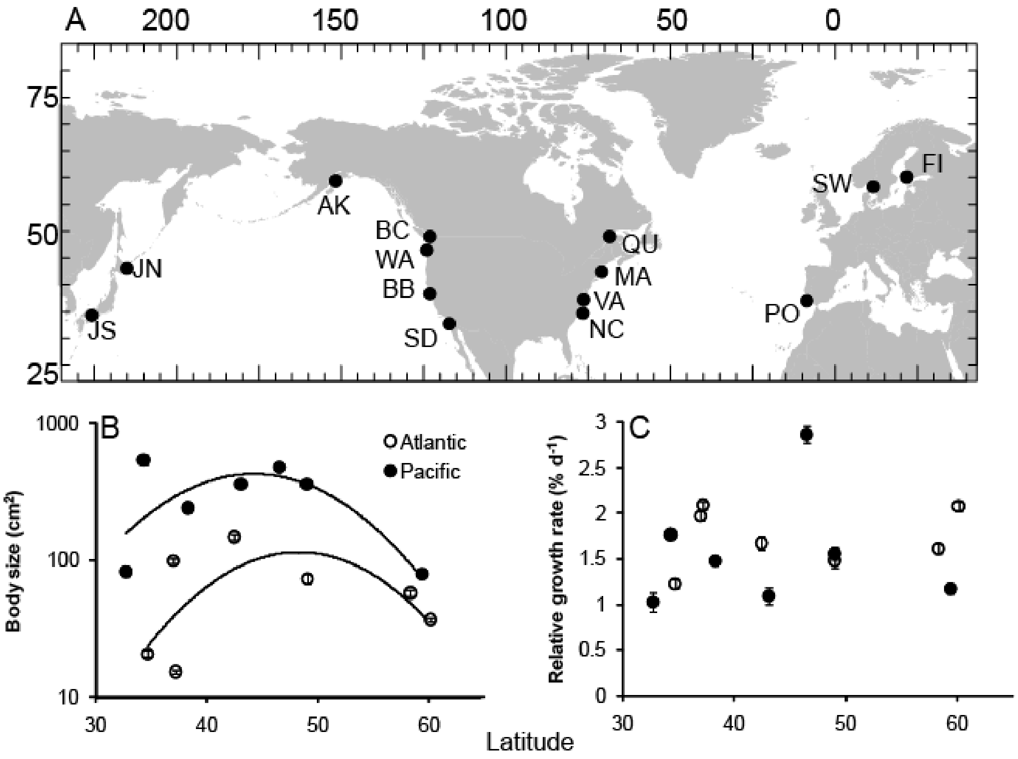

Figure 2. (A) Fourteen sites in the *Zostera* Experimental Network sampled for (B) size and (C) relative growth rate of eelgrass (*Zostera marina*) in summer 2011. Site codes and information provided in Supplementary Material Appendix 1 Tables A1-A3.

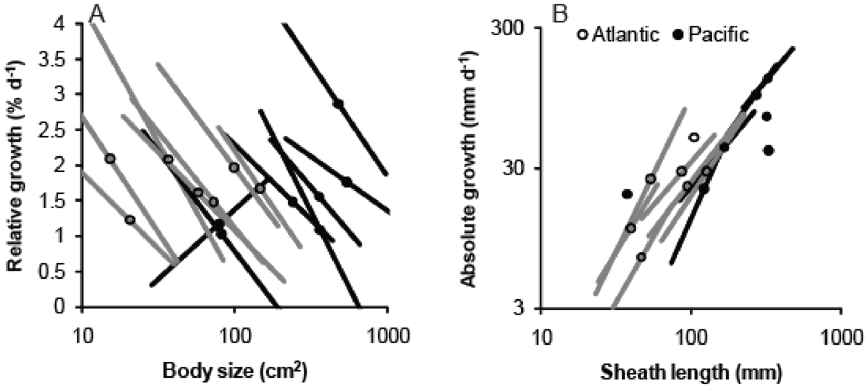

Figure 3. Form-function relationships of eelgrass (*Zostera marina*) in summer 2011 across 14 sites in the northern hemisphere. (A) Productivity as a function of body size. (B) Leaf extension as a function of sheath length. Lines show reduced major axis fit at each site individually (N=32-178 shoots measured per site), with a point at each site mean. Panel (B) shows means without slopes at four sites where AGR and size were uncorrelated. Regression statistics are provided in Supplementary Material Appendix 3 Table A5.

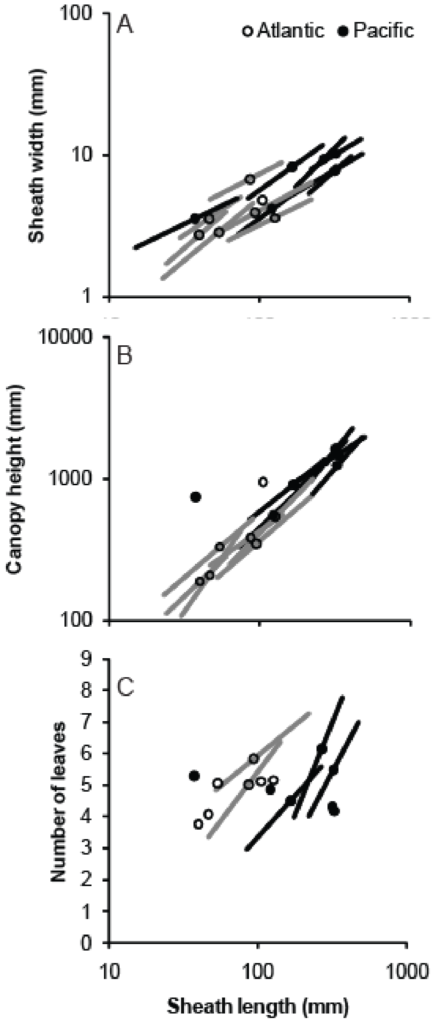

Figure 4. Allometric relationships among traits of eelgrass (*Zostera marina*) within and across 14 globally-distributed sites in summer 2011. A) Sheath width, B) maximum length, and C) number of leaves as a function of sheath length. Each point shows mean values at a site in the Atlantic (open points, grey lines) or Pacific Ocean (black points and lines). Lines are included when sites demonstrated significant correlation between variables and show the slopes from reduced major axis regression. Regression statistics are provided in Supplementary Material Appendix 3 Table A5.

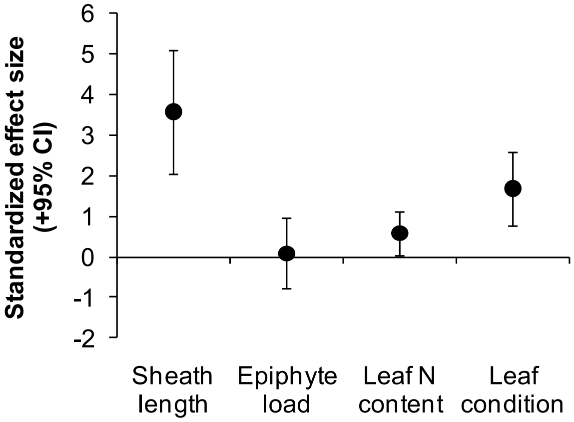

Figure 5. Response of eelgrass (*Zostera marina*) growth to three stressors. Growth was based on daily leaf extension per shoot, with sheath length as a covariate, e.g., Fig. 3B. Standardized effect size shows mean effect size of each stressor divided by standard error, based on linear models from 13 sites (Supplementary Material Appendix 4 Table A7), then combined for global mean and 95% confidence interval. Stressors were considered continuous variables across *Z. marina* shoots in 40 plots per site. Epiphyte load is defined as chlorophyll-*a* µg per gDW *Z. marina*. Nitrogen limitation declines with % nitrogen in *Z. marina* leaves. Increased leaf condition indicates less damage.