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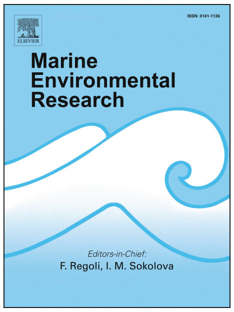

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A tale of two algal blooms: negative and predictable effects of two common bloom-forming macroalgae on seagrass and epiphytes

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RUNNING TITLE: Two macroalgal blooms on seagrass

Abstract

Recent evidence suggests macroalgal blooms may play a role in the worldwide decline in seagrass, but the shape of the functional relationship between seagrass health and dominant bloom-forming macroalgae is poorly characterized. We tested whether the impact of varying abundances of two cosmopolitan bloom-forming macroalgal genera caused linear/quasi-linear or sudden threshold changes in measures of eelgrass, *Zostera marina,* meadow health. We conducted two caging experiments in a shallow *Z. marina* bed (~1 m depth) in Bodega Harbor, California, USA where we maintained six densities within the range of natural abundances of macroalgae, *Ulva* (0-4.0 kg m^{-2}) and *Gracilariopsis* (0-2.0 kg m^{-2}), as well as uncaged controls over a 10-week period. Shoot density, blade growth, and epiphyte load were measured every two weeks and algal treatments reset. We did not find support for threshold transitions between algal abundance and measures of seagrass bed health using sigmoidal and broken-stick regression analyses for each data set; these models are commonly used to identify threshold patterns in ecological shifts. Instead, final measurements of shoot density and epiphyte load were best modelled as linear or slightly non-linear declines with increasing *Ulva* abundance. A negative linear relationship also existed between shoot density and *Gracilariopsis* abundance and a trend towards linear negative effects on epiphyte load. The similar shape of these functional relationships across different types of algae suggests the relationship may be generalizable. At algal abundances that are commonly observed, we found smooth and predictable negative impacts to *Z. marina* by decline in shoot density and potential impacts to food webs by loss of epiphytes rather than sudden threshold shifts or "ecological surprises". Our work contrasts with the growing body of

literature suggesting highly non-linear shifts in response to human impact; thus, it is important to broaden understanding of shifts to more than just pattern but to the processes that drive different patterns of shifts.

Keywords: seagrass decline, macroalgal blooms, epiphyte load

Introduction

Marine ecosystems globally have been undergoing regime shifts from one state to another, usually undesirable, state along gradients of environmental stressors such as climate warming, nutrient input, and changes in consumer pressure (see reviews by Conversi et al., 2014; Dudgeon et al., 2010; Hughes et al., 2010; Mollmann et al., 2014), motivating research on the patterns of these functional responses (defined as the shape of the relationship between predictor and response variables). Patterns of shifts in species or communities across stressor gradients can vary from smooth and gradual transitions, best described as linear or quasi-linear (sensu Conversi et al., 2014), to sudden, catastrophic declines, which are highly nonlinear and are often associated with a critical threshold (Conversi et al., 2014; Scheffer and Carpenter, 2003). Sudden shifts are thought to be common responses to anthropogenic stressors, may be maintained by positive feedbacks (e.g., Unsworth et al., 2015; York et al., 2017), and can be extremely difficult to predict (Ceccherelli et al., 2018; Hughes et al., 2018; Roca et al., 2016; Scheffer and Carpenter, 2003; Viaroli et al., 2008). For example “ecological surprises”, or unpredicted degradative shifts, have been documented in coral reefs (McCook, 1999), savannahs (Ludwig et al., 1997), and lakes (Carpenter et al., 1999; reviewed in Scheffer et al., 2001). In contrast, other systems respond in predictable, linear or quasi-linear ways to changes in environmental stressors such as nutrient levels in estuaries (e.g., Nedwell et al. 1999) and urbanization in streams (Morley and Karr, 2002). These response types can provide early warning signs of transitions because responses occur incrementally as stressors intensify. Thus, evaluating the shape of the functional response of species or communities to common stressors is of key importance in order to overcome the formidable management challenges regime shifts often present (Suding and Hobbs, 2009).

Seagrasses are important foundation species that have been experiencing global regime shifts along gradients of environmental stressors such as nutrient enrichment, sedimentation, and increased temperature (reviewed in Orth et al., 2006; York et al., 2017), yet their functional response to key stressors has not been fully characterized. One well-known driver of loss is nutrient enrichment from developed watersheds that results in phytoplankton blooms or excessive epiphyte loads on seagrass blades that block light (Hughes et al. 2004, Burkholder et al., 2007; Cardoso et al., 2004; Orth et al., 2006, Hitchcock et al. 2017). There is a growing body of evidence that implicates nutrient-driven blooms of macroalgae as a biotic stressor that can also drive seagrass loss. It is well known that bloom-forming macroalgae, such as opportunistic green (*Ulva*, *Cladaophora)* and red *(Gracilaria, Gracilariopsis)* algae, grow quickly in response to nutrient input (e.g., Fong et al., 1993; Kamer et al., 2001; McGlathery, 1995). Resultant macroalgal blooms have caused declines in seagrasses in the genus *Zostera* on both sides of the Atlantic Ocean by reducing available light and/or creating toxic biogeochemical conditions (Han et al., 2016; Hauxwell et al., 2001; Hughes et al., 2018; Mcglathery, 2001; Pulido and Borum, 2010; Valiela et al., 1997; see Appendix S1 for a more detailed review), and a meta-analysis suggests that macroalgal effects may vary across major bloom-forming genera (Thomson et al., 2012). Theory predicts that positive feedbacks should result in threshold responses to stressors (e.g., Scheffer and Carpenter, 2003) and some empirical evidence has demonstrated positive feedbacks in seagrass communities, such as seagrasses stabilizing sediment and grazers reducing epiphytes and macroalgae (for reviews see Maxwell et al., 2017; O'Brien et al., 2017; Roca et al., 2016; Unsworth et al., 2015; York et al., 2017, for analysis of long term data see van der Heide et al., 2007). However, the shape of the macroalgal stressor/seagrass response curve has not been characterized as most experimental studies include a limited range of bloom conditions (Han et al., 2016; Huntington and Boyer, 2008; Olyarnik and Stachowicz, 2012 and Supplemental Table S1). Because seagrass systems are thought to be characterized by positive feedbacks, we predicted that the functional response between seagrass and our macroalgal stress gradients would be highly non-linear.

It is especially important to evaluate the shape of the functional response of foundation species, such as seagrasses, to stressors as they support many ecosystem functions, including habitat and trophic support to a whole community (e.g., Scott et al., 2018; York et al., 2017). Seagrasses provide habitat to both epiphytic algae and mesograzers that comprise a key grazing function that supports upper trophic levels (Baden et al., 2010; Scott et al., 2018). Although epiphytes depend on seagrass for habitat, nutrient enrichment may cause increases in both epiphytes (Borum 1985, Frankovich and Fourqurean 1997, reviewed by Hughes et al. 2004) and macroalgae (Han et al., 2016; Huntington and Boyer, 2008; Olyarnik and Stachowicz, 2012), with over all negative effects on seagrasses (Hessing-Lewis et al., 2011; Hughes et al., 2018). An additional consequence of nutrient-stimulated blooms of free-floating macroalgae that raft onto seagrass is an increase in competition with epiphytes for light and nutrients (see Cardoso et al. 2004), which may cause a decline in epiphyte loading on *Z. marina*. While this may alleviate some negative impacts of epiphytes to *Z. marina*, there may be cascading impacts to trophic support for mesograzers (Hughes et al., 2004, 2018; Scott et al., 2018). Thus, characterizing the shape of the functional response of seagrass and its epiphytes to a macroalgal stress gradient is key to fully understanding the impacts of stressors on the functioning of seagrass communities.

While links have been made between macroalgal blooms and seagrass and epiphyte decline, these studies have not evaluated seagrass responses along a gradient of macroalgal stress to identify the shape of the functional response. We manipulated the abundance of two common bloom forming macroalgae in a California *Zostera marina* bed to determine whether the seagrass system would respond in a predictable linear/quasi-linear fashion or experience an abrupt threshold shift in response to the stressor of macroalgal loading. We asked: (1) will there be similar responses of seagrass and epiphytes to increased abundances of two dominant genera of bloom forming macroalgae? If so, can we (2) identify whether the response to increased abundance of each macroalgal species is a sudden threshold transition or smooth and predictable? Whether macroalgal loads cause a smooth, predictable degradation of seagrass and its epiphytes or whether catastrophic loss occurs above critical loads is key knowledge needed to fully understand community transitions.

Methods

Macroalgal genera

Dominant bloom-forming macroalgae in seagrass beds are usually either sheet-like or filamentous green (McGlathery, 2001; Valiela et al., 1997) or coarsely branching red (Hauxwell et al., 2003, 2001; Huntington and Boyer, 2008) algae that respond to nutrient addition with rapid increases in growth (Fong et al., 1993; Kamer et al., 2001; McGlathery, 1995). Blooms of green algae can produce floating mats that raft over seagrass, blanketing the beds with various abundances and depths (McGlathery 2001), though some can also intercalate between seagrass shoots or near the sediment (Hessing-Lewis et al., 2015). In contrast, branching red algae generally form masses that intercalate within the bases of seagrass shoots (Huntington and Boyer, 2008). Previous studies showed separately that red or green algal additions can have negative impacts on seagrass (see Appendix S1: Table S1.1), but did not test multiple levels of algal addition (but see Hauxwell et al. 2001, Huntington & Boyer 2008, Rasmussen et al. 2012 for 3 treatments). Our study compared impacts of 2 genera of macroalgae that commonly occur in seagrass beds and included multiple treatment levels to determine the shape of the seagrass community response. One algal genus was *Ulva*, which we identified as *expansa*, but since species-level distinctions are complicated by considerable morphological plasticity and we did not key out every specimen, we hereafter call it *Ulva* (as in Olyarnik and Stachowicz, 2012). The other genus is *Gracilariopsis*, and as *Gracilariopsis* is difficult to key to species, and often requires molecular techniques for identification (e.g., Lyra et al., 2015), hereafter we refer to it as *Gracilariopsis.*

Experimental design

Two field experiments assessed changes over time in seagrass health, measured as shoot density, blade growth rate, and epiphyte load, with additions of two common macroalgae. A seagrass bed near the mouth of Bodega Harbour, California, USA (38°18'41.81"N, 123° 3'37.63"W) with a range in tidal height of -0.24 to +2.00 m relative to mean lower low water was the site for both experiments. Bodega Harbor is nearly completely flushed each tidal cycle and receives very little freshwater input outside the rainy season (November-April) (Olyarnik and Stachowicz, 2012). It is episodically subjected to upwelled and advected nutrient-rich oceanic water. Large areas of the benthos are cover by continuous meadows of *Zostera marina*. Prior to the experiments, all existing macroalgae were removed from 44 1 m^2 plots. To retain (or exclude) algae, 5-sided cages (4 vertical sides and a horizontal lid) with dimensions of 1 m^3 constructed from a PVC frame and hardware mesh with 2.5 cm x 2.5 cm openings were placed on all plots; the 1m height allowed algae to float up and down with the tides if they did so naturally, but maintained experimental treatments (Green et al., 2014).

For one experiment, six treatments of *Ulva* were added to seagrass plots with densities of 0, 1.0, 1.5, 2.0, 3.0, and 4.0 kg m^{-2} wet weight (n=4 for algal treatments; n=5 for no addition plots used in both experiments (see below)). Marked but uncaged control (UCC) plots (n=4) evaluated artefacts due to cages alone. There were no differences due to cages for any response variable but epiphyte load, which was reduced by cages (see Appendix S2). Treatments were based upon Olyarnik and Stachowicz (2012) finding strong negative impacts, with shoot density approaching 0 at 4.0 kg m^{-2} of *Ulva* during one year of their study. This was the highest biomass for *Ulva* found in their nearly 4 year study, was over double the next highest biomass, and caused massive loss of shoots. Thus, we added a gradient of algal abundance below this value to identify the pattern of the transition to these very low shoot densities. While this cannot eliminate the possibility of a threshold at even higher biomass additions, we chose to use values within ranges found in the literature (see Table S1) and that would capture the pattern across a wide range of the stressor gradient.

The other caging experiment evaluated the impact of the branching red alga, *Gracilariopsis.* There were six treatments of macroalgae—0, 0.75, 1.0 1.5, 1.75, and 2.0 kg m^{-2} wet weight (n=3). Additions of *Gracilariopsis* were determined from Huntington and Boyer (2008) who found strong negative effects at 1.7 kg m^{-2} but not 0.325 kg m^{-2}. Both the 0 kg m^{-2} and UCC plots were used for both experiments.

Treatments were initiated by collecting the appropriate algae, weighing out the randomly assigned densities for each experimental unit with a hanging fish scale, and placing the algae within experimental plots. To prevent trapping fish within cages, a PVC pipe was moved back and forth throughout the plot prior to securing cages. The same procedure was replicated on UCC plots as well. This likely disturbed the epiphyte community, so we began measuring epiphytes in week 2. We used a shovel to sever rhizomes to a depth of ~30 cm around each plot to prevent movement of nutrients and photosynthate from outside the experimental area. Every two weeks (see below) we collected all algae from within each plot, measured its biomass, and added or removed macroalgae to re-establish initial treatment levels. The amount of macroalgae present in each plot after each two-week period estimated the persistence of macroalgae over time and treatment. Overall, *Ulva* biomass remained constant at the treatment levels except between the last two weeks, while *Gracilariopsis* biomass was reduced between each interval (Appendix S3). Despite this reduction in biomass over time, we used the experimental algal biomass that we maintained every 2 weeks in our statistical analyses as loss or gain within a mat is a natural process after mat deposition and therefore are part of the response to the treatments.

Field and Laboratory Methods

Both experiments ran for ten weeks from 10 July - 12 September 2012; previous work demonstrated that algal mats rafting onto intertidal mudflat communities could last up to 5 months (Green and Fong, 2015) and that they had significant community-level effects within this timeframe (Green et al., 2014). We sampled all plots within both experiments initially and five times over the 10-week duration approximately every 14 days at the spring low tides. Sampling occurred in a 0.25 m x 0.25 m (0.0625 m^2) quadrat placed in a different predetermined location within each plot for each sampling event. Thus the same location within each plot was sampled during a particular sampling period, but a new location was determined each sampling period, so that a location was never resampled. We counted the number of seagrass shoots (see Hauxwell et al., 2001 for method) and normalized density to shoots $\cdot$ m^{-2}. We collected three shoots from each plot to quantify epiphyte load. Shoots were separated into individual blades and both sides were scraped with a microscope slide to remove epiphytes (method adapted from Kendrick and Lavery, 2001; Short et al., 1995). Epiphytes from each blade were composited for each shoot and transferred to separate pre-weighed aluminium foil, dried at 60^o C to a constant weight, and dry weighed. Epiphyte load per shoot was calculated as the average of the 3 shoots per plot. Epiphyte load $\cdot$ m^{-2} was calculated as the average epiphyte dry weight (g) on the three collected shoots multiplied by the total number of shoots$\cdot$ m^{-2} (epiphyte load = epiphyte biomass (g$\cdot$ shoot^{-1}) * #shoots $\cdot$ m^{-2}).

Two weeks prior to the end of the experiment at least four shoots per plot were marked to measure seagrass growth. Two holes were punched through the shoots within the sheath using a needle (method adapted from Duarte and Kirkman 2001). The first hole was punched approximately 5 cm from the sediment and the second directly above it to make them distinguishable from other damage or grazing scars. After two weeks, shoots were collected and growth of each blade measured as the distance from the initial mark on the outer sheath (which does not elongate) to the hole on each interior blade. The tissue between the hole in the sheath and in each blade is comprised of new tissue as seagrass grows from a basal meristem (see Kendrick and Lavery, 2001; Short et al., 1995). Lengths of new blades with no holes were also measured. The total length of new tissue from each blade was summed for a given shoot and averaged for all shoots from a plot for average total blade elongation (cm $\cdot$ shoot^{-1}) (see Duarte and Kirkman 2001). This insured that blades of all sizes were included in growth measurements.

Threshold Analysis and Model Fitting

We tested for a threshold shift in response variables (shoot density, growth, epiphyte load per shoot, and epiphyte load per m^2 from the final week 10 measurement) in response to macroalgal abundance with two common approaches: (1) testing the fit of a sigmoid function and (2) conducting piecewise regression (Samhouri et al., 2010; Toms and Lesperance, 2003). Figure 1 (a) shows the function:

$$R = \frac{C_1}{1+\frac{C_2}{S}^{-t}} \qquad \text{(Equation 1)}$$

where R = the ecosystem response variable, S = the stressor on the system, C_1 is the y-axis starting value, and t is varied to determine the steepness in the relationship between the ecosystem response and stressor at point C_2. As the value of t declines, the shape of the negative relationship between the stressor and ecosystem response switches from being a very abrupt threshold transition (e.g. t=50) to a very smooth relationship (e.g. t=1). We used the non-linear regression, nls, routine (R Core Team, 2015) and bbmle package (Bolker, 2008) in R to estimate values for parameters C_1, C_2, and t for each of our seagrass response variables using maximum likelihood estimation (as in Samhouri et al. 2010). In cases where there was not support for a sharp threshold transition (e.g. t close to or less than 1), the smooth sigmoid model was compared by Akaike Information Criterion, using the correction for small sample sizes (AICc), to two other stress-response models based on their ecological relevance to the possible effect of macroalgae on seagrass and their epiphytes: (1) steady negative decline (linear) across the full range of the stressor and (2) rapid decline at low values of the stressor (exponential decay). If AICcs were similar (ΔAICc<4; although Burnham et al. 2011 accepted differences ΔAICc>2 as similar, they also suggest using >4 as more conservative so we chose the latter), we chose multiple models. Table 1

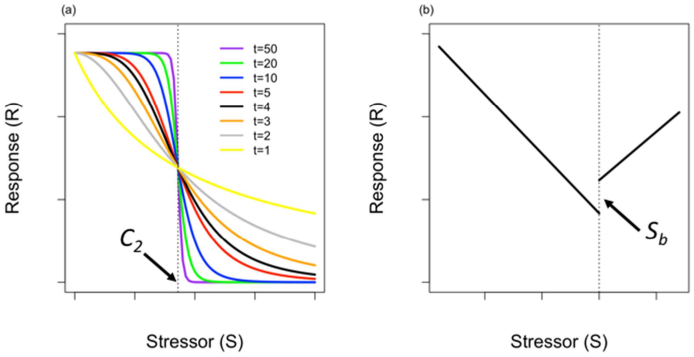

Figure 1. Examples of possible ecosystem response (R) to a stressor (S) following a threshold pattern either through (a) a sigmoid function (Eq. 1) or (b) a piecewise regression (Eq. 2) model with breakpoint at S_b. The different colours of the lines in the sigmoid (a) example represent a gradient from a steep threshold response (purple, t=50) at point C_2 (dotted line) to smooth, predictable relationship (yellow, t=1).

lists all models and comparisons; non-linear R^2 values were estimated by squaring the correlation between predicted and actual response values.

As a second test for threshold behavior, which could accommodate a broader range of functional relationships, we conducted piecewise regression through the iterative search method in R (see method in Crawley 2007, R Core Team 2015). In this case, two linear regressions:

$$R = b_1 + m_1{*}S \text{ when } S \leq S_b\text{, and}$$

$$R = b_2 + m_2{*}S \text{ when } S \geq S_b \quad \text{(Equation 2)}$$

were conducted to describe the data before and after a break-point, S_b (Figure 1 b). The breakpoint that yielded a model with the lowest residual mean standard error (MSE) was selected. We show any significant piecewise models (see similar analysis in Sutula et al., 2014) and these models were also compared by ΔAICc to the linear, exponential, and sigmoid models described above.

All analyses were conducted independently for the two (*Ulva* and *Gracilariopsis*) experiments. We used repeated measures ANOVA to assess temporal responses of shoot density and epiphyte load (measured every 2 weeks) to macroalgal abundance; results are presented in Appendix S4 and S5. UCC plots were not included in analyses, as they do not represent an experimental treatment but were compared to 0 kg m^{-2} plots to assess cage effects in Appendix S2.

Results

Ulva experiment

The data did not support the existence of a steep transition or threshold relationship as *Z. marina* shoot density declined incrementally across the gradient of increasing *Ulva* abundance (Figure 2 a). The maximum likelihood estimate (MLE) of *t* for the sigmoid function was 1.55, resulting in a smooth curve (Fig 2 a, green) similar in shape to the exponential decay model (Fig 2 a, blue). The piecewise model (Figure 2 b) was

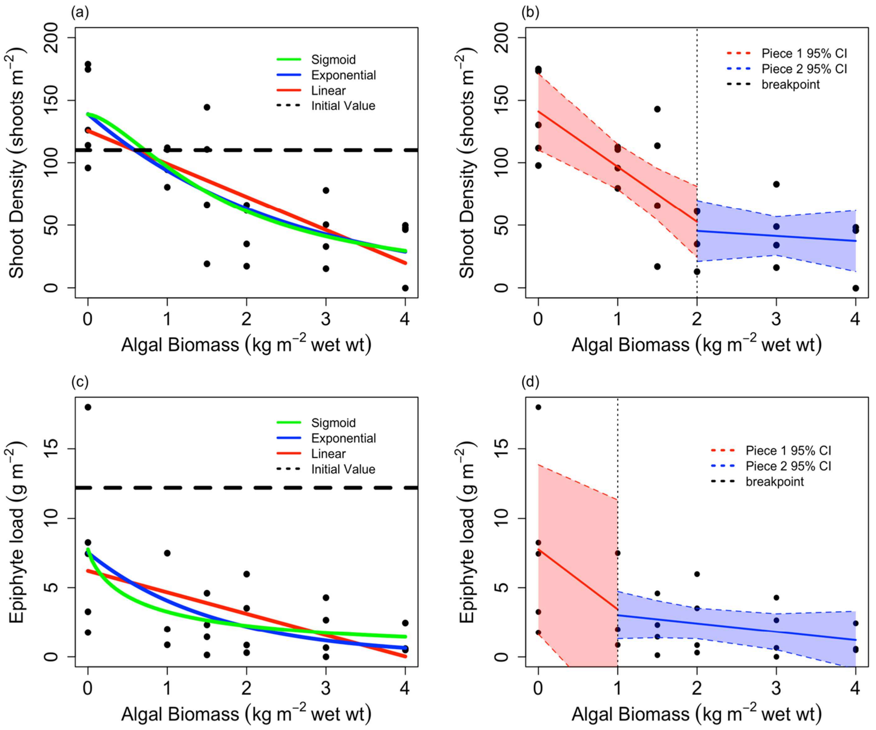

Figure 2. *Zostera marina* shoot density (n=25) and epiphyte load (g) per m^2 (n=23) in response to *Ulva* abundance (kg m^{-2}). Linear, exponential and sigmoid models were fit to *Z. marina* shoot density (a) and epiphyte load (c) (g m^{-2}). Black dotted horizontal lines indicate initial values (n=25). Piecewise regression with 95% confidence intervals for each linear piece (shaded areas) are also plotted for (b) shoot density with breakpoint S_b=2 (p<0.001, R^2=0.56) and (d) epiphyte load (g m^{-2}) with breakpoint S_b=1 (p=0.04, R^2=0.04). Vertical dotted lines are the breakpoints for each piecewise regression.

significant with a breakpoint at S_b=2 but the model was not preferred by AICc comparison (Table 1). Based upon our selection criteria for AICc, the exponential model was selected.

Table 1. Model fitting of linear, non-linear, and piecewise regression models using maximum likelihood parameter estimation. The regression models examined the relationship between macroalgal abundance (*S*) and all seagrass responses (*R*). Includes comparison of linear (R = b + mS), exponential (R = a*e^{bS}), and sigmoid ($R = \frac{C_1}{1+\frac{C_2}{S}^{-t}}$) least squares regression models and piecewise regression by ΔAICc for each measurement. We also include data sets with no significant relationships. Models determined to be preferred by ΔAICc are in bold.

Response (R)	Algal species (S)	Form	Equation (MLE)	Adjusted R^2	P-value	ΔAICc
Shoot density	*Ulva*	Linear	$R = 125.45 - 26.44S$	0.5207	<0.0001	3.1
		Exponential decay	**$R = 138.74e^{-0.39S}$**	**0.5939**	**<0.0001**	**0.0**
		Sigmoid	$R=138.5/[1+(1.72/S)^{-1.55}]$	0.6009	0.001	2.4
		Piecewise	$R= 137.28 – 36.06S$ when $S\le2$, $R= 68 – 8S$ when $S\ge2$	0.5554	<0.001	7.2
	Gracilariopsis	**Linear**	**$R = 148.51 - 42.97S$**	**0.3912**	**0.0025**	**0.0**
		Exponential decay	**$R = 147.94e^{-0.37S}$**	**0.3914**	**<0.01**	**1.1**
		Sigmoid	$R=141.8/[1+(1.68/S)^{-2.82}]$	0.4741	0.0796	1.6
		Piecewise	$R= 137.6 + 15.65S$ when $S\le1$, $R= 140.2 – 44.4S$ when $S\ge1$	0.3843	0.0268	7.9
Growth	*Ulva*	Linear	$R = 59.04 – 7.86S$	0.0205	0.2441	0.0
		Exponential decay	$R = 57.55e^{-0.15S}$	0.0556	0.3723	0.3
		Sigmoid	$R=54.5/[1+(3.46/S)^{-4.54}]$	0.1075	0.5655	2.0
		Piecewise	$R= 42.9 -12.5S$ when $S\le1$,	0.0253	0.3446	4.0

			$R= 70.6 - 12.5S$ when $S \geq 1$			
	Gracilariopsis	Linear	$R = 62.27 – 3.56S$	-0.0517	0.8009	0.0
		Exponential decay	$R = 61.62e^{-0.049S}$	0.0030	0.8370	0.0
		Sigmoid	$R=65.8/[1+(2.19/S)^{-5.05}]$	0.0465	0.7305	2.3
		Piecewise	$R= 42.9 + 91.6S$ when $S \leq 1$, $R= 89.3 – 23.4S$ when $S \geq 1$	0.1112	0.2271	3
Epiphyte load (g/shoot)	*Ulva*	Linear	$R = 0.0491 - 0.0022S$	-0.0428	0.7585	0.0
		Exponential decay	$R = 0.049e^{-0.046S}$	0.0044	0.7719	0.0
		Sigmoid	NF*	--	--	--
		Piecewise	$R= 0.054 – 0.019S$ when $S \leq 2$, $R= 0.16 – 0.034S$ when $S \geq 2$	-0.0404	0.5489	6.9
	Gracilariopsis	Linear	$R = 0.0585 - 0.0035S$	-0.0517	0.8012	0.0
		Exponential decay	$R = 0.058e^{-0.061S}$	0.0585	0.8116	0.0
		Sigmoid	$R=0.06/[1+(3.49/S)^{-2.73}]$	0.0879	0.8850	3.1

		Piecewise	$R = 0.053 + 0.003S$ when $S \leq 0.75$, $R = 0.045 + 0.003S$ when $S \geq 0.75$	-0.1098	0.7734	5.5
Epiphyte load (g/m^2)	*Ulva*	Linear	$R = 6.20 - 1.55S$	0.2238	0.0131	2.4
		Exponential decay	$\boldsymbol{R = 7.51e^{-0.62S}}$	**0.3330**	**0.0156**	**0.0**
		Sigmoid	$R=7.75/[1+(0.68/S)^{-0.83}]$	0.3476	0.481	2.4
		Piecewise	$R = 7.2 - 0.45S$ when $S \leq 1$, $R = 2.6 - 0.45S$ when $S \geq 1$	0.2475	0.0386	5.6
	Gracilariopsis	Linear	$R = 9.41 - 3.43S$	0.0669	0.1417	0.0
		Exponential decay	$R = 9.01e^{-0.38S}$	0.0997	0.2248	0.4
		Sigmoid	$R=8.73/[1+(1.59/S)^{-3.57}]$	0.1497	0.4625	2.4
		Piecewise	$R=7.7 + 6.6S$ when $S \leq 1$, $R=18.6 - 8.3S$ when $S \geq 1$	0.0994	0.2454	6.6

Epiphyte load per m^2 was negatively impacted by *Ulva* abundance but did not exhibit a threshold pattern. The sigmoid curve was smooth with a MLE for $t < 1$ (Fig 2 c, green). The exponential decay (Fig 2 c, blue) model is slightly preferred over the linear (Fig 2 c, red) and sigmoid (Fig 2 c, green) models by ΔAICc (Table 1). In addition, the adjusted R^2 value was higher for the exponential model than linear (0.33 vs. 0.22). The piecewise model was significant with a breakpoint S_b=1 (Figure 2 d) but was not preferred by AICc. Compared to initial levels ($\bar{x}$ = 12.2 ± 1.2 SEM g m^{-2}) average epiphyte load (g m^{-2}) decreased at least 3-fold in all treatments except for the 0 kg m^{-2} (Figure 2 c).

There was no relationship between *Ulva* abundance and growth of *Z. marina* blades (Figure 3 a). Total blade elongation (cm) per shoot was highly variable with a range from 2 to 171 cm shoot^{-1} ($\bar{x}$ =

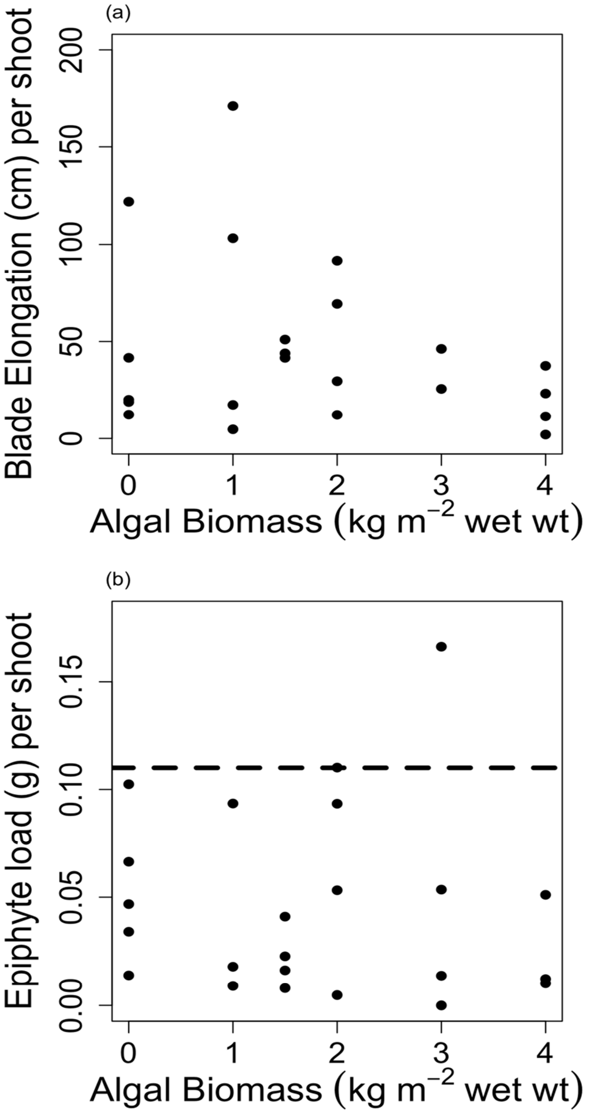

Figure 3. Scatter plots of responses with no significant relationship to *Ulva* abundance, (a) shoot growth over last two-week period (n=22) and (b) epiphyte load (g) per shoot (n=23). Black dotted horizontal lines indicate initial values (n=25). Note that there is no initial value for growth because this is a measurement over a two-week period.

45.3 ± 9.1 SEM cm shoot^{-1}). While there were no differences by treatment, blade elongation appeared to be lower and less variable in the highest biomass treatment. There was also no relationship between *Ulva* abundance and epiphyte load on individual shoots (g shoot^{-1}) (Figure 3 b). Mean epiphyte load per shoot was initially 0.11 ± 0.01 g and none of the treatments recovered to these levels.

Gracilariopsis experiment

There was a significant negative linear or quasi-linear (exponential decay) relationship between *Gracilariopsis* abundance and final shoot density (Figure 4 a). The sigmoid curve was smooth with MLE of *t*=2.8, but this

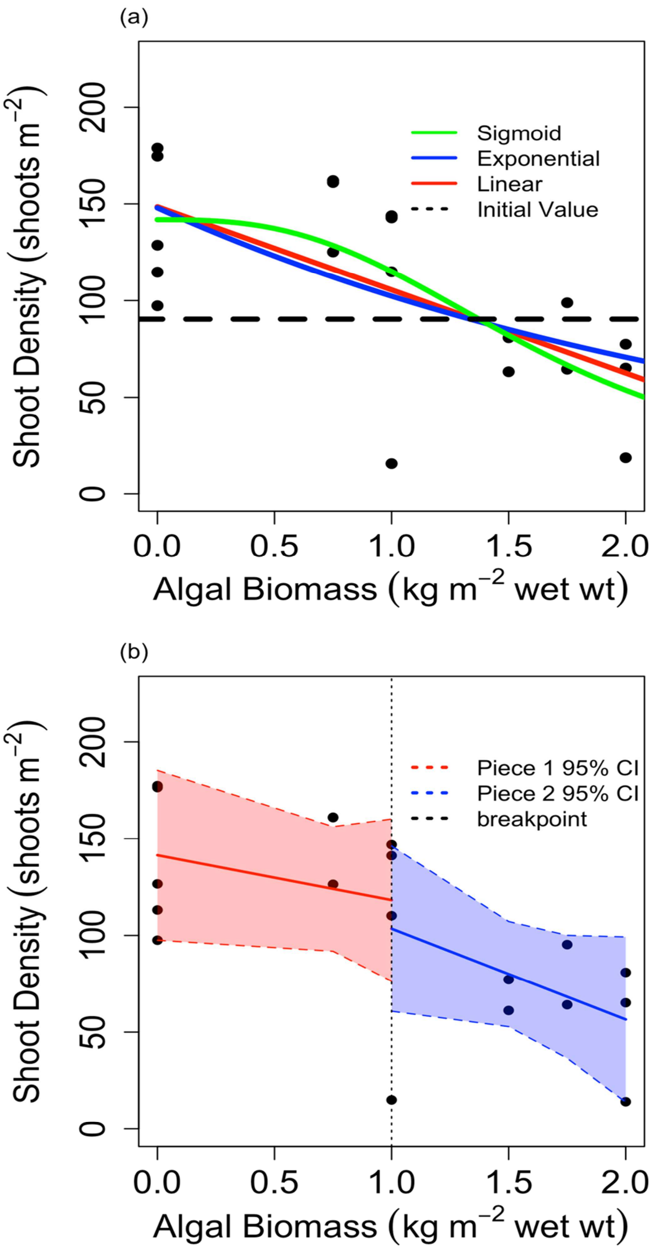

Figure 4. Response of shoot density to *Gracilariopsis* abundance (kg m^{-2}) comparing (a) linear, exponential and sigmoid models (n=19) and (b) piecewise regression for shoot density with 95% confidence intervals at breakpoint S_b=1 (p=0.03, R^2=0.25). Black dashed horizontal lines indicate initial values (n=25), vertical dotted lines are the breakpoints for the piecewise regression.

parameter was not significant (Table 1). While the piecewise model was significant with the breakpoint S_b=1, it was least preferred by ΔAICc (Table 1). As there was no difference according to ΔAICc between the linear and exponential decay models, we included both as preferred models (Table 1).

There were no significant relationships between *Gracilariopsis* abundance and final measurements of blade elongation (cm shoot^{-1}), epiphyte load per shoot, or epiphyte load per m^2. Rather, blade elongation (cm shoot^{-1}) over the final two weeks was highly variable (Figure 5 a). Although there was a trend towards a negative linear (p=0.14) relationship when epiphyte load (g) was considered at the m^{-2} scale, this trend is weak and primarily driven by a few high values (Figure 5c).

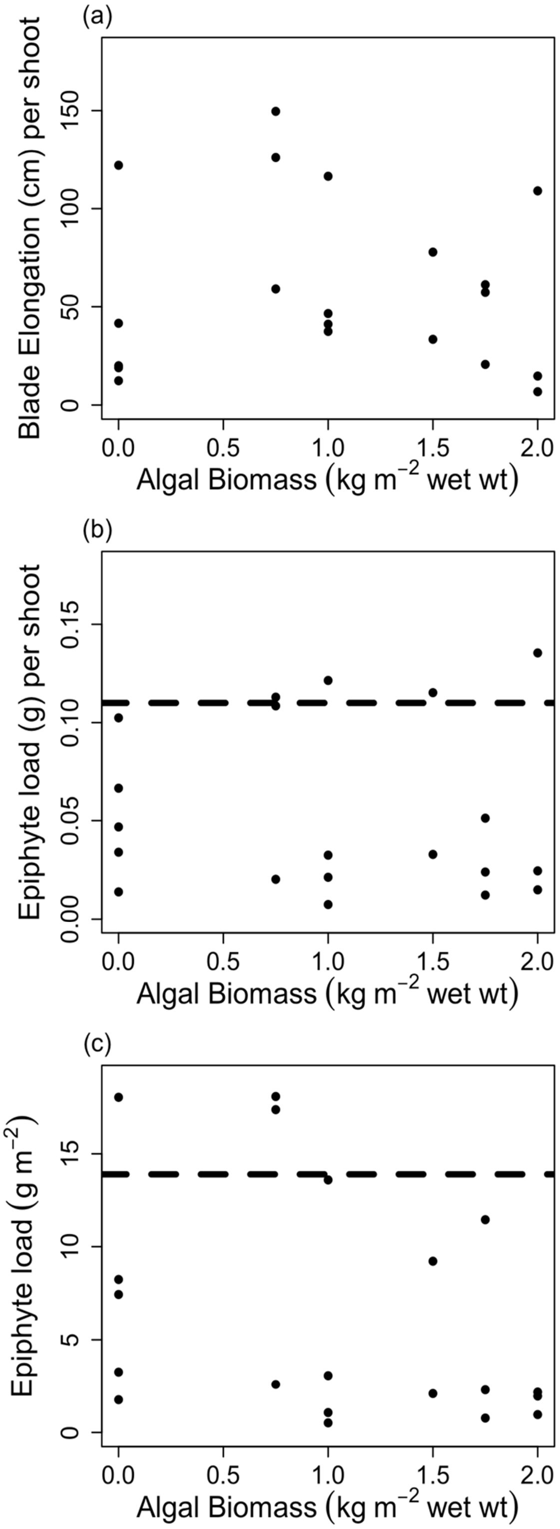

Figure 5. Scatter plots of responses with no significant relationship to *Gracilariopsis* abundance, (a) shoot growth over last two-week period (n=19), (b) epiphyte load (g) per shoot (n=20), and (c) epiphyte load per meter (n=19). Black dotted horizontal lines indicate initial values (n=20). Note that there is no initial value for growth because this is a measurement over a two-week period.

As in the *Ulva* experiment, none of the treatments recovered to the initial epiphyte load values.

Discussion

We documented a linear or quasi-linear functional relationship between the biotic stress gradient produced by macroalgal blooms and decline of *Zostera marina*, a critical foundation species of seagrass. This result contrasts with patterns found for many other foundation species that exhibited strongly non-linear or threshold functional responses to stressors (e.g., forested systems in Ellison et al. 2005 and coral reefs in Hughes et al. 2010). Several have argued that threshold responses, or phase-shifts, may be the “new normal” in systems subject to human disturbance because examples of strongly non-linear shifts have become so numerous across terrestrial, aquatic, and marine systems worldwide (see examples in Scheffer and Carpenter 2003, Folke et al. 2004). Highly non-linear shifts have also been predicted for seagrass beds (e.g. Viaroli et al. 2008, Unsworth et al. 2015, Hughes et al. 2018). However, when we tested seagrass response across a gradient of macroalgal stress we found the functional relationship was more similar to the incremental changes in response to global warming exhibited by alpine plants and salt marsh/mangrove systems. For example, Lesica and McCune (2004) found the majority of alpine plants tested declined linearly in relation to increased temperatures. There was also an incremental shift from dominance by salt marsh plants to invasion by mangroves as winter temperatures increased in temperate latitudes (Saintilan et al., 2014). Similarly, we found that health of *Z. marina* declined incrementally with increased abundance of macroalgae, and this pattern of decline was consistent for two bloom-forming algal species. While our experimental results do not rule out the possibility of a threshold shift at even higher macroalgal biomasses, our experiment did include the highest levels measured in the field (see Olyarnik and Stachowicz 2012). Thus, for a wide range of this stressor gradient, the relationship between the community of interest (seagrass) and the environmental stressor (macroalgae) was predictable and gradual rather than being a tipping point with a resultant “ecological surprise” (*sensu* King 1995, Lindenmayer et al. 2010).

A linear or quasi-linear functional response of seagrass to macroalgal stress implies that the mechanisms that may produce non-linearities in some seagrass systems may not have large effects in all seagrass systems, an important consideration for managing these systems. Strongly non-linear or threshold responses occur when feedbacks in a system are strong (Muthukrishnan and Fong, 2014; Scheffer and Carpenter, 2003), including abiotic processes and strong interspecific interactions (Hughes et al., 2018; Maxwell et al., 2017). Feedbacks that may stabilize seagrass include sediment stabilization maintaining a clear water state and grazers that may limit negative effects of nutrient enrichment (Maxwell et al., 2017; van der Heide et al., 2007). However, it is possible that the feedbacks that typically occur in seagrass systems are context-dependent. For example, Bodega Harbor receives limited terrestrial runoff and is strongly tidally flushed twice daily (Olyarnik and Stachowicz 2012), resulting in estuarine water that is largely free of suspended sediments or the influence of anthropogenic nutrients that may stimulate epiphyte loads. Hessing-Lewis et al. (2011) also found that up-welling influenced, high flow seagrass systems were not negatively affected by high loads of macroalgae. Therefore, in the context of Bodega Bay and other systems like it, feedbacks that stabilize sediments and limit increases in epiphytes may not have strong effects on seagrass health. However, in other systems that receive more terrestrial nutrients and sediment, the effects of these feedbacks may strengthen and drive strong nonlinearities. Thus, in order to manage seagrass ecosystems, it is important to broaden our understanding of shifts beyond just pattern but to the processes that drive these different patterns.

We found that epiphytes on seagrass, at least at the lower abundances found in our study (e.g. compare to mean July values in Williams and Ruckelhaus, 1993), declined linearly or quasi-linearly with the biotic stress of added macroalgae. This relationship was driven by the decline in seagrass itself rather than a decrease in epiphyte cover per shoot. As in our study, others found that degradation or replacement of foundation species caused cascading effects, including losses of higher trophic levels as their habitat, food source, or both disappeared (tropical rain forests, Turner 1996; kelp forests, Graham 2004; grasslands, Krauss et al. 2010; coral reefs, Kayal et al. 2012). In seagrass systems, many organisms rely on epiphytes as a food resource (Hughes et al., 2004, 2018), including epifaunal invertebrates (Thayer et al., 1978) that may in turn be a food resource to juvenile fish (Marsh, 1973). However, there can be complex interactions between macroalgae, seagrass, epiphytes, and invertebrates that do not always result in a cascade of negative effects (Scott et al., 2018). For example, macroalgae may have positive effects on invertebrates that can utilize it as a food resource (Everett, 1991; Whalen et al., 2013), but negative effects on other invertebrates that avoid it (Hughes et al. 2018). In another study, seagrass was indirectly affected by predation and nutrient enrichment, which directly controlled mesograzers and epiphytic algae (Baden et al., 2010). Negative effects to epiphytes in our system were strongest for *Ulva*, possibly due to greater light attenuation from the sheet-like morphology compared to the more open branching pattern of *Gracilariopsis*; a meta-snalysis found *Gracillaria*, a similar genus to *Gracilariopsis,* had weaker negative effects than *Ulva*, though, as in our study the differences were highly variable (Thomson et al. 2012), possibly reflecting these complex interactions. *Ulva* also had strong negative effects on trophic support in intertidal mudflats (Green et al., 2014, Green and Fong 2015). Thus, it is important to extend our approach in future work to assess the relationship between epiphyte loss and invertebrate and fish abundance to fully understand the impact of this community transition.

We hypothesize that, while biotic and abiotic context likely affects the negative relationship between macroalgae and seagrass communities, in systems without strong feedback effects the changes will be to the rate of decline (slope) and background shoot density in the absence of macroalgae (intercept) rather than the overall linear pattern. To test this hypothesis, our relatively simple experimental approach could be utilized in other locations; however, we found linear or quasi-linear negative effects to *Zostera marina* and its epiphytes at abundances of *Ulva* and *Gracilariopsis* that are found to occur naturally in seagrass beds around the world (see studies with similar species from East Coast USA, Hauxwell et al. 2001; Australia, Cummins et al. 2004; Portugal, Cardoso et al. 2004; Japan, Sugimoto et al. 2007; West Coast USA, Huntington and Boyer 2008, Olyarnik and Stachowicz 2012; Denmark, Rasmussen et al. 2012). Further, our study was conducted near the mouth of Bodega Harbor in California, in an expansive eelgrass bed under high flow and flushing conditions (Olyarnik and Stachowicz, 2012); under this best-case scenario, we still identified negative effects of macroalgal loads. Unless nutrient input into systems that support seagrass is reduced it is likely that macroalgal blooms will continue to occur, propagating further seagrass decline with concurrent trophic disruptions. However, our study showed that the pattern of this degradation, at least in some systems, can be linear or quasi-linear, not an ecological surprise or sudden transition. The discovery of a smooth and predictable x, y (stressor-response) relationship is critical information for resource managers because, rather than managing for unpredictable and catastrophic crashes, managers can monitor incremental increases in macroalgal biomass as an indicator of future declines in seagrass heath and initiate management action before negative effects become severe.

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Highlights: A tale of two algal blooms, Bittick et al.

- Seagrass shoot density is negatively impacted by the biotic stressor of macroalgal loading
- Epiphyte abundance is also negatively impacted by increased macroalgal load
- These patterns were true for two genera of macroalgae that are common worldwide
- The functional response of seagrass and epiphytes to macroalgae was quasi-linear and predictable
- With the predictable response, managers can monitor macroalgae as an indicator of future declines