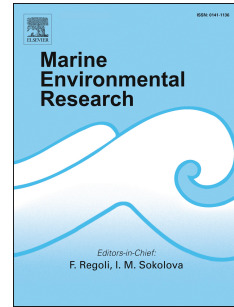


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A tale of two algal blooms: Negative and predictable effects of two common bloom-forming macroalgae on seagrass and epiphytes

S.J. Bittick, M. Sutula, P. Fong



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

3 **S.J. Bittick^{1*}, M. Sutula², and P. Fong¹**

4 ¹Department of Ecology and Evolutionary Biology, University of California Los Angeles,
5 621 Charles E. Young Drive South, Los Angeles, California 90095-1606, USA

6 ²Southern California Coastal Water Research Project, 3535 Harbor Boulevard, Costa
7 Mesa, CA 92626, USA

8 *Corresponding author: Orcid ID [0000-0001-7891-7482](https://orcid.org/0000-0001-7891-7482), bittick@zoology.ubc.ca,
9 Current affiliation: Department of Zoology, Biodiversity Research Centre, University of
10 British Columbia, 2212 Main Mall, Vancouver, BC V6T 1Z4

11 RUNNING TITLE: Two macroalgal blooms on seagrass

12 **Abstract**

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

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

38 **Keywords:** seagrass decline, macroalgal blooms, epiphyte load

39

40 **Introduction**

41 Marine ecosystems globally have been undergoing regime shifts from one state to
42 another, usually undesirable, state along gradients of environmental stressors such as
43 climate warming, nutrient input, and changes in consumer pressure (see reviews by
44 Conversi et al., 2014; Dudgeon et al., 2010; Hughes et al., 2010; Mollmann et al., 2014),
45 motivating research on the patterns of these functional responses (defined as the shape of
46 the relationship between predictor and response variables). Patterns of shifts in species or
47 communities across stressor gradients can vary from smooth and gradual transitions, best
48 described as linear or quasi-linear (*sensu* Conversi et al., 2014), to sudden, catastrophic
49 declines, which are highly nonlinear and are often associated with a critical threshold
50 (Conversi et al., 2014; Scheffer and Carpenter, 2003). Sudden shifts are thought to be
51 common responses to anthropogenic stressors, may be maintained by positive feedbacks
52 (e.g., Unsworth et al., 2015; York et al., 2017), and can be extremely difficult to predict
53 (Ceccherelli et al., 2018; Hughes et al., 2018; Roca et al., 2016; Scheffer and Carpenter,
54 2003; Viaroli et al., 2008). For example “ecological surprises”, or unpredicted
55 degradative shifts, have been documented in coral reefs (McCook, 1999), savannahs
56 (Ludwig et al., 1997), and lakes (Carpenter et al., 1999; reviewed in Scheffer et al.,
57 2001). In contrast, other systems respond in predictable, linear or quasi-linear ways to

58 changes in environmental stressors such as nutrient levels in estuaries (e.g., Nedwell et al.
59 1999) and urbanization in streams (Morley and Karr, 2002). These response types can
60 provide early warning signs of transitions because responses occur incrementally as
61 stressors intensify. Thus, evaluating the shape of the functional response of species or
62 communities to common stressors is of key importance in order to overcome the
63 formidable management challenges regime shifts often present (Suding and Hobbs,
64 2009).

65 Seagrasses are important foundation species that have been experiencing global
66 regime shifts along gradients of environmental stressors such as nutrient enrichment,
67 sedimentation, and increased temperature (reviewed in Orth et al., 2006; York et al.,
68 2017), yet their functional response to key stressors has not been fully characterized. One
69 well-known driver of loss is nutrient enrichment from developed watersheds that results
70 in phytoplankton blooms or excessive epiphyte loads on seagrass blades that block light
71 (Hughes et al. 2004, Burkholder et al., 2007; Cardoso et al., 2004; Orth et al., 2006,
72 Hitchcock et al. 2017). There is a growing body of evidence that implicates nutrient-
73 driven blooms of macroalgae as a biotic stressor that can also drive seagrass loss. It is
74 well known that bloom-forming macroalgae, such as opportunistic green (*Ulva*,
75 *Cladaophora*) and red (*Gracilaria*, *Gracilariopsis*) algae, grow quickly in response to
76 nutrient input (e.g., Fong et al., 1993; Kamer et al., 2001; McGlathery, 1995). Resultant
77 macroalgal blooms have caused declines in seagrasses in the genus *Zostera* on both sides
78 of the Atlantic Ocean by reducing available light and/or creating toxic biogeochemical
79 conditions (Han et al., 2016; Hauxwell et al., 2001; Hughes et al., 2018; Mcglathery,
80 2001; Pulido and Borum, 2010; Valiela et al., 1997; see Appendix S1 for a more detailed

81 review), and a meta-analysis suggests that macroalgal effects may vary across major
82 bloom-forming genera (Thomson et al., 2012). Theory predicts that positive feedbacks
83 should result in threshold responses to stressors (e.g., Scheffer and Carpenter, 2003) and
84 some empirical evidence has demonstrated positive feedbacks in seagrass communities,
85 such as seagrasses stabilizing sediment and grazers reducing epiphytes and macroalgae
86 (for reviews see Maxwell et al., 2017; O'Brien et al., 2017; Roca et al., 2016; Unsworth
87 et al., 2015; York et al., 2017, for analysis of long term data see van der Heide et al.,
88 2007). However, the shape of the macroalgal stressor/seagrass response curve has not
89 been characterized as most experimental studies include a limited range of bloom
90 conditions (Han et al., 2016; Huntington and Boyer, 2008; Olyarnik and Stachowicz,
91 2012 and Supplemental Table S1). Because seagrass systems are thought to be
92 characterized by positive feedbacks, we predicted that the functional response between
93 seagrass and our macroalgal stress gradients would be highly non-linear.

94 It is especially important to evaluate the shape of the functional response of
95 foundation species, such as seagrasses, to stressors as they support many ecosystem
96 functions, including habitat and trophic support to a whole community (e.g., Scott et al.,
97 2018; York et al., 2017). Seagrasses provide habitat to both epiphytic algae and
98 mesograzers that comprise a key grazing function that supports upper trophic levels
99 (Baden et al., 2010; Scott et al., 2018). Although epiphytes depend on seagrass for
100 habitat, nutrient enrichment may cause increases in both epiphytes (Borum 1985,
101 Frankovich and Fourqurean 1997, reviewed by Hughes et al. 2004) and macroalgae (Han
102 et al., 2016; Huntington and Boyer, 2008; Olyarnik and Stachowicz, 2012), with over all
103 negative effects on seagrasses (Hessing-Lewis et al., 2011; Hughes et al., 2018). An

104 additional consequence of nutrient-stimulated blooms of free-floating macroalgae that
105 raft onto seagrass is an increase in competition with epiphytes for light and nutrients (see
106 Cardoso et al. 2004), which may cause a decline in epiphyte loading on *Z. marina*. While
107 this may alleviate some negative impacts of epiphytes to *Z. marina*, there may be
108 cascading impacts to trophic support for mesograzers (Hughes et al., 2004, 2018; Scott et
109 al., 2018). Thus, characterizing the shape of the functional response of seagrass and its
110 epiphytes to a macroalgal stress gradient is key to fully understanding the impacts of
111 stressors on the functioning of seagrass communities.

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

125

126 **Methods**127 *Macroalgal genera*

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

148 ***Experimental design***

149 Two field experiments assessed changes over time in seagrass health, measured as
150 shoot density, blade growth rate, and epiphyte load, with additions of two common
151 macroalgae. A seagrass bed near the mouth of Bodega Harbour, California, USA
152 (38°18'41.81"N, 123° 3'37.63"W) with a range in tidal height of -0.24 to +2.00 m relative
153 to mean lower low water was the site for both experiments. Bodega Harbor is nearly
154 completely flushed each tidal cycle and receives very little freshwater input outside the
155 rainy season (November-April) (Olyarnik and Stachowicz, 2012). It is episodically
156 subjected to upwelled and advected nutrient-rich oceanic water. Large areas of the
157 benthos are cover by continuous meadows of *Zostera marina*. Prior to the experiments,
158 all existing macroalgae were removed from 44 1 m² plots. To retain (or exclude) algae, 5-
159 sided cages (4 vertical sides and a horizontal lid) with dimensions of 1 m³ constructed
160 from a PVC frame and hardware mesh with 2.5 cm x 2.5 cm openings were placed on all
161 plots; the 1m height allowed algae to float up and down with the tides if they did so
162 naturally, but maintained experimental treatments (Green et al., 2014).

163 For one experiment, six treatments of *Ulva* were added to seagrass plots with
164 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
165 for no addition plots used in both experiments (see below)). Marked but uncaged control
166 (UCC) plots (n=4) evaluated artefacts due to cages alone. There were no differences due
167 to cages for any response variable but epiphyte load, which was reduced by cages (see
168 Appendix S2). Treatments were based upon Olyarnik and Stachowicz (2012) finding
169 strong negative impacts, with shoot density approaching 0 at 4.0 kg m⁻² of *Ulva* during
170 one year of their study. This was the highest biomass for *Ulva* found in their nearly 4 year

171 study, was over double the next highest biomass, and caused massive loss of shoots.
172 Thus, we added a gradient of algal abundance below this value to identify the pattern of
173 the transition to these very low shoot densities. While this cannot eliminate the possibility
174 of a threshold at even higher biomass additions, we chose to use values within ranges
175 found in the literature (see Table S1) and that would capture the pattern across a wide
176 range of the stressor gradient.

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

182 Treatments were initiated by collecting the appropriate algae, weighing out the
183 randomly assigned densities for each experimental unit with a hanging fish scale, and
184 placing the algae within experimental plots. To prevent trapping fish within cages, a PVC
185 pipe was moved back and forth throughout the plot prior to securing cages. The same
186 procedure was replicated on UCC plots as well. This likely disturbed the epiphyte
187 community, so we began measuring epiphytes in week 2. We used a shovel to sever
188 rhizomes to a depth of ~30 cm around each plot to prevent movement of nutrients and
189 photosynthate from outside the experimental area. Every two weeks (see below) we
190 collected all algae from within each plot, measured its biomass, and added or removed
191 macroalgae to re-establish initial treatment levels. The amount of macroalgae present in
192 each plot after each two-week period estimated the persistence of macroalgae over time
193 and treatment. Overall, *Ulva* biomass remained constant at the treatment levels except

194 between the last two weeks, while *Gracilariopsis* biomass was reduced between each
195 interval (Appendix S3). Despite this reduction in biomass over time, we used the
196 experimental algal biomass that we maintained every 2 weeks in our statistical analyses
197 as loss or gain within a mat is a natural process after mat deposition and therefore are part
198 of the response to the treatments.

199 *Field and Laboratory Methods*

200 Both experiments ran for ten weeks from 10 July - 12 September 2012; previous
201 work demonstrated that algal mats rafting onto intertidal mudflat communities could last
202 up to 5 months (Green and Fong, 2015) and that they had significant community-level
203 effects within this timeframe (Green et al., 2014). We sampled all plots within both
204 experiments initially and five times over the 10-week duration approximately every 14
205 days at the spring low tides. Sampling occurred in a 0.25 m x 0.25 m (0.0625 m²) quadrat
206 placed in a different predetermined location within each plot for each sampling event.
207 Thus the same location within each plot was sampled during a particular sampling period,
208 but a new location was determined each sampling period, so that a location was never
209 resampled. We counted the number of seagrass shoots (see Hauxwell et al., 2001 for
210 method) and normalized density to shoots · m⁻². We collected three shoots from each plot
211 to quantify epiphyte load. Shoots were separated into individual blades and both sides
212 were scraped with a microscope slide to remove epiphytes (method adapted from
213 Kendrick and Lavery, 2001; Short et al., 1995). Epiphytes from each blade were
214 composited for each shoot and transferred to separate pre-weighed aluminium foil, dried
215 at 60° C to a constant weight, and dry weighed. Epiphyte load per shoot was calculated as
216 the average of the 3 shoots per plot. Epiphyte load · m⁻² was calculated as the average

217 epiphyte dry weight (g) on the three collected shoots multiplied by the total number of
218 shoots $\cdot m^{-2}$ (epiphyte load = epiphyte biomass (g \cdot shoot $^{-1}$) * #shoots $\cdot m^{-2}$).

219 Two weeks prior to the end of the experiment at least four shoots per plot were
220 marked to measure seagrass growth. Two holes were punched through the shoots within
221 the sheath using a needle (method adapted from Duarte and Kirkman 2001). The first
222 hole was punched approximately 5 cm from the sediment and the second directly above it
223 to make them distinguishable from other damage or grazing scars. After two weeks,
224 shoots were collected and growth of each blade measured as the distance from the initial
225 mark on the outer sheath (which does not elongate) to the hole on each interior blade. The
226 tissue between the hole in the sheath and in each blade is comprised of new tissue as
227 seagrass grows from a basal meristem (see Kendrick and Lavery, 2001; Short et al.,
228 1995). Lengths of new blades with no holes were also measured. The total length of new
229 tissue from each blade was summed for a given shoot and averaged for all shoots from a
230 plot for average total blade elongation (cm \cdot shoot $^{-1}$) (see Duarte and Kirkman 2001).
231 This insured that blades of all sizes were included in growth measurements.

232 ***Threshold Analysis and Model Fitting***

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

$$238 \quad R = \frac{c_1}{1 + \frac{c_2}{S}^{-t}} \quad (\text{Equation 1})$$

239 where R = the ecosystem response variable, S = the stressor on the system, C_1 is
 240 the y-axis starting value, and t is varied to determine the steepness in the relationship
 241 between the ecosystem response and stressor at point C_2 . As the value of t declines, the
 242 shape of the negative relationship between the stressor and ecosystem response switches
 243 from being a very abrupt threshold transition (e.g. $t=50$) to a very smooth relationship
 244 (e.g. $t=1$). We used the non-linear regression, `nls`, routine (R Core Team, 2015) and
 245 `bbmle` package (Bolker, 2008) in R to estimate values for parameters C_1 , C_2 , and t for
 246 each of our seagrass response variables using maximum likelihood estimation (as in
 247 Samhuri et al. 2010). In cases where there was not support for a sharp threshold
 248 transition (e.g. t close to or less than 1), the smooth sigmoid model was compared by
 249 Akaike Information Criterion, using the correction for small sample sizes (AICc), to two
 250 other stress-response models

251 based on their ecological
 252 relevance to the possible effect
 253 of macroalgae on seagrass and
 254 their epiphytes: (1) steady
 255 negative decline (linear) across
 256 the full range of the stressor
 257 and (2) rapid decline at low values
 258 of the stressor (exponential decay).
 259 If AICcs were similar ($\Delta AICc < 4$;

260 although Burnham et al. 2011 accepted differences $\Delta AICc > 2$ as similar, they also suggest
 261 using > 4 as more conservative so we chose the latter), we chose multiple models. Table 1

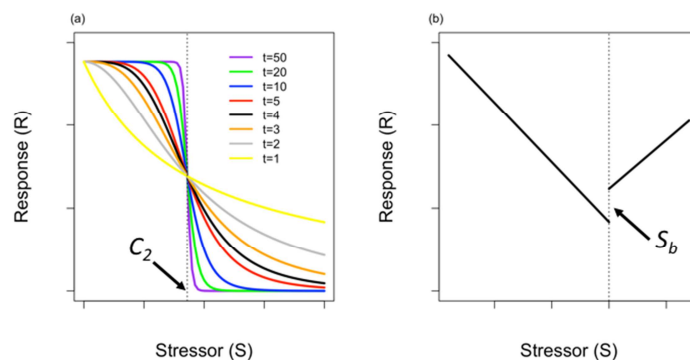


Figure 1. Examples of possible ecosystem response (R) to a stressor (S) following a threshold pattern either through (a) a sigmoid function (Eq. 1) or (b) a piecewise regression (Eq. 2) model with breakpoint at S_b . The different colours of the lines in the sigmoid (a) example represent a gradient from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

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

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

$$268 \quad R = b_1 + m_1 * S \text{ when } S \leq S_b, \text{ and}$$

$$269 \quad R = b_2 + m_2 * S \text{ when } S \geq S_b \text{ (Equation 2)}$$

270 were conducted to describe the data before and after a break-point, S_b (Figure 1 b). The
271 breakpoint that yielded a model with the lowest residual mean standard error (MSE) was
272 selected. We show any significant piecewise models (see similar analysis in Sutula et al.,
273 2014) and these models were also compared by $\Delta AICc$ to the linear, exponential, and
274 sigmoid models described above.

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

281

282 **Results**

283 *Ulva* experiment

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

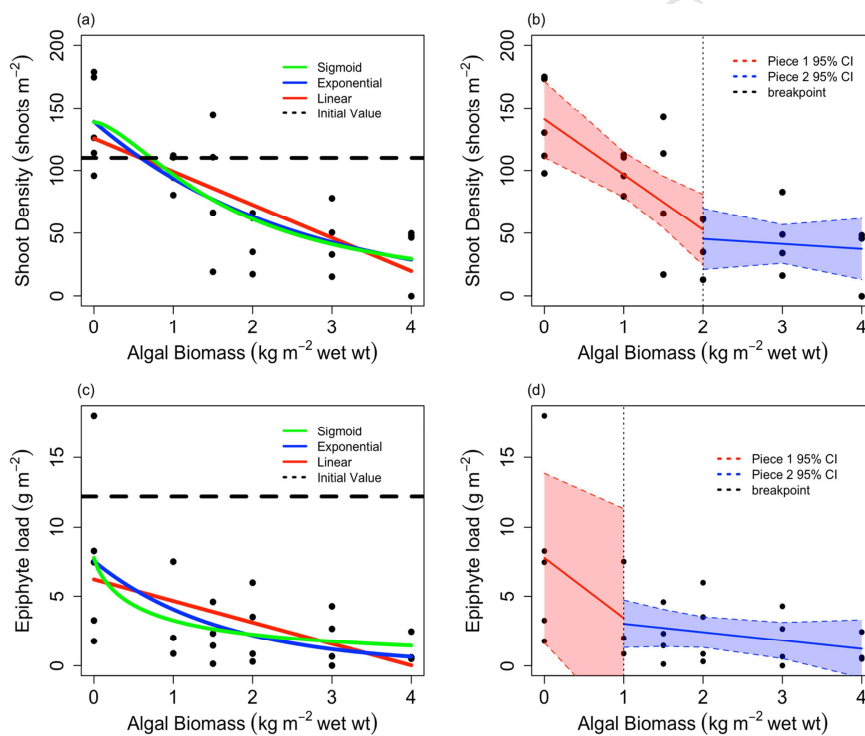


Figure 2. *Zostera marina* shoot density ($n=25$) and epiphyte load ($g\ m^{-2}$) per m^2 ($n=23$) in response to *Ulva* abundance ($kg\ m^{-2}$). Linear, exponential and sigmoid models were fit to *Z. marina* shoot density (a) and epiphyte load (c) ($g\ m^{-2}$). Black dotted horizontal lines indicate 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.

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

292 **Table 1.** Model fitting of linear, non-linear, and piecewise regression models using
293 maximum likelihood parameter estimation. The regression models examined the
294 relationship between macroalgal abundance (S) and all seagrass responses (R). Includes
295 comparison of linear ($R = b + mS$), exponential ($R = a * e^{bS}$), and sigmoid ($R = \frac{c_1}{1 + \frac{c_2}{S}}$)
296 least squares regression models and piecewise regression by Δ AICc for each
297 measurement. We also include data sets with no significant relationships. Models
298 determined to be preferred by Δ AICc are in bold.

Response (R)	Algal species (S)	Form	Equation (MLE)	Adjusted R ²	P-value	ΔAICc
Shoot density	<i>Ulva</i>	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 $S \leq 2$, $R= 68 - 8S$ when $S \geq 2$	0.5554	<0.001	7.2
	<i>Gracilariopsis</i>	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 $S \leq 1$, $R= 140.2 - 44.4S$ when $S \geq 1$	0.3843	0.0268	7.9
Growth	<i>Ulva</i>	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 $S \leq 1$,	0.0253	0.3446	4.0

		$R = 70.6 - 12.5S$ when $S \geq 1$				
<i>Gracilariopsis</i>	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)	<i>Ulva</i>	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
<i>Gracilariopsis</i>	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)	<i>Ulva</i>	Linear	$R = 6.20 - 1.55S$	0.2238	0.0131	2.4
		Exponential decay	$R = 7.51e^{-0.62S}$	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
	<i>Gracilariopsis</i>	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

299

300

301
 302 Epiphyte load per m² was negatively impacted by *Ulva* abundance but did not
 303 exhibit a threshold pattern. The sigmoid curve was smooth with a MLE for $t < 1$ (Fig 2 c,
 304 green). The exponential decay (Fig 2 c, blue) model is slightly preferred over the linear
 305 (Fig 2 c, red) and sigmoid (Fig 2 c,
 306 green) models by ΔAICc (Table 1).
 307 In addition, the adjusted R² value
 308 was higher for the exponential model
 309 than linear (0.33 vs. 0.22). The
 310 piecewise model was significant
 311 with a breakpoint $S_b=1$ (Figure 2 d)
 312 but was not preferred by AICc.
 313 Compared to initial levels ($\bar{x} = 12.2$
 314 ± 1.2 SEM g m⁻²) average epiphyte
 315 load (g m⁻²) decreased at least 3-fold
 316 in all treatments except for the 0 kg
 317 m⁻² (Figure 2 c).

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

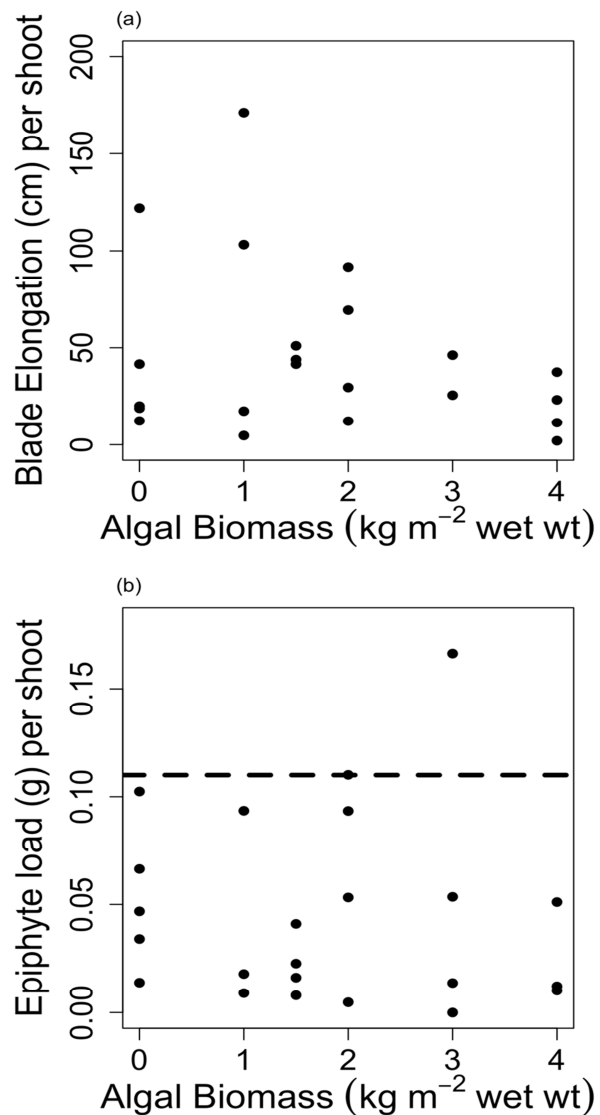


Figure 3. Scatter plots of responses with no significant relationship to *Ulva* abundance, (a) shoot growth over last two-week period (n=22) and (b) epiphyte load (g) per shoot (n=23). Black dotted horizontal lines indicate initial values (n=25). Note that there is no initial value for growth because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

324 45.3 ± 9.1 SEM cm shoot⁻¹). While there were no differences by treatment, blade
 325 elongation appeared to be lower and less variable in the highest biomass treatment. There
 326 was also no relationship
 327 between *Ulva* abundance
 328 and epiphyte load on
 329 individual shoots (g shoot⁻¹)
 330 (Figure 3 b). Mean epiphyte
 331 load per shoot was initially
 332 0.11 ± 0.01 g and none of
 333 the treatments recovered to
 334 these levels.

335 *Gracilariopsis*

336 experiment

337 There was a
 338 significant negative linear
 339 or quasi-linear (exponential
 340 decay) relationship between
 341 *Gracilariopsis* abundance
 342 and final shoot density
 343 (Figure 4 a). The sigmoid
 344 curve was smooth with
 345 MLE of $t=2.8$, but this

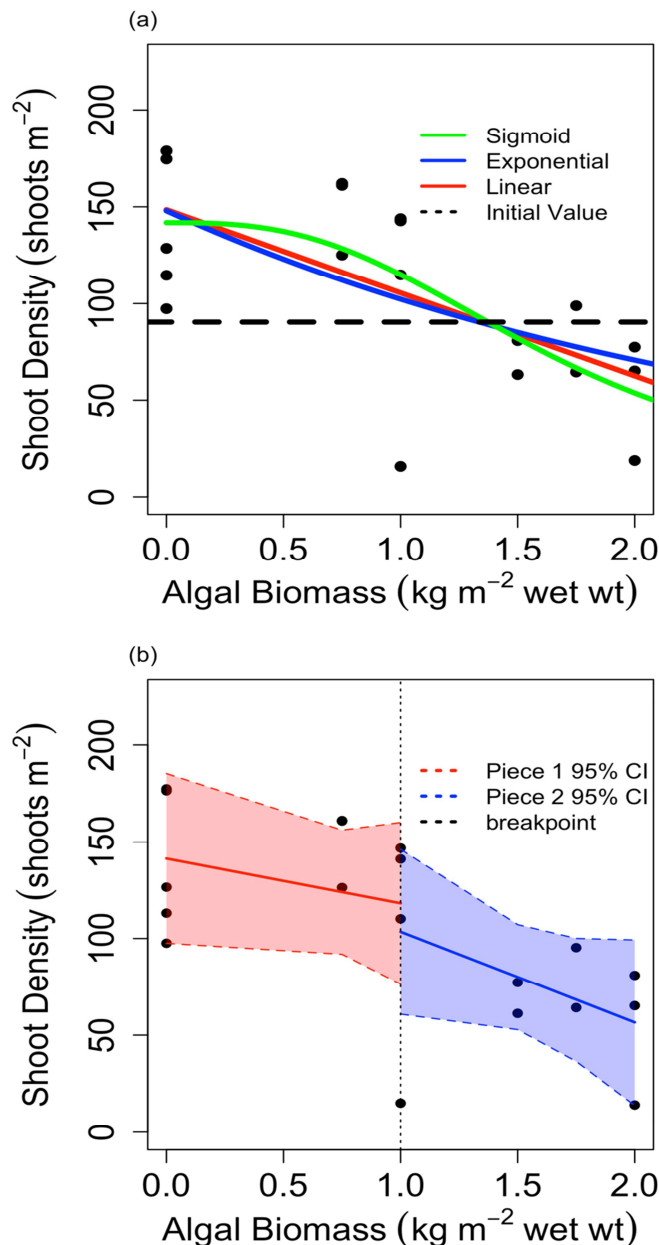
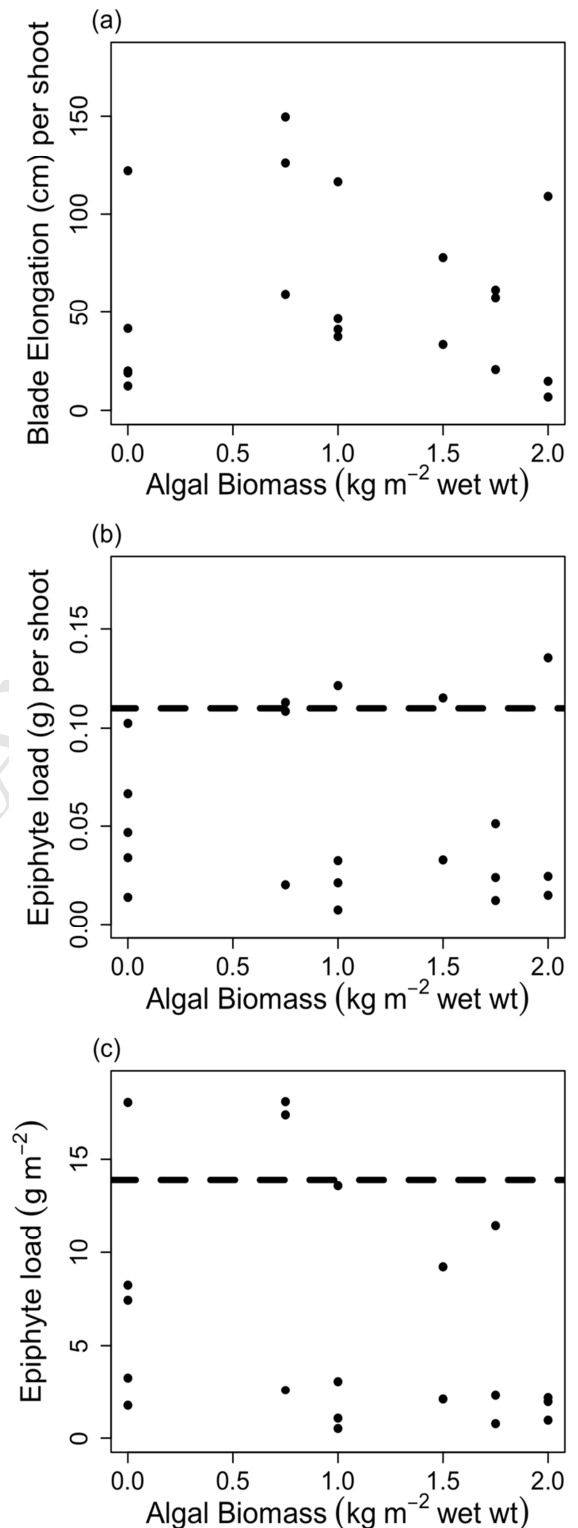


Figure 4. Response of shoot density to *Gracilariopsis* abundance (kg m⁻²) comparing (a) linear, exponential and sigmoid models (n=19) and (b) piecewise regression for shoot density with 95% confidence intervals at breakpoint $S_b=1$ ($p=0.03$, $R^2=0.25$). Black dashed horizontal lines indicate initial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

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

353 There were no significant relationships
 354 between *Gracilariopsis* abundance and final
 355 measurements of blade elongation (cm shoot^{-1}),
 356 epiphyte load per shoot, or epiphyte load per m^2 .
 357 Rather, blade elongation (cm shoot^{-1}) over the final
 358 two weeks was highly variable (Figure 5 a).
 359 Although there was a trend towards a negative
 360 linear ($p=0.14$) relationship when epiphyte load (g)
 361 was considered at the m^{-2} scale, this trend is weak
 362 and primarily driven by a few high values (Figure
 363 5c).

364 **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.



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

367 **Discussion**

368 We documented a linear or quasi-linear functional relationship between the biotic
369 stress gradient produced by macroalgal blooms and decline of *Zostera marina*, a critical
370 foundation species of seagrass. This result contrasts with patterns found for many other
371 foundation species that exhibited strongly non-linear or threshold functional responses to
372 stressors (e.g., forested systems in Ellison et al. 2005 and coral reefs in Hughes et al.
373 2010). Several have argued that threshold responses, or phase-shifts, may be the “new
374 normal” in systems subject to human disturbance because examples of strongly non-
375 linear shifts have become so numerous across terrestrial, aquatic, and marine systems
376 worldwide (see examples in Scheffer and Carpenter 2003, Folke et al. 2004). Highly non-
377 linear shifts have also been predicted for seagrass beds (e.g. Viaroli et al. 2008, Unsworth
378 et al. 2015, Hughes et al. 2018). However, when we tested seagrass response across a
379 gradient of macroalgal stress we found the functional relationship was more similar to the
380 incremental changes in response to global warming exhibited by alpine plants and salt
381 marsh/mangrove systems. For example, Lesica and McCune (2004) found the majority of
382 alpine plants tested declined linearly in relation to increased temperatures. There was also
383 an incremental shift from dominance by salt marsh plants to invasion by mangroves as
384 winter temperatures increased in temperate latitudes (Saintilan et al., 2014). Similarly, we
385 found that health of *Z. marina* declined incrementally with increased abundance of
386 macroalgae, and this pattern of decline was consistent for two bloom-forming algal
387 species. While our experimental results do not rule out the possibility of a threshold shift

388 at even higher macroalgal biomasses, our experiment did include the highest levels
389 measured in the field (see Olyarnik and Stachowicz 2012). Thus, for a wide range of this
390 stressor gradient, the relationship between the community of interest (seagrass) and the
391 environmental stressor (macroalgae) was predictable and gradual rather than being a
392 tipping point with a resultant “ecological surprise” (*sensu* King 1995, Lindenmayer et al.
393 2010).

394 A linear or quasi-linear functional response of seagrass to macroalgal stress
395 implies that the mechanisms that may produce non-linearities in some seagrass systems
396 may not have large effects in all seagrass systems, an important consideration for
397 managing these systems. Strongly non-linear or threshold responses occur when
398 feedbacks in a system are strong (Muthukrishnan and Fong, 2014; Scheffer and
399 Carpenter, 2003), including abiotic processes and strong interspecific interactions
400 (Hughes et al., 2018; Maxwell et al., 2017). Feedbacks that may stabilize seagrass include
401 sediment stabilization maintaining a clear water state and grazers that may limit negative
402 effects of nutrient enrichment (Maxwell et al., 2017; van der Heide et al., 2007).
403 However, it is possible that the feedbacks that typically occur in seagrass systems are
404 context-dependent. For example, Bodega Harbor receives limited terrestrial runoff and is
405 strongly tidally flushed twice daily (Olyarnik and Stachowicz 2012), resulting in
406 estuarine water that is largely free of suspended sediments or the influence of
407 anthropogenic nutrients that may stimulate epiphyte loads. Hessing-Lewis et al. (2011)
408 also found that up-welling influenced, high flow seagrass systems were not negatively
409 affected by high loads of macroalgae. Therefore, in the context of Bodega Bay and other
410 systems like it, feedbacks that stabilize sediments and limit increases in epiphytes may

411 not have strong effects on seagrass health. However, in other systems that receive more
412 terrestrial nutrients and sediment, the effects of these feedbacks may strengthen and drive
413 strong nonlinearities. Thus, in order to manage seagrass ecosystems, it is important to
414 broaden our understanding of shifts beyond just pattern but to the processes that drive
415 these different patterns.

416 We found that epiphytes on seagrass, at least at the lower abundances found in
417 our study (e.g. compare to mean July values in Williams and Ruckelhaus, 1993), declined
418 linearly or quasi-linearly with the biotic stress of added macroalgae. This relationship
419 was driven by the decline in seagrass itself rather than a decrease in epiphyte cover per
420 shoot. As in our study, others found that degradation or replacement of foundation
421 species caused cascading effects, including losses of higher trophic levels as their habitat,
422 food source, or both disappeared (tropical rain forests, Turner 1996; kelp forests, Graham
423 2004; grasslands, Krauss et al. 2010; coral reefs, Kayal et al. 2012). In seagrass systems,
424 many organisms rely on epiphytes as a food resource (Hughes et al., 2004, 2018),
425 including epifaunal invertebrates (Thayer et al., 1978) that may in turn be a food resource
426 to juvenile fish (Marsh, 1973). However, there can be complex interactions between
427 macroalgae, seagrass, epiphytes, and invertebrates that do not always result in a cascade
428 of negative effects (Scott et al., 2018). For example, macroalgae may have positive
429 effects on invertebrates that can utilize it as a food resource (Everett, 1991; Whalen et al.,
430 2013), but negative effects on other invertebrates that avoid it (Hughes et al. 2018). In
431 another study, seagrass was indirectly affected by predation and nutrient enrichment,
432 which directly controlled mesograzers and epiphytic algae (Baden et al., 2010). Negative
433 effects to epiphytes in our system were strongest for *Ulva*, possibly due to greater light

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434 attenuation from the sheet-like morphology compared to the more open branching pattern
435 of *Gracilariopsis*; a meta-analysis found *Gracillaria*, a similar genus to *Gracilariopsis*,
436 had weaker negative effects than *Ulva*, though, as in our study the differences were
437 highly variable (Thomson et al. 2012), possibly reflecting these complex interactions.
438 *Ulva* also had strong negative effects on trophic support in intertidal mudflats (Green et
439 al., 2014, Green and Fong 2015). Thus, it is important to extend our approach in future
440 work to assess the relationship between epiphyte loss and invertebrate and fish abundance
441 to fully understand the impact of this community transition.

442 We hypothesize that, while biotic and abiotic context likely affects the negative
443 relationship between macroalgae and seagrass communities, in systems without strong
444 feedback effects the changes will be to the rate of decline (slope) and background shoot
445 density in the absence of macroalgae (intercept) rather than the overall linear pattern. To
446 test this hypothesis, our relatively simple experimental approach could be utilized in
447 other locations; however, we found linear or quasi-linear negative effects to *Zostera*
448 *marina* and its epiphytes at abundances of *Ulva* and *Gracilariopsis* that are found to
449 occur naturally in seagrass beds around the world (see studies with similar species from
450 East Coast USA, Hauxwell et al. 2001; Australia, Cummins et al. 2004; Portugal,
451 Cardoso et al. 2004; Japan, Sugimoto et al. 2007; West Coast USA, Huntington and
452 Boyer 2008, Olyarnik and Stachowicz 2012; Denmark, Rasmussen et al. 2012). Further,
453 our study was conducted near the mouth of Bodega Harbor in California, in an expansive
454 eelgrass bed under high flow and flushing conditions (Olyarnik and Stachowicz, 2012);
455 under this best-case scenario, we still identified negative effects of macroalgal loads.
456 Unless nutrient input into systems that support seagrass is reduced it is likely that

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457 macroalgal blooms will continue to occur, propagating further seagrass decline with
458 concurrent trophic disruptions. However, our study showed that the pattern of this
459 degradation, at least in some systems, can be linear or quasi-linear, not an ecological
460 surprise or sudden transition. The discovery of a smooth and predictable x, y (stressor-
461 response) relationship is critical information for resource managers because, rather than
462 managing for unpredictable and catastrophic crashes, managers can monitor incremental
463 increases in macroalgal biomass as an indicator of future declines in seagrass health and
464 initiate management action before negative effects become severe.

465
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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