How much is too much? Identifying benchmarks of adverse effects of macroalgae on the macrobenthic community in estuarine intertidal flats

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Abstract

Eutrophication is the accumulation of organic matter typically in response to anthropogenically - enhanced nutrient inputs. In shallow estuaries, macroalgal blooms are a symptom of eutrophication, causing a cascade of adverse ecosystem effects. Confidence in the use of macroalgae as an indicator of eutrophication in estuaries is limited by the lack of quantitative data on benchmarks of adverse effects, which are used to inform thresholds. To determine a benchmark of adverse effects of macroalgal abundance on macrobenthic faunal communities in intertidal flats, manipulative experiments were conducted in two sites in Bodega Harbor and two sites in Upper Newport Bay, California, USA. At each site, twenty - four cages maintained six treatments of macroalgae for eight weeks, with mat depths of 0, 1.0, 1.5, 2.5, 3.5 and 5 cm comprised mostly of bloom-forming green macroalgae in the genus *Ulva*. Mats 1 cm deep, equivalent to a biomass of 110 to 120 g dry weight (dw) m^{-2} or 840 to 930 g wet weight m^{-2} (estimated by regression analysis), resulted in the reduction of macrofaunal abundance by at least 67% and species richness by at least 19% within two weeks at three of four sites. Loss was attributed to the decline of key functional groups. Surface deposit feeders were eliminated from one site at Bodega Harbor within four weeks and at one site in Upper Newport Bay within six weeks, while 1 cm mats negatively affected suspension feeders and herbivores in Bodega Harbor. In contrast, the other site at Upper Newport Bay was not affected by macroalgal treatment, likely due to an initial community comprised of a high proportion of subsurface deposit feeders tolerant of stressful environments. Macroalgal abundances as low as 110 to 120 g dw m^{-2} had significant and rapid negative effects on macrobenthic invertebrates, providing a critical benchmark for adverse effects of macroalgal blooms on ecosystem health. *Synthesis and applications:* Due their responsiveness to nutrient enrichment and negative effects in aquatic ecosystems, macroalgal abundance is a reliable indicator of eutrophication in estuaries. This work provides quantitative data on adverse effects that can inform managers when macroalgal abundance has reached critical levels.

Introduction

Management of coastal ecosystems increasingly relies on biological assessment to quantify the ecological condition of habitats and the extent and magnitude of adverse effects of anthropogenic stressors (Borja *et al.* 2011). Biological indicators have an advantage over chemical indicators as they integrate the effects of chemical concentrations over time and provide a stronger linkage to ecosystem effects (Karr 1991). Significant advances have been

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made in developing quantitative tools that utilize information on biological response indicators such as benthic macroinvertebrates to quantify benchmarks (Fuschman *et al.* 2006). Diagnostic tools to quantify the effects of nutrient enrichment have been slower in development for estuaries, in part because of the complexity of pathways in which ecosystems respond to excess nutrients, site-specific factors that mitigate ecosystem response, and a lack of quantitative data regarding thresholds of adverse effects particularly on management endpoints of concern (Borja *et al.* 2011).

Primary producers such as phytoplankton or macroalgae are typically used as biological indicators of nutrient enrichment in estuaries (Bricker *et al*. 2003, Zaldivar *et al.* 2008, Borja *et al.* 2011). While phytoplankton blooms are common responses to nutrient enrichment in deeper, subtidal-dominated estuaries (Kemp *et al.* 2005), macroalgal blooms are more common in shallow subtidal and intertidal-dominated systems (Brush and Nixon 2010). Some macroalgae, especially opportunistic green algae in the genus *Ulva*, can take up large amounts of excessive nutrients from both the water column and sediment, store a portion for future use, and simultaneously undergo rapid growth (Kamer *et al.* 2004, Kennison *et al*. 2011). As a result of these nutrient and growth strategies, macroalgae can bloom rapidly, outpace grazer control (Worm and Lotze 2006), and cover extensive sections of intertidal flats and subtidal habitat (Nezlin *et al*. 2007) for long durations (Green 2011). These macroalgal blooms outcompete other primary producers and can blanket intertidal flats and subtidal sediments, resulting in hypoxia, disruption of biogeochemical cycling, and reduced abundance and diversity of benthic invertebrates (Raffaelli *et al*. 1998, Bolam *et al.* 2000, Young 2009) often leading to adverse trophic-level effects on birds and fish (Fleeger *et al.* 2008, Spruzen *et al*. 2008). The causal mechanisms for adverse effects of macroalgal blooms on benthic invertebrates have been well studied. Labile organic matter associated with macroalgal biomass stimulates sediment oxygen demand (Lavery and McComb 1991) causing a shallowing of the zone of sediment anoxia. This shallowing is accompanied by high concentrations of pore water ammonia and sulfide that are toxic to surface deposit feeders that often reside just below the sediment surface (Gianmarco *et al.* 1997, Kristiansen *et al*. 2002).

Although causal mechanisms for adverse effects of macroalgal blooms on benthic invertebrates are well documented, few studies have identified thresholds at which these adverse effects occur. Most studies have been correlative, relating macroalgal abundance to infaunal and epifaunal community structure (e.g., Bona 2006). Collectively, these studies lack control over exogenous factors that can mediate biological response; only controlled field experiments that manipulate macroalgal abundance can show causal relationships between biomass and changes to benthic community structure without the influence of confounding factors. In two separate manipulative experiments in the Baltic Sea, Norkko and Bonsdorff (1996) added 2.05 kg wet weight (ww) m^{-2} and Cummins *et al.* (2004) added approximately 4.5 kg ww m^{-2} of macroalgae in a one-time addition to benthic plots and measured infaunal responses after approximately four weeks. Both studies found that macroalgal additions resulted in a significant loss of infaunal and epifaunal species richness compared to no-algae controls. These studies had only a single algal density and only a single time point was monitored; recent work demonstrated duration of exposure was an important factor in establishing thresholds (Green and Fong In Review). This study was the first manipulative field experiment that featured multiple treatment levels of algae as well as tight control over duration of treatment. The shortcoming of this study was a lack of resolution between plots cleared bi-weekly, (a control treatment) and mat depths of 1.5 cm (185 g dw m^{-2}; dry weight based on regression analysis, this study), the next highest treatment level where strong adverse effects were observed. Without varying macroalgal abundance across an intermediate range of treatments, it is unknown if negative effects on benthic diversity would have occurred at lower biomass.

Ecological thresholds have been defined as "the point at which there is an abrupt change in an ecosystem quality, property or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem" (Groffman *et al.* 2006). Thresholds can be further distinguished as "resistance" thresholds (e.g., an abrupt decline in condition following an initial zone of no effect) and "exhaustion" thresholds (a sharp transition to zero slope at the end of a stressor gradient at which point the response variable reaches a natural limit (Cuffney *et al.* 2010). Others have associated

ecological thresholds with the concept of resilience and a transition between alternate stable states (Resiliance Alliance and Sante Fe Institute 2004). Here, we utilize the concept of "benchmark" to refer to a region along the stressor - response threshold curve in which adverse effects have been empirically documented under a set of environmental conditions. Thus, as benchmarks provide essential information about known points where thresholds have been passed, they begin to narrow in on the range where thresholds occur and where management action may be needed.

The objective of this study was to document benchmarks of adverse effects to benthic macrofaunal community structure along a stress gradient of varying macroalgal abundance on intertidal flats as they developed over eight weeks. Moreover, we repeated our experiments in two sites in each of two estuaries in different latitudes, one in northern and one in southern California, to determine if there was a common threshold despite differences in climate, hydrology, and sediment characteristics.

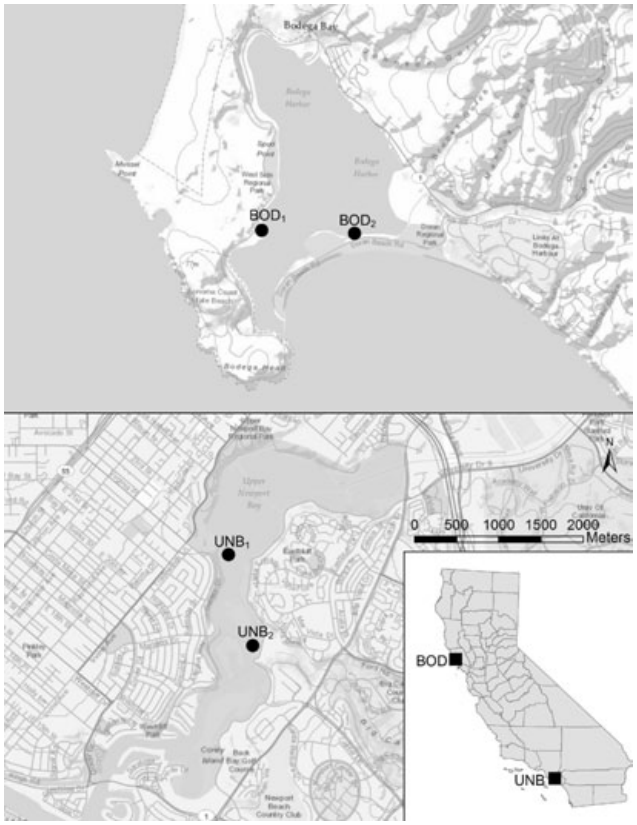

Figure 1. Map showing study sites in Bodega Harbor and Upper Newport Bay: Bodega Harbor Site 1 (BOD_1), Bodega Harbor Site 2 (BOD_2) Upper Newport Bay Site 1 (UNB_1), and Upper Newport Bay Site 2 (UNB_2).

Methods

We conducted a single factor experiment maintaining six abundances of macroalgae (*Ulva* spp.) in experimental plots on intertidal flats and measured the response of the faunal community every two weeks. Although macroalgae can be found from intertidal to subtidal habitats, we chose to focus on estuarine intertidal flats for this study, as monitoring of macroalgae is most cost-effective in this zone (Scanlan *et al.* 2007). Treatment abundances, maintained as mat thickness among the treatments but transformed to biomass (see results), were representative of the range found in estuaries across a range of eutrophication, and maintained for eight weeks to understand the relationship between abundance and duration of algal blooms. The experiments were conducted from July to October 2011.

Study Sites

Two experiments were conducted in Bodega Harbor (referred to as BOD_1 and BOD_2), northern California (38° 19' 25" N, 123° 02' 52" W) (Figure 1) and two in Upper Newport Bay (referred to as UNB_1 and UNB_2), southern California (33° 38′ 29.11″ N, 117° 53′ 7.91″ W). Bodega Harbor is a tidally well-flushed bay with seasonal freshwater input, sediments with a high percentage of sand (Grosholz *et al.* 2000), and a moderately developed watershed. Upper Newport Bay's principle freshwater source drains a large highly urbanized watershed and has sediments dominated by fine-grained clays and silts (Nezlin *et al*. 2007).

While there are many differences between the estuaries, we chose to assess differences in organic and percent sand content as both of these factors have been shown to be important in the distribution of benthic macrofauna (Levin and Talley 2000, Pelletier *et al.* 2010). We assessed initial sediment organic content and percent sand at each of the four sites by taking cores (2.5 cm id, 5 cm deep) from within randomly selected plots within each site. Organic content (n = 17 per site) was obtained by determining ash free dry mass. Percent sand (n = 20 per site) was assessed by sonicating wet samples with a sodium metaphosphate solution and sieving them through a 63 µm screen. One-factor nested analysis of variance (ANOVA) with sites nested in estuary was used to assess differences in sediment organic content and percent sand between sites.

Experimental Set Up

For each of the 4 experiments, 24 plots spaced 1 m apart were selected along a 50 m transect on wide intertidal flats following an elevational contour at approximately 0.75 m above MLLW. Plots were >10 meters from the vegetation in Upper Newport Bay, while in Bodega Harbor flats are broad with little slope so cages were placed greater than 50 m from the vegetation to insure daily submersion. Macroalgae for treatments were collected from each study area. The dominant genus of macroalgae at both sites was *Ulva*, including mixed assemblages of *U. expansa, U. intestinalis, U. lactuca* and *U. prolifera.* The remainder was in the genera *Gracilaria, Gracilariopsis, Ceramium,* and *Cladophora.* To maintain treatment abundances of macroalgae within our plots, 1.0 x 1.0 x 0.6 m (L x W x H) enclosures were constructed from black plastic mesh (1 cm mesh opening size), reinforced with plastic-coated rebar and cable ties. Uncoated rebar was attached to each corner with cable ties and pushed at least 50 cm into the sediment to prevent cages from floating. Walls of each cage were pushed at least 2 cm into the sediment and a lid secured with cable ties to prevent macroalgae from floating in or out. Treatment abundances were within the range of those found on intertidal mudflats in California (Kamer *et al*. 2001, Kennison 2008, Green 2011, Green *et al.* unpublished). Treatments were comprised of 0, 1, 1.5, 2.5, 3.5, and 5 cm of algae dominated by *U. expansa* in Bodega Harbor and by *U. intestinalis* in Upper Newport Bay. To facilitate comparisons of our mat depth treatments with earlier relevant literature, we regressed mat depth with measures of wet weight and dry weight from Green *et al.* (unpublished).

Algal mat depths were adjusted for loss due to decomposition or gain due to growth every two weeks by measuring mat depth in five haphazardly chosen locations within each plot and adding or removing macroalgal biomass evenly within plots. For no-biomass treatments all macroalgae within enclosures were removed by combing the sediment to a maximum depth of approximately 1 cm. We disturbed sediments in all plots equally. We chose to mimic continuous cover of macroalgal mats over eight weeks instead of a single depositional event based on field surveys of mat duration (Green and Fong In Review).

Quantification of Macrofauna

We quantified the responses of infauna and epifauna to macroalgal mat depth treatments by collecting cores (5 cm id, 10 cm deep) initially and every two weeks for eight weeks. Sampling dates coincided with the spring tides of each month. All measurements and cores were taken at least 10 cm from the cage walls to reduce possible edge effects. We were interested in macrofauna thus core contents were rinsed through 1 mm mesh using site water. Organisms were preserved immediately using 10% buffered formalin and transferred to 70% ethanol after at least 48 hours. Macrofauna were sorted using a dissecting microscope and identified to lowest taxonomic category possible. Total macrofauna was summed from the categories. Functional groups were assigned to the following categories: herbivore, omnivore, scavenger, subsurface deposit feeder, surface deposit feeder, and suspension feeder (see Appendix Table A1). Species richness was calculated to assess the effects of macroalgal mat depth on diversity over eight weeks. At all sites omnivores and scavengers comprised less than 1% of the total population thus were included in richness assessments but were not analyzed individually. At BOD_1, subsurface deposit feeders comprised only 5% of the community across all sampling dates and treatments while at BOD_2 they comprised <1% and were therefore not analyzed. At UNB_1 and UNB_2, suspension feeder populations were approximately 2% of total macrofauna across all sampling dates and treatments and were not analyzed.

For each site, repeated - measures ANOVAs compared mean total macrofauna, species richness and functional groups among macroalgal treatments over time. Data were transformed as necessary to meet the assumptions of ANOVA. Some data were transformed to ranks but did not violate the assumptions regarding rank transformed data and RM-ANOVA (Seaman *et al.* 1994).

Results

There were significant positive linear relationships between wet weight and mat depth for both *U. expansa* and *U. intestinalis* (Figure 2). Arrows indicate wet biomasses that correspond to experimental mat depth treatments. There were also positive linear relationships between wet and dry weights for both species (Figure 2). Overall, dry weights were approximately 13 and 11% of

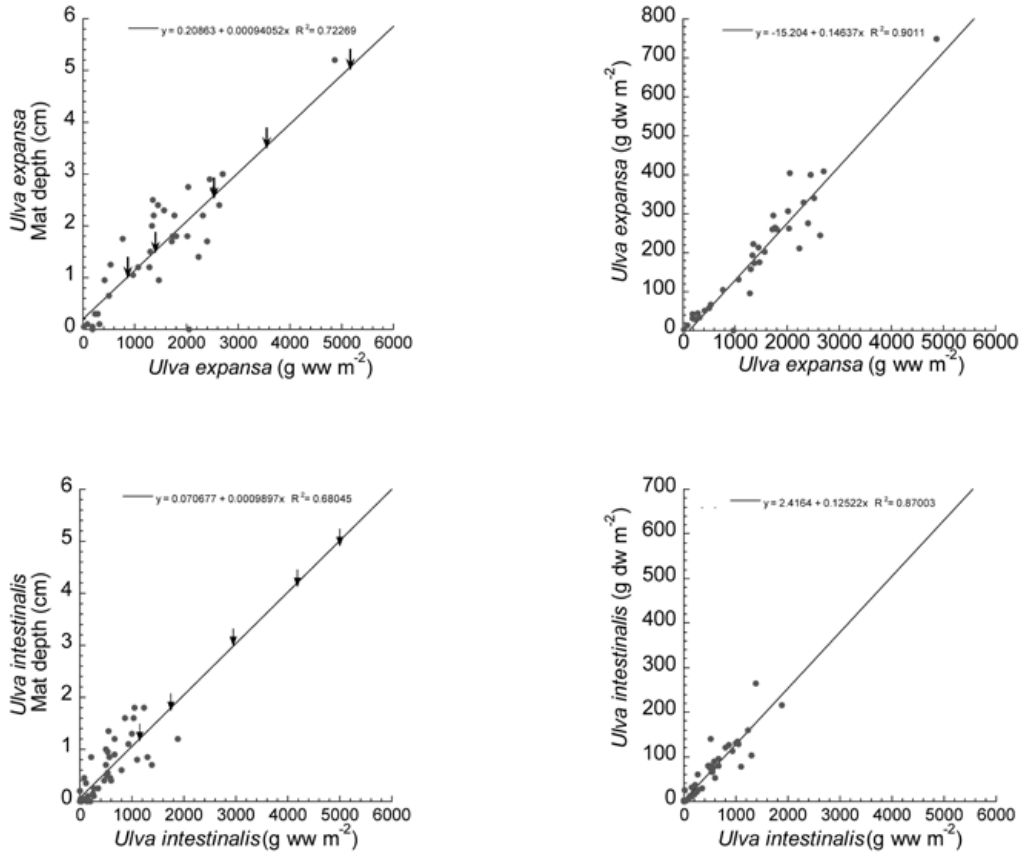

Figure 2. Regression analysis for mat depth and biomass for *U. expansa* and *U. intestinalis*. Experimental treatments are indentified by arrows.

wet weights for *U. expansa* and *U. intestinalis* respectively.

Initial sediment organic content and percent sand were significantly different between estuaries and between sites within estuaries (Table 1). Sediments from Upper Newport Bay had nearly three times more organic matter than sediments from Bodega Harbor (Table 2). Additionally, BOD_1 had 2.4 times higher percent organic content than BOD_2. Sediments at UNB_2 had approximately 20% greater organic content than sediments from UNB_1. Overall, Bodega Harbor sites had 63% more sand than sediments collected from Upper Newport Bay. BOD_2 had slightly more sand than BOD_1.

Overall, benthic invertebrate densities increased dramatically over time in no-algal treatments (0 cm) in BOD_1 compared to other sites (note differences in x axis scale), with mean maximum values 5 times higher than BOD_2 and exceeding both sites in UNB by an order of magnitude.

We found that mat depths as low as 1 cm caused reductions in total macrofaunal abundance for three of our four sites. At BOD_1, plots with 0 cm had more total macrofauna than any plot with mats and

Table 1. A nested one-factor ANOVA to compare initial sediment characteristics between estuaries and sites within estuaries.

Characteristic	Source	*d.f.*	*SS*	*F*	*p*
Percent Sand	Estuary	1	63880	368.76	<0.0001
	Site (Estuary)	2	1360.94	3.93	0.0238
Organic Content	Estuary	1	16.3	102.96	<0.0001
	Site (Estuary)	2	3.97	12.56	<0.0001

Table 2. Mean (+s.e.) sediment characteristics between estuaries and sites within estuaries.

	Sediment Characteristics			
	BOD_1	BOD_2	UNB_1	UNB_2
Organic Content	0.68 (+0.03)	0.28 (+0.01)	1.18 (+0.03)	1.74 (+0.19)
Percent Sand	87.67 (+0.73)	91.70 (+3.76)	27.70 (+1.72)	38.65 (+4.12)

macrofauna increased over eight weeks resulting in a significant interaction between treatment and time (Table 3; Figure 3). By week 2, 0 cm plots had nearly 15 times more total macrofauna than plots with 1 cm and 20 times more invertebrates on average than plots with 5 cm treatments.

Like BOD_1, at BOD_2 our lowest mat depth treatment caused adverse effects on total macrofaunal abundance. In BOD_2, total macrofauna in 0 cm treatments remained elevated compared to all treatments with mats where total macrofauna tended to decrease over eight weeks resulting in a significant interaction (Table 3; Figure 3). Declines in macrofauna were rapid, with differences between treatments with and without macroalgae evident after just two weeks. Declines also increased in magnitude with increasing algal biomass. Macrofaunal abundance in 0 cm treatments was nearly 4 times higher than in 1 cm treatments and 24 times higher on average than macrofauna in 5 cm treatments. This pattern remained relatively constant over the duration of the experiment.

Table 3. Results of repeated measures ANOVA for total macrofauna for each experiment varying macroalgal biomass. Interactions calculated by Wilks Lambda.

Source	*d.f.*	*F*	*P*
A. BOD_1			
Between Subjects (Treatment)	5	18.911	<0.0001
Within Subjects (Time)	4	29.29	<0.0001
Time*Treatment	20	3.599	0.0001
Residual	21		
B. BOD_2			
Between Subjects (Treatment)	5	5.349	0.0069
Within Subjects (Time)	4	27.541	<0.0001
Time*Treatment	20	2.237	0.0186
Residual	21		
C. UNB_1			
Between Subjects (Treatment)	5	8.283	0.0003
Within Subjects (Time)	4	13.619	<0.0001
Time*Treatment	20	0.856	0.6380
Residual	21		
D. UNB_2			
Between Subjects (Treatment)	5	0.204	0.9570
Within Subjects (Time)	4	11.775	0.0002
Time*Treatment	20	1.545	0.1070
Residual	21		

Negative effects were also seen at UNB_1 under the lowest mat depth (Table 3; Figure 3); both time and treatment had significant effects on total macrofauna. However negative effects took longer to occur at this site than in Bodega, as macrofauna remained at initial levels for up to four weeks in some of the intermediate mat depth treatments. Rapid effects of macroalgae occurred only with the two thickest mat treatments. Despite differences in timing, all treatments with added macroalgae had significantly lower abundances of total macrofauna after eight weeks.

Unlike the other sites, total macrofauna collected from UNB_2 were unaffected by treatment (Table 3; Figure 3). However fluctuations in total macrofaunal abundance across eight weeks resulted in an effect of time.

Overall, benthic diversity was higher at Bodega than Upper Newport Bay (Figure 4, Table 4, note scale change). For details of species composition see Appendix Table A1.

In three of the four experiments, species richness was affected by mat depth and time (Table 4). BOD_1 had the highest diversity; across all treatments and sampling dates, there was an average of 5.19 (+0.02) species per sample (Figure 4). In the 0 cm treatment, species richness nearly doubled after just two weeks. Species richness in any macroalgal treatment was no more than 56% of the richness found in 0 cm treatments after four weeks. However, richness increased again in nearly all of the treatments in

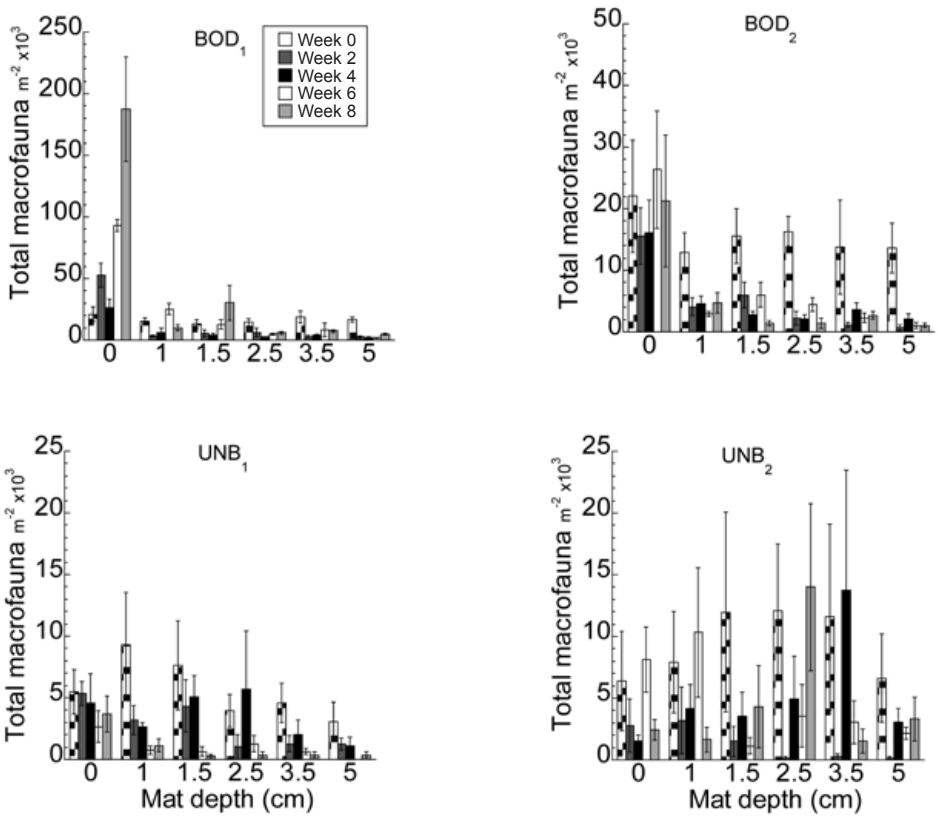

Figure 3. Total macrofauna from mat density treatments at Bodega Harbor and Upper Newport Bay: Bodega Harbor Site 1 (BOD_1), Bodega Harbor Site 2 (BOD_2) Upper Newport Bay Site 1 (UNB_1), and Upper Newport Bay Site 2 (UNB_2).

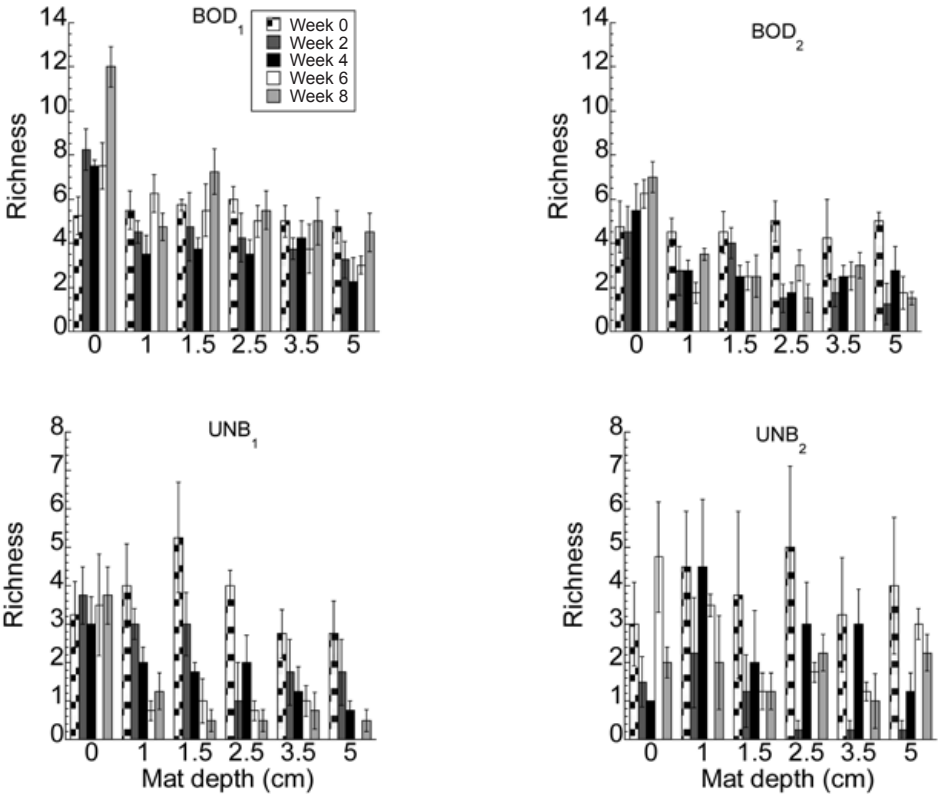

Figure 4. Species richness from mat density treatments at Bodega Harbor and Upper Newport Bay: Bodega Harbor Site 1 (BOD_1), Bodega Harbor Site 2 (BOD_2) Upper Newport Bay Site 1 (UNB_1), and Upper Newport Bay Site 2 (UNB_2).

Table 4. Results of repeated measures ANOVA for species richness for each experiment varying macroalgal biomass. Interactions calculated by Wilks Lambda.

Source	d.f.	F	P
A. BOD_1			
Between Subjects (Treatment)	5	12.302	<0.0001
Within Subjects (Time)	4	6.231	0.0037
Time*Treatment	20	1.737	0.058
Residual	21		
B. BOD_2			
Between Subjects (Treatment)	5	4.322	0.009
Within Subjects (Time)	4	4.825	0.011
Time*Treatment	20	1.692	0.067
Residual	21		
C. UNB_1			
Between Subjects (Treatment)	5	9.768	0.0001
Within Subjects (Time)	4	11.757	0.0002
Time*Treatment	20	1.096	0.383
Residual	21		
D. UNB_2			
Between Subjects (Treatment)	5	0.808	0.559
Within Subjects (Time)	4	16.912	<0.0001
Time*Treatment	20	1.415	0.159
Residual	21		

weeks 6 and 8 resulting in an effect of time (Table 4). The increase in richness in the 0 cm treatment across eight weeks and the decrease and subsequent increase in the other treatments resulted in a nearly significant interaction. This recovery was mostly due to the recruitment of low abundances of rare species.

Diversity was lower at BOD_2 than BOD_1 with 3.28 (+0.02) species collected per sample on average across treatments and sampling dates and highest in the 0 cm treatment (Figure 4). After two weeks of cover, 1 cm mats resulted in a 39% loss of species richness when compared to the treatment without macroalgae. Richness at BOD_2 was highest in the 0 cm compared to treatments with macroalgae resulting in an effect of treatment (Table 4). In general, richness increased in the 0 cm treatment and decreased after 2 weeks and remained lower in all macroalgal treatments.

Macroalgal mats of all depths had strong negative effects on species richness at UNB_1 (Table 4; Figure 4). After two weeks, 0 cm plots had 1.7 times greater richness than plots with mats at UNB_1, which resulted in an effect of treatment. All plots with macroalgae lost richness over eight weeks, resulting in an effect of time.

Like total macrofauna, species richness was affected by time but not treatment at UNB_2 (Table 4; Figure 4). Every treatment showed a decline in the number of species after two weeks and then an increase. The greatest increase in number of species occurred in the 0 cm treatment during week 6, where richness was 1.6 times greater than in the same treatment during week 0. The increase was due to recruitment of a few uncommon species that disappeared two weeks later.

Macroalgal mats affected functional group composition at all four sites. At BOD_1 surface deposit feeders was the dominant functional group, comprising 45% of total macrofauna (Table 5; Figure 5). After two weeks, all groups including herbivores, surface deposit feeders, and suspension feeders were nearly eliminated in all treatments with macroalgae but not in the 0 cm treatment. Some recovery occurred in all trophic groups in 1 and 1.5 cm treatments during weeks 6 and 8. However, treatments with 2.5 cm and greater mat depths never showed recovery of macrofauna, which resulted in a significant interaction.

In contrast to BOD_1, the benthic community at BOD_2 was dominated by suspension feeders, which made up approximately 63% of total macrofauna. At BOD_2 herbivores, surface deposit feeders, and suspension feeders had higher abundances in the treatment without mats than treatments with macroalgae and losses occurred within two weeks (Table 5; Figure 6). For example, herbivores were completely eliminated in 2.5 and 5 cm treatments in week 2 while suspension and surface deposit feeders lost approximately 80% of individuals in the 1 cm treatment when compared to 0 cm during week 2. Some recovery of suspension feeders occurred during week 6 and herbivores populations increased in week 8 in a few treatments but neither of these resulted in a significant interaction.

Surface deposit feeders were the only functional group to show a treatment effect at UNB_1 (Table 5; Figure 7). Surface deposit feeders were eliminated in 5 cm treatments after just two weeks and effectively eliminated in 1.5 cm treatments and greater after four weeks. Herbivores declined in all treatments over eight weeks resulting in an effect of time. Some recovery of herbivores occurred in the 1.5 and 2.5 cm treatments due to increased abundances of epibenthic gastropods. Subsurface deposit feeders (which

Table 5. Results of repeatd measures ANOVA for functional groups for each experiment varying macroalgal biomass. Interactions calculated by Wilks Lambda.

Source	d.f.	F	P
A. BOD_1 Herbivores			
Between Subjects (Treatment)	5	37.634	<0.0001
Within Subjects (Time)	4	20.003	<0.0001
Time*Treatment	20	3.296	0.0003
Residual	21		
B. BOD_1 Surface Deposit Feeders			
Between Subjects (Treatment)	5	23.064	<0.0001
Within Subjects (Time)	4	30.659	<0.0001
Time*Treatment	20	4.693	<0.0001
Residual	21		
C. BOD_1 Suspension Feeders			
Between Subjects (Treatment)	5	164.55	<0.0001
Within Subjects (Time)	4	6.366	0.0034
Time*Treatment	20	4.858	<0.0001
Residual	21		
D. BOD_2 Herbivores*			
Between Subjects (Treatment)	5	5.183	0.004
Within Subjects (Time)	4	0	1
Time*Treatment	20	1.711	0.063
Residual	21		
E. BOD_2 Surface Deposit Feeders			
Between Subjects (Treatment)	5	4.448	0.008
Within Subjects (Time)	4	2.379	0.098
Time*Treatment	20	2.232	0.011
Residual	21		
F. BOD_2 Suspension Feeders			
Between Subjects (Treatment)	5	9.453	0.0001
Within Subjects (Time)	4	16.267	<0.0001
Time*Treatment	20	1.046	0.43
Residual	21		
G. UNB_1 Herbivores			
Between Subjects (Treatment)	5	2.076	0.116
Within Subjects (Time)	4	8.321	0.001
Time*Treatment	20	1.338	0.199
Residual	21		
H. UNB_1 Surface Deposit Feeders			
Between Subjects (Treatment)	5	8.275	0.0003
Within Subjects (Time)	4	7.353	0.002
Time*Treatment	20	1.336	0.201
Residual	21		
I. UNB_1 Subsurface Deposit Feeders*			
Between Subjects (Treatment)	5	2.164	0.104
Within Subjects (Time)	4	0	1
Time*Treatment	20	0.701	0.806
Residual	21		
J. UNB_2 Herbivores			
Between Subjects (Treatment)	5	1.275	0.317
Within Subjects (Time)	4	8.886	0.0007
Time*Treatment	20	0.5026	0.953
Residual	21		
K. UNB_2 Surface Deposit Feeders*			
Between Subjects (Treatment)	5	7.362	0.0006
Within Subjects	4	0	1
Time*Treatment	20	1.211	0.284
Residual	21		
L. UNB_2 Subsurface Deposit Feeders			
Between Subjects (Treatment)	5	0.426	0.824
Within Subjects	4	10.097	0.0004
Time*Treatment	20	1.877	0.036
Residual	21		

*Rank transformed

made up approximately 15% of total invertebrate abundances) reached their highest post initial abundances in the 2.5 cm treatments after four weeks but were not affected by either treatment or time.

UNB_2 was the only site dominated by subsurface deposit feeders (Figure 8), comprising approximately 56% of total macrofauna across all sampling dates and treatments. However, variable responses due to treatment and time resulted in a significant interaction (Table 5; Figure 8). Overall, subsurface deposit feeders seemed to reach highest densities in intermediate mat depths. Surface deposit feeders declined in all treatments until week 6 where they recovered slightly in 0 and 5 cm resulting in an effect of treatment. Herbivores likewise declined in all treatments with some recovery during week 4 but they never returned to their initial abundances resulting in an effect of time.

Discussion

We established a benchmark of macroalgal abundance and duration where loss of key benthic invertebrate functional groups (surface deposit feeders, suspension feeders, and herbivores) occurred. These strongly negative effects occurred at similar levels in two very different estuaries and at our thinnest macroalgal mat depth treatment, corresponding to biomass levels of approximately 110 to 120 g dw m^{-2} (estimated from regressions). This effect level fell within the range of biomass commonly found during field surveys, suggesting many California estuaries are currently experiencing negative effects of macroalgal mats and therefore clearly identifying a need for management action (McLaughlin *et al.* In Review). Previous studies showed that macroalgal mats resulted in anoxic and sulfidic environments that are detrimental to

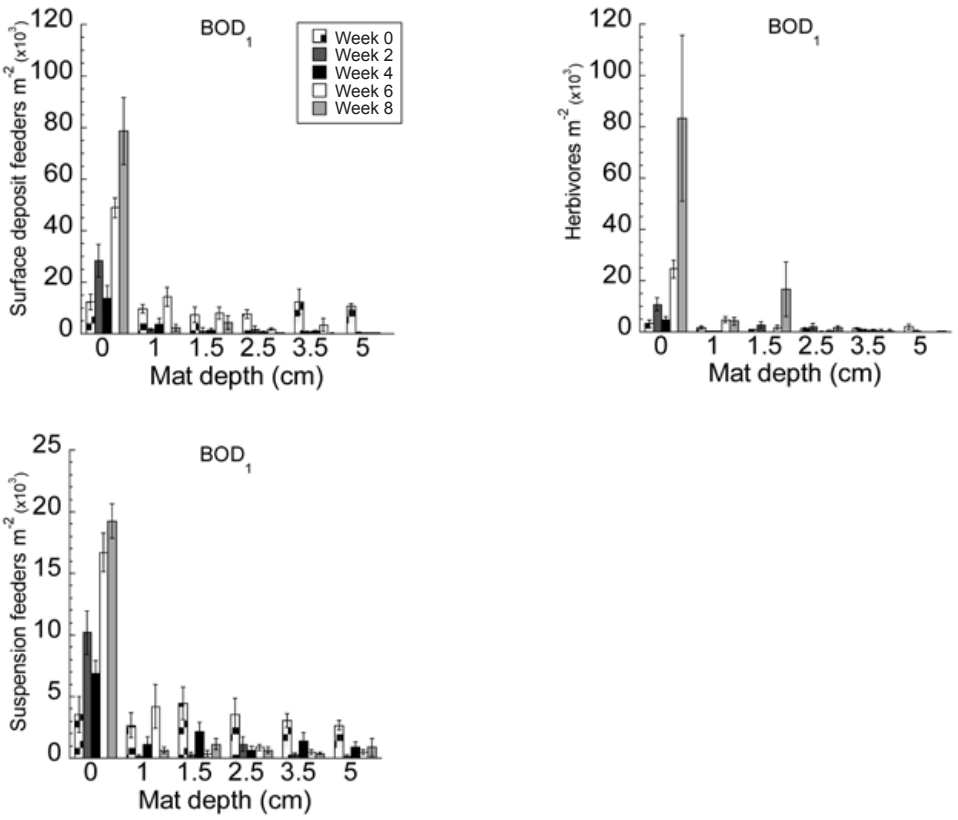

Figure 5. Response of macrobenthic functional groups to macroalgal density at Bodega Harbor Site 1 (BOD_1) for surface deposit feeders, herbivores, and suspension feeders.

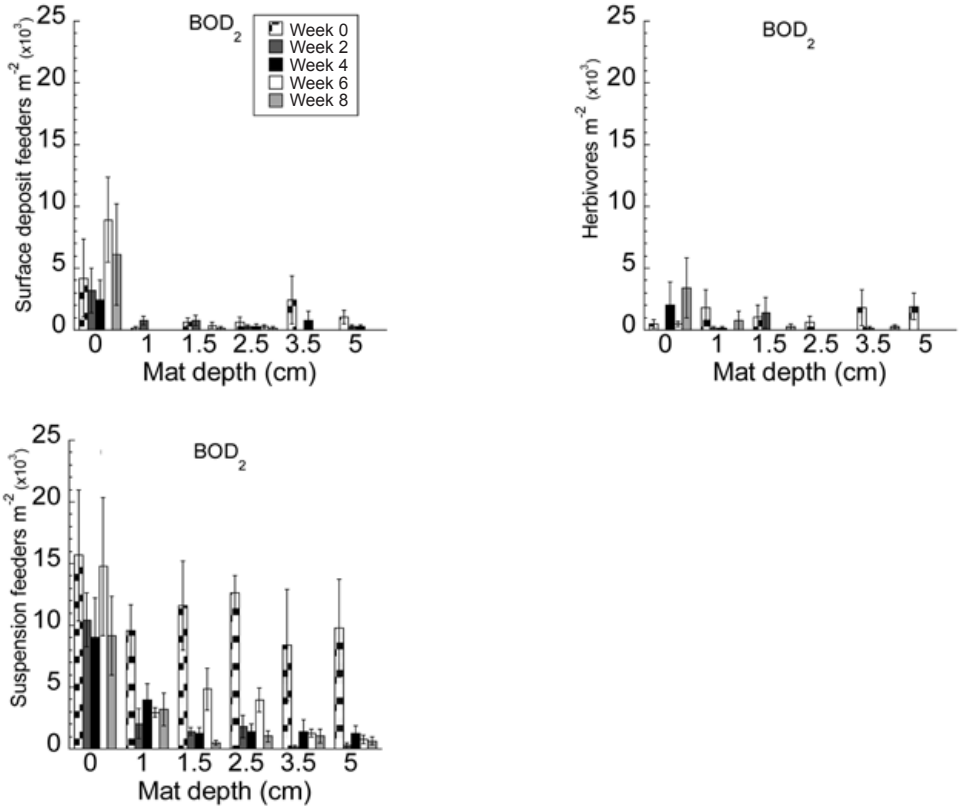

Figure 6. Response of macrobenthic functional groups to macroalgal density at Bodega Harbor Site 2 (BOD_2) for surface deposit feeders, herbivores, and suspension feeders.

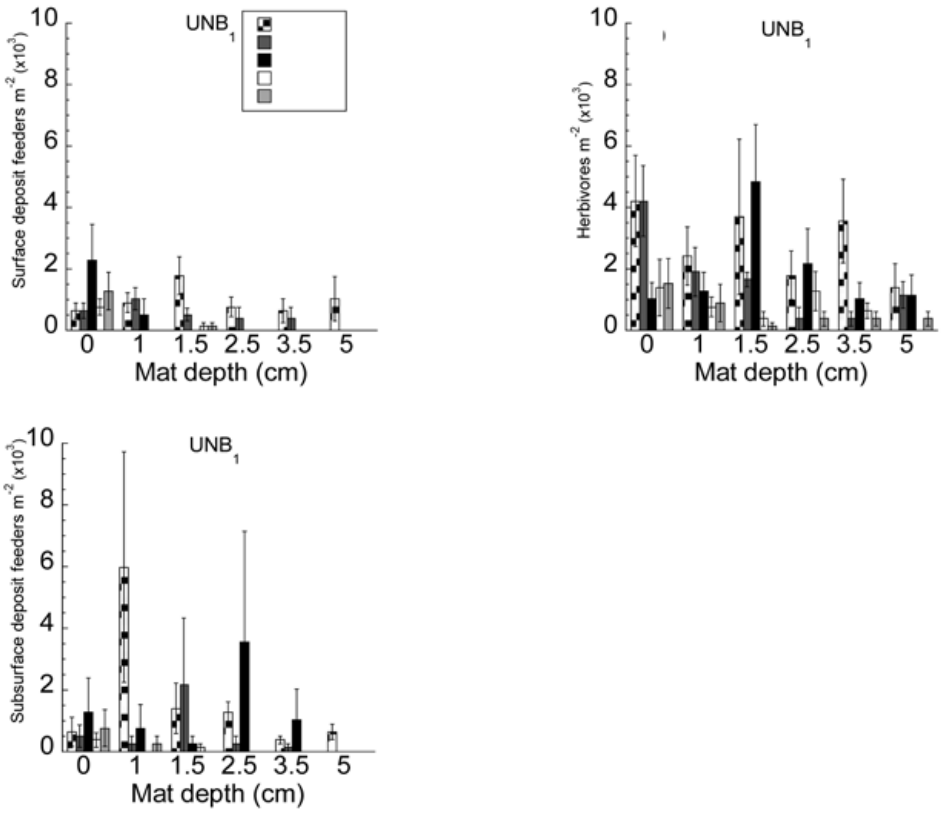

Figure 7. Response of macrobenthic functional groups to macroalgal density at Upper Newport Bay Site 1 (UNB_1) for surface deposit feeders, herbivores, and suspension feeders.

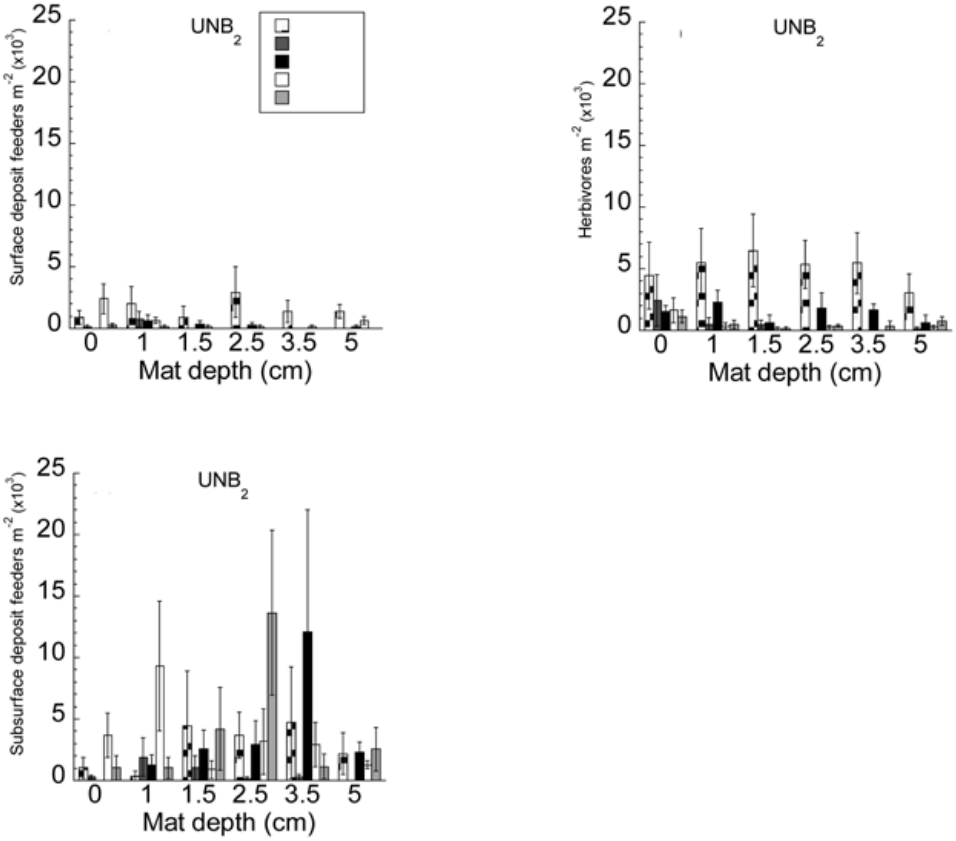

Figure 8. Response of macrobenthic functional groups to macroalgal density at Upper Newport Bay Site 2 (UNB_2) for surface deposit feeders, herbivores, and suspension feeders.

surface deposit feeders, suspension feeders, and herbivores (Llanso 1991, Auffrey *et al*. 2004) but not subsurface deposit feeders (Grieshaber and Volkel 1998). Adverse effects were found in BOD_1, BOD_2 and UNB_1 due to the initial dominance of these sensitive groups within the benthic community. Loss of sensitive taxa could have catastrophic consequences on ecosystem function due to changes in biogeochemical cycling (Waldbusser *et al.* 2004) and trophic support (Posey *et al.* 1995, Wilson Jr. and Vogel 1997, Grosholz *et al.* 2000). UNB_2 was likely less affected by macroalgae because the initial community had the highest proportion of subsurface deposit feeders, which may be indicative of a shifted baseline due to a history of anthropogenic stress (toxicants, excessive sedimentation, etc.) at that site (Gamito *et al.* 2012). Thus, our study suggests that some areas of Upper Newport Bay are chronically above our established benchmark. This is likely to have ecosystem - level effects as communities dominated by subsurface deposit feeders are unlikely to support ecosystem functions such as biogeochemical cycling (Waldbusser *et al.* 2004) and trophic transfer (Posey *et al.* 2002).

In this study we found strong negative effects of even the thinnest macroalgal mats, establishing a benchmark of the lowest observed effect level documented in the literature thus far (110 g dw m^{-2}). One field survey supports this benchmark; Bona (2006) found a loss of deep burrowing deposit feeders, critical to biogeochemical cycling and trophic support, when *Ulva* biomass exceeded approximately 90 g dw m^{-2} (700 g ww m^{-2}). Conceptually, we believe that this "lowest observed effect" benchmark lies between a resistance threshold (defined as an abrupt decline in condition following an initial zone of no effect) and an exhaustion threshold (*sensu* Cuffney *et al.* 2010 - a sharp transition to zero slope at the end of a stressor gradient). In a field survey in eight California estuaries, Sutula *et al.* (In Review) identified an exhaustion threshold of 175 g dw m^{-2} where the oxygen penetration in sediments approached zero. Similarly, Green and Fong (In Review) documented a complete shift from surface to subsurface deposit feeders occurred at approximately 185 g dw m^{-2}, an abundance that also corresponded to high concentrations of pore water sulfide (Green and Fong In Review). Sutula *et al.* (In Review) determined a "reference envelope" – defined as the physical, chemical or biological characteristics of sites found in the best available condition according to the variable of interest (Stoddard *et al.* 2006) in a wide range of estuaries in California. They established that macroalgal biomasses of 3 to 15 g dw m^{-2} had no negative effects on sediment oxygen penetration depths in intertidal flats. Together these studies have begun to define the range of macroalgal abundance – between 15 and 110 g dw m^{-2} - within which a resilience threshold occurs. However, clearly more studies with intermediate abundances of algae are needed to more closely define this resilience threshold.

We found that the duration that mats remained on the benthos often interacted with macroalgal abundance to modify their impact on macrofaunal abundance and diversity. Thus far, attempts to identify adverse effects of macroalgae on benthic invertebrates have been based on a single application (Cardoso *et al.* 2004). Prior to this study and Green and Fong (In Review), no study has taken duration of cover into account. Macroalgal mats, subject to transport by currents, may move long distances over short periods of time (FangLi *et al.* 2011); therefore it is impossible to determine how long a given mat has been on the benthos in a typical simple snap shot measure. In our study, many, but not all, effects occurred after just two weeks of macroalgal cover with significant losses to total macrofauna, species richness and functional groups critical to trophic support. In some cases, negative effects took over 4 weeks, especially at intermediate mat depth treatments, suggesting that there may be some ameliorating effect if mats are ephemeral. However, Green (2011) showed that mats routinely cover large areas of benthos for durations exceeding 8 weeks in eutrophic estuaries. In addition, several other studies using comparable macroalgal abundances have similarly shown changes in macrobenthic structure in two weeks or less (Bolam *et al.* 2000, Osterling and Pihl 2001, Franz and Friedman 2002). Since devastating effects to macrobenthic abundance, diversity and community structure can occur rapidly, we recommend that duration of bloom be considered in use of macroalgae in assessments of estuarine condition and that routine monitoring of macroalgal abundance be undertaken, particularly in sensitive habitats and during bloom seasons.

Moreover, we clearly demonstrated a benchmark of macroalgal abundance at which severe and rapid impacts to macrobenthic estuarine communities occurred, representing one of two studies to

document effects in a field experiment that controlled duration as well as abundance (Green and Fong In Review). Macroalgal biomasses of approximately 110 to 120 g dw m^{-2} negatively affected the abundance and diversity of critical infauna and epifauna, often within just two weeks. Future studies that maintain macroalgal abundances below 100 g dw m^{-2} may inform where the resistance threshold may ultimately lie. In this study we targeted critical macrobenthic taxa in two sites in each of two estuaries such that generalizations about the effects of macroalgae on the benthic community could be made. The quantitative information from our study can inform nutrient - related water quality goals and restoration targets through improved assessments of eutrophication in estuaries.

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Appendix

Table A1. List of taxa and functional group. Means and standard errors for each taxon for initial and final sampling weeks. Functional group abbreviations: H = Herbivores, O = Omnivores, P = Predators, SC = Scavengers, SSDF = Subsurface Deposit Feeders, SDF = Surface Deposit Feeders, SF = Suspension Feeders.

Site	Genus	species	FNX Group	Week 0 Mean	Week 0 SE	Week 8 Mean	Week 8 SE
BOD_1	Allorchestes	angusta	H	0.02	0.02	0.13	0.11
BOD_1	Ampithoe	laceterosa	H	0.02	0.02	0.02	0.02
BOD_1	Ampithoe	plumosa	H	0	0	0.08	0.04
BOD_1	Ampithoe	sectimanus	H	0	0	0.02	0.02
BOD_1	Aoroides	exilis	SF	0	0	0.08	0.05
BOD_1	Aoroides	intermedia	SF	0	0	0.04	0.03
BOD_1	Aoroides	inermis	SF	0	0	0.15	0.09
BOD_1	Axiothella	rubrocincta	SSDF	0.17	0.08	0.32	0.1
BOD_1	Boccardia	proboscidea	SDF	0.21	0.21	0.02	0.02
BOD_1	Cryptomya	californica	SF	0	0	0.66	0.23
BOD_1	Cumella	vulgaris	P	0	0	0.34	0.13
BOD_1	Drilonereis	falcata	P	0.06	0.04	0	0
BOD_1	Emplectonema	gracile	P	0	0	0.02	0.02
BOD_1	Exogone	acutipalpa	H	1.29	0.32	16.5	7.93
BOD_1	Grandidierella	japonica	H	0.36	0.15	0.53	0.36
BOD_1	Hemigrapsis	oregonensis	O	0.04	0.03	0.15	0.05
BOD_1	Leptochelia	dubia	SDF	9.83	1.1	14.27	6.32
BOD_1	Monocorophium	insidiosum	SF	2.12	0.31	2.53	1.18
BOD_1	Nebalia	kensleyi	SC	0	0	0.42	0.16
BOD_1	Notomastus	tenuis	SSDF	0	0	0.02	0.02
BOD_1	Nutricola	tantilla	SF	1.19	0.3	0.42	0.16
BOD_1	Oligochaeta		SSDF	0.17	0.09	2.55	0.65
BOD_1	Phoronis	sp	SF	0.02	0.02	0	0
BOD_1	Photis	lacia	SF	0	0	0.17	0.11
BOD_1	Rhepoxynius	heterocuspidatus	P	0.66	0.25	0.51	0.13
BOD_1	Scoletoma	luti	P	0.36	0.14	0.83	0.32
BOD_2	Allorchestes	angusta	H	0.02	0.02	0.15	0.11
BOD_2	Boccardia	proboscidea	SDF	0.53	0.14	0.4	0.19
BOD_2	Cryptomya	californica	SF	0	0	0.66	0.23
BOD_2	Drilonereis	falcata	P	0.17	0.07	0.19	0.1
BOD_2	Emplectonema	gracile	P	0	0	0.02	0.02
BOD_2	Eohaustorius	estuarius	H	0.02	0.02	0	0
BOD_2	Eteone	spilotus	P	0.02	0.02	0.02	0.02
BOD_2	Exogone	acutipalpa	H	0.13	0.07	0.32	0.22
BOD_2	Grandidierella	japonica	H	1.1	0.4	0.32	0.23
BOD_2	Hemigrapsis	oregonensis	O	0	0	0.06	0.05
BOD_2	Leptochelia	dubia	SDF	0.98	0.55	0.66	0.66
BOD_2	Monocorophium	insidiosum	SF	6.62	1.24	1.02	0.58
BOD_2	Nebalia	kensleyi	SC	0	0	0.02	0.02
BOD_2	Notomastus	tenuis	SSDF	0	0	0.02	0.02
BOD_2	Nutricola	tantilla	SF	4.42	0.55	0.91	0.28
BOD_2	Nutricola	lordi	SF	0.13	0.13	0	0
BOD_2	Phoronis	sp	SF	0.11	0.11	0	0
BOD_2	Rhepoxynius	heterocuspidatus	P	1.17	0.24	0.21	0.07
BOD_2	Scoletoma	luti	P	0.28	0.1	0.42	0.22

Table A1. Continued

Site	Genus	species	FNX Group	Week 0 Mean	Week 0 SE	Week 8 Mean	Week 8 SE
UNB_1	Acteocina	inculta	H	0.66	0.18	0.32	0.11
UNB_1	Capitella	capitata	SSDF	1.38	0.47	0.04	0.04
UNB_1	Cerithidea	californica	H	0	0	0.21	0.09
UNB_1	Eteone	lighti	P	0.49	0.14	0.08	0.04
UNB_1	Grandidierella	japonica	H	2.17	0.5	0.08	0.07
UNB_1	Monocorophium	insidiosum	SF	0.15	0.11	0	0
UNB_1	Musculista	senhousia	SF	0	0	0.02	0.02
UNB_1	Oligochaeta		SSDF	0.34	0.25	0.13	0.11
UNB_1	Polydora	nuchalis	SDF	0	0	0.02	0.02
UNB_1	Pseudopolydora	paucibranchiata	SDF	0.34	0.08	0.08	0.08
UNB_1	Streblospio	benedicti	SDF	0.08	0.04	0.02	0.02
UNB_1	Tagelus	affinis	SDF	0.04	0.03	0.02	0.02
UNB_1	Tethygeneia	opata	H	0.02	0.02	0	0
UNB_2	Acteocina	inculta	H	509.5	122.67	63.69	46.64
UNB_2	Allorchestes	angusta	H	106.15	68.43	21.23	21.23
UNB_2	Ampithoe	valida	H	84.92	50.08	42.46	29.36
UNB_2	Capitella	capitata	SSDF	318.44	175.67	2972.08	1034.88
UNB_2	Cerithidea	californica	H	0	0	21.23	21.23
UNB_2	Eteone	lighti	P	360.9	103.91	21.23	21.23
UNB_2	Exogone	sp A	H	42.46	29.36	0	0
UNB_2	Grandidierella	japonica	H	4267.06	827.37	275.98	110.49
UNB_2	chironomid	larvae	SDF	42.46	29.36	0	0
UNB_2	Marphysa	angelensis	H	21.23	21.23	21.23	21.23
UNB_2	Monocorophium	insidiosum	SF	127.38	55.29	21.23	21.23
UNB_2	Musculista	senhousia	SF	21.23	21.23	0	0
UNB_2	Oligochaeta		SSDF	2271.52	954.16	934.08	547.47
UNB_2	Perampithoe	mea	H	21.23	21.23	63.69	35.13
UNB_2	Polydora	nuchalis	SDF	63.69	46.64	0	0
UNB_2	Pseudopolydora	paucibranchiata	SDF	721.79	252.74	0	0
UNB_2	Streblospio	benedicti	SDF	339.67	142.75	21.23	21.23
UNB_2	Tagelus	affinis	SDF	106.15	61.18	21.23	21.23
UNB_2	Tethygeneia	opata	H	0	0	42.46	29.36