Context-Dependent Eelgrass–Macroalgae Interactions Along an Estuarine Gradient in the Pacific Northwest, USA

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Abstract Land-based eutrophication is often associated with blooms of green macroalgae, resulting in negative impacts on seagrasses. The generality of this interaction has not been studied in upwelling-influenced estuaries where oceanic nutrients dominate seasonally. We conducted an observational and experimental study with *Zostera marina* L. and ulvoid macroalgae across an estuarine gradient in Coos Bay, Oregon. We found a gradient in mean summer macroalgal biomass from 56.1 gdw 0.25 m^{-2} at the marine site to 0.3 gdw 0.25 m^{-2} at the riverine site. Despite large macroalgal blooms at the marine site, eelgrass biomass exhibited no seasonal or interannual declines. Through experimental manipulations, we found that pulsed additions of macroalgae biomass (+4,000 mL) did not affect eelgrass in marine areas, but it had negative effects in riverine areas. In upwelling-influenced estuaries, the negative effects of macroalgal blooms are context dependent, affecting the management of seagrass habitats subject to nutrient inputs from both land and sea.

Keywords *Zostera marina* · *Ulva* · Species interactions ·
Estuarine gradient · Oceanic upwelling · Oregon

Introduction

Eutrophication of coastal waters worldwide is associated with the loss of seagrass habitat (Orth et al. 2006; Waycott et al. 2009). Among a host of ecosystem perturbations associated with increased anthropogenic nutrient input to coastal waters, land-based nutrient loading and associated macroalgal blooms are of key concern due to their deleterious effects on seagrass meadows (Burkholder et al. 2007) and the associated loss of the many vital ecosystem functions and services associated with these habitats (Barbier et al. 2011; Duarte 2000). Compared to seagrasses, macroalgae can exhibit high productivity and increases in biomass over relatively short periods of time, stemming from its superior ability to sequester nutrients (Hauxwell et al. 2001; Valiela et al. 1997). Blooms of green macroalgae (primarily of the family Ulvaceae; hereafter referred to as "ulvoids") have been shown to range from roughly 650 g dw m^{-2} (Hog Island Bay, Virginia, USA; Havens et al. 2001) to upwards of 1,800 gdw m^{-2} (Venice Lagoon, Italy; Sfriso et al. 1992). On the Oregon coast, research in Coos Bay has documented maximum summer bloom conditions of ~750 gdw m^{-2} (Pregnall and Rudy 1985), almost four times as dense as the threshold for negative impacts on seagrass in Chesapeake Bay, USA (Bricker et al. 2003).

The interactions that result from these productivity differences between seagrass and macroalgae are complex, and their outcomes may depend on both environmental conditions, as well as the ability of seagrass to influence these interactions via feedbacks associated with their strong engineering capabilities (Carr et al. 2010; Havens et al. 2001; Valiela et al. 1997). Light attenuation by macroalgal canopies is one primary cause of seagrass loss under eutrophic conditions (Hauxwell et al. 2001; Krause-Jensen et al. 1996; Valiela et al. 1997) and can be exacerbated by water column nutrient enrichment (Burkholder et al. 1992), shifts in oxygen level due to senescence of the macroalgae (Hauxwell et al. 2001), and other indirect processes, such as increased turbidity (Carr et al. 2010).

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The various biogeochemical changes associated with macroalgal canopies in seagrass beds have been reviewed by McGlathery (2001) and Burkholder et al. (2007) and include hypoxia in the water column, anoxia in the sediment, as well as the associated microbial activity and production of sulfide-containing compounds associated with low oxygen environments. The additive and interactive effects of the numerous physical and biogeochemical processes produced by macroalgae canopies within seagrass beds suggest that there may be diverse outcomes to these interactions depending on the environmental context in which they occur.

Growing evidence suggests that seagrass response to nutrient enrichment via interactions with macroalgae can result in negative, neutral, and potentially positive effects, with changing interaction dynamics through time and space (e.g., Armitage et al. 2005; Eriksson et al. 2007; Jorgensen et al. 2007). This context dependency of species interactions not only helps inform basic community structure theory (e.g., Bronstein 1994; Hacker and Gaines 1997; Menge and Sutherland 1987) but, along with other ecological research on context dependency, is necessary to translate broad-scale ecological generalities into management initiatives that address the idiosyncrasies of natural systems, such as the outcomes of biological invasions (Hacker and Dethier 2006; Hacker et al. 2011), human alteration of food webs (Salomon et al. 2010), and ecosystem engineering (Crain and Bertness 2006).

To explore this context dependency in more detail, we investigated the interaction between seagrass, *Zostera marina* L. (hereafter referred to as "eelgrass") and ulvoid macroalgae across an estuarine gradient in South Slough, a branch of Coos Bay, located on the southern coast of Oregon, USA (Fig. 1). This is a characteristic "upwelling-influenced" estuary in the Pacific Northwest, where the influence of the nearshore California Current System is particularly strong at the estuary's mouth (Hickey and Banas 2003; Roegner and Shanks 2001). In this system and other upwelling-influenced estuaries in this region (e.g., Yaquina Bay), marine-derived nutrient inputs dominate over land-based loading during the low precipitation summer months (Brown and Ozretich 2009; Rumrill 2006) and are strongly associated with blooms of green macroalgae (Brown et al. 2007; Kaldy and Brown, US EPA, unpublished data). Along the relatively undisturbed South Slough estuary, blooms at the mouth of the bay are equivalent in height and biomass to those associated with seagrass declines in other systems (e.g., Hauxwell et al. 2001) but are much greater than macroalgae production in other regions of the estuary. In this study, we were primarily interested in determining how macroalgae abundance and gradients in physicochemical conditions along the estuarine gradient affected macroalgae–eelgrass

interactions. We used a comparative experimental approach (e.g., Dayton 1971; Menge et al. 2004), and the sites located along the estuarine salinity gradient address two primary questions: (1) What is the temporal relationship between macroalgae and eelgrass production at different sites within the estuary? (2) How does the direction and magnitude of macroalgae–eelgrass interaction strength change between sites and through time? Based on results from this study, we discuss potential mechanisms influencing interactions along the estuarine gradient and implications for eutrophication management.

Methods

Study System

Coos Bay is located in Southern Oregon (43.35° N, 124.34° W; Fig. 1) and lies adjacent to Cape Arago, a region of strong, persistent upwelling within the California Current Large Marine Ecosystem (Rumrill 2006). The mean monthly upwelling index (Pacific Fisheries Environmental Laboratory (2011), station 42° N 125° W) for the summer months of this study (June–October) was 51.6 ± 13.97 m^3 s^{-1}100 m^{-1} coastline (2007) and 81.00 ± 22.95 m^3 s^{-1}100 m^{-1} coastline (2008; 2000–2010, 10-year summer mean of 116.05 ± 11.9 m^3 s^{-1}100 m^{-1}). Throughout the winter months, an average of 142 cm of rainfall enters the estuary, compared to less than 10 cm within the summer months (Rumrill 2006). The research was conducted in The South Slough National Estuarine Research Reserve (SS NERR) located in a southern branch of the larger Coos Bay estuary (Fig. 1). The South Slough is approximately 9 km long, with an average width of 600 m, wet surface area of 783 ha, and a volume of 2 million m^3 (Harris et al. 1979). It is composed of 222 ha of intertidal habitat (mudflats, seagrass beds (95 ha), tidal marshes) and 16 ha of subtidal channels. Tidal flushing rates within the South Slough are high, with an estimated tidal prism of 9.34 million m^3 (Harris et al. 1979). Eelgrass beds are not continuous throughout South Slough, but relatively large, contiguous, perennial eelgrass meadows are present throughout its length. We used three sites with large eelgrass meadows for the research, including Barview (marine), Valino (polyhaline), and Danger (riverine; Fig. 1). These sites are representative of the overall estuarine gradient in this system and are distinguishable by salinity, temperature, and nutrient parameters (Table 1).

Eelgrass–Macroalgal Observational Patterns

Eelgrass and macroalgae parameters were measured on a monthly basis during the summer months (June–September)
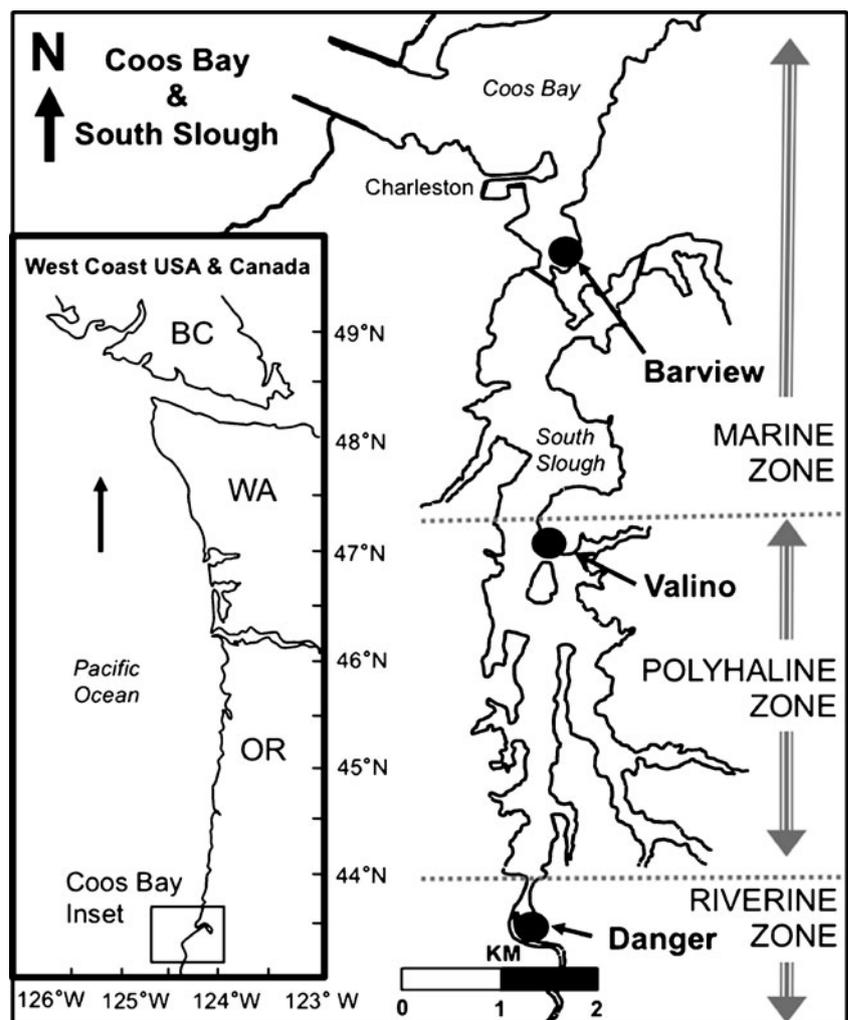
and bi-monthly during the winter months (November, January, April) from June 2007 to April 2009. Eelgrass density through time was monitored along a permanent 100 m transect line haphazardly located in each eelgrass bed perpendicular to the channel edge, at approximately +0.1 MLLW (corresponding to maximum density of eelgrass shoots; Thom et al. 2003). Density of shoots was counted in 0.5 m×0.5 m quadrats (0.25 m^2) at 10 m intervals along each transect line (n=10 per site). Thirty eelgrass shoots were haphazardly sampled from the eelgrass bed (adjacent to transect) at each site. Eelgrass was returned to the lab, measured for length and width, scraped of epiphytes, scored for percent blade desiccation, and then dried (60°C for 24 h) and weighed. The desiccation index developed by Boese et al. (2003) was used to quantify the percentage of blade area with non-pigmented (bleached) necrotic tissue. Biomass at the quadrat scale (0.25 m^{-2}) was extrapolated by multiplying mean biomass per shoot by mean shoot density within the quadrats. Macroalgae biomass was collected from quadrats (0.25 m^{-2}) haphaz-

ardly placed within each site (n=5–9 per site) by clipping the macroalgae sheets at the edge of the quadrat and removing it from around the eelgrass shoots. All ulvoid macroalgae was cleaned with freshwater and scraped to remove epiphytes and sediment and then dried (60°C for 24 h) and weighed.

Eelgrass–Macroalgal Interaction Experiment

We manipulated macroalgal biomass during the summer months of 2007 and 2008 to measure its interaction with eelgrass. Macroalgae treatments, which consisted of the pulse addition and removal of macroalgae, were applied twice (August, September) in 2007 and three times (June, July, August) in 2008 to permanently marked eelgrass plots (0.5 m× 0.5 m). Treatment plots were blocked haphazardly at each site (n=9 per treatment), within tidal heights spanning −0.1 to +0.3 MLLW (encompassing the elevation of the permanent transect lines).The macroalgae addition treatment involved anchoring sheet-form ulvoids (including the species *Ulva*

Table 1 Physicochemical differences among the study sites along (Barview, Valino, Danger) the South Slough NERR estuarine gradient

Site	Barview (marine)		Valino (polyhaline)		Danger (riverine)	
Season	Summer	Winter	Summer	Winter	Summer	Winter
Mean temperature±SE (°C) range (min–max)	13±0.01 (8–20)	10±0.01 (5–23)	15±0.01 (9–21)	11±0.01 (3–21)	17±0.01 (4–25)	10±0.01 (0–22)
Mean salinity±SE (psu) range (min–max)	33±0.01 (0–37)	29±0.02 (0–37)	32±0.01 (0–35)	26±0.02 (0–32)	19±0.05 (0–33)	10±0.04 (0–35)
Mean nitrate (NO_3^-)+nitrite (NO_2^-)±SE range (min–max) (mg/L (top), and µM (bottom))	0.15±0.01 (0.02–0.39), 10.72±0.68 (1.18–27.74)	0.16±0.00 (0.00–0.35), 11.25±0.33 (0.29–25.04)	0.11±0.01 (0.01–0.26), 7.95±0.87 (0.61–18.80)	0.15±0.01 (0.01–0.38), 10.71±0.59 (0.36–27.20)	0.06±0.01 (0.00–0.42), 4.12±0.64 (0.37–30.06)	0.28±0.01 (0.06–0.66), 20.02±0.97 (4.00–47.33)
Mean phosphate (PO_4^{3-})±SE range (min–max) (mg/L (top), and µM (bottom))	0.05±0.00 (0.02–0.07), 1.64±0.04 (0.51–2.43)	0.03±0.00 (0.01–0.09), 1.13±0.02 (0.33–3.09)	0.05±0.00 (0.02–0.09), 1.64±0.07 (0.57–3.06)	0.03±0.00 (0.01–0.06), 1.03±0.03 (0.36–1.88)	0.02±0.01 (0.00–0.05), 0.59±0.07 (0.04–1.68)	0.01±0.00 (0.00–0.12), 0.40±0.04 (0.02–4.05)

Mean temperature and salinity data (±SE) from YSI datasondes (Yellow Springs Instruments Model 6600) located in the water column adjacent to each intertidal site. Data collected at 15-min intervals and averaged over summer (June–September 2007–2009) and winter (October–May 2007–2009) seasons (min and max range of values also reported). Nutrient grab samples (nitrate + nitrite, phosphate) collected at flood and ebb tide adjacent to datasondes on a near-monthly basis (System Wide Monitoring Protocol (SWMP) protocol; http://cdmo.baruch.sc.edu/). Mean high and low tide average values (± SE) reported for 2007–2008. Nutrient data acquired and reported in milligrams per liter and converted to micromolars using the conversions NO_3^- +NO_2^- µM/71.39 and PO_4^{3-} µM/32.9. Water column data acquisition protocol and data storage implemented by the NERR SWMP: National Oceanic and Atmospheric Administration, Office of Ocean and Coastal Resource Management, National Estuarine Research Reserve System-wide Monitoring Program. 2004. Centralized Data Management Office, Baruch Marine Field Lab, University of South Carolina (http://cdmo.baruch.sc.edu/). All flagged data not meeting SWMP quality check protocol removed from this summary

linza and *Ulva lobata*; Gabrielson et al. 2006) on the top of the sediment using metal stakes and ropes strung across the plot. Care was taken to ensure that the eelgrass was not blanketed by macroalgae or damaged by the stakes or ropes. The macroalgae removal treatment consisted of carefully removing all macroalgae from the quadrat area, including attached thalli and macroalgae partially embedded in the substrate. A control was established in which macroalgae anchors were applied without manipulating the natural abundance of macroalgae. For the addition treatments, macroalgae was collected from Barview (the marine site) and then added based on volumetric quantification (Robbins and Boese 2002). We added 4,000 mL macroalgae to each plot at all the sites which was equivalent to ~160 gdw 0.25 m^{-2} (=~650 gdw m^{-2}), representing a doubling of the average quantity of macroalgae found at the marine site during the peak bloom summer months. Depending on the timing of low tide (when access to the eelgrass beds was possible), ulvoid macroalgae was either gathered for the addition treatments during the same day as the treatment application, or it was held overnight in cold seawater before applying the treatment the following day.

Eelgrass density per replicate plot was counted during each re-visit to the sites. In addition, redox potential was measured three times in different locations within each plot using an Orion Star probe (Thermo Electron Corporation) fitted with a platinum electrode. At the termination of the experiment (October 2008), all aboveground and below-ground material was collected from within the experimental plots. Eelgrass was returned to the lab, measured for length and width, scraped of epiphytes, and then dried (60°C for 24 h) and weighed. Sediment samples from the top 3 cm of each plot were also obtained and later dry sieved to determine the grain size distribution of sand (>63 µm, larger rocks and wood removed) and silt (<63 µm).

Statistical Analyses

All statistical analyses were conducted using the *R* platform (R Development Core Team 2009). We analyzed observational eelgrass and macroalgae trends separately using linear mixed effect models (*lme* in *R nlme* package, Pinheiro et al. 2009) with site, season, and site×season, as fixed effects. A random effect term was included in this model structure to incorporate the nestedness of temporal sampling (month within season within year). Macroalgae biomass was log-transformed, and eelgrass biomass was square root-transformed in order to improve homoscedasticity and normality assumptions in these models. The analysis of variance techniques used throughout this analysis was robust to inequality of variance and non-normality given the balanced design and large sample size used in these analyses (Underwood 1997). To determine the relationship between

macroalgae and eelgrass biomass through time, a correlation permutation test (non-normal time series) was conducted on non-transformed monthly averages.

For the analysis of the experimental data, eelgrass density (square root-transformed) was analyzed using a linear mixed effects model (fixed effects: treatment×site×year (2007 vs. 2008), random effects: treatment nested in block). Relative change in density was calculated at the end of the growing seasons in summer 2008 (August 2008) as the change in eelgrass density relative to the initial (August 2007) eelgrass densities. We calculated interaction strength values for both addition and removal manipulations as: treatment − control (based on the raw difference index; Berlow et al. 1999). Comparisons between sites were made using a linear mixed effects model (fixed effect=site, random=experimental block) with square root-transformed interaction strengths as the response. Deviations from normality were assessed by employing a generalized linear model (glm) with a Poisson distribution. Results from glm models were compared to linear mixed effect model outcomes but never resulted in differences in treatment effects. Interaction strength by site was also assessed by determination of significant departures from zero (neutral interaction) using Student's t test with modifications for unequal variance. At the experiment termination (October 2008) aboveground and belowground biomass, shoot length, sediment grain size (sand/silt), and redox potential were analyzed using a linear mixed effect model (fixed effects: site×treatment, random effect: experimental block), with data transformations when appropriate. A priori comparisons were conducted using planned linear contrasts and were judged significant when $p<0.05$ (Kuhn et al. 2010). Graphs were produced using the ggplot2 package (Wickham 2009).

Results

Eelgrass–Macroalgal Observational Patterns

Patterns in macroalgae biomass were highly site and season specific (Table 3), with the greatest mean monthly summer biomass at the Barview site, where marine influence is the greatest (Fig. 2; Table 2). Mean summer macroalgal biomass differed among all sites (linear contrasts $p<0.05$) and was 83% lower at Valino, in the polyhaline zone, and 99% lower at Danger, located in the riverine zone (Fig. 2; Table 2). Among-site differences and rank order in mean macroalgal biomass persisted between seasons (summer vs. winter), except for differences between Barview and Valino, which were not apparent during the winter (linear contrasts $p>0.05$). Biomass changes between summer and winter were most marked at Barview, followed by Valino (Fig. 2, linear contrasts $p<0.05$). Very little macroalgae biomass was
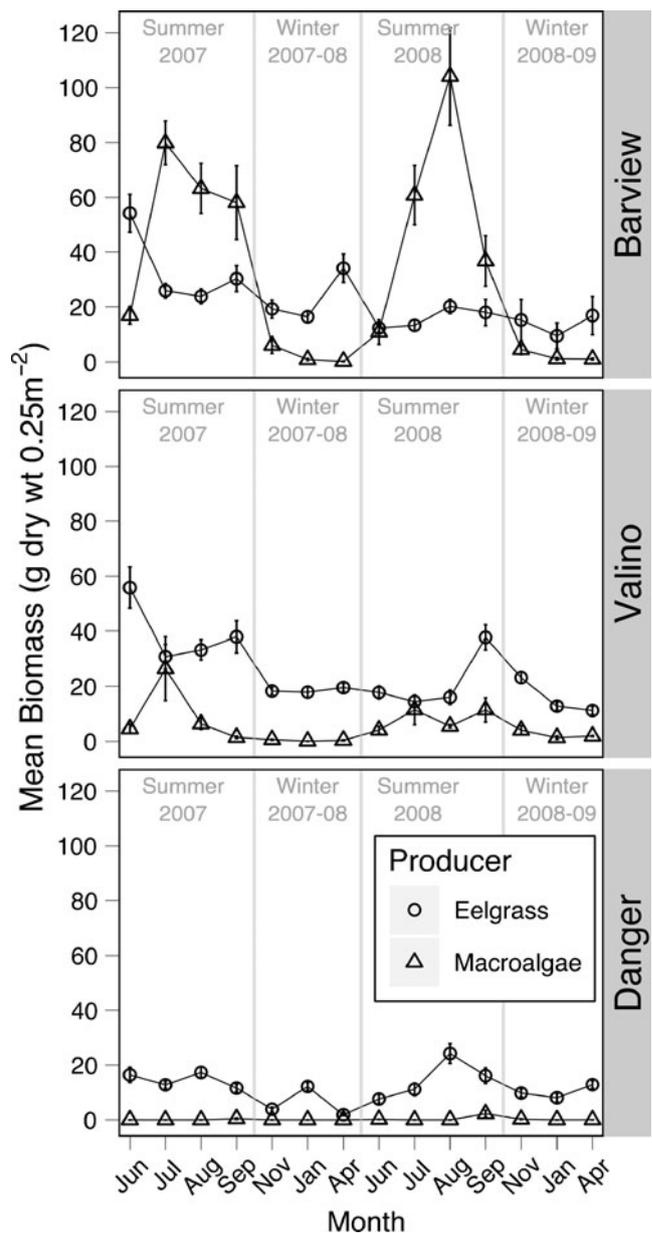

Fig. 2 Mean (± SE) macroalgae and seagrass biomass at three sites located along the estuarine gradient within South Slough, Coos Bay, Oregon, USA from June 2007 to April 2009 (Barview—marine, Valino—polyhaline, Danger—riverine). Macroalgae biomass $N=$ 6 quadrats site^{-1} month^{-1} g dry wt 0.25 m^{-2}. Eelgrass biomass $N =$ 10 quadrats site^{-1} month^{-1} g dry wt 0.25m^{-2} (shoot density (0.25m^{-2})× mean shoot biomass (g dry wt))

quantified at Danger (Fig. 2; Table 2), and no seasonal differences were observed (linear contrasts $p>0.05$).

In contrast, mean eelgrass biomass did not show strong seasonal variation at any of the sites, but differences between sites were found (Fig. 2; Table 3). Mean eelgrass shoot density and length were similar at Barview and Danger, but density was greater and shoot length was shorter at Danger (Tables 2 and 3; linear contrasts $p>0.05$). Desiccation index was low at all sites (<2% average blade

Table 2 Mean macroalgae and eelgrass parameters measured during observational study at three sites (Barview—marine, Valino—polyhaline, Danger—riverine) along the South Slough NERR estuarine gradient (June 2007–April 2009)

Site	Barview (marine)		Valino (polyhaline)		Danger (riverine)	
Season	Summer	Winter	Summer	Winter	Summer	Winter
Macroalgae biomass (mean g dw 0.25 m^{-2})	56.1±5.3	2.2±0.6	9.7±2.3	1.4±0.4	0.3±1.3	0.1±0.2
Eelgrass biomass (mean g dw 0.25 m^{-2})	24.8±1.9	18.6±2.3	30.5±2.1	17.1±0.8	14.6±1.0	8.1±0.7
Eelgrass shoot density (mean shoot 0.25 m^{-2})	28.5±1.6	22.9±2.6	23.4±1.2	21.4±0.9	33.2±1.9	34.0±2.7
Eelgrass shoot length (mean cm)	106.1±9.9	76.6±5.7	108.1±7.1	91.0±6.4	74.4±5.4	45.4±5.7
Dessication index (mean % blade surface)	1.56±0.25	0	0.63±0.18	0	0.76±0.22	0

Mean values determined from pooled samples of all summer and winter months sampled. Summer months=June, July, August, September; winter months=November, January, April. Sample sizes: macroalgae biomass area^{-1}=6 quadrats site^{-1} month^{-1}, eelgrass density area^{-1}=10 quadrats site^{-1} month^{-1}, eelgrass shoot biomass, length, and dessication index=30 shoots site^{-1} month^{-1}

desiccation), with values of zero for the winter months (Table 2). Interannual and seasonal variation in eelgrass biomass showed no relationship to temporal trends in macroalgae biomass at any of the sites (permutation test: Barview (rho=0.07, $p=0.76$); Valino (rho=0.23, $p=0.39$), Danger (rho=0.19, $p=0.45$).

Eelgrass–Macroalgal Interaction Experiment

Eelgrass densities in the eelgrass–macroalgal interaction experiment were affected by both site, treatment, and year (Fig. 3; Table 4). At Barview, treatment effects (both addition and removal; Fig. 3; Table 4) were only observed as the experiment progressed through 2008 (Fig. 3; linear contrasts, $p<0.05$). At Valino, eelgrass density did not vary with treatment, but did vary temporally (Fig 3; linear

contrasts, $p<0.05$). At Danger, the addition treatment effects appeared in 2007 and endured through 2008, with no effect of removal (Fig. 3; linear contrasts, $p<0.05$).

Taking into account relative change through time and differences from the control treatments, interaction strengths also differed between sites (Fig. 4; Table 4). For the addition treatment, differences occurred across all sites (Table 4; linear contrasts, $p<0.05$). With addition of macroalgae, interaction strength of macrophytes on eelgrass at Danger was negative, suggesting competition (t test, $p<0.001$), but was not different from zero (neutral interaction) at Barview and Valino (Fig. 4 addition; t test, $p<0.001$). Removal interaction strengths also varied among sites (Fig. 4 removal; Table 4), with positive (facilitative) interaction strengths at Barview that were different from zero (t test, $p<0.001$) and neutral effects (t test, $p>0.05$) at both Valino and Danger. The quantity of

Table 3 Linear mixed effect model results from eelgrass–macroalgae observational study

Response	Sample size (N)	Fixed effect	df fixed effect, df error	F (p)
Macroalgae biomass	258	Site	2, 240	0.9**
		Season	1, 1	51.13 ns
		Site × season	2, 240	100.09***
Eelgrass biomass	420	Site	2, 402	46.77***
		Season	1, 1	6.97 ns
		Site × season	2, 402	0.46 ns
Eelgrass density	420	Site	2, 402	14.54***
		Season	1, 1	2.29 ns
		Site × season	2, 402	2.92*
Eelgrass length	1,261	Site	2, 1243	214.75***
		Season	1, 1	10.17 ns
		Site × season	2, 1243	13.74***

Effects of season (summer vs. winter) or site on producer biomass (g dw 0.25 m^{-2}) at three sites (Barview—marine, Valino—polyhaline, Danger—riverine) along the South Slough NERR estuarine gradient. Differences between sites compared across both summer and winter seasons (fixed effect=site)

ns no significant differences ($p>0.05$)
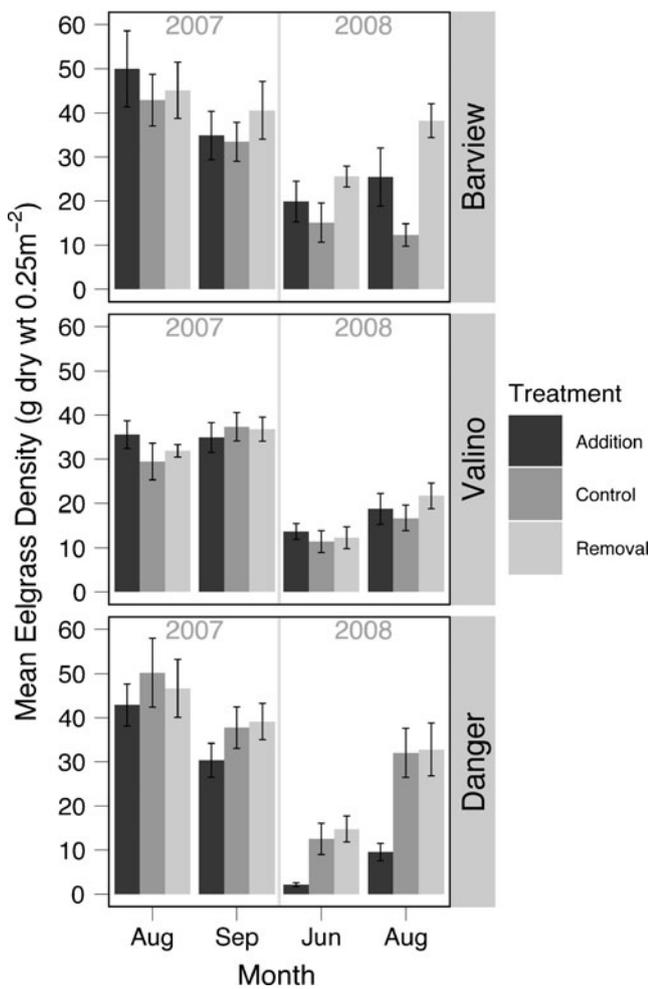
*$p<0.05$; **$p<0.001$; ***$p<0.0001$

Fig. 3 Mean (±SE) eelgrass densities (0.25 m^{-2}) in eelgrass–macro-algae manipulation experimental plots at three sites ($N=27$ plots site^{-1} month^{-1}) along the South Slough estuarine gradient (Barview—marine, Valino—polyhaline, Danger—riverine). The first and last month sampled (2007 and 2008) is shown here, and is a subset from all months sampled

macroalgae removed was not constant across sites due to the natural differences in macroalgae abundance between sites (Table 2). For instance, the average volume macroalgae removed at Danger during August 2007 and 2008 (13.3 mL) was 1% that of Barview (1,318 mL) and 4% that of Valino (345 mL).

At the termination of the experiment (October 2008), variation among sites persisted, but treatment effects on the eelgrass (Fig. 5) and sediment (Table 5) parameters measured did not. Site effects were apparent for aboveground biomass (fixed effect: site, $F_{2,62}=19.6$, $p<0.001$), belowground biomass (fixed effect: site, $F_{2,63}=9.8$, $p<0.001$) and shoot length (fixed effect: site, $F_{2,59}=44.0$, $p<0.001$). Valino had increased aboveground and belowground biomass compared to both Barview and Danger (linear contrasts $p<0.05$), and average blade length was also greatest at Valino, followed by Barview, then Danger (Fig. 5; linear contrasts $p<0.05$). No full model effects of treatment or treatment×site (fixed effects, $p>0.05$) were found for any of these parameters. Sand-to-silt ratio and redox potential also varied with site, but not treatment (Table 5). Across-treatment sand/silt was greater at Barview and Valino than Danger (Table 5; linear contrasts, $p<0.05$), and redox potential was lower across all treatments at Barview relative to Valino and Danger (Table 5; linear contrasts, $p<0.05$).

Discussion

Context Dependency of Eelgrass–Macroalgae Interactions

Our results show that interactions between eelgrass and macroalgae, often negative under eutrophic conditions (see reviews: Burkholder et al. 2007; McGlathery 2001), can vary dramatically across sites located along an estuarine

Table 4 Linear mixed effect model results from eelgrass–macroalgae manipulation experiment. Effects of treatment and season-year on eelgrass density (shoots 0.25 m^{-2}) at three sites (Barview—marine, Valino—polyhaline, Danger—riverine) along the South Slough NERR estuarine gradient. Interaction strengths (treatment−control) differences for addition and removal also reported

Response	Sample size	Fixed effect	df fixed effect, df error	F (p)
Eelgrass density	729	Site	2, 687	3.82*
		Treatment	2, 16	8.37**
		Year	1, 687	224.01***
		Site×treatment	4, 687	10.97***
		Site×year	2, 687	1.36 ns
		Treatment×year	6, 287	4.96*
		Site×treatment×year	4, 687	4.06*
Addition interaction strength	27	Site	2, 16	19.39***
Removal interaction strength	27	Site	2, 16	7.29*

ns no significant differences ($p>0.05$)

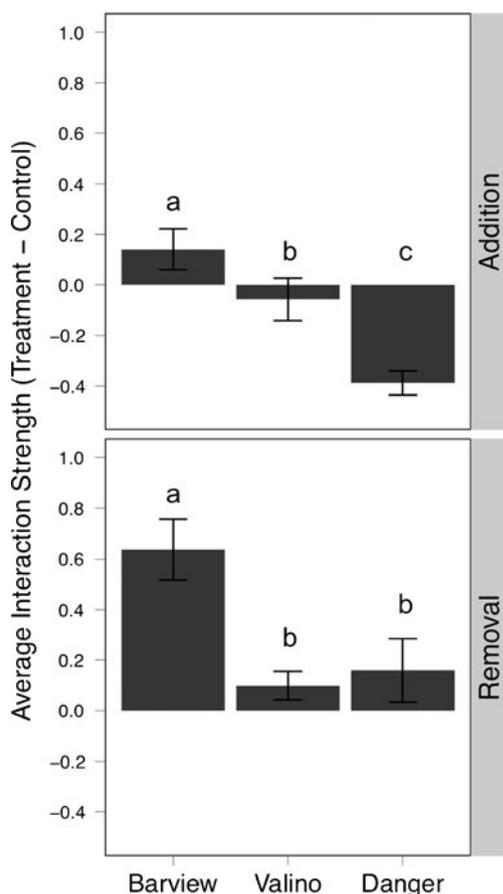*$p<0.05$; **$p<0.001$; ***$p<0.0001$

Fig. 4 Mean (± SE) eelgrass density response to the macroalgae manipulation experiment (N=27 plots site^{-1} month^{-1}). Addition and removal treatments at three sites along the South Slough estuarine gradient (Barview—marine, Valino—polyhaline, Danger—riverine). Interaction strength calculated as the difference between manipulated and control treatments for the relative change in eelgrass density from initial (August 2007) to final (October 2008) experiment conditions. Significant differences between sites indicated by letter annotations (t-test linear contrast conducted independently for each treatment)

Fig. 5 Eelgrass parameters measured at the end of the eelgrass–macroalgae experiment (October 2008) at three sites (N=27 plots site^{-1}) along the South Slough estuarine gradient (Barview—marine, Valino—polyhaline, Danger—riverine): *a* Mean (± SE) aboveground eelgrass biomass (mean g dw 0.25 m^{-2}). *b* Mean (± SE) belowground eelgrass biomass (mean g dw 0.25 m^{-2}). *c* Mean (± SE) eelgrass length (centimeters). Significant differences between sites indicated by *letter annotations* (t-test linear contrast conducted independently for each parameter)

gradient within an ocean upwelling-influenced estuary. We found that eelgrass and macroalgae interactions ranged from neutral or slightly positive in the more marine-influenced zones of the estuary, to strongly negative at the riverine, freshwater-influenced site (Fig. 4). We also found that while removing macroalgae resulted in either positive or neutral responses of eelgrass depending on the site, additions of macroalgae also had slightly positive or neutral effects on eelgrass, except at the riverine site where macroalgae is naturally sparse and the interactions were uniformly negative (Figs. 4 and 5). These treatment effects became significant during the second year of this experiment (Fig. 3), indicating that macroalgae effects only become apparent when blooms persist through time. It is likely that a combination of factors mediate the balance between the positive, as well as the negative, effects of
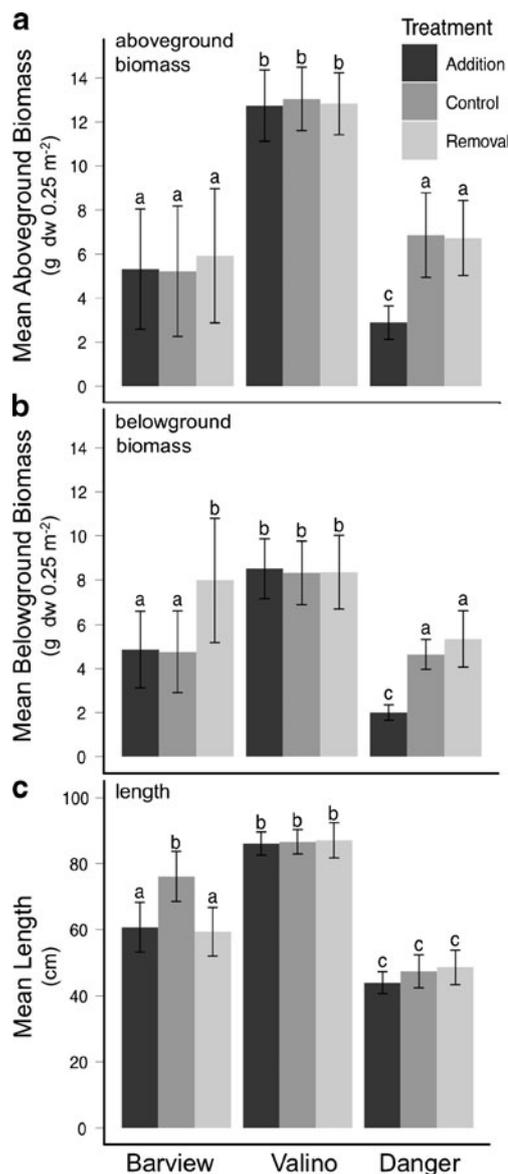
macroalgae on eelgrass and that this balance is tipped in one direction or the other depending on the physical conditions or site context within the estuary.

The experimental results are supported by the patterns of eelgrass and macroalgae at the different sites observed through time (Fig. 2). Despite large macroalgal blooms at the marine site throughout summer 2007 and 2008, eelgrass biomass was either unchanged or changed only slightly from year to year, with no correlation between trends in

Table 5 Physical sediment parameters (sand/silt, redox potential) measured at the different estuarine gradient sites (Barview—marine, Valino—polyhaline, Danger—riverine) at the termination of the experimental macroalgae manipulation (October 2008)

	Treatment	Site			Mixed effect model results		
		Barview (marine)	Valino (polyhaline)	Danger (riverine)	Fixed effect	*df* fixed effect, *df* error	*F* (*p*)
Sand (g)/silt (g)	Control	5.0±1.0	6.2±1.0	3.1±1.6	Site	2, 64	10.3**
	Addition	5.5±0.9	5.8±0.6	2.0±0.3	Treatment	2, 64	0.39 ns
	Removal	5.7±1.2	8.6±2.7	1.7±0.2	Site×treatment	4, 64	0.76 ns
Redox potential (mV)	Control	−335.0±15.2	−171.0±41.2	−143.2±8.4	Site	2, 64	61.2***
	Addition	−336.3±21.5	−182.6±43.3	−186±19.0	Treatment	2, 64	1.2 ns
	Removal	−309.2±14.1	−173.4±40.7	−147.7±10.7	Site×treatment	4, 64	0.38 ns

$N=27$ plots site^{-1}. Linear mixed effects modeling results reported

ns no significant differences ($p>0.05$)

*$p<0.05$; **$p<0.001$; ***$p<0.0001$

macroalgae and eelgrass biomass throughout the annual cycle (Fig. 2). Similar results were found at the polyhaline and riverine sites, but these sites also had macroalgal abundances that were lower than that of eelgrass and were a small fraction of those at the marine site (Fig. 2). Thus, while other studies have found that increased macroalgae productivity is often correlated with declines in seagrass density and biomass (Burkholder et al. 2007), we found no concurrent seasonal patterns or correlations with seagrass biomass.

Mechanisms Responsible for Eelgrass–Macroalgae Interactions

The variability of outcomes between eelgrass and macroalgae at different sites along the estuarine gradient points to some potential mechanisms that might be controlling this interaction. Our findings show that the potential negative effects of macroalgae blooms are magnified in the riverine site of this estuary and tempered in the marine reaches of the estuary, where other mechanisms may lead to neutral or positive effects of macroalgae on eelgrass.

While we did not measure water column light attenuation during this study, evidence suggests that the riverine reaches may be more light-limited than other zones of this estuary. Turbidity is generally higher (20–30 NTU) with more frequent high pulse events associated with storm events at Danger than at the other sites (Rumrill 2006). Elevated turbidity levels can be related to decreased water column light levels, which may affect eelgrass photosynthetic capabilities (Moore et al. 1997; Thom et al. 2008; Zimmerman et al. 1995). Because eelgrass at this site (Danger) may have pre-existing physiological stress associated with low light levels, additional reduction of light by the macroalgae addition treatment could have had a larger impact on plants. Reduction in light, as well as decreased salinity (Nejrup and Pedersen 2008), may be key factors related to the shorter shoot length found at this site (Table 2). Due to this small plant morphology, macroalgae additions held in place at the sediment surface may have covered a greater extent of the shoot's photosynthetic surface than the longer blades able to extend beyond the imposed macroalgae canopy at Barview and Valino (Fig. 5 c; Tables 2 and 3).

Other key mechanisms known to negatively affect seagrass are associated directly with the sediment environment and macroalgae degradation. It is currently unclear what factors are limiting macroalgal blooms at the polyhaline and riverine sites, but parameters such as water column nutrients, salinity, temperature, light, and grazing are likely key (Table 1; Cohen and Fong 2004; Hauxwell et al. 1998; Nelson et al. 2008; Rivers and Peckol 1995).The average biomass of macroalgae was very low at Danger during all months sampled and likely the result of macroalgal drift into this region of the estuary (Fig. 2; Table 2). The physicochemical factors limiting the distribution of ulvoids in this region may also have acted to degrade macroalgae additions at a greater rate than elsewhere in the estuary, which potentially could have altered the nutrient conditions in the sediment and contributed to decreased oxygen (redox potential) with macroalgae additions (Table 5). Differences in macroalgae degradation rates may have resulted in differences in the duration of the addition treatments across sites. At all sites, we observed that the imposed macroalgae canopy created by the addition treatment remained for the duration of the week during which the low tide series occurred. We do not know how long this treatment endured as subtidal site re-visitations were not conducted. Thus, our repeated summer macroalgae manipulations are to be treated and interpreted as pulse, rather than sustained

treatments. Among-site differences in sediment grain size also exist along the estuarine gradient (Table 5; Rumrill 2006). The dominance of finer, silty sediments at the riverine site could have exacerbated anoxia and depressed gas exchange with seagrass shoots (Ralph et al. 2006). Furthermore, our experimental manipulation structure itself may have affected sedimentation rates at this site, which may increase shoot burial. While we found significant negative effects of macroalgae addition on both above-ground and belowground eelgrass biomass at this site (Fig. 5), we found no conclusive evidence that this was correlated with the factors discussed here (increased silt load or decreased redox potential; Table 5). This is surprising because this experiment was meant to accentuate interactions that occur primarily at the sediment interface, by not allowing macroalgae to drift horizontally or vertically within the eelgrass bed. Further experiments that replicate the natural movement of macroalgae within seagrass beds are thus necessary to fully understand the mechanisms at play in these intertidal environments.

In the middle reaches of the estuary, at Valino, eelgrass was not affected by macroalgae manipulations (Figs. 3, 4, and 5). In this zone of the estuary, elevated eelgrass shoot biomass and longer shoot morphology (Tables 2 and 3; Fig. 5) may have allowed eelgrass to adapt to the conditions by extending beyond the macroalgae–sediment interface where they are less susceptible to the negative effects of light reduction, decreased oxygen levels, and sedimentation. Belowground biomass was also greater at this site, but its role in stress mitigation (Hemminga 1998) in this system has not been well investigated. In other systems, it has been found to allow seagrass to withstand periods of shading by acting as a source of carbohydrates (Peralta et al. 2002). We found no effects of macroalgal removal at this site or at Danger, which is expected given the low macroalgae biomass in this region of the estuary.

Contrary to the riverine site, the marine site shows little evidence that mechanisms associated with light reduction and changes in the sediment associated with ulvoid macro-algae are acting negatively on eelgrass. Redox potential was lower in the marine zone at the end of the experiment than at the other two sites (Table 5) and within the low range of reported values for seagrasses (Terrados et al. 1999). However, these large negative values did not vary by treatment and are consistent with the hypothesis that Z. marina can adapt to low oxygen sediment conditions that may be associated with macroalgae blooms in this zone of the estuary, depending on the nature of the water column conditions (Terrados et al. 1999). Additionally, it does not appear that the macroalgal canopies occupy a sufficient portion of the water column, or are dense enough to negatively affect eelgrass in these intertidal systems. While snorkeling, we observed that the un-manipulated macro-

algal canopy occupied a 5–20-cm layer above the sediment during high tide, and we documented repeated macroalgae accumulations that blanketed many of the seagrass shoots at low tide during our sampling. These values contrast with canopy heights of 20–75 cm found along a gradient of nutrient loading in shallow, subtidal Waquoit Bay, Massachusetts, but lie within the critical heights associated with eelgrass declines (9–12 cm) in experimental macroalgae manipulations conducted in this system (Hauxwell et al. 2001). In our system, most large seagrass shoots appear to emerge from macroalgae accumulations, thereby reducing the photosynthetic stress associated with macroalgae canopy formation. In the experimental conditions, we mimicked these conditions, allowing eelgrass blades to protrude beyond the artificial canopy attached to the sediment. Given the size of our manipulation plots (0.25 m^{-2}), we expect that some edge effects, including shading from adjacent, non-manipulated macroalgae canopies, would be present across all of our experimental treatment plots within a site. Such edge effects caused by differences in baseline algal abundance may be one contributing factor to the observed differences in treatment effects between sites. We did not explicitly measure light attenuation within the macroalgae accumulations at this site, however, and future investigation of light attenuation within intertidal seagrass beds is warranted.

Mechanisms associated with light and sediment may be balanced or even overshadowed by the potential positive effects of the canopy structure during times of low tide exposure; such mechanisms have not received sufficient research attention in intertidal seagrass systems. At low tide, intertidal seagrass beds are exposed to both heat and desiccation stress, key factors limiting their upper intertidal distribution (Boese et al. 2005). However, a covering of macroalgae that can retain moisture and protect the seagrass from direct exposure may alleviate these stressors. No major signs of desiccation stress (i.e., bleaching) were observed at any of the study sites (Table 2). The values that we recorded were lower (average summer month desiccation values of 0.63–1.6%) than those recorded at a similar tidal height in Yaquina Bay (5%) (Boese et al. 2003) where macroalgae blooms also occur (Kentula and DeWitt 2003). Another potential positive effect of macroalgae layers on seagrass, although not investigated here, is the translocation of dissolved organic carbon from macroalgae to seagrass shoots. This has been observed in other seagrass species and related to increased growth under low light conditions (Brun et al. 2003).

While macroalgae addition had no negative effect on eelgrass in the marine zone, removal of macroalgae had a positive effect, suggesting that while eelgrass co-exists with macroalgae, macroalgal removal may improve the conditions for eelgrass. Therefore, while we did not find any

evidence for negative macroalgae effects under ambient and manipulated (2×ambient) bloom conditions, the baseline population of eelgrass at this site may already be subject to some degree of sub-lethal stress due to the presence of macroalgae. These results should be interpreted cautiously due to the nature of the removal treatment at this site. Macroalgae removal, while thorough, was also pulsed and only maintained during monthly low tide sampling events, and without a retaining structure, algae was able to repopulate these plots sometime after the manual exclusion. In fact, each time we returned to this site, macroalgal abundance had fully recovered to pre-removal levels. This was the case at all sites, but due to the high baseline macroalgal abundance at the marine site, the potential for macroalgae to re-enter removal plots was likely highest here, which may reflect the large positive effects found only at this site (Fig. 4).

Management Implications

Key to eutrophication management initiatives is an understanding of the ultimate direction and magnitude of seagrass–macroalgae interactions. Currently, along with nutrient criteria and seagrass metrics as secondary symptoms, macroalgal parameters are considered primary indicators of eutrophication and are used as assessment criteria of nutrient enrichment in the USA (Bricker et al. 2003). The use of macroalgae as a bioindicator is based on studies from land-based, anthropogenic eutrophication, where the macroalgae–seagrass interaction has been primarily documented as negative (Burkholder et al. 2007 review). However, growing evidence from this study and other upwelling-influenced estuaries (Brown and Ozretich 2009; Jorgensen et al. 2010) suggests that this metric of eutrophication status may not be appropriate in regions of estuaries where eelgrass can coexist with macroalgal blooms.

We caution that adaptive management strategies and continued monitoring of these nearshore benthic habitats and water quality nutrient criteria are necessary in coastal areas with growing human populations, such as the Pacific Northwest. Additional nitrogen loading, among other factors, could potentially increase macroalgal biomass to higher levels than observed or manipulated in this study. Research from the Pacific Northwest and around the world show that nitrogen addition rates rarely saturate ulvoid growth (Kamer et al. 2004; Nelson et al. 2008; Teichberg et al. 2010). While our results indicate that eelgrass may not be negatively affected by increases in macroalgae biomass in the marine-dominated regions of the estuary, increased production in the riverine reaches of the estuary has potentially negative consequences. The specific factors limiting macroalgal growth in the riverine reaches of this estuary are not known. However, based on trends from eutrophic

estuaries (Kamer et al. 2004) and the currently low phosphate concentrations in this region of the estuary (Table 1; similar to other upwelling-influenced Oregon estuaries; Brown et al. 2007), macroalgal production may currently be constrained by low watershed nutrient loading in this region of the estuary (O'Higgins and Rumrill 2007; Fry et al. 2003).While our research documents the current state of macroalgal–eelgrass interactions of one upwelling estuary, the high degree of context dependency found both within this estuary and in comparison to other eutrophic estuaries suggests the need for continued monitoring and research on the mechanisms underlying these important ecological interactions in a wider variety of estuarine systems.

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