

# Eutrophication decreases salt marsh resilience through proliferation of algal mats



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## ABSTRACT

Globally, many estuaries are affected by nutrient loading from human land uses in the surrounding watersheds. One consequence of increased nutrient levels is proliferation of opportunistic macroalgae. We sought to understand spatial and temporal dynamics of ephemeral macroalgal mats and to examine their effects on salt marsh in a eutrophic estuary in central California. A time series analysis spanning 80 years revealed that algal wrack has increased exponentially in frequency on the salt marsh, and was highly correlated with nutrient concentrations in the estuary, which have increased along with fertilizer use. Analysis of sediment  $\delta^{15}\text{N}$  showed a dramatic increase in nutrient loads attributable to agricultural fertilizer over the past 50 years. We monitored 15 salt marsh plots along the bank edge and detected a negative relationship between algal wrack cover and salt marsh cover, flowering, and canopy height. Moreover, algal wrack led to retreat of vegetation from the bank edge, and increased bank erosion. We also experimentally added algal wrack to salt marsh edge plots. Algal addition decreased salt marsh cover, flowering, and canopy height, and increased retreat rate. By integrating time series analyses, isotope data, algal and marsh monitoring and manipulative experiments, we have identified robust linkages between increased anthropogenic nutrient loading, increased algal wrack cover, reduction in marsh resilience and conversion of marsh habitat to mudflat through bank erosion. Decreasing nutrient inputs to eutrophic estuaries is thus essential for conservation and restoration of salt marshes and enhancing their resilience in the face of sea level rise.

## 1. Introduction

Estuaries have been altered by human activities for centuries. Wetlands have been “reclaimed” for agricultural and urban land uses, freshwater has been diverted, and overfishing has restructured trophic interactions (Kennish, 2002). As coastal populations of humans continue to grow, one threat of particular concern is increased nutrient inputs from fertilizer, livestock waste, and fossil fuel composition; this nutrient enrichment can lead to eutrophication, the increase in the rate of supply of organic matter (Nixon, 1995). The majority of US estuaries are currently considered moderately to highly eutrophic (Bricker et al., 2008; Greene et al., 2015). Nutrient loading can enhance some desired ecosystem services, such as increasing fish production and catch in the Nile River delta (Oczkowski et al., 2009). However, many negative

effects of eutrophication reverberate through estuarine ecosystems, for instance harming fish communities through decreases in oxygen concentrations (Diaz and Rosenberg, 1995; Powers et al., 2005) and degrading seagrass beds through algal blooms (Valiela et al., 1997).

Salt marshes are valued habitats in temperate estuaries, providing ecosystem services including water quality improvement, shoreline protection, fisheries support, and carbon sequestration (Gedan et al., 2009; McLeod et al., 2011). Salt marshes are nitrogen limited (Valiela and Teal, 1979), and fertilization with nitrogen enhances above-ground productivity (Boyer et al., 2001; Nelson and Zavaleta, 2012). But nitrogen enrichment can decrease below-ground production, which can impede the ability of marshes to build elevation through subsurface organic accretion and thus limit their ability to track sea level rise (Turner et al., 2009; Deegan et al., 2012; Watson et al., 2014). While

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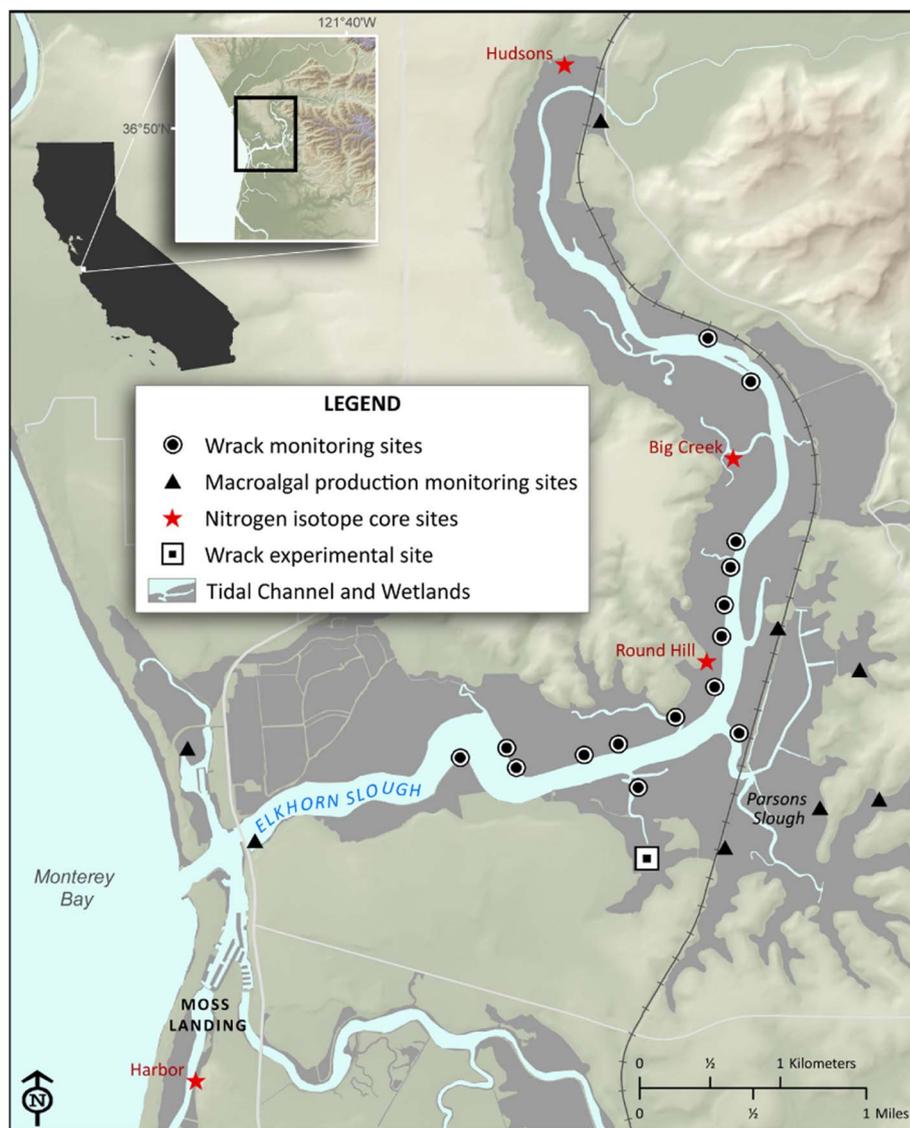


Fig. 1. Study sites. The wrack monitoring sites were used for the observational study of wrack deposition and effects on marsh in 2014–5. The macroalgal production monitoring sites are the mudflat plots monitored for algal production 2009–2016. The wrack experimental site indicates the location of the wrack addition experiment in 2014.

plot-scale experiments with high nutrient addition levels can generate strong responses from the marsh, more realistic application of nutrients leads to much milder responses (Johnson et al., 2016). Whether nutrient loading enhances or degrades salt marsh resilience in the face of sea level rise may vary across different marshes, and remains a controversial topic among marsh ecologists (Morris et al., 2013; Graham and Mendelssohn, 2014).

One characteristic of nutrient loading in estuaries is proliferation of opportunistic macroalgae (Duarte, 1995; Fletcher, 1996; Valiela et al., 1997). While macroalgae are a natural component of estuarine ecosystems, they have likely increased over past decades in many estuaries, though time series documentation is rare (Raffaelli, 1999). Macroalgal blooms are well-known to have negative impacts on seagrass beds through shading (Hauxwell et al., 2001). Effects of macroalgal blooms on salt marsh vegetation are less well understood. Macroalgal wrack that drifts onto the marsh can potentially benefit marsh plants by providing nutrients. Mesocosm experiments have demonstrated the transfer of nutrients from macroalgae to marsh plants (Boyer and Fong, 2005; Watson et al., 2015) and increased marsh plant growth with macroalgal addition (Newton and Thornber, 2013). However, macroalgal wrack also can have negative effects above ground through shading, and below ground, as decomposing algae

increase sediment hypoxia and sulfide concentrations (Caffrey et al., 2002b). Field experiments have revealed negative effects on above-ground plant growth (Hulzen et al., 2006; Newton and Thornber, 2013) while laboratory mesocosm experiments showed negative effects on both above- and below-ground biomass (Watson et al., 2015). The effects of algal wrack may depend on duration or intensity of exposure. For instance for mudflat invertebrates, thin algal mats increase diversity while thick algal mats decrease it (Green and Fong, 2015). For salt marshes, it is possible that short-term or low-level exposure to algal wrack provides beneficial nutrient subsidies, while more intense exposure is harmful.

The lower edge of a salt marsh is a front between alternate stable states, mudflat and marsh (McGlathery et al., 2013). This boundary is very dynamic, and in many estuaries, where sediment supply has been decreased by human activities such as river diversion and damming, marsh loss and bank erosion are common (Fagherazzi et al., 2013). Nutrient loading can have direct effects on marsh edges, with decreased plant allocation to roots and higher microbial decomposition rates, leading to lower bank stability and increased bank erosion rates (Deegan et al., 2012). Nutrient loading may also have indirect effects on the marsh-mudflat boundary through disturbance by algal wrack, but previous considerations of the role algal wrack may play in shifts

between alternative stable states, from marshes to mudflats have been speculative (Hartig et al., 2002; Byer et al., 2004). Projected acceleration in the rate of sea level rise will also cause shifts from marshes to mudflats, where insufficient sediment supply is available to allow marshes to build upwards at a rate matching the rising waters (Kirwan and Megonigal, 2013). Fucoid algae have been shown to increase sedimentation, but decrease seedling colonization in salt marshes (Tyrrell et al., 2015). Thus, an understanding of coastal marsh resilience to sea level rise should incorporate the potential role of algal wrack in affecting the boundary between marshes and mudflats.

We conducted an extensive, multi-faceted investigation to understand the spatial and temporal dynamics of algal mats and their effects on salt marsh plants. Our study system was Elkhorn Slough, a highly eutrophic estuary (Hughes et al., 2011) that has undergone significant marsh loss due to multiple causes (Van Dyke and Wasson, 2005). One goal of our study was to examine long-term changes. We used a GIS analysis of aerial photos to detect changes in algal wrack coverage over time, and correlated patterns with nutrient concentrations. We analyzed dated sediment cores for nitrogen stable isotope ratios to reconstruct changes in nutrient loads over time. In addition to long-term temporal patterns, we were also interested in short-term temporal dynamics. We monitored macroalgal mats on mudflats adjacent to salt marshes to understand seasonality of macroalgal production in the estuary, and how it corresponds with the marsh growing season. Another goal of the investigation was to understand spatial patterns of algal wrack distribution across the salt marsh plain. We used GIS analysis of aerial imagery and field monitoring to determine whether there are predictable hotspots of wrack disturbance on the marsh. A final goal of the study was to examine the effects of algal wrack at the salt marsh-mudflat boundary. We conducted correlative surveys and a manipulative experiment to determine how different levels of exposure to algal wrack affect the marsh, allowing us to explore whether there may be benefits at low levels but harm at high levels of exposure. In addition to examining effects on plant health, we also quantified wrack effects on the dynamics of the marsh-mudflat boundary, the critical front for marsh resilience in the face of sea level rise.

## 2. Methods

### 2.1. Study system

Elkhorn Slough is located in the middle of Monterey Bay in central California (Fig. 1). The undiked portions of the estuary, where we focused our study, have a similar tidal range as the adjacent open coast, with a mean daily tidal range of 1.6 m and an annual maximum of 2.5 m. Salinity averages 30–32 ppt year-round due to strong marine influence, although it can drop temporarily during heavy rainfall events. There is extensive agriculture in the watershed surrounding the estuary, dominated by heavily fertilized row crops such as strawberries and lettuce (Caffrey et al., 2002a). Nutrient concentrations in the estuary are high, and much of the estuary is moderately to highly eutrophic (Hughes et al., 2011). Water quality impairment from nutrient loading has been linked to eelgrass declines (Hughes et al., 2013) and lower fish diversity and abundance (Hughes et al., 2015). Macroalgal mats are common at Elkhorn Slough and are comprised primarily of *Ulva intestinalis* and *U. lactuca* (Schaadt, 2005). In this study, we refer to mats of *Ulva* that have drifted on to the salt marsh simply as “algal wrack”. *Ulva*, a cosmopolitan genus, naturally occurs in coastal systems throughout the world (Abbott et al., 1992). It is considered an inferior competitor when nutrients are not artificially enriched, but switches to over-dominance in nutrient-loaded conditions (Sfriso et al., 1992; Burkholder et al., 2007).

Elkhorn Slough has the most extensive salt marshes in California south of San Francisco Bay. A single species, pickleweed (*Salicornia pacifica*), dominates salt marsh vegetation, and was the only species present in our field monitoring and experimental plots. Pickleweed is a

woody perennial succulent that forms large clones that spread through vegetative growth. The clones appear to persist for many years, perhaps even decades, with little evidence for successful colonization of the existing marsh plain by sexually produced shoots, except in areas where large disturbances have created extensive bare space. Elkhorn Slough has lost about half of the acreage of salt marsh that was evident in maps 150 years ago, mostly due to diking and draining that occurred during the early 1900s, but also due to gradual dieback in undiked areas more recently (Van Dyke and Wasson, 2005).

### 2.2. Algal wrack spatial and temporal characterization across marsh ecosystem

In order to characterize spatial patterns of algal wrack distribution and changes over time, we used ArcGIS for Desktop v.10.2 to analyze 15 aerial photos of Elkhorn Slough, ranging from 1931 through 2014 (Table S1). We used photos only from the peak growing period, April–November. A grid of 50 × 50 m<sup>2</sup> cells was draped over the entire Elkhorn wetland area along the main channel in marshes that were never diked, creating a total of 2214 cells. Our analysis was limited to wrack on the marsh; we did not examine adjacent mudflats, because of logistic difficulty with photos taken at different inundation levels and because our primary interest in this study is macroalgal effects on marshes (Fig. S1). We examined each cell for each photograph at a scale of 1:2000, and visually assessed whether wrack was present or absent. Algal wrack was considered present in a cell when one or more features within a cell appeared bright white in color; dead algal wrack appears bright white in all types of imagery including panchromatic (black and white), true color, and color infrared. In contrast, live algal mats were difficult to identify in the panchromatic imagery that was used between 1931 and 1976 and therefore live algal mats were excluded from the analysis for all years. The total number of all cells with algal wrack marked as “present” were then summed for each image examined, and compared across years in order to assess changes in wrack abundance over time. Frequency of algal wrack presence in each individual cell was also tallied for all years combined in order to assess any spatial patterns of algal wrack distribution across the marsh. We used linear regression to detect temporal trends in wrack cover (lm function in R, v. 3.2.2; R Core Team, 2015; and used this same software for all temporal analyses and regressions in this study, and log transformed data when appropriate). We recognize that the use of a limited number aerial photographs for analysis of macroalgal wrack trends over time fails to account for temporal variation at smaller time-scales. There certainly is extensive variation in algal abundance across the year, and so a more accurate assessment would be obtained by averaging ten photos per year. Unfortunately, we had a limited number of photographs available during the growing season where light angle was appropriate to detect algal wrack and where the tide was below the marsh, especially for earlier years. The resulting analysis thus has a larger error associated with each individual year than would have been the case with multiple photographs per year; the increased noise makes detecting a signal (temporal trend) less likely.

### 2.3. Temporal changes in fertilizer sales and estuarine nutrient concentrations

To determine how fertilizer use in the surrounding watershed has changed over time we examined nitrogen fertilizer sales for Monterey County, CA and California from 1925 to 2013 using the California Department of Food and Agriculture (CDFA) – Fertilizing Materials Tonnage Reports ([https://www.cdfa.ca.gov/is/fldrs/Fertilizer\\_Tonnage.html](https://www.cdfa.ca.gov/is/fldrs/Fertilizer_Tonnage.html) for years 1991–2013; earlier reports available by Public Records Act request from CDFA). Tonnage reports were only available for Monterey County starting in 1971. We estimated fertilizer sales (in tons nitrogen) for Monterey County for 1925–1969 (1970 data were not available) by calculating the percent of sales in California

coming from Monterey County from 1971 to 2008 (mean = 4.2%  $\pm$  0.72 SD). Since the mean and SD were consistent across nearly four decades, we assumed that the percentage was consistent from 1925 to 1969, and calculated the annual fertilizer sales in Monterey County by multiplying the annual California fertilizer sales by 4.2%.

To determine trends in water column nitrate values in Elkhorn Slough, we constructed a time series drawing on different sources for different periods: 1970 to 1972 (Smith, 1973), 1974 to 1976 (Nybakken et al., 1977), 1977 from the California Central Coast Regional Water Quality Control Board, and 1989 to 2015 Elkhorn Slough National Estuarine Research Reserve (ESNERR). We also examined the relationship between fertilizer sales and nitrate concentrations.

Historical changes in nitrogen isotopic composition were examined at four locations across Elkhorn Slough. Sediment cores (50–60 cm in length) were analyzed at one cm increments for stable nitrogen isotopic composition using a Finnegan Delta IX continuous flow isotope ratio mass spectrometer (CF-IRMS) using standard methods (McClelland et al., 1997; McKinney et al., 2001). Cores were collected using a Russian peat corer, a side filling coring device that prevents compaction (Aquatic Research Instruments, Hope, ID). Chronological control was provided using downcore profiles of  $^{210}\text{Pb}$  and  $^{226}\text{Ra}$  (Supplemental Methods). The stable nitrogen isotope composition of the soil is expressed as a per mill difference relative to the reference standard (air- $\text{N}_2$ ) such that  $\delta^{15}\text{N} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$  where  $R$  is the ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  (Mariotti, 1983). Duplicates were run every five samples with a typical difference of 0.09‰. Here, we interpret increasing sedimentary  $\delta^{15}\text{N}$  signatures as reflecting historic increases in nitrogen inputs, in accordance with previous studies demonstrating linkages between high N loads and high stable nitrogen isotope ratios (Kreitler et al., 1978; Fry and Allen, 2003; Fry et al., 2003). Enrichment in  $\delta^{15}\text{N}$  signatures is often the result of fractionation that occurs with denitrification. While synthetic fertilizer has a nitrogen stable isotope signature similar to atmospheric air ( $\delta^{15}\text{N} = 0$ ; Aly et al., 1982), denitrification can fractionate nitrogen stable isotopes as denitrifying bacteria take up  $^{14}\text{N}$  at a faster rate than  $^{15}\text{N}$ , leaving the remaining dissolved inorganic nitrate enriched in  $^{15}\text{N}$  (Lehmann et al., 2003; Oczkowski et al., 2008). Support for the interpretation of  $^{15}\text{N}$  enrichment as a result of fertilizer application is supported by previous surveys of nitrogen stable isotopes in agriculturally dominated areas, such as the Mississippi River, the Nile Delta, and Portuguese Lagoons (Fry and Allen, 2003; Castro et al., 2007; Oczkowski et al., 2008).

#### 2.4. Macroalgal production and seasonality

To monitor algal production over time, we established a permanent plot 100  $\times$  50 m in size at each of eight intertidal mudflats in Elkhorn Slough (Fig. 1). We sampled percent cover of green macroalgae (*Ulva* spp.) at each plot, approximately once per month, from 2010 to 2016, during tides below Mean Lower Low Water (MLLW); these plots span elevations of approximately 0 cm below MLLW to 50 cm above MLLW. We determined percent cover using a modified random point contact (RPC) method described by Nedwell et al. (2002). We surveyed plots from nearby upland positions using a rifle scope with crosshairs mounted to a tripod. Transects were run across the entire plot area by moving the scope at  $\sim 10^\circ$  angles, looking through the scope and recording if the crosshairs intercepted algae, for a total of 100 points. We tallied points to generate percent cover of algae.

#### 2.5. Monitoring of algal wrack dynamics and effects on marsh edge

We characterized algal wrack and effects on the marsh at 15 sites along the main channel of Elkhorn Slough (Fig. 1). Methods are summarized here and detailed in the Supplement. During monthly boat surveys, we assigned wrack along the marsh edge an index score of 0–3 based on cover and thickness. To examine whether this wrack index

correlated with marsh health and habitat loss, we used the average of the index across the four summer months in 2014 for each site. To determine whether our algal wrack index correlated with biomass of algal wrack on the marsh, we harvested wrack biomass once during the monitoring period and weighed each sample before and after drying.

In order to characterize marsh plant health at each of the sites, we assessed a 0.5  $\times$  0.5 m quadrat centered on each monitoring plot in August 2014. Percent cover of succulent marsh plant tissue was assessed by dropping a metal rod at 16 intercepts and tallying the number of intercepts where the rod touched succulent tissue. Succulent tissue was chosen as a more sensitive response variable because woody pickleweed tissue can persist in this perennial even in stressed plants. Percent flowering was assessed by searching for flowers on marsh plants in each of five equal sections of the quadrat separated by string; we then tallied the percent of the rows that had flowers. Maximum canopy height was assessed by using a meter stick to measure the tallest stem in the quadrat.

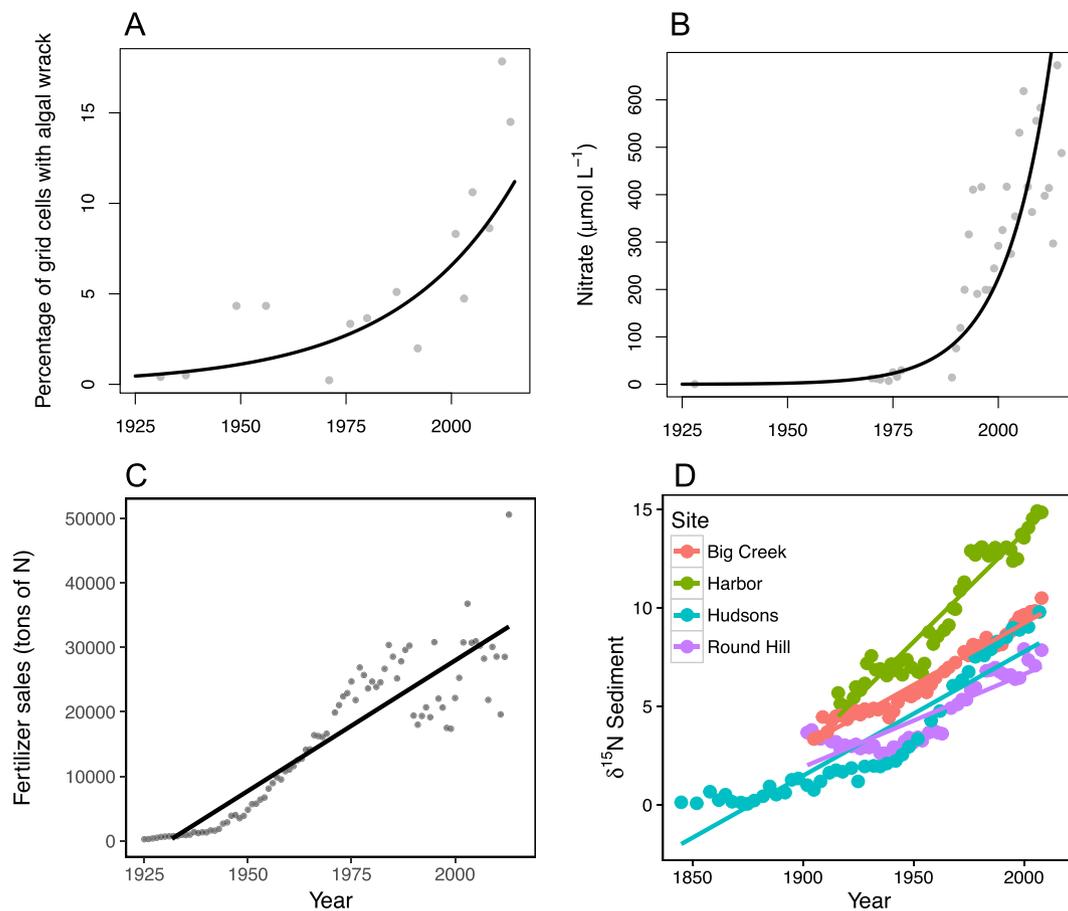
To assess habitat change rates at each site, we took identical measurements in January 2014 and 2015. A one-year interval was chosen rather than the shorter summer *Ulva* monitoring period because habitat effects can take months to manifest. We ran a transect tape perpendicular to the shoreline, from our plot markers (set about 2 m landward of the bank edge) to the bank edge. We measured the distance to the most seaward succulent marsh plant tissue (the live marsh edge) and to the bank edge. We then calculated the difference between the measurements made a year apart as the bank erosion rate and the vegetation retreat rate, respectively. We quantified the number of holes > 1 cm in diameter (large holes in this estuary are made only by the crab *Pachygrapsus crassipes*) within a 0.5  $\times$  0.5 m quadrat held vertically on the bank edge just below the marsh edge. To estimate the role of physical forcing of bank erosion through tidal scour, we deployed erodible plasters for two weeks in June 2015, spanning a period of strong spring tides, and weighed the plasters before and after deployment (see Supplement for details).

To examine the relationship between the algal wrack index and the potential response variables, we conducted simple linear regressions. Linear regressions were appropriate based on the distribution of the data for all analyses except flowering, where a logarithmic regression was used.

#### 2.6. Experimental test of algal wrack effects on low marsh edge

To test the effect of different time lengths of wrack exposure on salt marsh health and habitat change, we conducted a field experiment (methods are summarized here, with more detail in the Supplement). We conducted the experiment on a former levee near the lower elevational limit for salt marsh in the estuary (Fig. 1). Ten plots received no wrack; ten were covered with wrack (applied at approximately 1500 g/m<sup>2</sup> dry weight) for 8 weeks (May–July); ten were covered with wrack for 12 weeks (May–September). All plots (wrack and control) were fenced and a mesh placed on top to retain the wrack. We assessed the plots in early May 2014, prior to initiating wrack addition, in late July, for flowering during the reproductive peak, and in late September, for all other parameters. We surveyed the plots a year later, in September 2015, to assess recovery.

To evaluate salt marsh response, we assessed marsh plants within a 0.5  $\times$  0.5 m quadrat placed within each plot. Percent cover of succulent vegetation, percent flowering, and maximum canopy height were assessed with the same methods as described above for the field surveys. We also collected succulent marsh plant biomass (snipped all succulent growing tips with scissors) as a proxy for recent production from 0.15  $\times$  0.15 m quadrats located outside the focal assessment area, using a different portion of the plot in September 2014 vs. 2015 to avoid resampling the same area. Biomass samples were dried and weighed. To evaluate potential vegetation retreat, we assessed the location of the seaward pickleweed boundary by measuring the



**Fig. 2.** Temporal changes in algal wrack, nitrate concentrations and fertilizer sales over historical period. (A) Results of analysis of photographs from 15 years between 1931 and 2014, showing the percentage of grid cells (2500 m<sup>2</sup>,  $N = 2214$ ) with algal wrack present. (B) Trend in annual nitrate concentrations collected from lower Elkhorn Slough from 1928, 1971–72, 1974–1977, and 1989–2015. (C) Annual fertilizer sales in Monterey County, CA from 1925 to 2013 measured in tons of nitrogen. The period from 1925 to 1969 was estimated using California state totals by multiplying the mean % sales ( $4.2\% \pm 0.72$  SD) of Monterey County from 1971 to 2008. (D)  $\delta^{15}\text{N}$  values (‰) over time (1848–2008) at four sites around Elkhorn Slough. Lines represent modeled trends.

distance to the most seaward succulent tissue from four stakes along the seaward plot boundary; positive numbers were used for vegetation seaward of stakes, negative numbers for landward. We used Analysis of Variance (ANOVA) to test for effect of the three treatments on the various response variables, with a Tukey HSD post-hoc test for pair-wise comparisons of treatments. We used a Pearson's Chi-square test to determine effect of the treatments on flowering in pickleweed.

### 3. Results

#### 3.1. Algal wrack spatial and temporal characterization across marsh ecosystem

We detected significant increases in algal wrack (log transformed) on marshes over time ( $R^2 = 0.56$ ,  $P = 0.0014$ ; Fig. 2a). Results of the GIS spatial analysis of algal wrack indicates low wrack abundance (e.g. fewer than 5% of cells observed with wrack present per year) between 1931 and 1980 followed by a significant increase in wrack abundance between 1992 and 2014 (Fig. 2a, Fig. S1). A maximum of 18% of cells were observed to contain algal wrack in May 2012.

Our analysis of spatial patterns (Fig. 3), summing all instances of wrack presence per cell over time, revealed that marsh edges along the main channel are exposed to wrack much more frequently than other areas. All edges are not equally affected; some edges have much more frequent wrack occurrence than others. Areas of persistent accumulation of wrack can be seen at selected locations throughout the estuary (Fig. 3). In the marsh interior, there were no clear patterns of spatial

distribution; all areas seem to occasionally be exposed to wrack.

#### 3.2. Changes in nutrient loading

We detected a significant increase in water column nitrate concentrations (log transformed) in the estuary over time ( $R^2 = 0.89$ ,  $P < 0.0005$ , Fig. 2b), as well as a significant increase in fertilizer use in the surrounding watershed ( $R^2 = 0.84$ ,  $P < 0.0005$ ; Fig. 2c). Significant increases in sediment  $\delta^{15}\text{N}$  values were also found at all four coring locations (Harbor:  $R^2 = 0.93$ ,  $P < 0.0005$ ; Round Hill:  $R^2 = 0.76$ ,  $P < 0.0005$ ; Big Creek:  $R^2 = 0.96$ ,  $P < 0.0005$ ; Hudsons:  $R^2 = 0.86$ ,  $P < 0.0005$ ; Fig. 2d). Pre-1920s  $\delta^{15}\text{N}$  values ranged from 0.5‰ at the upper Slough, to 5.6‰ near the mouth of the estuary, with sites in the middle slough averaging 3–4‰. There was a rise in sediment nitrogen stable isotope ratios beginning in the 1940s that mirrored the increase in fertilizer sales in the watershed. Values in the upper and lower slough are most enriched in  $^{15}\text{N}$ , at 9.5‰ over background values. In the mid-slough, values are enriched over background values by 4–7‰.

Fertilizer sales showed a significant relationship with nitrate concentrations ( $R^2 = 0.14$ ,  $P = 0.033$ ; Fig. S2a). Nitrate concentrations correlated significantly with algal wrack cover from the GIS time series analysis ( $R^2 = 0.62$ ,  $P = 0.012$ ; Fig. S2b). Fertilizer sales and water column nitrate also correlated significantly with  $\delta^{15}\text{N}$  values; for this regression we used the Harbor core since it is closest to the most extensive fertilizer inputs to the estuary (Fertilizer:  $R^2 = 0.87$ ,  $P < 0.0005$ ; Nitrate:  $R^2 = 0.51$ ,  $P = 0.006$ ; Fig. S2c–d).

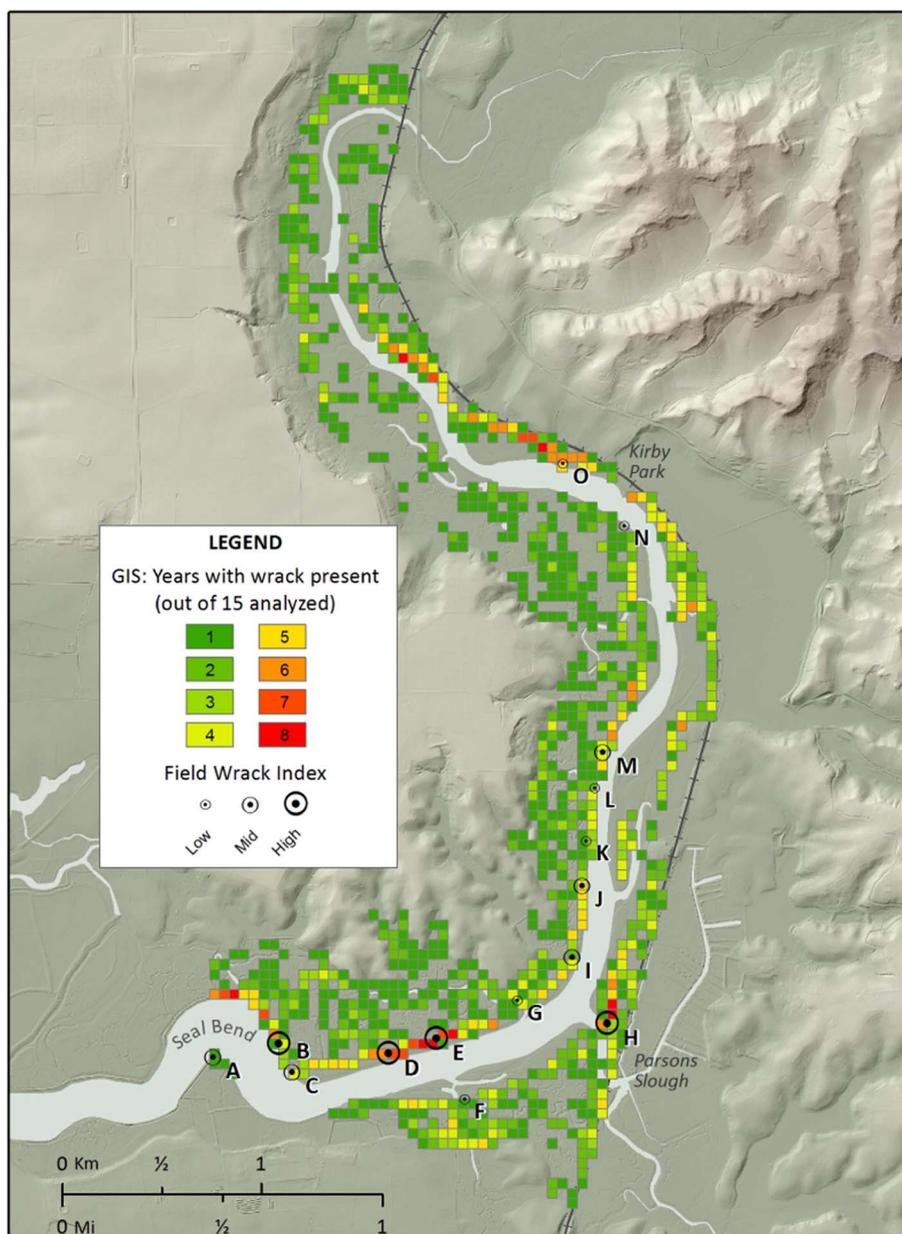


Fig. 3. Spatial patterns of algal wrack on marsh. Grid cells show the results of analysis of aerial photographs from 15 years between 1931 and 2014, with color-coding indicating frequency with which each cell had algal wrack present. Circles of different sizes show relative wrack index values at 15 sites (labeled A–O) monitored with field surveys in 2014. Wrack index scores of 0–3 were assigned in monthly surveys June–September, and these were summed over the four months. Low = cumulative wrack index 0–2.5; Mid = 2.6–5.0; High = 5.1–7.5.

### 3.3. Macroalgal production and seasonality

Macroalgal production in the estuary was high throughout the estuary during the monitoring period (2010–2016). The percent cover of macroalgae at the eight sampled sites ranged from 23% on average in winter to 50% on average in the summer (Fig. 4). The peak in cover varied somewhat across years, but always occurred in spring or summer with the highest average coverage reaching 98% in April 2016.

### 3.4. Monitoring of algal wrack dynamics and effects on marsh edge

Our algal wrack index obtained during boat-based assessments of the 15 sites along the Elkhorn Slough channel proved to be a reliable indicator of wrack biomass: there was a strong correlation between the average of the wrack index over summer 2015 (June–September) and the dry weight of wrack collected at the 15 sites ( $R^2 = 0.64$ ,

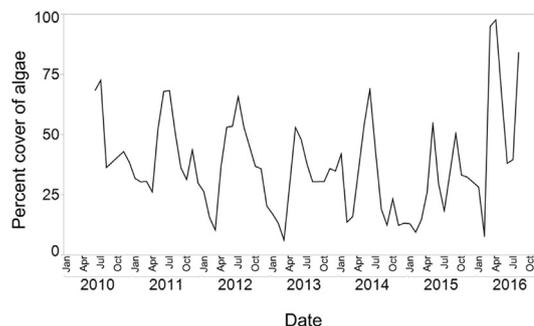


Fig. 4. Seasonality of macroalgal production. Mean algal production typically peaks during summer months and is lowest during winter months.



Fig. 5. Algal wrack at marsh edge. *Top*: Fresh algal mats draped on salt marsh edge along main channel, with recent bank erosion visible as chunks adjacent to marsh. (Photo: K. Wasson); *Bottom*: Dried algal wrack on salt marsh edge; in foreground, wrack has been removed to reveal salt marsh underneath, which looks unhealthy compared to impacted marsh to right and back of photo. (Photo: L. Gray).

$P = 0.0003$ ) (Fig. S3a). The average dry weight of wrack was  $359 \text{ g/m}^2$  across all sites, with a range of  $0\text{--}1422 \text{ g/m}^2$ .

Deposition of algal wrack along the channel banks was sometimes very high (Fig. 5), but spatially variable. Some sites repeatedly scored high on the index, while others scored low (Fig. S4). The sites with highest cumulative cover (B, D, E, H) were located near hotspots identified by the time series analysis (Fig. 3). The average algal wrack index was 0.97, with averages for individual sites ranging from 0.1 to 1.7. The average duration of wrack cover over the four summer months was 2.1 months, but ranged from 0 to 4 months across the sites. There was a significant correlation ( $R^2 = 0.32, P = 0.029$ ) between the Summer 2014 index across the 15 sites and the index in June 2015, suggesting spatial patterns of deposition are similar across years (Fig. S3b).

Algal wrack correlated negatively with all three indicators of marsh health that we assessed. There was a significant negative correlation between the wrack index and percent cover of succulent marsh tissue ( $R^2 = 0.39, P = 0.013$ ) (Fig. 6a). In addition, there was a significant negative correlation between the wrack index and percent flowering ( $R^2 = 0.29, P = 0.041$ ) (Fig. 6b). There was also a marginally significant negative correlation between the wrack index and maximum canopy height ( $R^2 = 0.23, P = 0.0069$ ) (Fig. S3c).

Algal wrack correlated with both indicators of marsh habitat loss. There was a very strong relationship between the algal wrack index and vegetation retreat rate ( $R^2 = 0.67, P = 0.0002$ ) (Fig. 6c), and a weaker but still highly significant relationship with bank erosion rate ( $R^2 = 0.41, P = 0.0096$ ) (Fig. 6d). The vegetation retreat rate did not correlate with plaster loss (proxy for physical forcing by tidal erosion)

( $R^2 = 0.11, P = 0.26$ ), and showed a weak relationship with crab holes ( $R^2 = 0.23, P = 0.07$ ) (Fig. S5a,c). The bank erosion rate was correlated with plaster loss ( $R^2 = 0.36, P = 0.023$ ) as well as crab holes ( $R^2 = 0.55, P = 0.0016$ ) (Fig. S5b,d).

### 3.5. Experimental test of algal wrack effects on low marsh edge

Prior to the initiation of the wrack treatments, in the May 2014 assessment, plots assigned to the three different treatments did not differ significantly in ANOVA conducted on each parameter (Fig. S6). In the July 2014 assessment of flowering, we found flowers only in the “no wrack” treatment, a significant result (Pearson’s Chi-square,  $P = 0.025$ ). In the September 2014 assessment, we found the “no wrack” treatment differed significantly from the two wrack treatments for two indicators of plant health (Fig. 7, Table S2), pickleweed succulent biomass and pickleweed percent cover; the 8 and 12 week wrack cover treatments did not differ significantly from each other. For the third indicator of plant health, maximum canopy height, all three treatments differed; canopy height was far higher in the “no wrack” than “wrack” treatments, and it was also greater in the 8 vs. the 12 week wrack treatment. Significantly less vegetation retreat occurred in the “no wrack” vs. wrack treatments; the two wrack treatments were not significantly different. The control “no wrack” treatment had lower marsh health in September 2014 than May 2014 (Fig. S6), and had undergone some vegetation retreat, presumably in response to the extensive trampling from weekly visits to the plots.

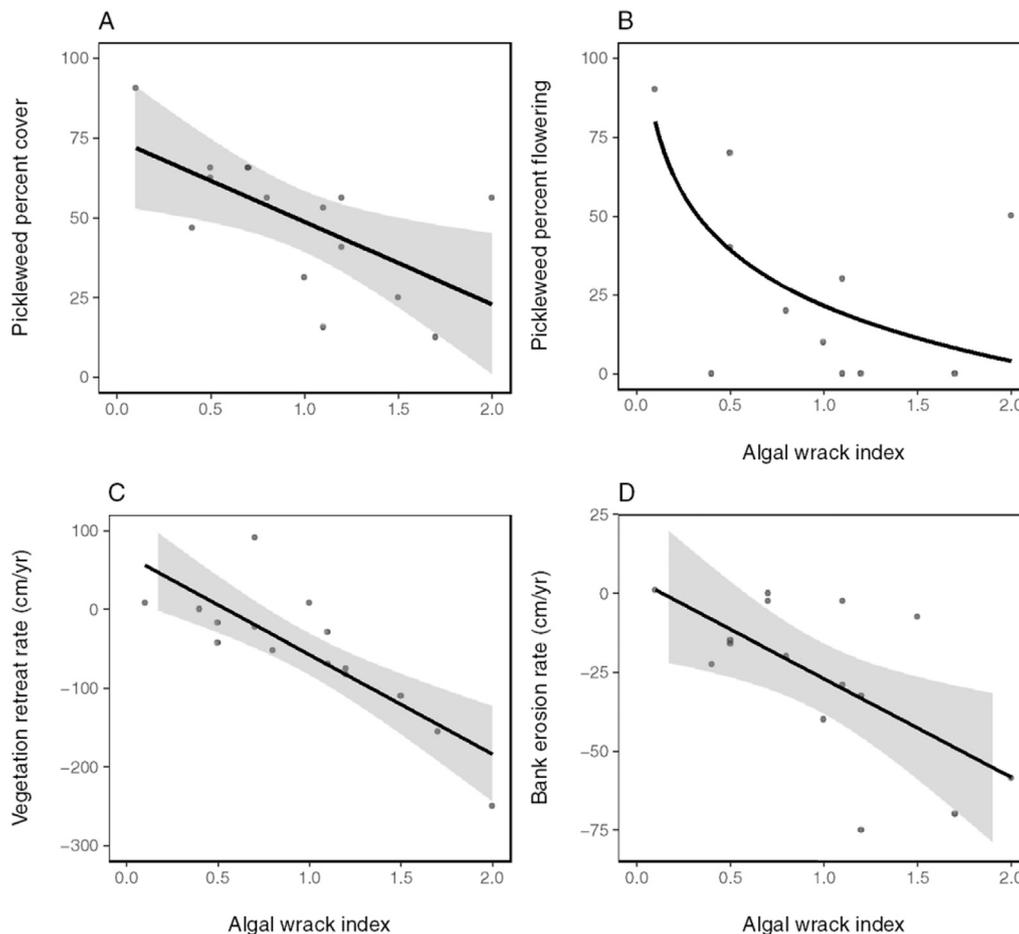
In September 2015, the plots had not yet recovered (Fig. S6, Table S3). The “no wrack” treatment was significantly different from both wrack treatments for two indicators (canopy height and vegetation retreat), and significantly different from just the 8 week treatment for the other two indicators (biomass and percent cover). The 8 and 12 week wrack treatments were not significantly different from each other for any of the indicators of marsh health.

## 4. Discussion

### 4.1. Temporal patterns of eutrophication

Our time series spanning eight decades showed that macroalgal wrack on the salt marsh has increased over time, concurrent with nutrient concentrations and fertilizer use. The strong correlation observed between wrack and nutrient concentrations over time suggests fertilizers intended for crops such as lettuce and strawberries in this watershed are inadvertently also growing sea lettuce (*Ulva*) in Elkhorn Slough. While the relationship between nutrient loading and increases in macroalgal abundance is well known, primarily from comparative studies of estuaries with different nutrient loading levels (Duarte, 1995, Valiela et al., 1997), there are relatively few studies quantifying change in nutrients and macroalgae at a single site over extended periods of time. Raffaelli (1999) demonstrated an increase between the 1950s and 1980s in a Scottish estuary using repeat field survey data. Repeated field surveys have also been useful for detecting decreases in macroalgae likely resulting from better nutrient management practices; Sfriso et al. (2003) demonstrated a decrease in macroalgae in Venice Lagoon between the 1980s and 1990s, while Krause-Jensen et al. (2012) and Rasmussen et al. (2015) revealed decreases in Danish coastal waters between the 1990s and 2000s. We do not know of a macroalgal time series as long as ours (80 years). Multi-decadal studies of changes in estuaries are rare, but critical for wise stewardship of coastal resources (Cloern et al., 2015). The remote sensing technique we used could readily be applied to other locations to look at changes in frequency of wrack in photos over time.

Our  $\delta^{15}\text{N}$  analysis also provided a deeper temporal perspective on nutrient loading, examining current nutrient signatures relative to those from the period before the widespread use of synthetic fertilizers. Both decadal and centennial demonstrations of nutrient loading, relative to



**Fig. 6.** Correlations between algal wrack index and marsh attributes. The wrack index was averaged across June–September 2014 sampling dates for each of the 15 stations. Significant correlations were obtained with A: succulent percent cover of marsh, B: percent of marsh that was flowering, C: vegetation retreat rate, and D: bank erosion rate. Linear regressions were used for A, C and D; logarithmic regression was used for B. Black lines are the modeled trends and gray areas represent 95% confidence interval (A, C and D).

baselines, are useful for informing regulatory efforts, because such demonstrations quantify the increase in nutrients likely due to anthropogenic activities. Here, the reconstruction of changes in stable nitrogen isotope ratios provide firm evidence for historical increases in nitrogen availability and thus for expanded presence of *Ulva* at Elkhorn Slough.

On a shorter time scale, our field monitoring of intertidal macroalgal production revealed marked seasonal patterns. Macroalgae peak in summer, which coincides with the salt marsh growing season. A similar result was found by Hulzen et al. (2006) in the Netherlands. The coincident timing of growth of algae and marsh increases the potential for disturbance of the latter by the former.

#### 4.2. Spatial patterns of wrack deposition

Some disturbances in nature are unpredictable, but this one – algal wrack deposition on the salt marsh – seems to have some predictability. Hulzen et al. (2006) working in the Scheldt estuary of the Netherlands found that the low marsh border accumulates a high proportion of algal wrack in the Scheldt estuary of the Netherlands. Our results for Elkhorn Slough are similar: the marsh boundary with the mudflats of the main channel of the estuary had a greater frequency of algal wrack cover in our 80 year time series than did the marsh interior. However, not all portions of the marsh edge are equally affected. Our time series analysis identified “hotspots” where algal wrack was found more frequently. Likewise, our field monitoring revealed that some marsh edges were exposed to wrack repeatedly within the same season, and that those same areas were likely to be exposed a year later as well; these results

are very similar to ones from Hulzen et al. (2006). In a different study focusing on marsh disturbance by wrack consisting of marsh debris, not algae, creek bends where water velocities slowed appeared to accumulate the most wrack (Fischer et al., 2000). At Elkhorn Slough, the areas where algal wrack accumulated are predominantly west or south-facing edges, possibly due to wind waves or current patterns. These marsh edges face chronic stress and are particularly vulnerable. Design of marsh restoration projects could take such predictability of disturbance into account by avoiding extensive representation of edges facing the directions most prone to wrack accumulation.

#### 4.3. Negative effects of algal wrack on marsh edge

Both our field monitoring of marsh edges exposed to variable levels of wrack and our controlled field experiment manipulating exposure to wrack revealed negative effects of wrack on marsh plants: decreased canopy height, percent cover, and flowering, and increased rate of vegetation retreat. The monitoring enabled us to compare sites with variable frequency and duration of exposure to wrack, and the experiment included longer and shorter periods of wrack exposure. Given that marshes are nutrient-limited, we might have expected that low intensities or shorter duration of exposure to wrack might be beneficial, while high levels are damaging. However, we found no such bell-shaped curve of effects. Hulzen et al. (2006) also found a linear relationship with frequency of wrack removal and marsh growth and cover. We thus concur with Watson et al. (2015): high nutrient loads manifested as massive algal blooms can exacerbate coastal marsh loss. A recent study found that seagrass wrack on marshes can lead to loss of

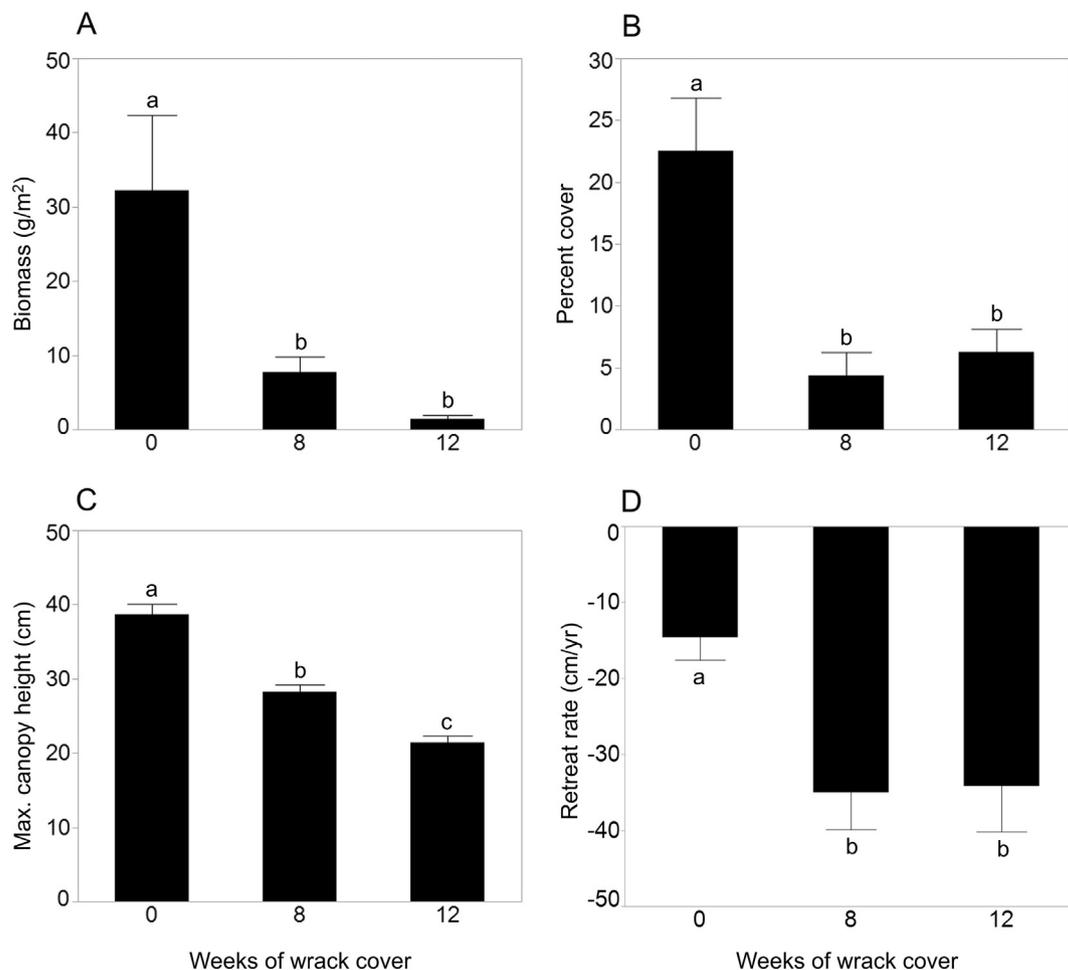


Fig. 7. Effects of algal wrack on pickleweed. There was a strong effect of algal wrack on A) pickleweed succulent biomass, B) pickleweed percent cover, C) maximum canopy height of pickleweed, and D) vegetation retreat rate. The negative values for retreat rate indicate landward migration. All data were collected in September 2014, about one week after the end of the experiment. Error bars represent standard error. The three different treatments (no wrack, 8 weeks of wrack, and 12 weeks of wrack cover) are on the x-axis. Lower case letters denote significant differences ( $P < 0.05$ ) (Table S2) among treatments.

carbon sequestration, a key ecosystem service provided by marshes (Macreadie et al., 2013), and we suspect that algal wrack can likewise lead to loss of valued services provided by marshes.

Field studies and laboratory mesocosm studies have mostly demonstrated negative effects of ephemeral macroalgae such as *Ulva* on the annual marsh grass *Spartina* (Hulzen et al., 2006, Newton and Thornber, 2013, Watson et al., 2015); to our knowledge ours is the first demonstration of negative effects of *Ulva* wrack on the perennial succulent *Salicornia*. While we did not examine the mechanisms by which wrack affected the marsh plants, we suspect they are similar between the species. Hulzen et al. (2006) measured virtually complete reduction of light under algal mats of any thickness, directly affecting above-ground biomass as well as carbon storage. Watson et al. (2015) found decaying *Ulva* in sediments resulted in high ammonia, sulfides and organosulfur compounds, reducing below-ground biomass at low concentrations, and above- and below-ground biomass at high concentrations. While field experiments have shown mixed benefits of fucoid algae to salt marsh plants and dynamics (increased sedimentation and growth, but decreased colonization by seedlings, Tyrrell et al., 2015), only laboratory mesocosm studies have demonstrated any benefits of more ephemeral macroalgae such as *Ulva* to salt marsh plants (Boyer and Fong, 2005, Newton and Thornber, 2013). Watson et al. (2015) found that negative effects of *Ulva* are exacerbated by increased inundation, and suggest that the benefits that have been demonstrated are an artifact of laboratory conditions where lack of inundation prevents soil anoxia typical in the field. Furthermore, estuaries with

big algal blooms tend to have such high nutrient concentrations that nutrient subsidies from algae would not provide an important benefit (Newton and Thornber, 2013). Thus, it appears that under realistic conditions, algal wrack only has negative, not positive effects on salt marshes. While a recent study (Johnson et al., 2016) found that salt marsh communities may only show mild responses when exposed to realistic types, amounts, and delivery methods of nitrogen, it appears that the marsh responses to nitrogen-fueled algal production and subsequent wrack deposition on the marsh may be much stronger.

#### 4.4. Multiple stressors and limits to marsh resilience

The lower edge of the salt marsh is a dynamic front for marsh expansion or contraction, and is rarely in equilibrium (Fagherazzi et al., 2013). We have demonstrated the negative effect of wrack on marsh edges, with both our experiment and field monitoring showing retreat of the marsh edge linked to wrack exposure. In the experiment, the marsh edge had not recolonized its former more seaward position a full year after wrack treatments were halted; marsh retreat was persistent. The monitoring, conducted on higher bank edges along the main channel of the estuary, also detected increased bank erosion with wrack (the experimental addition of wrack was conducted in an area with shallow slopes and no clear bank edges so this could not be examined). After vegetation is degraded, banks are weakened because there is no above-ground vegetation buffering waves and no below-ground root matter holding sediment (Barbier et al., 2008, Fagherazzi

et al., 2013). While decline in marsh cover on the marsh plain can be reversible, bank erosion is not, in this low sediment system. The elevation undergoes a sharp drop of 20–100 cm when chunks of bank erode (Fig. 5), and in the absence of a massive sediment supply, this means that marsh has permanently converted to mudflat. Mudflat and marsh are thus alternate stable states at the bank edge in this estuarine system, and wrack can cause state shifts beyond the limits of marsh resilience.

While we have focused on one stressor to the marsh edge, algal wrack, this stressor does not operate in isolation. Marsh edges are inherently unstable, and will retreat if loss due to erosion exceeds sediment supply (Fagherazzi et al., 2013). Elkhorn Slough has experienced both increased erosion due to increased tidal currents resulting from an artificial harbor mouth, and decreased sediment supply due to river diversion (Watson et al., 2011). Eutrophication also likely has negative effects other than wrack; monitoring data reveal subsidence of the marsh plain (C. Endris, unpublished data) that may be related to increased microbial activity or decreased below-ground organic matter accumulation such as has been demonstrated for other nutrient-loaded marshes (Deegan et al., 2012). During the period of our monitoring and experiment, California was experiencing unusually high water levels, and perhaps related to this, monitoring data showed retreat of the lower marsh vegetation edge even at sites not affected by wrack (K. Wasson, A. Woolfolk, unpublished data). This may explain why even the low wrack monitoring sites, and the control plots in the experiment underwent some vegetation retreat at the marsh edge (although we cannot rule out a cage effect). Furthermore, unavoidable trampling associated with weekly visits to the experimental sites appears to have negatively affected the entire marsh area, such that even the control plots had less cover and biomass at the end of the experiment than the start. The lack of recovery of the wrack plots even after a full year may thus be due to the combined effect of wrack, higher water levels, and trampling. In another example, Watson et al. (2015) showed that macroalgae have much stronger negative effects in highly inundated sediments, so wrack and sea level rise are likely to have synergistically negative effects on marsh resilience. Likewise, Brewer et al. (1998) found an interaction between (non-algal) wrack and marsh elevation. We thus conclude that in order to understand marsh resilience at the mudflat boundary, it is critical to examine both abiotic drivers such as water levels and sediment supply and biotic drivers such as algal wrack and crab burrowing, as well as the interactions among them.

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## Appendix A. Supplementary methods and analyses

Supplementary details on the methods employed and additional analyses of the results related to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.05.019>.

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## APPENDIX A. Supplementary methods and analyses

### Methods

#### *Sediment radioisotope dating*

To date sediment accumulation, 10-12 subsamples per core were dried and introduced into a Ge well detector (GL 20203, Canberra, Meridian, CT) for measurement of  $^{210}\text{Pb}$ ,  $^{214}\text{Pb}$ , and  $^{137}\text{Cs}$ . For each core, excess  $^{210}\text{Pb}$  activities were calculated by subtracting the  $^{214}\text{Pb}$  activity from the total  $^{210}\text{Pb}$  activity. Sediment accumulation rates and chronologies were generated using a linear regression of the natural log of excess  $^{210}\text{Pb}$  activity vs. depth, assuming a constant rate of  $^{210}\text{Pb}$  supply (Appleby and Oldfield 1978):

$$A = A_0 e^{(-\lambda/s)x}$$

where  $A$  is the  $^{210}\text{Pb}$  activity at a given depth,  $A_0$  is the initial activity of excess  $^{210}\text{Pb}$  at the marsh surface,  $\lambda$  is the radioactivity decay constant for  $^{210}\text{Pb}$  ( $0.03101 \text{ y}^{-1}$ ),  $s$  is the accretion rate in  $\text{cm y}^{-1}$ , and  $x$  is the depth of the core (cm). Accretion rates were cross-checked using radio-cesium chronologies: the first appearance of  $^{137}\text{Cs}$  was assigned an age of 1954, and the peak an age of 1968, in line with the timeline of radioactive fallout from historical munitions testing (Robbins and Edgington 1975). To confirm chronologies, sediment total lead concentrations were also analyzed using an ICP-AES instrument following four-acid pretreatments. For two of the four cores, accretion rates generated from  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$  dating were in strong agreement: in those cases, mean accretion rates from  $^{210}\text{Pb}$  dating were adopted. For one of the other cores, accretion rates from  $^{210}\text{Pb}$  age-modeling were found to be significantly greater than those from  $^{137}\text{Cs}$  dating ( $0.73 \text{ cm y}^{-1}$  vs.  $0.46 \text{ cm y}^{-1}$ ), while at another site accretion rates from  $^{210}\text{Pb}$  age-modeling were found to be significantly less than those from  $^{137}\text{Cs}$  dating ( $0.31 \text{ cm y}^{-1}$  vs.  $0.58 \text{ cm y}^{-1}$ ). In these cases, total lead concentrations were examined to see which age model associated high lead concentration depths with ages between the 1960s to early 1980s (e.g., Hornberger et al. 1999), and the model was adopted which fitted the lead concentration data the best.

#### *Monitoring of algal wrack dynamics and effects on marsh edge*

To select our 15 sites, we picked the GPS coordinates of the sites a priori using aerial imagery to spread the sites fairly evenly along the middle region of the main channel. We had no sites in the lower region near the mouth because the banks there consist of artificial berms that are higher than natural banks. We had no sites in the upper channel because waters are too shallow for easy boat access. Many more of our sites were located on the northwestern bank of the channel than the southeastern simply due to logistics; the southern bank is not accessible by boat in many places due to a shallow mudflat in front of the marsh. At each of the 15 sites, we had two PVC markers located 10 m apart, set back about 2 m from the bank edge. We conducted our assessments in front of each marker and then took the average value of the two markers to characterize that site.

Since our long-term monitoring of macroalgal production on the mudflat revealed that algae peak in summer, we conducted surveys approximately monthly between June-September 2014, and again in June 2015 to examine whether patterns were consistent across years. Surveys were conducted at low tides when the marsh was well above the waterline. In each of these five months (June, July, August, September 2014 and June 2015), we approached each site by boat and assessed the level of algal wrack coverage from a few meters offshore. The assessment plot was a rectangle approximately 100 cm long (centered on the PVC marker) and 50 cm wide (extending from the marsh edge landward). Wrack abundance was classified in each plot on a

scale of zero to three. 0: zero algal wrack or trace amounts (<2% cover), 1: light algal wrack cover (<50% cover of thin layer < 1 cm thick or <20% cover of thick layer), 2: medium algal wrack cover (up to 100% cover of thin layer or <50% cover of thick layer), 3: high wrack cover (>50% cover of thick layer). To improve the repeatability and rigor of these qualitative assessments, two observers independently scored the wrack and then compared index values; when they differed, more observations of the plot were made until consensus was reached.

To determine whether our algal wrack index correlated with biomass of algal wrack on the marsh, we quantified algal wrack biomass once during the monitoring period. In June 2014, we placed 0.15 x 0.15 m quadrats about 1 m outside the monitoring plots at each site and collected all feasibly removable wrack on the marsh (we stopped when about 95% of the wrack had been collected, because the final 5% was tangled up in marsh stems and removal would destroy the plant). We harvested the wrack near but outside the monitoring plots so that we would not affect the results of the next months' monitoring or the health of the marsh. The wrack was dried and weighed, and the average of the two collections per site (one outside each PVC marker) taken.

Plasters were deployed at each site to estimate physical forcing of erosion by currents. Each plaster was made from a single batch of plaster mix consisting of 8.5 liters plaster of Paris to 3.5 liters water. The plasters were poured into silicone cupcake molds. Before the plasters began to solidify two 3 cm stainless steel hex bolts were placed in each mold. Plasters sat on the laboratory counters in a dry room until they solidified after which they were placed in a drying oven for approximately 24 hrs. Each plaster was labeled with a unique identifier and individually weighed before deployment. Plasters were attached to metal rods with a 5 x 5 cm piece of 19-gauge galvanized steel hardware cloth anchored to the rod with zip ties. The hex bolts in each plaster were threaded through the gauges in the hardware cloth and anchored using stainless steel washer and nuts. The plasters were inserted in the bank edge about 10 cm below the marsh edge for both steep and gradual sloping banks. Following a 14-day deployment during a period of extreme tides near the summer solstice, plasters were retrieved, disassembled and dried in the drying oven and reweighed. Percent loss of plaster was used as a proxy for tidal scour.

#### *Experimental test of algal wrack effects on low marsh edge*

Thirty 1 x 1 m plots were placed along a narrow (approximately 3 m wide), 70 m long berm, covered with a monoculture of pickleweed. This berm, which is at the lower end of marsh elevation in the estuary (about 1.3-1.5 m NAVD88, or 0-20 cm below Mean High Water), was considered an appropriate analogue to low natural marsh edges in the estuary. It is located in an area targeted for marsh restoration through sediment addition, and was chosen because marsh damage here would soon be reversed by sediment addition. The plots were located at the very edge of the marsh along the berm, spaced at least 50 cm apart, in areas of at least 80% cover by pickleweed. Each plot was surrounded by 20 wooden stakes (about 2.5 cm wide, protruding from the sediment about 60 cm) intended both to mark the plots and retain the wrack. Plots were randomly assigned to three treatments, wrack addition for 8 weeks or 12 weeks, or no wrack addition (control). The growing season for pickleweed is mainly May-October, treatments corresponding to about 40% vs. 60% of the growing season were chosen. Wrack addition begun in late May 2014 and ended in late July and late September, respectively for the 8 and 12 week treatments. Wrack was collected from different sites within Elkhorn Slough, where blooms were abundant near road access. Initially, approximately 1500 g *Ulva* spp. per m<sup>2</sup> (dry weight) were added to the wrack addition plots, which was at the upper end of the range observed in the field

monitoring, but lower than the maximum occurring in the estuary. Plots were surveyed 1-2 times per week. Drift wrack was removed from the no wrack addition plots, and supplemental wrack at a 2-3 cm thick layer (0-750g/m<sup>2</sup> dry weight) was added to wrack addition plots, where tidal forcing removed initially placed wrack. In late June in order to compensate for this effect, a mesh was placed over all plots, including the plots under the no cover treatment, to prevent wrack from leaving the plot. The mesh was placed over the stakes at a height greater than the highest pickleweed stalk of the plot. For the remainder of the 12 week experimental period, the mesh was retained on the all the plots, but temporarily removed as needed to replenish wrack. Control plots were visited with equal frequency and intensity as wrack plots, to ensure there was no difference in trampling.

### Citations

- Appleby, P.G., and F. Oldfield. 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210 Pb to the sediment. *Catena* **5**:1-8.
- Hornberger, M.I., S.N. Luoma, A. van Geen, C. Fuller, and R. Anima. 1999. Historical trends of metals in the sediments of San Francisco Bay, California. *Marine Chemistry*. **64**:39-55.
- Robbins, J.A., and D.N. Edgington. 1975. Determination of recent sedimentation rates in Lake Michigan using Pb-210 and Cs-137 *Geochimica et Cosmochimica Acta* **39**:285-304.

**Table S1. Historical aerial photographs used for GIS analysis.**

DATE	TYPE	RESOLUTION	ORIGIN
May 1931	panchromatic	0.63 m pixel <sup>-1</sup>	Western Gulf Oil Co./Fairchild Aerial Surveys, Inc.
November 1937	panchromatic	0.66 m pixel <sup>-1</sup>	U.S. Department of Agriculture/Fairchild Aerial Surveys, Inc.
August 1949	panchromatic	0.66 m pixel <sup>-1</sup>	U.S. Department of Agriculture/Park Aerial Surveys, Inc.
May-June 1956	panchromatic	0.6 m pixel <sup>-1</sup>	U.S. Department of Agriculture/Aero Service Corp.
May 1971	panchromatic	0.67 m pixel <sup>-1</sup>	U.S. Department of Agriculture/Western Aerial Contractors
April 1976	panchromatic	0.4 m pixel <sup>-1</sup>	California Department of Transportation
April 1980	color infrared	0.52 m pixel <sup>-1</sup>	California Coastal Commission/Western Aerial Photographs, Inc.
April 1987	color infrared	0.51 m pixel <sup>-1</sup>	Moss Landing Marine Labs/Western Aerial Photographs, Inc.
May 1992	color infrared	0.53 m pixel <sup>-1</sup>	Elkhorn Slough Foundation/Aerial Data Systems
May 2001	color infrared digital ortho	0.6 m pixel <sup>-1</sup>	County of Monterey/HJW GeoSpatial, Inc.
April 2003	true color digital	0.5 m pixel <sup>-1</sup>	California Department of Fish and Game Air Services
June 2005	color infrared digital ortho	1.0 m pixel <sup>-1</sup>	U.S. Department of Agriculture/National Agriculture Imagery Program
June 2009	color infrared digital ortho	1.0 m pixel <sup>-1</sup>	U.S. Department of Agriculture/National Agriculture Imagery Program
May 2012	color infrared digital ortho	1.0 m pixel <sup>-1</sup>	U.S. Department of Agriculture/National Agriculture Imagery Program
June 2014	color infrared digital ortho	1.0 m pixel <sup>-1</sup>	U.S. Department of Agriculture/National Agriculture Imagery Program

**Table S2.** Results from experimental test of algal wrack effects on low marsh edge, using ANOVA and Tukey-Kramer HSD tests to identify differences among “no wrack” and “wrack” treatments, in September 2014.

**(A) Pickleweed succulent biomass**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	5289.109	2	2644.55	7.3463	<b>0.0028</b>
	Error	9719.566	27	359.98		

(ii) Tukey's HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>12 weeks</b>	30.78	8.485	<b>0.0033</b>
<b>0 weeks</b>	<b>8 weeks</b>	24.49	8.485	<b>0.0201</b>
8 weeks	12 weeks	6.29	8.485	0.7414

**(B) Pickleweed percent cover**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	1989.9387	2	994.969	11.7498	<b>0.0002</b>
	Error	2286.356	27	84.68		

(ii) Tukey's HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	18.14	4.115	<b>0.0004</b>
<b>0 weeks</b>	<b>12 weeks</b>	6.26	4.115	<b>0.0014</b>
12 weeks	8 weeks	4.38	4.115	0.8918

**Table S2 (continued)**

**(C) Max. canopy height**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	1518.05	2	759.025	62.7437	<b>&lt;0.0001</b>
	Error	326.625	27	12.097		

(ii) Tukey's HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	17.30	1.555	<b>&lt;0.0001</b>
<b>0 weeks</b>	<b>12 weeks</b>	10.45	1.555	<b>&lt;0.0001</b>
<b>8 weeks</b>	<b>12 weeks</b>	6.85	1.555	<b>0.0004</b>

**(D) Vegetation retreat rate**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	2672.862	2	1336.43	5.8476	<b>0.0078</b>
	Error	6170.661	27	228.54		

(ii) Tukey's HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>8 weeks</b>	<b>0 weeks</b>	20.43	6.761	<b>0.0146</b>
<b>12 weeks</b>	<b>0 weeks</b>	19.59	6.761	<b>0.0195</b>
8 weeks	12 weeks	0.84	6.761	0.9915

**Table S3.** Results from experimental test of algal wrack effects on low marsh edge, using ANOVA and Tukey-Kramer HSD tests to identify differences among “no wrack” and “wrack” treatments, in September 2015.

**Pickleweed succulent biomass**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	3248.478	2	1624.24	4.6125	<b>0.0189</b>
	Error	9507.725	27	352.14		

(ii) Tukey-Kramer HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	24.84	8.392	<b>0.0169</b>
0 weeks	12 weeks	17.37	8.392	0.1152
12 weeks	8 weeks	7.47	8.392	0.6510

**Pickleweed percent cover**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	446.689	2	223.344	4.4497	<b>0.0214</b>
	Error	1355.201	27	50.193		

(ii) Tukey-Kramer HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	9.39	3.168	<b>0.0167</b>
<b>0 weeks</b>	<b>12 weeks</b>	5.63	3.168	0.1963
12 weeks	8 weeks	3.76	3.168	0.4711

**Table S3 (continued)**

**Max. canopy height**

(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	632.217	2	316.108	9.2847	<b>0.0009</b>
	Error	919.250	27	34.046		

(ii) Tukey-Kramer HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	10.65	2.609	<b>0.0010</b>
<b>0 weeks</b>	<b>12 weeks</b>	8.45	2.609	<b>0.0086</b>
12 weeks	8 weeks	2.20	2.609	0.6800

**Seaward pickleweed boundary**

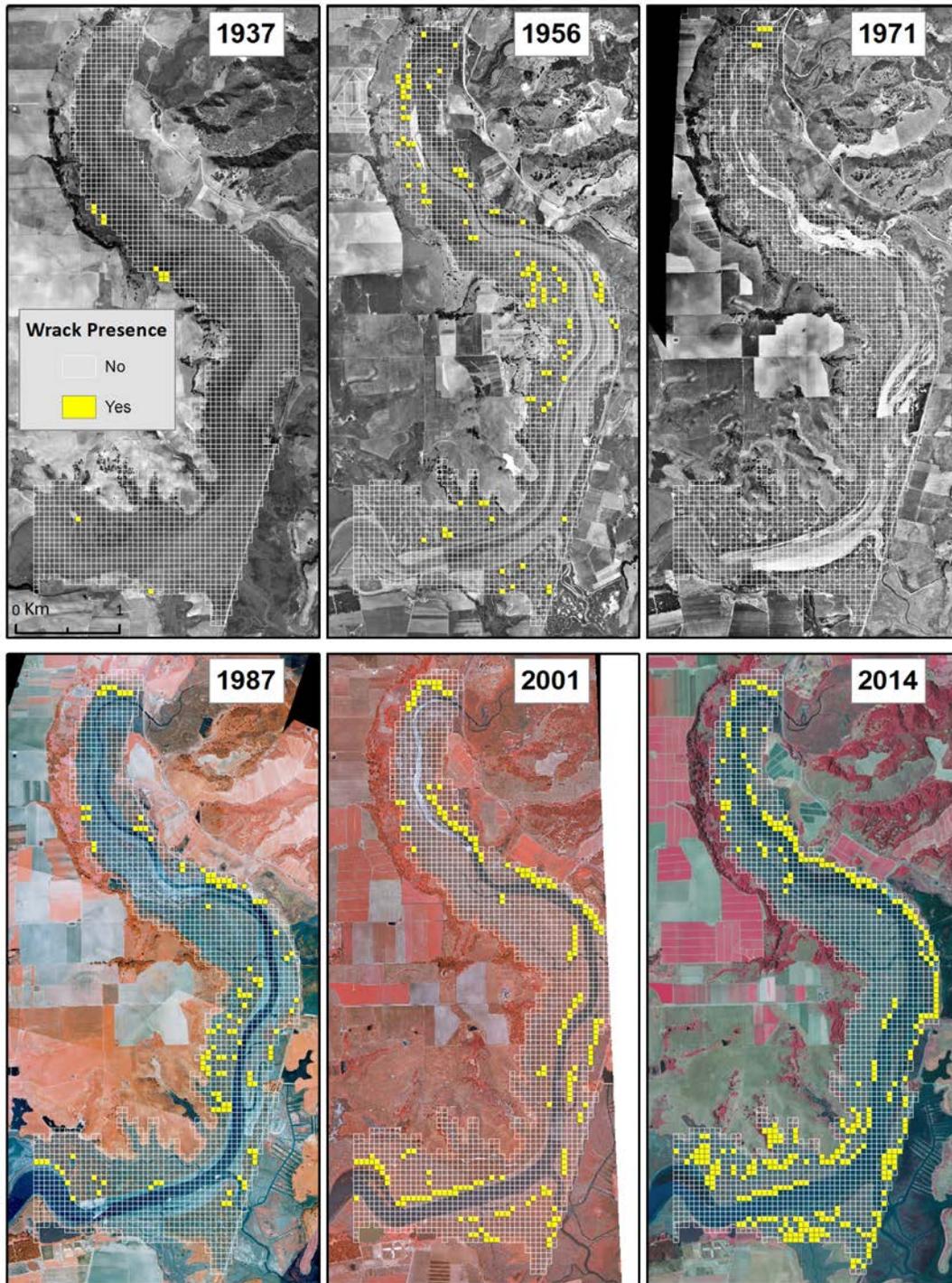
(i) Full randomized ANOVA test between all treatments

<i>Source</i>		<i>SS</i>	<i>df</i>	<i>Mean Square</i>	<i>F</i>	<i>P</i>
Treatment	<b>Hypothesis</b>	13968.40	2	6984.20	14.3702	<b>&lt;0.0001</b>
	Error	13122.54	27	486.02		

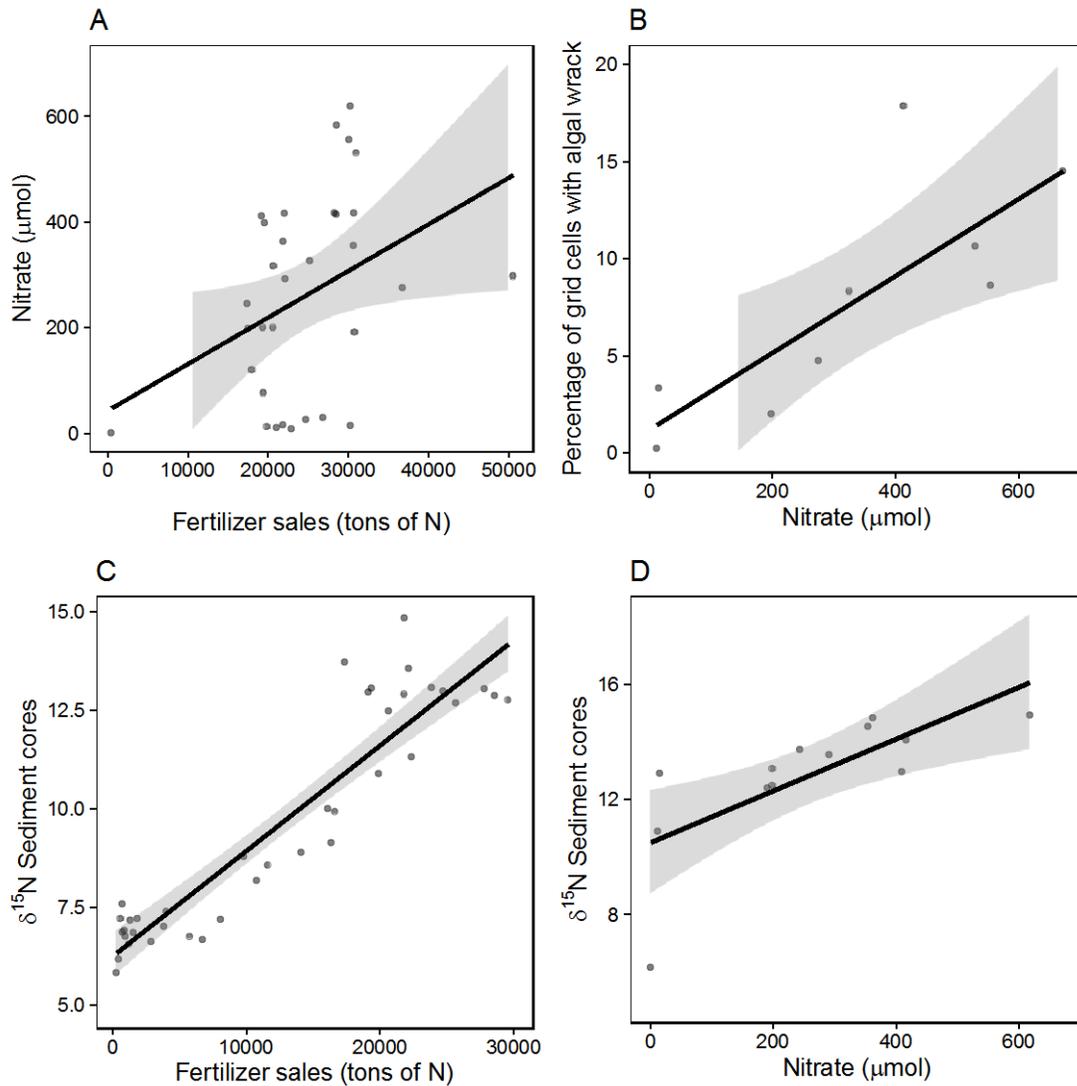
(ii) Tukey-Kramer HSD multiple comparison test among treatments

<i>Treatment 1</i>	<i>Treatment 2</i>	<i>Mean Difference (1-2)</i>	<i>Std. Error</i>	<i>P</i>
<b>0 weeks</b>	<b>8 weeks</b>	48.84	9.859	<b>&lt;0.0001</b>
<b>0 weeks</b>	<b>12 weeks</b>	41.92	9.859	<b>0.0006</b>
12 weeks	8 weeks	6.92	9.859	0.7644

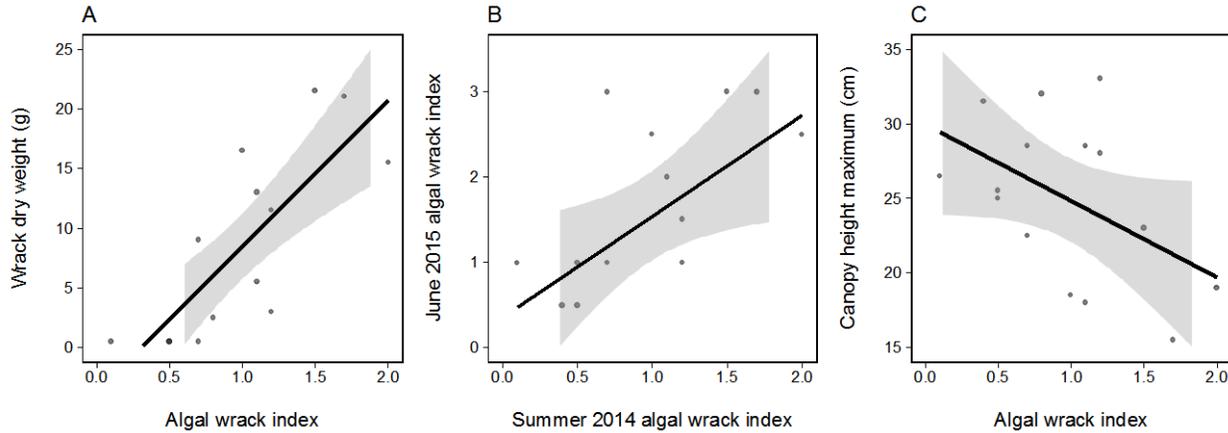
**Figure S1. Increase in algal wrack over time.** The results of GIS analysis of six of the fifteen aerial photos are presented, showing an increase in the number of grid cells with algal wrack present over time.



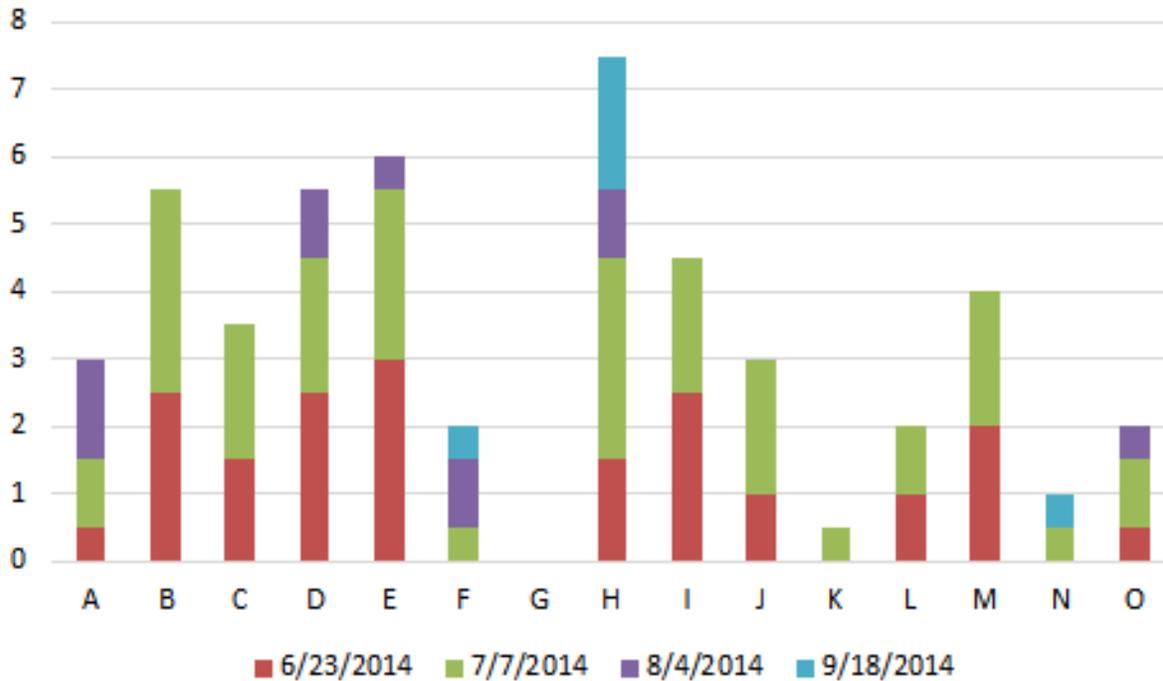
**Figure S2. Correlations of fertilizer, nitrates, nitrogen isotopes and wrack.** A: Relationship between fertilizer sales in Monterey County and nitrate concentrations in Elkhorn Slough. B: Relationship between nitrate concentrations and percent of GIS grid cells with algal wrack. C-D: Relationship between  $\delta^{15}\text{N}$  values (‰) from Harbor site core with C: Fertilizer sales and D: water column nitrate. Black lines are the modeled trends and grey areas represent 95% confidence interval.



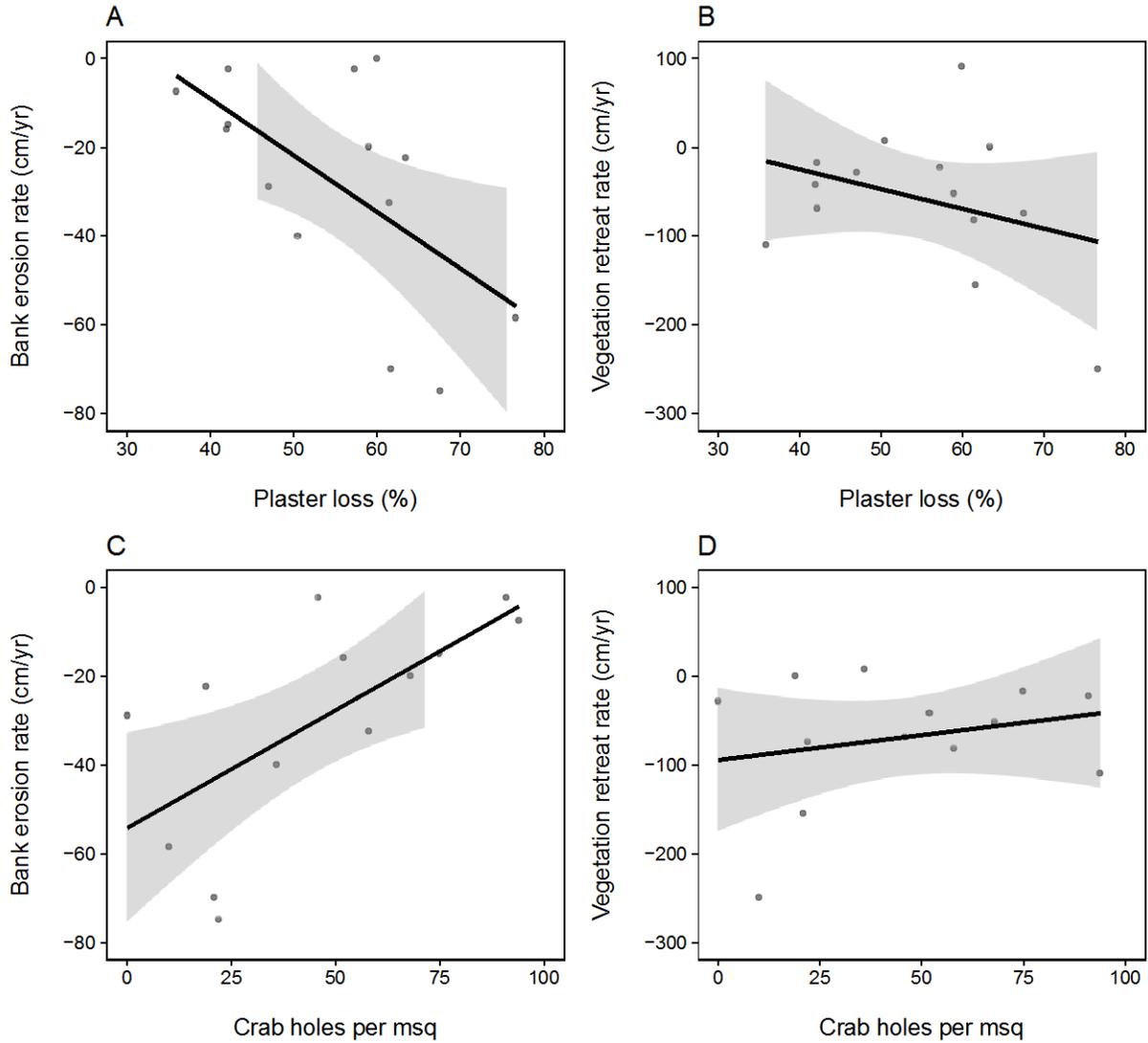
**Figure S3. Correlations with algal wrack index.** The wrack index was averaged across June-September 2014 sampling dates for all 15 stations. A significant correlation was obtained with A: dry weight of wrack harvested from the plots in June 2014 and B: algal wrack index for June 2015. C: The correlation between the wrack index and maximum pickleweed canopy height of marsh was marginally significant. Black lines are the modeled trends and grey areas represent 95% confidence interval.



**Figure S4. Contrasts among sites in algal wrack deposition patterns.** The 15 sites are lettered A-O (see Figure 3). The stacked bars represent the extent of algal wrack (scored with index 1-3) at different sampling dates June-September 2014.



**Figure S5. Correlations with vegetation retreat and bank erosion.** A and B: Correlations between plaster loss rate (a proxy for physical erosion forcing) and bank erosion rate and vegetation retreat rate, respectively. C and D: Correlations between crab holes and bank erosion and vegetation retreat, respectively. A and C were significant; B was non-significant; C was marginally significant. Black lines are the modeled trends and grey areas represent 95% confidence interval.



**Figure S6. Time series of marsh response to experimental manipulations.** First column: biomass, second column: percent succulent cover, third column: maximum canopy height, fourth column: seaward pickleweed boundary relative to markers (negative numbers indicate inland movement). Lower case letters denote significant differences ( $P < 0.05$ ) (Table S3) among treatments. Error bars represent standard error of the mean.

