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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 $\delta^{15}N$ 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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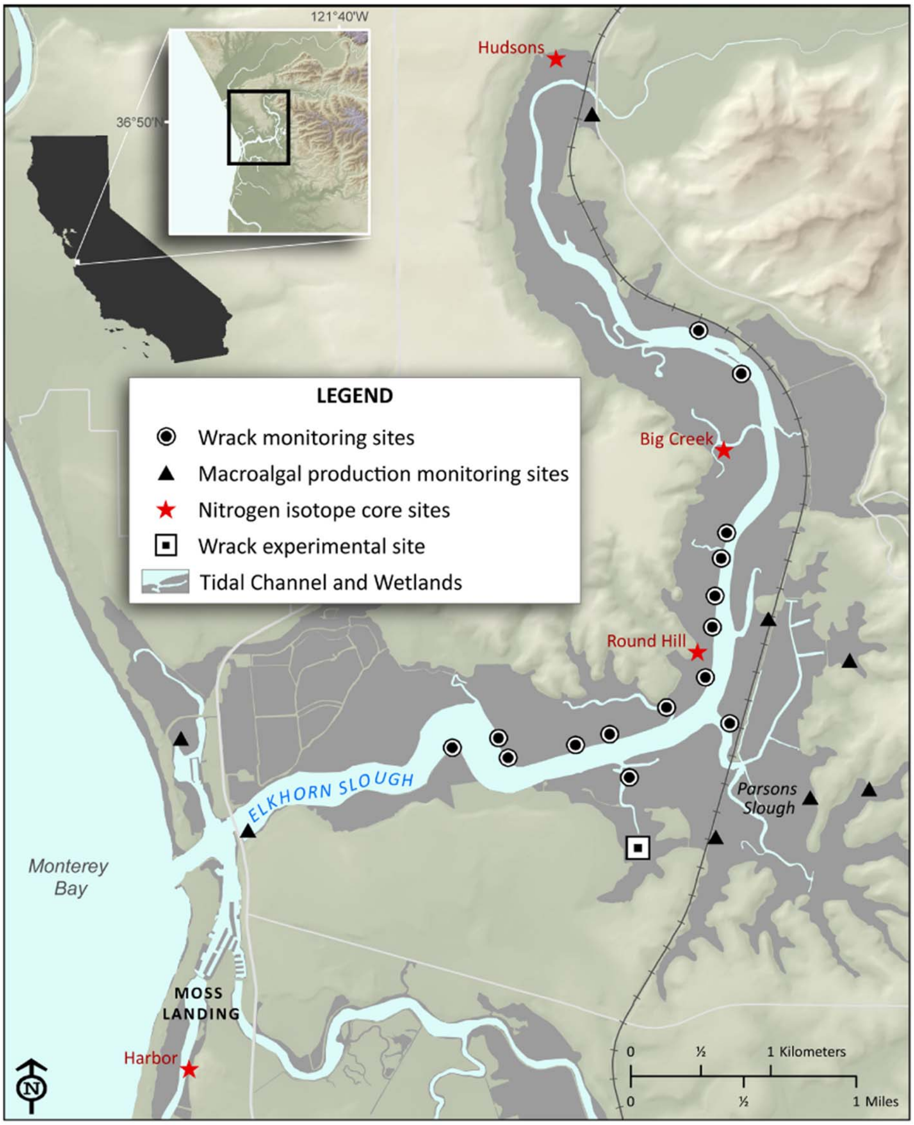

Fig. 1. Study sites. The wrack monitoring sites were used for the observational study of wrack deposition and effects on marsh in 2014–5. The macroalgal production monitoring sites are the mudflat plots monitored for algal production 2009–2016. The wrack experimental site indicates the location of the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