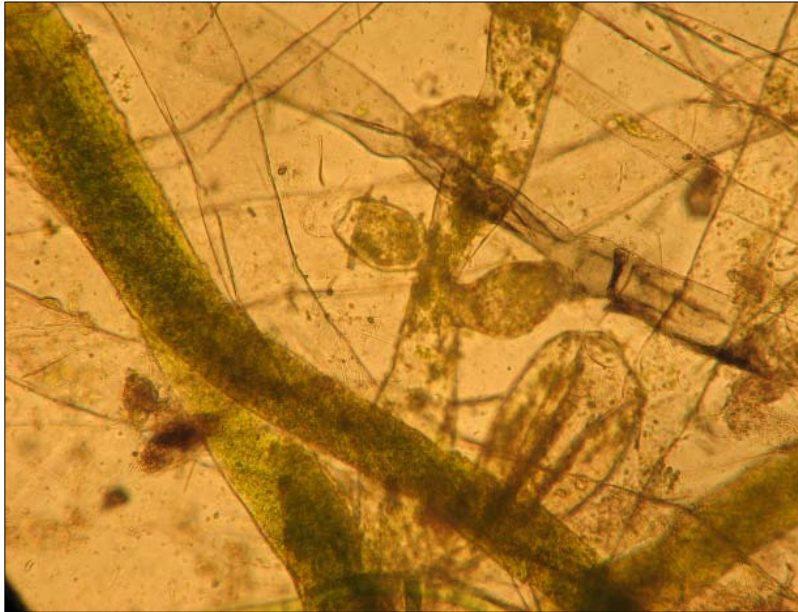


Algal response to removal of the invasive cordgrass *Spartina densiflora* in a salt marsh at Humboldt Bay, CA



Simona Augytė
Department of Ecology and Evolutionary Biology
University of Connecticut
and
Andrea Pickart
U.S. Fish and Wildlife Service

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6800 Lanphere Rd.
Arcata, CA 95521
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Abstract

There are few published studies examining the effects of invasive vascular plants on co-occurring non-vascular species, despite the fact photoautotrophic algae and cyanobacteria exist at the base of the marine food web. This study tested whether the removal of the invasive dense-flowered cordgrass (*Spartina densiflora*) resulted in an increase in biomass of micro- and macroalgae in a salt marsh located in northern California. The site was sampled over a two-year time period, and percent cover of benthic algae was measured using a point-intercept technique in treated and control areas. Treatment consisted of mechanical removal of *S. densiflora*. The functional groups green filamentous and green sheet algae as well as diatoms and cyanobacteria were found. Growth peaks in algal biomass were significantly lower in the control compared to the treated areas. In addition, successional trends were observed in treated plots. These results suggest that the presence of *S. densiflora* lowered both algal biomass and functional group diversity in an invaded salt marsh, with implications for resulting trophic cascades.

Introduction and Purpose

Dense-flowered cordgrass (*Spartina densiflora*) was first introduced into Humboldt Bay in the mid-1800s and has spread and invaded over 90% of the Bay's salt marsh habitat (Pickart 2001). It has been documented to displace native vascular plant species through competition (Fenkel & Boss 1988, Kittelson & Boyd 1997). Recent work in Humboldt Bay salt marshes showed that *S. densiflora*-invaded sites had lower diversity and abundance of terrestrial invertebrates compared to restored sites (Mitchell 2012). A *Spartina* canopy can shade out ephemeral algal species (Van Raalt et al. 1976), thereby favoring grazers that feed on cordgrass detritus instead of algal biomass. Lagarde (2012) showed that native salt marsh had greater net ecosystem productivity despite its lower above-ground biomass, compared to *S. densiflora*-dominated marsh at a site in Humboldt Bay. Since 2004, restoration efforts have been carried out at Humboldt Bay National Wildlife Refuge (HBNWR) to remove *S. densiflora* using mechanical methods (Pickart 2012).

Plants are essential components in coastal wetlands as they regulate important processes such as nutrient cycling, sedimentation rates, and hydrology (Bertness 1988, Leonard & Luther 1995). Non-vascular plants (micro- and macroalgae) and cyanobacteria are important primary producers, and provide food sources for invertebrates and fish, and in turn are largely controlled by these grazers and their predators in complex trophic cascades (Sullivan & Moncreiff 1990, Silliman & Bertness 2002). Other studies conducted in Pacific Coast estuaries show considerable changes in plant species composition and broader-scale alterations of salt marsh ecosystem processes after the invasion of *Spartina alterniflora* (Grosholz et al. 2009). For example, in San Francisco Bay, the invasive *Spartina* hybrid has shifted the wetland food-web from algal-based to detritus-based, thereby altering the amount of biomass as well as the types of invertebrates present in the Bay (Levin et al. 2006).

In addition to providing primary productivity, cyanobacteria may be early colonizers of bare mud in salt marshes and important contributors of nitrogen to salt marshes (Carpenter et al. 1978), thereby contributing to colonization by successive higher plants (Jones 1974). Other salt-tolerant marine algae provide 'habitat-amelioration' in physically and biologically stressed environments where they have been shown to facilitate colonization of vascular plants in salt marshes and seagrasses in sandy habitats with low substrate nutrient and high light levels (Bertness & Callaway 1994). Reports of algae in East Coast marshes have documented both cyanobacteria and green filamentous algae (e.g. *Rhizoclonium* Kützing) as early successional spring species (Blum 1968).

Light intensity is one of the main factors that governs the composition of micro- and macroalgae in salt marsh communities (Sullivan and Daiber 1976). However, an excess amount of light from the removal of canopy cover in a California salt marsh produced marsh soils with harsher physical properties and shifted the microalgal community to become diatom-dominant (Whitcraft & Levin 2007). Furthermore, vascular plants can affect the quality and quantity of light that reaches the soil surface and thus control the amount of biomass and the timing of edaphic algal growth (Seliskar et al. 2002). A study in a salt marsh in Massachusetts showed that increases in light penetration with the removal of *Spartina* were directly correlated to an immediate increase in the growth of benthic algae on the marsh surface followed by its consumption by marsh animals (Buchsbaum et al. 2009).

The main objective of this study was to test whether the removal of the invasive dense-flowering cordgrass (*S. densiflora*) would lead to an increase in diversity and biomass of micro-

and macroalgae and in the salt marsh. In addition, we wanted to assess changes in functional group dominance over time in treated compared with control areas. Results could help elucidate the impacts of *S. densiflora* removal on the base of the food-web, with implications for higher trophic levels -- specifically fish, birds, and small mammals.

Methods

Sampling was conducted in four permanent experimental treatment areas (15m x 15m) at Humboldt Bay National Wildlife Refuge (HBNWR), CA (Fig. 1) from September 2008 through August 2010. The treatment areas were part of a larger study that assessed the effectiveness of mechanical removal treatments on *S. densiflora* eradication (Pickart 2012). Treatment areas were similar in their topography, tidal elevation and soil type, and were located so that replicated treatment areas were stratified into moderate (<60%) and high (>60%) *Spartina* cover. Treatment consisted of the use of a hand-held metal-bladed brushcutter to mow all *S. densiflora*, followed by shallow subsurface “grinding” of rhizomes. Mowed *S. densiflora* was subsequently raked and removed. This resulted in the removal of all *S. densiflora* canopy, as well as the exposure of bare muddy substrate in those areas where *S. densiflora* had been present. Brushcutting was performed in August 2008.

In each 15m x 15m treatment area, a total of 5 transects were placed using systematic spacing with a random start. A 30 cm x 30 cm quadrat was placed at six randomly selected, permanent sample points along each 15-m transect. Using a gridded quadrat, thirty randomly selected points were used to measure percent cover based on point intercepts of each algal functional group in the quadrat. Sampling was conducted during the low tide at 14 time intervals over two years.

Algae were placed into one of four functional groups based on morphology; green filamentous, green sheet, diatoms, and cyanobacteria. Any unknown algae were identified at the Humboldt State University Cryptogamic Herbarium laboratory using microscopy and dichotomous keys (Gabrielson et al. 2004, Gabrielson et al. 2006). Data analysis was done with R statistical software.

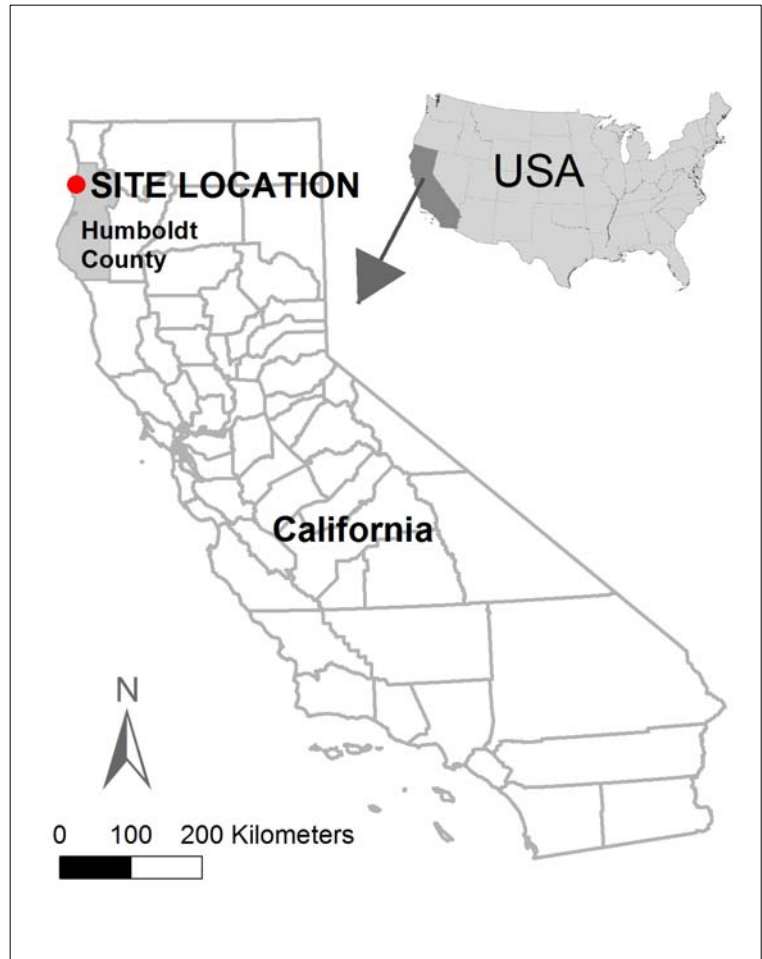


Figure 1. Study site location, Humboldt County, CA.

Results

Change in algal abundance over time

The total algal cover in the salt marsh displayed seasonal peaks around April and May for both years in both the control and treatment areas (Fig. 2). A two-way general linear model revealed that there was a significant difference in the mean algal cover in the treated vs. control areas over time ($p < 0.001$). In the spring of 2009, mean total algal cover peaked at 9% in control and 17% in treated areas (Fig. 3). By summer, total cover declined to 7% for the control and 5% for the treated areas. The following spring of 2010, total algal cover peaked at 18% in control and 32% in treated areas, declining to 4% in control and 16% in treated areas by summer. A strong correlation was found between the individual time steps and total algal cover for the mechanical treatment ($r^2=0.338$, $p=0.0172$) compared with the control ($r^2= 0.049$, $p=0.545$).

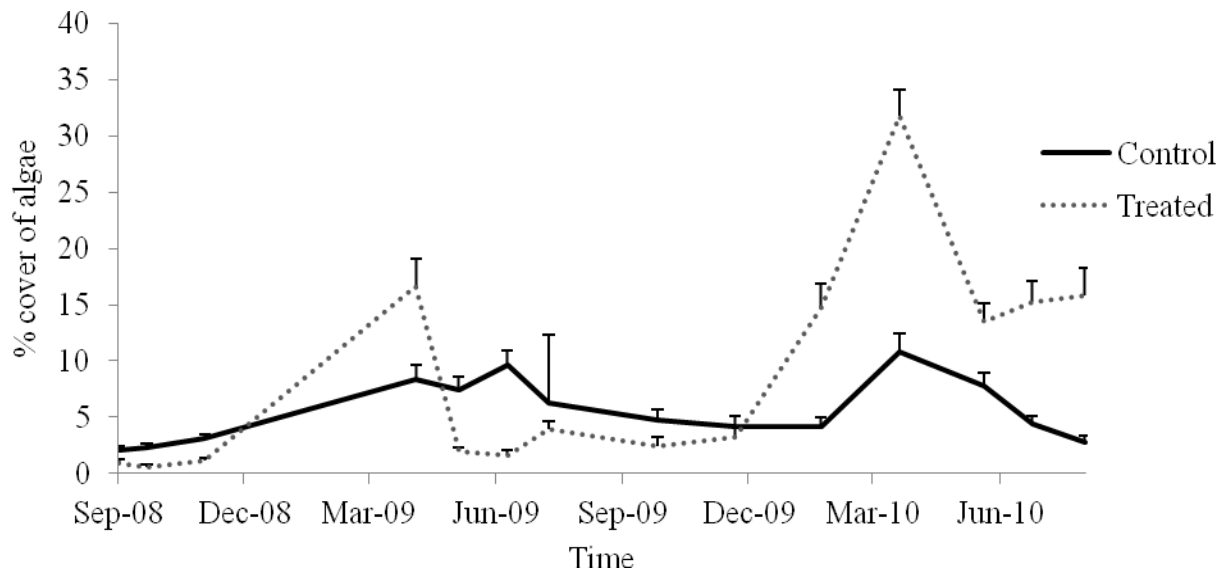


Figure 2. Mean percent total algal cover for the control and treated areas over a two year time period (2008-2010). Standard error bars are included.

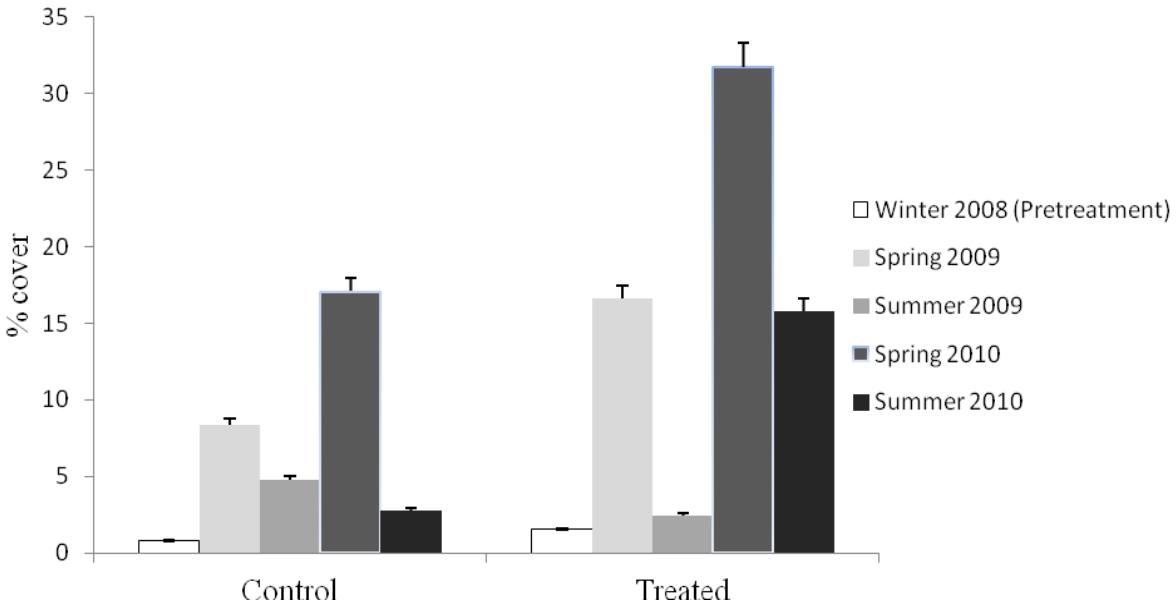


Figure 3. Changes in mean total algal cover over two years (2008-2010) in control and treated areas. Standard error bars are included.

Successional trends

In the control areas, most of the algal cover was formed by the green filamentous group in both years. The seasonal peaks were in April for the first year and June for the second year, of 10% and 11% cover, respectively (Fig. 4a). The rest of the year, algal cover ranged from 2-4% cover. In the treated areas, green filamentous algae and diatoms reached their first seasonal peak in April at 10% and 8% cover respectively, after which they rapidly decreased in abundance to less than 1% (Fig. 4b). During the first winter, diatoms increased to 2% but over the next year decreased to less than 1%. The second year peak for the filamentous algae was in March at 32% cover. Cyanobacteria were not present until November of the second year at 1% cover followed by a gradual increase to 13% in August.

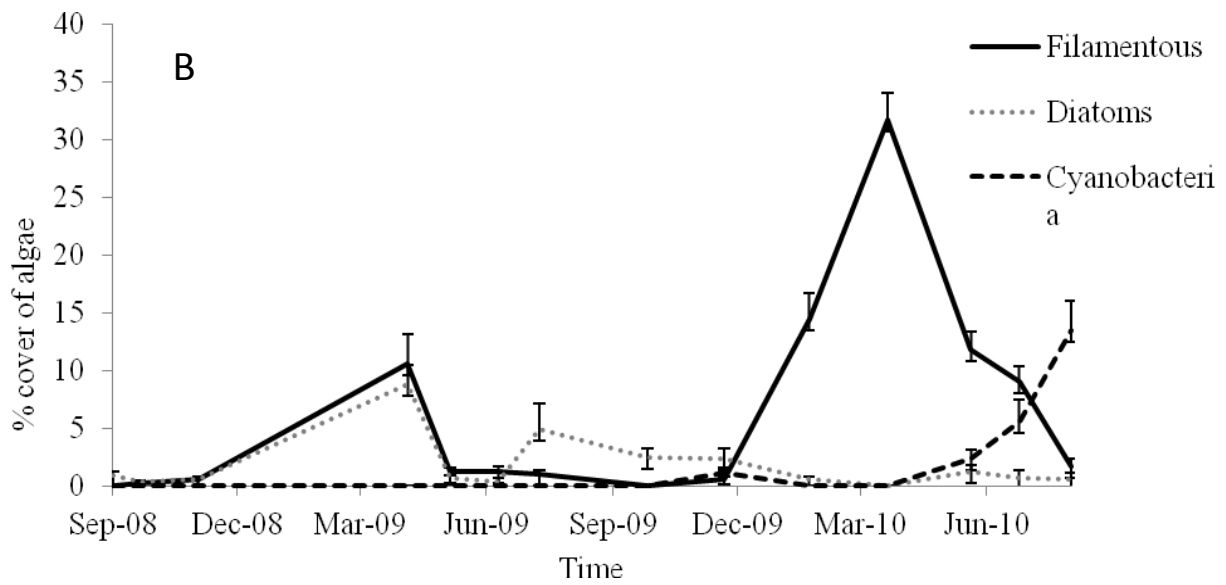
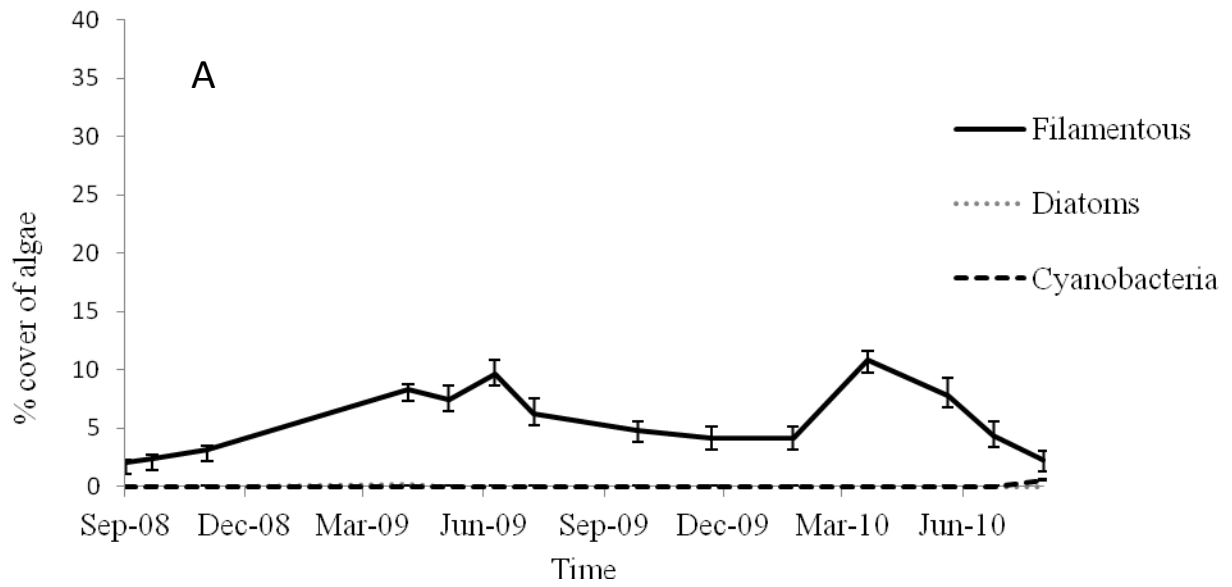


Figure 4. Total percent cover of algae based on three functional groups; diatoms, green filamentous, and cyanobacteria over time for the control (a) and treated (b) areas. Standard error bars are included.

Algal species composition

All the macroalgae found were in the phylum Chlorophyta. The green filamentous group consisted of four algal species: *Cladophora columbiana* F.S. Collins, *Rhizoclonium riparium* (Roth) Harvey, *Chaetomorpha linum* (O.F. Müller) Kützing, *Vaucheria longicaulis* Hoppaugh (Figs. 5 - 8). Only one taxon (*Ulva* sp. Linnaeus) was present in the green sheet group (Fig. 9). Cyanobacteria (Fig. 10) and diatoms (Fig. 11) were not identified to the species level.

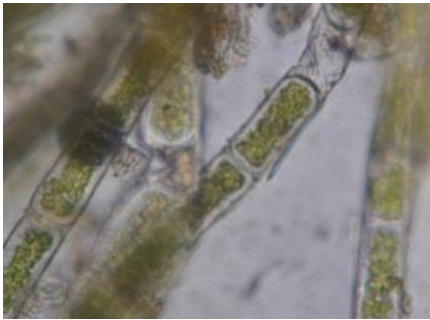


Figure 5. *Rhizoclonium riparium*.
Photos by Simona Augytė.

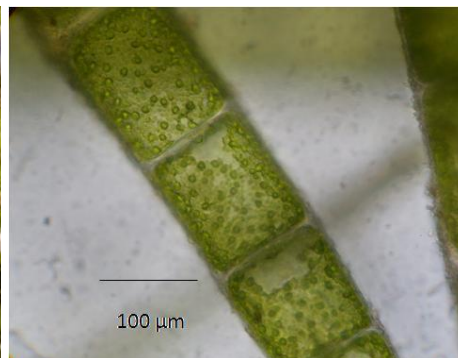


Figure 6. *Chaetomorpha linum*.
Photos by Simona Augytė.

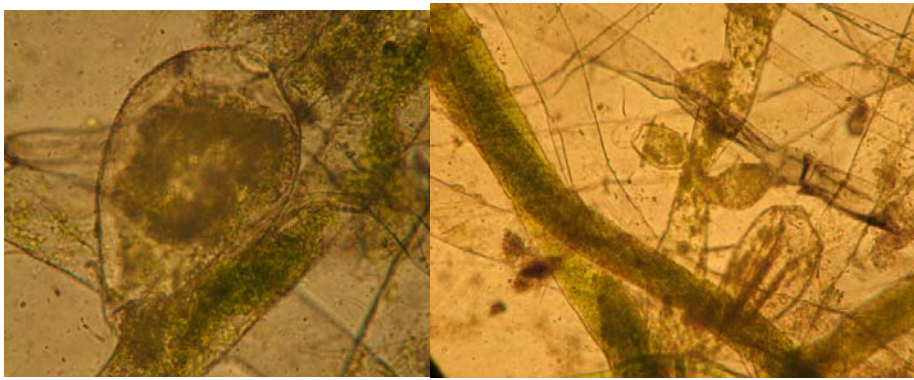


Figure 7. *Vaucheria longicaulis* in the field and under a scope showing reproductive features.
Photos by Simona Augytė.



Figure 8. *Cladophora columbiana*.



Figure 9. *Ulva* sp. Photos by Simona Augytė.

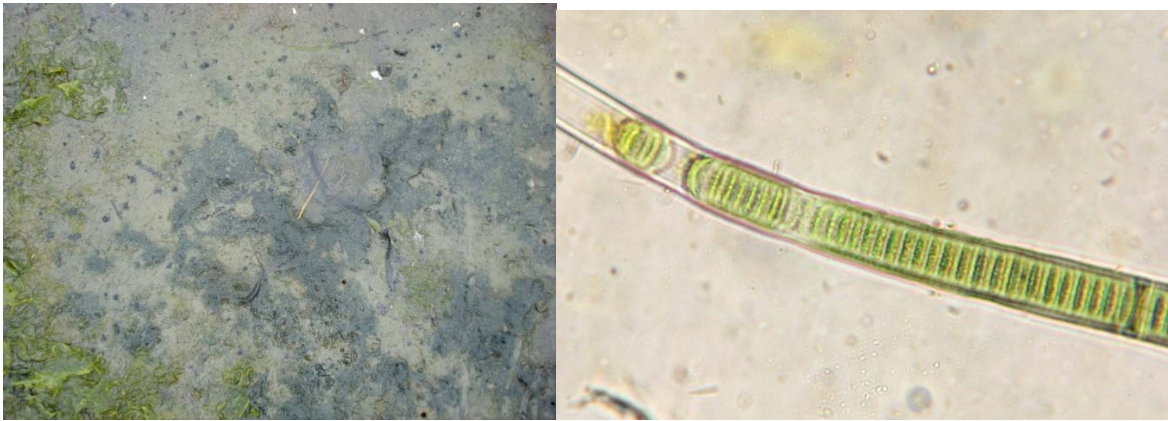


Figure 10. Cyanobacterial mats and magnified using a microscope. Photos by Simona Augytė.

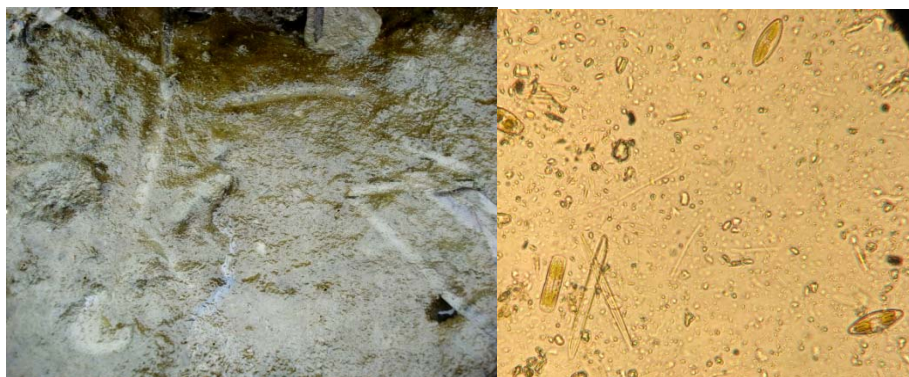


Figure 11. Diatoms in the field and magnified using a microscope. Photos by Simona Augytė.

Discussion

This study suggests that invasive *S. densiflora* lowered the abundance and diversity of algae and suppressed cyanobacteria at a northern California salt marsh. Removal of *S. densiflora* using mechanical methods resulted in an increase in total algal abundance and functional group diversity by the end of the second sampling year. The increase in light penetration is a likely cause of algal response in this experiment. A study in a southern California wetland found that the net primary productivity of both macro- and microalgae was limited by low light and desiccation stress (Zedler 1980). The green filamentous algae, diatoms, and cyanobacteria functional groups were more abundant in the treated than in the control area; these are species heavily dependent on light for establishment and growth.

Furthermore, this experiment suggests that there are successional trends in algal functional groups following *S. densiflora* removal, indicated by shifts in dominance over time. Early successional algae are fast to accumulate during the first stages of community development and tend to have high immigration abilities compared to late successional species that have high reproductive rates and are fast to accumulate when population densities are large (McCormick & Stevenson 1991). Both filamentous algae and diatoms appear to be early successional species, decreasing in abundance after their first spring peak, possibly due to grazing pressures. Diatoms remained low in abundance the second year and disappeared by the end of the second year. Cyanobacteria appear to be late successional, colonizing in large densities only late in the summer of the second year.

Coastal wetlands provide important habitat for fishes, shellfish and shorebirds and are particularly sensitive to introductions of non-native vegetation (Posey 1988, Daehler & Strong 1996). Invasive *Spartina* forms dense, monospecific stands that eliminate open mudflats, thus decreasing plant and animal biomass and diversity. The aggressive *Spartina* competes for space with native salt marsh vascular and non-vascular plants and may result in a shift in the invertebrate community composition from species that feed on algae to detritivores (Levin et al. 2006). These changes have already been observed in San Francisco Bay, California and Willapa Bay, Washington (Buchanan 2003). It is, therefore, reasonable to suggest that similar mechanisms operate in the Humboldt Bay salt marshes and our results illustrate how the removal of *S. densiflora* can lead to significant increases in the abundance and diversity of macro- and microalgae. These findings further suggest that the *S. densiflora* invasion has a negative effect on the growth and productivity of salt marsh algae and potentially the invertebrate communities that rely on algae as their principal food source.

Acknowledgments

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