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Effect of native and invasive cordgrass on *Macoma petalum* density, growth, and isotopic signatures

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Abstract

Ecosystem engineers can influence community and ecosystem dynamics by controlling resources, modifying the flow of energy or biomass, or changing physical characteristics of the habitat. Invasive hybrid cordgrass (*Spartina alterniflora* × *Spartina foliosa*) is an ecosystem engineer in salt marshes in San Francisco Bay, California, U.S.A. that raises intertidal elevations and may be either increasing C_4 plant carbon input into food webs or tying up carbon in a form that is not usable by consumers. A manipulative experiment compared abundance, growth, and stable isotope (δ^{13}C and δ^{15}N) composition of the clam *Macoma petalum* (=*M. balthica*) among native marsh, hybrid *Spartina*, and mudflats in central San Francisco Bay. We found higher densities (individuals m^{-2}) of *M. petalum* on mudflats compared to either native or hybrid *Spartina* ($p < 0.001$). *Macoma petalum* shell growth was significantly greater in mudflats than in either vegetation type in 2002 ($p = 0.005$) but not 2003. Differences in shell growth between native and hybrid *Spartina* were not significant. Stable isotope results showed differences between habitats in δ^{13}C but not δ^{15}N. Carbon signatures of *M. petalum* placed in *Spartina* were much more depleted than the isotopic signature of *Spartina*. Neither native nor hybrid *Spartina* appears to be a significant carbon source for *M. petalum* in San Francisco Bay, and we found no evidence that hybrid *Spartina* contributes carbon to *M. petalum* beyond what is provided by *S. foliosa*, despite the hybrid's much greater biomass. Our results show that loss of mudflat habitat, rather than increased input of C_4 carbon, is the greatest effect of the invasion of hybrid *Spartina* on *M. petalum*.

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1. Introduction

Although many habitats are being rapidly altered by invasive plants, we know comparatively little about the impacts of invasive plants in estuarine systems (Posey, 1988; Wainwright et al., 2000; Larned, 2003). Estuarine plants act as ecosystem engineers (sensu Jones et al., 1994) by providing habitat complexity aboveground and below, by stabilizing and oxygenating sediments (Ellison and Farnsworth, 2001; Williams and Heck, 2001), and by modifying water flow (Shi et al., 2000). Ecosystem engineers can control resources, including space, modify the flow of energy or biomass, or change physical characteristics of the habitat (Crooks and Khim, 1999; Crooks, 2002). Because of these effects, ecosystem engineers may influence the diversity and richness of organisms living in or around them (Crooks and Khim, 1999). The introduction of a non-indigenous ecosystem engineer into a new community may change habitat availability, nutrient cycling, productivity, hydrology, or other characteristics of the native system (Crooks, 2002). In a terrestrial example, annual grasses introduced into perennial grasslands in the western United States displace native species, change soil mineral content, and alter fire regimes (Bossard et al., 2000).

Our study examined the effects of two closely-related ecosystem engineers, native California cordgrass (*Spartina foliosa*) and invasive hybrid cordgrass (*Spartina alterniflora* × *S. foliosa*, hereafter hybrid *Spartina*) on a common benthic

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species, *Macoma petalum*. *Spartina* replaces mudflats or native vegetation with dense grass where it successfully invades, affecting available habitat for vertebrate (Goss-Custard and Moser, 1988) and invertebrate organisms (Hedge and Kriworken, 2000; Neira et al., 2005; Brusati and Grosholz, 2006). Hybrid *Spartina* in San Francisco Bay resulted from interbreeding between native California cordgrass (*S. foliosa*) and introduced *S. alterniflora* from the Atlantic coast of the United States (Daehler and Strong, 1996). Hybrid *Spartina* produces greater aboveground and belowground biomass, and stems with a higher C:N ratio (Brusati, 2004) than *S. foliosa*, possibly increasing the amount of C_4 plant material available to enter the estuarine food web.

This study examined the effects of native *Spartina foliosa*, hybrid *Spartina*, and mudflat habitat on abundance, growth, and stable isotope signatures of *Macoma petalum* (Bivalvia: Tellinidae) in San Francisco Bay. *Macoma petalum* is itself an introduced species and is much more common than most native bivalves. We chose itas our study organism because it occurs in both vegetated and unvegetated habitats (Brusati, 2004) and can serve as a proxy for the less-abundant native bivalves that live in this habitats. *Macoma petalum* can use both detritus and siphon feeding (Poulton et al., 2004). *Macoma petalum* populations in San Francisco Bay are genetically identical to *Macoma balthica* (J. Geller, unpub. data), a circum-Arctic species that lives in intertidal and subtidal habitats (Nichols and Thompson, 1982). San Francisco Bay is near the southern limit of the species' range (Nichols and Thompson, 1982).

We hypothesized that much greater differences in detritus availability and habitat structure created by hybrid *Spartina* relative to *Spartina foliosa* would cause differences in density, growth, and carbon source (reflected in stable isotope composition) of *Macoma petalum*. The hybrid produces up to six times more aboveground biomass than the native *S. foliosa* (Brusati, 2004; Grosholz et al., in press). Therefore, we would expect that if the hybrid is entering the food web, a much stronger *Spartina* signal would be reflected in the isotopic composition of the clams living within the hybrid compared to those in *S. foliosa* or on mudflats.

2. Study area

The study site was San Lorenzo marsh (37°40.22′N 122°09.70′W) in central San Francisco Bay. At this site, some hybrid *Spartina* clones are overgrowing *Spartina foliosa* while others are on mudflats ≥10 m from other vegetation (species identity confirmed by genetic analysis, D. Ayres, pers. comm.).

3. Methods

To compare clam densities among mudflat, *Spartina foliosa*, and hybrid *Spartina* areas, we ran four 50 m transects, two each through mudflats and vegetation, in Jan, June, Aug, and Dec 2002. Due to interspersion of native and hybrid *Spartina*, vegetation transects intersected both *Spartina* species and quadrats were unequally divided between them; the plant species was noted for each quadrat. Bivalves were counted at ten random points along each transect using a core 10 cm diameter × 5 cm deep washed through a 2 mm sieve. Different points were chosen each time with a random number generator. Transect count data were log + 1 transformed and compared among dates and habitats (hybrid *Spartina*, *S. foliosa*, mudflat) using Systat 9.0 (SPSS, 1998).

We examined *Macoma petalum* shell growth with a field enclosure experiment. *Macoma petalum* were collected from mudflats adjacent to the marsh, then immersed in a buffered seawater solution of calcein (250 mg L^{-1}) in the laboratory for 24 h (Kaehler and McQuaid, 1999). Clams were returned to the marsh and placed in 15 cm × 15 cm × 7 cm deep plastic containers filled with ambient sediment and covered with 1 mm mesh; sediment was sieved in 2003, but not 2002. Each replicate consisted of one container in *Spartina foliosa* or hybrid *Spartina* paired with another placed ∼5 m away on the mudflat, and each container held 8 clams (0.5–1.5 cm wide). In 2002, three *S. foliosa* and three hybrid *Spartina* replicates were placed in the field in May and June, and removed at 97 and 104 days, respectively. In 2003, clams were placed at 10 hybrid and 10 *S. foliosa* replicates in April and removed at 109 days, with 5 clams container^{-1}. Due to differences in caging methods, comparisons cannot be made between years. There was significant overlap in tidal range between mudflat, *S. foliosa*, and hybrid areas. The range of elevation in mudflats, although on average less than that of vegetated plots, overlapped with both *S. foliosa* and hybrid *Spartina* (Neira et al., 2005).

To measure growth, we photographed shells using a digital camera attached to a microscope with a fluorescent filter. The growing edge at the time of immersion in calcein fluoresces brightly, while new growth appears as a darker band on the shell's edge. Shell measurements were taken at three points on the edge of the right valve using Metamorph 4.5 (Universal Imaging Corp., 2000) and a mean growth per clam was calculated. We then used these data to estimate mean growth per container. Growth data were square-root transformed and tested for homoscedasticity with Cochran's *C* test. We compared growth in *Spartina foliosa* or hybrid *Spartina* containers to their paired mudflat containers using paired *t*-tests.

In 2003, we used stable isotopes of carbon and nitrogen from clams in the growth experiment to determine how these signatures of *Macoma petalum* changed between mudflat, *Spartina foliosa* or hybrid *Spartina* areas. The ratio of ^{13}C:^{12}C ($\delta^{13}C$) typically increases ∼1 ‰ from primary producer to consumers and can distinguish between different food sources such as C_4 plants (including *Spartina*), C_3 plants, and phytoplankton, while the ratio of ^{15}N:^{14}N ($\delta^{15}N$) increases ∼3 ‰ with each trophic level (Peterson, 1999).

We predicted that if hybrid *Spartina* detritus was entering the food web and being used by *Macoma petalum*, and assuming other carbon sources are equal among habitats, then clams from hybrid *Spartina* would be enriched in $\delta^{13}C$ and more similar to *Spartina* than clams from mudflats or *Spartina foliosa*. We did not attempt to determine the exact combination

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