

Effects of a Non-Native Crab on the Restoration of Cordgrass in San Francisco Bay [Ⓐ]

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ABSTRACT

Invasive species are known to alter the progress of ecological restoration, but effects of invasive consumers, and particularly those that can act through both trophic and physical disturbance mechanisms, remain poorly understood. Due to its impacts on vegetation and ability to alter marsh food webs, we predicted that a non-native crab, *Carcinus maenas* (European green crab), would negatively affect restoration plantings of a native cordgrass, *Spartina foliosa*¹ (California cordgrass), in San Francisco (SF) Bay, in contrast with neutral or positive impacts predicted for a native crab, *Hemigrapsus oregonensis* (yellow shore crab). We implemented an experiment in SF Bay using caged plots of planted *S. foliosa*, to which we added or did not add crabs. We compared responses among these treatments, cageless, and partially-caged controls. *Carcinus maenas* treatments had the greatest reduction in *S. foliosa* stem density from June through August, and the lowest stem density in August relative to all other treatments. *Hemigrapsus oregonensis* effects were similar to controls. Both crabs reduced small invertebrate abundance by ~50% and led to shifts in community composition relative to controls. Changes to the invertebrate community and subtle shifts in soil conditions may contribute to the apparent negative impact of *C. maenas*. Crab trapping revealed more *C. maenas* in areas with *Spartina* in SF Bay, suggesting it uses *Spartina* as a refuge and that these effects are especially relevant to restoration activities. These results add to our developing understanding that invasive consumers can affect the path and pace of restoration and thus warrant increased attention in restoration planning and management.

Keywords: *Carcinus maenas*, habitat restoration, invasive species, *Spartina*

🌿 Restoration Recap 🌿

- The density of restoration plantings of the native *Spartina foliosa* (California cordgrass) declined significantly in the presence of the non-native *Carcinus maenas* (European green crab), but not the native *Hemigrapsus oregonensis* (yellow shore crab). Specifically, we recommend restoring *S. foliosa* in sites where *C. maenas* abundances are low or can be controlled during early plant establishment.
- A trend toward lower nitrogen content in sediment with *C. maenas* present could further develop through direct effects on organic matter loss or indirect effects of a shifting invertebrate community and functions. Future work should explore how soil properties and restored vegetation interact and respond to invasive predator-induced changes to infaunal communities over longer time scales.
- Invasive consumers that are also habitat modifiers can alter the course of habitat restoration efforts and should garner greater attention in restoration of foundational plant species.

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Species that engineer their environments can be especially influential when they modify both abiotic conditions and co-occurring habitat-forming species. Engineers may positively influence habitat-forming species through facultative or mutualistic interactions (e.g., nutrient

deposition from wastes [Mosepele et al. 2009, Holdredge et al. 2010]), nutrient cycling (Andriuzzi et al. 2016), seed dispersal (Wilby et al. 2001, Mosepele et al. 2009) or oxygenation of water or sediment (Kilham 1982, Bertness 1985, Gereta and Wolanski 1998, Wolanski et al. 1999, Daleo and Iribarne 2009). Alternatively or concurrently, they may consume the habitat-forming species or otherwise negatively affect its size or geometry (Whicker and Detling 1988, Wilby et al. 2001, Daleo and Iribarne 2009, Holdredge et al. 2009, Mosepele et al. 2009, Gass and Binkley 2011). In either case, these effects may be in addition to indirect effects by engineers also altering the food web to the detriment or benefit of habitat-forming species through consumption of herbivores or organisms that modify soil conditions (ants, Zelikova et al. 2011; kangaroo rats, Prugh and Brashares 2012; crabs, Bertness and Coverdale 2013).

Perhaps not surprisingly, introduced species with strong engineering effects can have large impacts on structure and function of their invaded ranges and associated native species. Even in nature reserves, where human influence is limited, conservation and restoration goals can be undermined by the presence of invasive species (Usher 1986). In invaded systems, these species are often released from the predation and competition they experience in their native range. Resident predators or competitors can increase resistance to invasion but may not effectively reduce the density or spread of non-native species (Levine et al. 2004, Stachowicz and Byrnes 2006). In many cases, invaders establish and negatively impact habitat-forming species (Davis et al. 1998, Ford and Grace 1998). For example, *Myocastor coypus* (nutria) introduced to the southeastern USA decrease above- and belowground biomass of wetland vegetation through feeding, rooting and burrowing activities, ultimately leading to soil subsidence and decreased habitat availability for native wildlife (de Vos et al. 1956, Ford and Grace 1998, Maryland Department of Natural Resources, 2004). Feral *Ovis aries* (sheep) and *Capra hircus* (goat) intensely graze vegetation on islands, and their movement patterns additionally disturb vegetation, contribute to erosion, and reduce diversity, abundance and species richness of birds (Coblentz 1978, Van Vuren and Coblentz 1987). In freshwater systems, *Cyprinus carpio* (carp) and *Carassius auratus* (goldfish) can raze submerged aquatic vegetation through extensive grazing and increase turbidity and nutrient loads, consequently reducing zooplankton biomass (Richardson et al. 1995, Loughheed et al. 1998). These examples highlight the many and varied effects of engineering invaders on abiotic conditions and habitat structure and at multiple trophic levels.

Often, restoration efforts seek to establish or encourage the spread of habitat-forming species, as they create the foundations of dependent species assemblages. However, restoring habitat-building species requires understanding the interaction network within which the species is embedded; this includes both positive and negative

interactions that link community members (Halpern et al. 2007, Gagnon et al. 2020). Non-native species may alter these interaction networks, change physical structure, or alter disturbance regimes (Crooks 2002, Hensel et al. 2021) in different ways than resident species, complicating habitat restoration efforts. As such, pressure by invasive species on their invaded systems may influence the path, pace, and outcome of restoration efforts. Though invasive species' impacts in ecological systems are well known (Elton 1958, Gallardo et al. 2016), these impacts are not often studied or planned for in restoration settings.

Salt marshes are frequent targets for restoration as they provide valuable ecosystem services (e.g., dampening wave energy, sequestering carbon, and providing nursery and foraging habitat), but have been greatly diminished in the United States and globally by human activities (Zedler and Kercher 2005, Brophy et al. 2019). Salt marsh plant species' performance can be hindered and/or facilitated by invasive organisms (Ford and Grace 1998, Alberti et al. 2007, Bertness and Coverdale 2013). By better understanding the settings in which habitat-modifying invasive species will impact salt marsh vegetation, practitioners can choose sites and strategies more effectively and ultimately improve restoration outcomes.

Here, we investigate how the invasive *Carcinus maenas* (European green crab) can influence the outcome of native *Spartina foliosa* (California cordgrass) restoration in San Francisco Bay, California, USA. (We chose to use the species name *Spartina foliosa* in this manuscript but note that there is an ongoing dispute over whether to subsume *Spartina* into the larger monophyletic genus *Sporobolus* [Bortolus et al. 2019]). Recent work in other salt marsh systems leads to conflicting hypotheses regarding how *C. maenas* may impact habitat restoration efforts. In areas where it is introduced, this crab may indirectly benefit vegetation by controlling herbivorous crab populations (Bertness and Coverdale 2013, Coverdale et al. 2013) or directly harm it while foraging (Davis et al. 1998, Garbary et al. 2014, Howard et al. 2019). *Carcinus maenas* is a voracious food generalist that preys on benthic invertebrates and can significantly reduce their abundance, especially bivalves and surface feeding amphipods (Grosholz and Ruiz 1995, Grosholz et al. 2000). Infauna can affect sediment biogeochemistry through feeding activities, burrow formation, and sediment excavation (Aller 1982), which can affect sediment stabilization (Hall 1994), promote denitrification and phosphorus retention (Karlson et al. 2007) and move oxygen deeper into soils (Fenchel and Riedl 1970). Although *C. maenas* feeding activity is typically concentrated in the top few centimeters of sediment (Scherer and Reise 1981, Le Calvez 1987), it can also dig deeper pits to extract large clams (Cohen et al. 1995). Its foraging can result in lower sediment organic matter, redox potential and chlorophyll *a*, which lead to poor survivorship of tidal flat fauna (Neira et al. 2006). *Spartina foliosa*

could be affected by direct changes to soil conditions, or changes in composition and abundance of benthic epifaunal and infaunal organisms that could additionally influence soil characteristics and thus plant growth.

It is important to consider effects of native species' impacts on vegetation relative to introduced species. Densities and habitat preference of native vs. non-native crabs may affect how they use vegetation, and thus their impact in restoration settings. The native grapsid crab *Hemigrapsus oregonensis* (yellow shore crab) also occurs in and around *S. foliosa* patches throughout San Francisco Bay (Jensen et al. 2002). In California marshes, higher densities of another small, burrowing grapsid crab native to the region, *Pachygrapsus crassipes* (striped shore crab), can have positive or neutral effects on cordgrass cover (Walker et al. 2021). Though crabs can negatively impact vegetation through consumption or physical damage from their activities, they can also positively affect vegetation by aerating sediments (Bertness 1985) and through nutrient deposition from their wastes (Holdredge et al. 2009). Additionally, grapsid marsh crabs can facilitate a *Spartina*-mycorrhizal fungi mutualism by oxygenating sediment during formation of burrow networks, increasing the availability of nitrogen in soil and promoting the growth of *Spartina* species (Daleo et al. 2007). *Hemigrapsus oregonensis* may promote soil oxygenation in the process of creating burrows, expanding the aerobic layer in marsh sediments, in contrast to *C. maenas* that appear to create simple burrows for shelter and shallow feeding pits but do not create extensive burrow networks. *Hemigrapsus oregonensis* has a diet consisting primarily of small snails and bivalves, sessile diatoms and algae (Knudsen 1964). Though it is possible that *H. oregonensis* burrows directly disturb vegetation, there is no evidence in the literature to suggest that it directly harms vegetative tissues while foraging, contrary to the effects of the behavior of *C. maenas*. Its smaller size (maximum adult carapace width of 35 mm [Rathbun 1918], versus a maximum carapace width of 100 mm for *C. maenas* [Washington Department of Fish and Wildlife 2001]) may reduce its impact on the surrounding soils and thus on *S. foliosa*.

Here we evaluate the impacts of *C. maenas* and *H. oregonensis* on *S. foliosa* using a field cage enclosure experiment. We also assess the crabs' use of *Spartina* as habitat at various sites in San Francisco Bay to understand the relevance of these impacts. Considering the previous studies of crab impacts on their habitats in the context of *S. foliosa* restoration, we predicted that new plantings would be disturbed by *C. maenas* foraging activities, and that associated changes to abiotic conditions or the invertebrate prey community could indirectly influence *S. foliosa* growth. In contrast, we predicted that *H. oregonensis* would have a neutral or positive effect on *S. foliosa* due to its smaller size and oxygenation of sediment through deep, complex burrow formation. Previous work found that *Spartina*

in a nitrogen-limited environment responded positively to nitrogen additions (Boyer and Zedler 1998) and we expected *S. foliosa* to benefit from increased nutrient deposition with either crab's wastes. However, we expected *C. maenas* to reduce the epifaunal and infaunal invertebrate abundance and alter community composition to a greater extent than *H. oregonensis* due to the invader's frequent and intense foraging behavior, leading to a net negative impact on *S. foliosa* establishment and growth characteristics.

Methods

Local Restoration and Study Sites

Spartina alterniflora (smooth cordgrass) was introduced to San Francisco Bay in the 1970s (Callaway and Josselyn 1992, Daehler and Strong 1997). This non-native species then hybridized with the native *S. foliosa* (Daehler and Strong 1997), leading to local extirpation of the native cordgrass in most of the central and southern portions of the Bay (Ayres et al. 2003). There is currently an ongoing program to eradicate hybrid *Spartina* in San Francisco Bay, and a recent shift toward restoring native *S. foliosa* (California Coastal Conservancy's Invasive *Spartina* Project [ISP, www.spartina.org]). However, planting success of *S. foliosa* varies by site (Lewis and Thornton 2014). At some locations, the soil surrounding plantings of native cordgrass is riddled with pits and apparent damage to both the roots and shoots (W. Thornton, ISP, pers. obs.). This may be due to the actions of *C. maenas*, whose foraging activities damage and result in widespread loss of vegetative habitat in other locations (Garbary et al. 2014, Neckles 2015, Matheson et al. 2016).

The cage enclosure study was conducted at Tiscornia Marsh, in San Rafael, California (37.967203°N, -122.495293°W), an area actively undergoing *S. foliosa* restoration and expansion. We deployed crab traps at four sites in San Francisco Bay to assess the use of *Spartina* by *C. maenas* and *H. oregonensis*: Tiscornia Marsh (37.968654°N, -122.495661°W), San Rafael Restoration Site (SRRS; 37.961246°N, -122.490176°W), Brickyard Park (37.882777°N, -122.504058°W) and Giant Marsh (37.996759°N, -122.362872°W). It is difficult to distinguish *S. foliosa* from the *Spartina* hybrid in the field without genetic analysis, so for the purposes of this trapping we categorize all cordgrass at these sites as *Spartina* spp.

Carcinus maenas Effects on *S. foliosa* in the Field

We tested the effect of each crab species on *S. foliosa* and its associated biota using a field enclosure experiment over the summer of 2016 in Tiscornia Marsh. Plugs (5–10 stems) of *S. foliosa* were planted in sets of five in each of fifty plots (0.25 m²) with a 10cm buffer between the cage and cordgrass plantings. One plug was placed at each corner and one in the center imitating ISP methodology

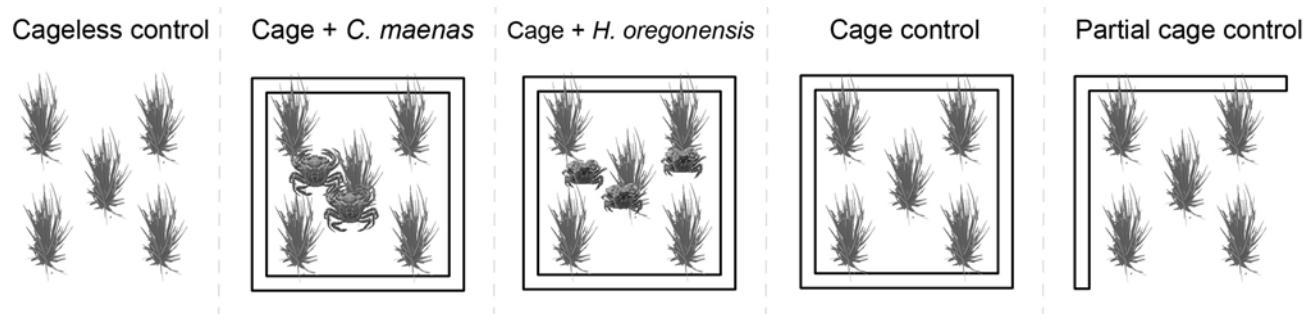


Figure 1. A depiction of the five experimental treatments.

for *S. foliosa* planting design (Figure 1) within open areas in an existing stand of *S. foliosa* (~2 ha) to ensure habitat suitability for transplanted cordgrass. Cage enclosure experiments can be a useful tool to assess crab impacts on vegetation and infaunal prey when potential cage artefacts are accounted for in the experimental design (Hall et al. 1990, Richards et al. 1999, Garbary et al. 2014). We used cage controls in addition to crab treatments to account for potential artefacts from the cages. Treatments consisted of (1) a cageless control, (2) two *C. maenas* in a cage, (3) three *H. oregonensis* in a cage, (4) a cage control with no crabs, or (5) a partial cage control (Figure 1, N=10 for each treatment) similar to the design in Neira et al. (2006). Summer surveys around San Francisco Bay guided sizes (*C. maenas*, 30–50mm; *H. oregonensis*, 12–19mm) and densities used (*C. maenas*, two per cage, abundance 2.8 ± 0.8 crabs/trap; *H. oregonensis*, three per cage, abundance 4.8 ± 0.6 crabs/trap, Gonzalez 2017), although preliminary trapping found no *C. maenas* present within the experimental area, and very few *H. oregonensis* (0.1 crabs/trap). Treatments were assigned randomly to plots placed at least one meter apart within the experimental area. Full cage controls allowed examination of *S. foliosa* growth with crabs and other wildlife excluded but represented potential artefacts of shading and reduced flow. Partial cage controls added shade but allowed more flow and access to wildlife. Cages (0.5 × 0.5 × 1 m height) were composed of PVC poles (1 cm in diameter) at the corners and enclosed in 6-mm Vexar mesh. Como et al. (2006) found no difference in infaunal abundance in caged and uncaged plots using 6-mm mesh. Cages had open bottoms and were buried ~15 cm in the sediment to limit escape of crabs. Cage lids were composed of a 0.5 m² piece of 6-mm mesh and were removable to allow for measurements and manipulations. Some crabs could not be located during sampling or may have been buried when counts were performed. Therefore, to be certain that crabs were present, a new set (one *C. maenas* and one *H. oregonensis* per treatment) of similarly sized crabs was added to each cage every month after July. Even with these additions, the number of crabs in treatments was within natural local densities.

Response of *S. foliosa*, Invertebrates and Soil Parameters

The total number of live stems and stand height estimated as the average of the five tallest stems in each plot (measured from the base of the stem) was recorded every month for five months as a proxy for *S. foliosa* survival and growth, respectively.

Two sediment cores per enclosure were taken at the end of five months using a 5-cm PVC corer to a depth of 10 cm. One core per 0.25m² plot was taken to evaluate invertebrate community composition and abundance, and one to evaluate percent carbon (C) and nitrogen (N) and organic matter (as in Neira et al. 2006). Invertebrates were sieved to capture individuals larger than 500µm, then preserved in 70% ethanol, sorted and identified to the lowest taxonomic level possible (species level for all but *Monocorophium* spp., *Corophiidae* spp. and *Ostracoda* spp.) (Table 1). We excluded annelids from analyses due to their poor preservation. From these data, species richness, abundance, Shannon-Wiener diversity index, total number of clams and amphipods, and community similarity were calculated.

Cores for sediment analyses were dried in an oven at 50°C. Samples were sieved through a 2-mm mesh screen, ground using a mortar and pestle and passed through a 500-µm mesh screen. Percent organic matter was determined by loss on ignition in a combustion oven at 500°C for three hours and expressed as a percentage of initial weight. Subsamples were analyzed for carbon and nitrogen using a Costech ECS 4010 CHNSO elemental analyzer (Pella and Colombo 1973).

Carcinus maenas Abundance in *Spartina*

To assess crab abundance within *Spartina*, we set out five Fukui collapsible multi-species marine traps (63 × 46 × 23 cm; 1.6 cm mesh) alternating with five minnow traps (21 × 37 cm, with 6 cm openings and 0.5 cm mesh) baited with sardine to gather a range of crab sizes and ages. We set out the traps approximately 10m apart in areas with and without *Spartina* at each site for a total of 10 traps in each area. We additionally evaluated whether crabs were

Table 1. Comparison of densities (mean \pm standard error) of benthic epifaunal and infaunal taxa, and total amphipods and bivalves, across treatments, grouped by order or roughly equivalent clade. The core (area of 15.7 cm² by 10 cm deep) was sieved through a 500 μ m mesh sieve. Annelids were excluded from analysis due to their poor preservation. Letters in parentheses: (i) for introduced or (n) for native.

Species	No Cage	<i>C. maenas</i>	<i>H. oregonensis</i>	Partial Cage	Full Cage
Amphipoda					
<i>Ampithoe valida</i> (i)	1.8 (0.7)	3.4 (2.2)	0.4 (0.4)	3.2 (1.1)	1.5 (1.0)
<i>Corophiidae</i> spp.	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)
<i>Grandidierella japonica</i> (i)	14.5 (2.8)	5.3 (1.6)	6.4 (2.6)	11.7 (2.1)	18.5 (4.6)
<i>Monocorophium acherusicum</i> (i)	1.4 (1.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Monocorophium</i> spp.	1.6 (1.1)	1.7 (1.6)	0.2 (0.2)	1.5 (0.5)	0.8 (0.5)
<i>Sinocorophium</i> c.f. <i>alienense</i> (i)	2.8 (3.6)	1.1 (2.2)	4.8 (7.0)	4.2 (8.3)	2.3 (1.7)
Cumacea					
<i>Nippoleucon hinumensis</i> (i)	6.9 (3.3)	1.9 (0.9)	1.0 (0.5)	6.3 (3.5)	7.8 (3.5)
Bivalvia					
<i>Gemma gemma</i> (i)	3.4 (2.0)	3.4 (1.4)	1.0 (0.6)	2.5 (0.7)	1.0 (0.4)
<i>Potamocorbula amurensis</i> (i)	3.5 (1.4)	1.1 (0.5)	5.0 (3.0)	1.8 (2.4)	6.3 (1.0)
<i>Limecola balthica</i> (i)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Isopoda					
<i>Gnorisphaeroma oregonensis</i> (n)	0.0 (0.0)	1.1 (1.1)	0.2 (0.2)	0.7 (0.7)	0.0 (0.0)
Ostracoda					
<i>Osstracoda</i> spp.	0.5 (0.4)	0.3 (0.2)	0.4 (0.2)	1.0 (0.5)	0.5 (0.5)
Cephalaspidea					
<i>Haminoea</i> c.f. <i>vesicula</i> (n)	0.4 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Tanaidacea					
<i>Sinelobus</i> c.f. <i>stanfordi</i> (i)	4.6 (2.9)	0.0 (0.0)	0.2 (0.2)	0.2 (0.2)	0.0 (0.0)
Total amphipods	22.1 (3.4)	11.6 (5.3)	11.8 (2.3)	21.8 (4.1)	23.3 (5.8)
Total bivalves	7.0 (2.9)	4.7 (1.5)	6.0 (3.6)	4.3 (1.5)	7.3 (3.4)

found more frequently in different substrates within each “*Spartina*” and “no *Spartina*” area by visually assessing approximate percentages of “riprap/rock/brick,” “mud,” and “*Spartina*”. Every 24 hours for three days, we removed the crabs from each trap and recorded the size and sex, and then rebaited and replaced the trap. Trapping took place between June and August in 2016.

Statistics

Statistical analyses were performed using R Statistical Software (version 4.0.3, R Core Team 2020). We used generalized linear models (GLM) to assess the interaction of site and *Spartina* presence on crab abundance. We also used GLMs to evaluate effect of treatment on change in stem density (number of stems per m²) between June and August, and stem density in August. This approach was chosen due to the ability of GLMs to accommodate for heteroscedastic variances, overdispersion and non-normal error distributions (Quinn and Keough 2002). The appropriate distribution for each model was chosen using goodness-of-fit statistics (Quinn and Keough 2002). We used the “emmeans” (estimate marginal means) package in R to conduct post-hoc pairwise comparisons, which uses the Kenward-Rogers method to calculate degrees of

freedom. We recognize that cage effects can become more severe with time, so we chose to focus analysis on the time period between June and August, before obvious cage effects, and before flowering (September) and senescence (September/October). Shannon-Weiner diversity index was calculated using the ‘diversity’ function in the vegan package in R (Oksanen et al. 2020). GLMs were used to test whether the total number of invertebrate individuals and species, Shannon-Weiner diversity index, number of amphipods, and soil characteristics (e.g., % nitrogen, % carbon, C:N and % organic matter) varied by treatment at the end of the experiment. The ‘metaMDS’ function in the vegan package was used to run the NMDS, which applies a square root transformation and calculates Bray-Curtis distances. Species vector correlations with NMDS axes based on 1,000 iterations were performed using the ‘envfit’ function to determine potential drivers of community composition. The 95% confidence interval ellipse area for the nMDS plot was also calculated using the vegan package (Oksanen et al. 2020). We tested for differences in community composition across treatments using a PERMANOVA and did pairwise comparisons using the ‘adonis’ function in the vegan package and the ‘pairwise.adonis’ function (Martinez Arbizu 2019).

Results

Response of *S. foliosa* to *C. maenas* in the Field

From June through August, *S. foliosa* stem density declined significantly more in *C. maenas* treatments than all other treatments. *Carcinus maenas* treatment plots lost 61% more stems over the course of the summer growing season than partial cage controls (Figure 2, emmeans pairwise contrast; $Z = -6.55, p < 0.001$), 66% more than cageless controls ($Z = -6.97, p < 0.001$), 59% more than plots with *H. oregonensis* ($Z = -6.49, p < 0.001$), and 31% more than cage controls

(Figure 2, $Z = -3.60, p = 0.003$). We found that the decline in stem density from June through August was reduced in *H. oregonensis* treatments relative to the cage control, but did not differ relative to cageless and partial control treatments (cage control: $Z = 3.09, p = 0.017$; cageless control: $Z = -0.635, p = 0.969$; partial cage control: $Z = -0.205, p = 1.00$).

Initially (June and July) there was no difference in *S. foliosa* response by treatment. Treatments began to diverge in August (Figure 3), where stem density was reduced by 90% in the *C. maenas* treatment relative to the cageless

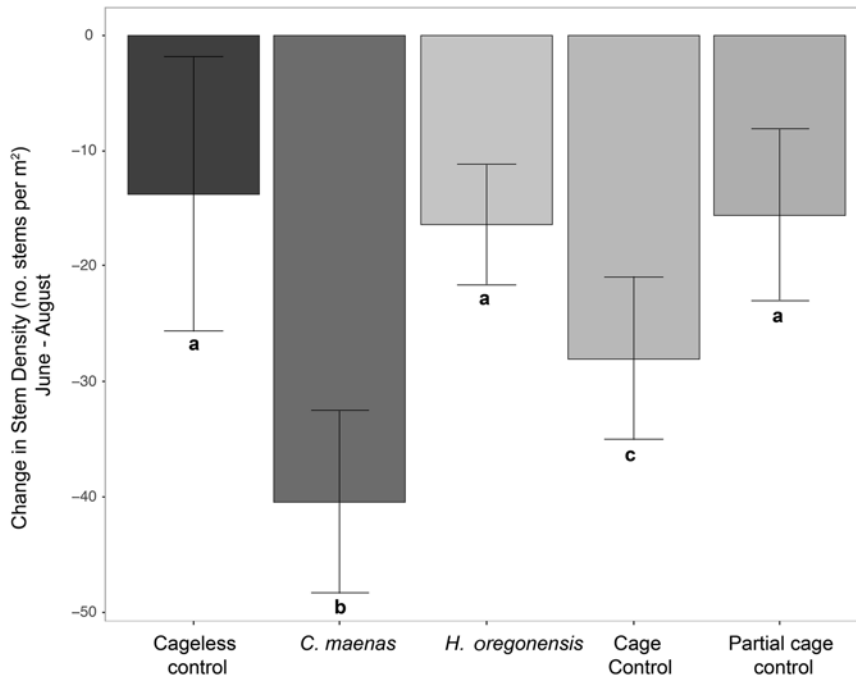


Figure 2. Bars represent the average decline in stem density (no. stems per m² plot) from June through August across treatments. Error bars show \pm one standard error about the mean. Shades of grey are according to treatment and letters denote significant differences among treatments.

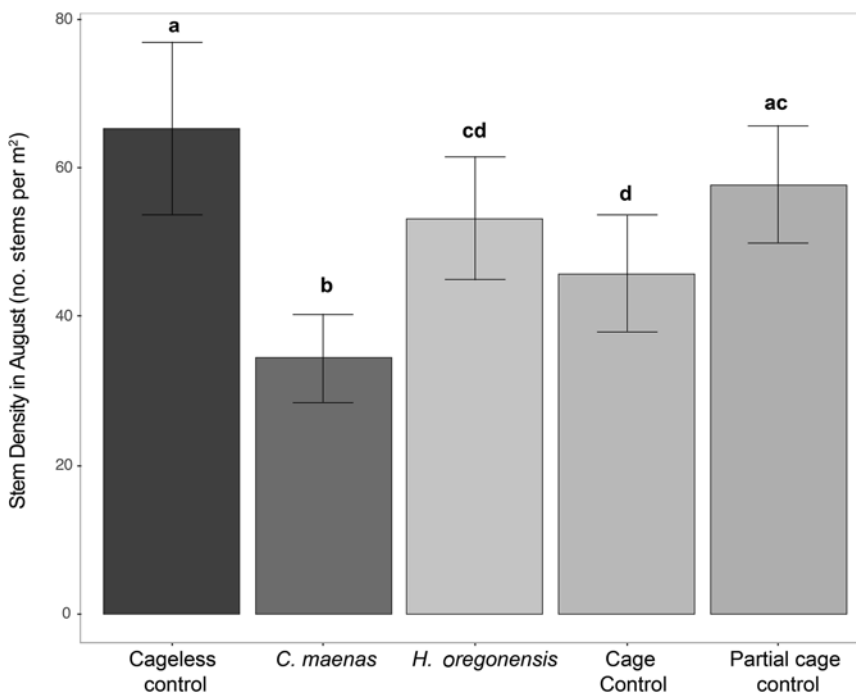


Figure 3. Bar plot shows the average stem density (no. stems per m² plot) across treatments in August, and error bars represent \pm one standard error. Shades of grey represent different treatments. Letters denote significant differences among treatments.

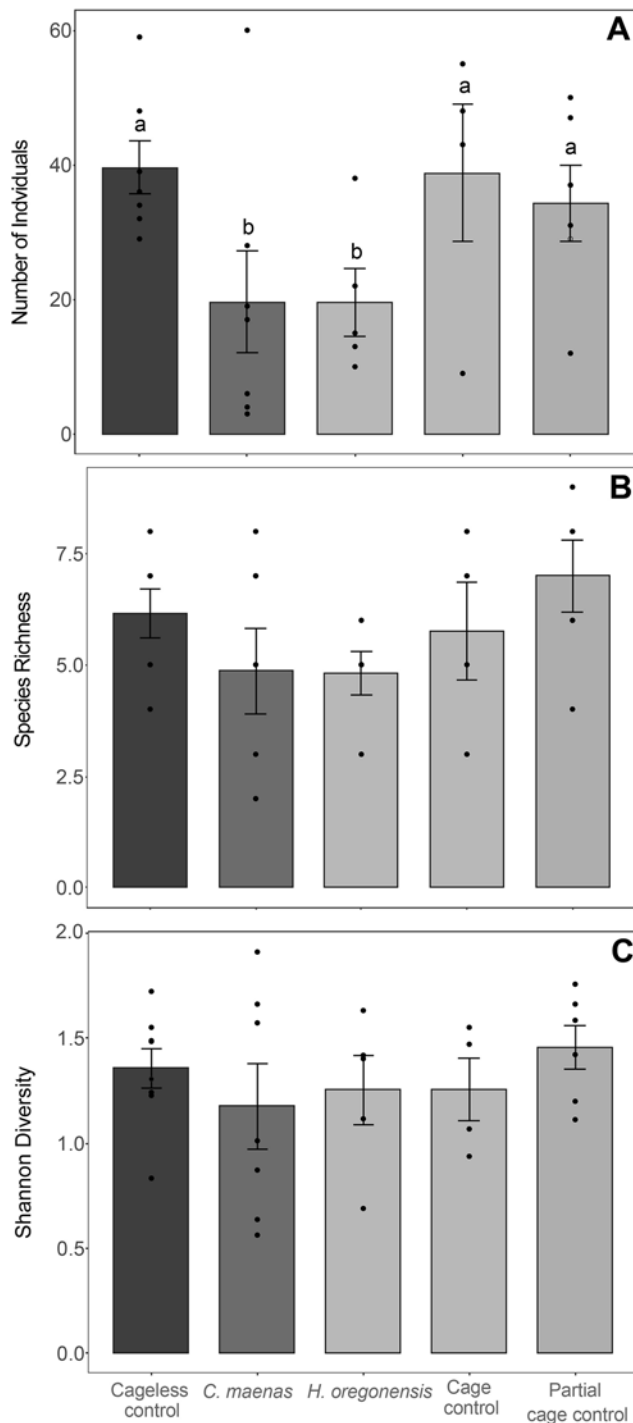


Figure 4. Bars show average (A) number of individuals, (B) species richness, and (C) Shannon-Weiner diversity index for invertebrates processed from one sediment core taken from each treatment plot at the end of the experiment. Individual data points are displayed in addition to the mean. Error bars denote \pm one standard error and different letters denote significantly different groups.

control ($Z = -9.45$, $p < 0.001$), 68% relative to the partial cage control ($Z = -7.46$, $p < 0.001$), 33% relative to the cage control ($Z = -4.10$, $p < 0.001$), and 55% relative to the *H. oregonensis* treatment ($Z = -6.30$, $p < 0.001$). Stem density in cages containing *H. oregonensis* was lower than cageless controls but did not differ from partial or cage control treatments (cageless control: $Z = -3.43$, $p = 0.005$; partial cage control: $Z = -1.34$, $p = 0.667$; cage control: $Z = 2.40$, $p = 0.114$). Stem density in full cage controls was significantly lower than cageless control treatments ($Z = -5.85$, $p < 0.001$) and partial controls ($Z = -3.71$, $p = 0.002$). There was no effect of treatment on the change of the average height of the five tallest stems from June through August or mean stem height in August ($p > 0.1$ for all).

3.2.1 Surface feeding and benthic macroinvertebrate community

There were 51% fewer soil macroinvertebrate individuals in the *C. maenas* treatment and 50% fewer individuals in the *H. oregonensis* treatment than in the cageless control (Figure 4A; $Z = 6.74$, $p < 0.001$, $Z = 5.978$, $p < 0.001$, respectively). Benthic invertebrate abundance in the full cage treatment and partial cage control treatments did not differ from cageless controls (respectively, $Z = 0.21$, $p = 0.999$; $Z = 1.54$, $p = 0.534$). Species richness decreased by ~13% in both the *C. maenas* and *H. oregonensis* treatments relative to the cageless controls, though these were not significant changes (Figure 4B, $Z = 1.02$, $p = 0.845$; $Z = 0.968$, $p = 0.870$, respectively). Shannon diversity was not affected by crab presence or cage controls (Figure 4C, $p > 0.1$ for all). There were 48% fewer amphipods in the *C. maenas* treatments compared with the cageless control treatment (Table 1, $Z = -4.83$, $p < 0.001$), and 47% fewer amphipods in the *H. oregonensis* treatment ($Z = -4.18$, $p < 0.001$). There were also 44% fewer amphipods in the *C. maenas* treatment than in the partial cage control ($Z = -4.00$, $p < 0.001$) and 50% fewer than in the cage control ($Z = -4.59$, $p < 0.001$). We found 42% fewer amphipods in the *H. oregonensis* treatment relative to the partial cage control ($Z = -3.49$, $p = 0.004$) and 49% fewer relative to the cage control ($Z = 4.08$, $p < 0.001$). Clam abundance did not differ in either the *C. maenas* or *H. oregonensis* treatment plots relative to controls ($p > 0.1$ for all). There were no differences in amphipod and clam abundances between crab treatments (amphipods: $Z = -0.114$, $p = 1.000$; clams: $Z = -0.956$, $p = 0.875$). Additionally, soil macroinvertebrate communities in the cageless control diverged significantly from communities in the *C. maenas* treatment (Figure 5, PERMANOVA, $r^2 = 0.19$, $p = 0.048$, *C. maenas*: adonis pairwise comparison; $r^2 = 0.168$, $p = 0.006$) and the *H. oregonensis* treatment (adonis pairwise comparison; $r^2 = 0.154$, $p = 0.047$). Communities among crab treatments seemed to diverge slightly but these differences were not significant ($r^2 = 0.074$, $p = 0.660$).

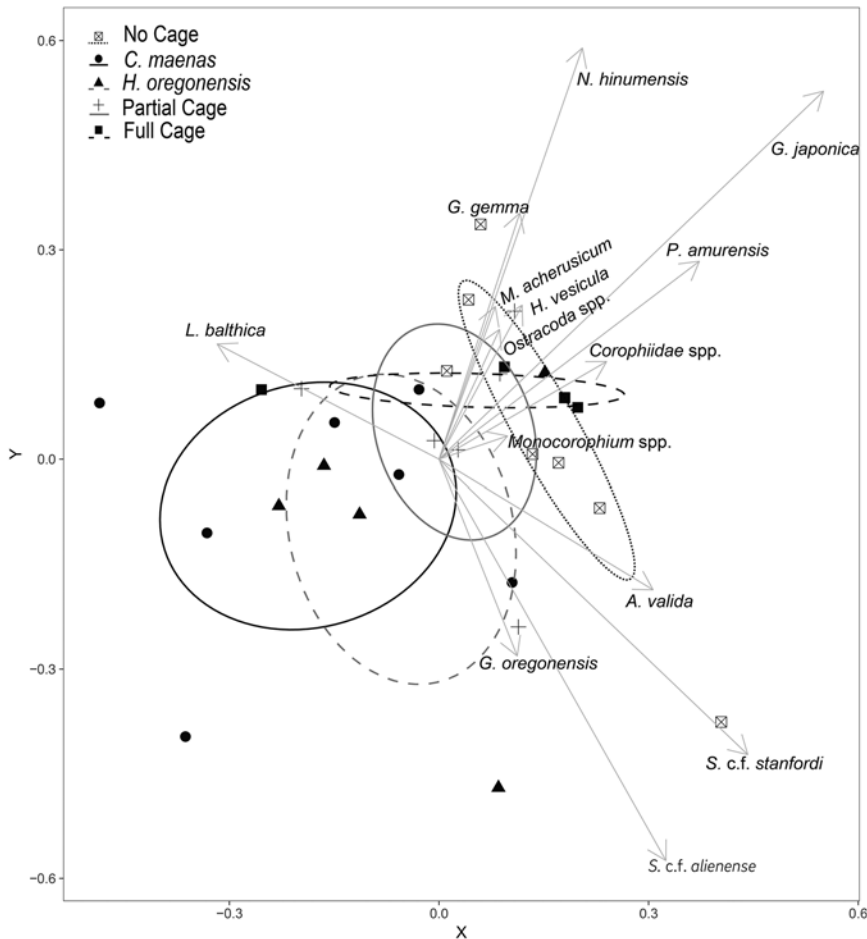


Figure 5. Non-metric multidimensional scaling (NMDS) of the Bray-Curtis dissimilarity matrix comparing benthic invertebrate (epifaunal plus infaunal) abundances from cores collected at the end of the experiment in October (Stress = 0.120, stress value <0.2 indicates a good fit of the model). Ellipses and shapes represent 95% confidence intervals around the group centroid. Species vectors represent coefficients of variation relative to the discriminant axes.

Soil Characteristics

There was no significant effect of treatment on soil measures (Figure 6). There was a trend of lower percent organic matter in *C. maenas* treatments relative to the cageless control (Figure 6A, $Z = -1.51$, $p = 0.558$). Percent nitrogen was 9% lower in plots with *C. maenas*, 7% lower in the cage control, 4% lower in the partial cage control and 3% lower in plots with *H. oregonensis* than in the cageless control treatment (Figure 6B, $Z = -1.23$, $p = 0.734$; $Z = -0.74$, $p = 0.947$; $Z = 0.56$, $p = 0.981$; $Z = -0.33$, $p = 0.997$, respectively). The average C:N ratio for the *C. maenas* treatment was slightly higher than all other treatments (Figure 6C, cageless control: $Z = 1.19$, $p = 0.760$; cage control: $Z = 1.05$, $p = 0.831$; *H. oregonensis*: $Z = 0.80$, $p = 0.929$; partial cage: $Z = 0.88$, $p = 0.905$, respectively).

C. maenas Abundance in *Spartina*

H. oregonensis counts were low at all sites except Tiscornia Marsh, where they were found more frequently in non-*Spartina* habitat composed primarily of riprap (Figure 7A, Mean CPUE of 4.87 vs. 0.47 in *Spartina*, $Z = 5.79$, $p < 0.001$). Abundance of *C. maenas* was relatively low (< 1 crab per trap per day) in all sites except Giant Marsh, where we found more *C. maenas* in *Spartina* habitats (Figure 7B, mean catch per unit effort or crabs/trap/day (CPUE) of 2.83

in *Spartina* vs. 0.77 in sites without *Spartina*, $Z = 3.79$, $p < 0.001$). Tiscornia Marsh had a high proportion of rocky substrate in the non-*Spartina* area, and the Giant Marsh site was composed entirely of *Spartina* and mud (Figure 7).

Discussion

As predicted, there was a negative response of *S. foliosa* to the presence of *C. maenas* in the field. Across treatments, plots experienced stem loss as *S. foliosa* recovered and established after being planted. From June through August, plots caged with *C. maenas* lost 31% more *S. foliosa* stems than cage controls, 61% more stems than partial cage controls, 66% more stems than cageless controls, and 59% more stems than plots with *H. oregonensis*. In August, stem density was reduced by 90% in the *C. maenas* treatment relative to the cageless control, 33% relative to the cage control, 68% relative to the partial cage control, and 55% relative to *H. oregonensis*. Intermediate effects in cage controls suggest that *C. maenas* itself was responsible for only a portion of the reduction in *S. foliosa* stem density from June through August. Cage effects were less prevalent in partial cage controls, suggesting that cages did not affect light penetration in a way that would substantially impact *S. foliosa* growth. Full cages may have altered water flow or sediment transport in such a way to inhibit *S. foliosa*

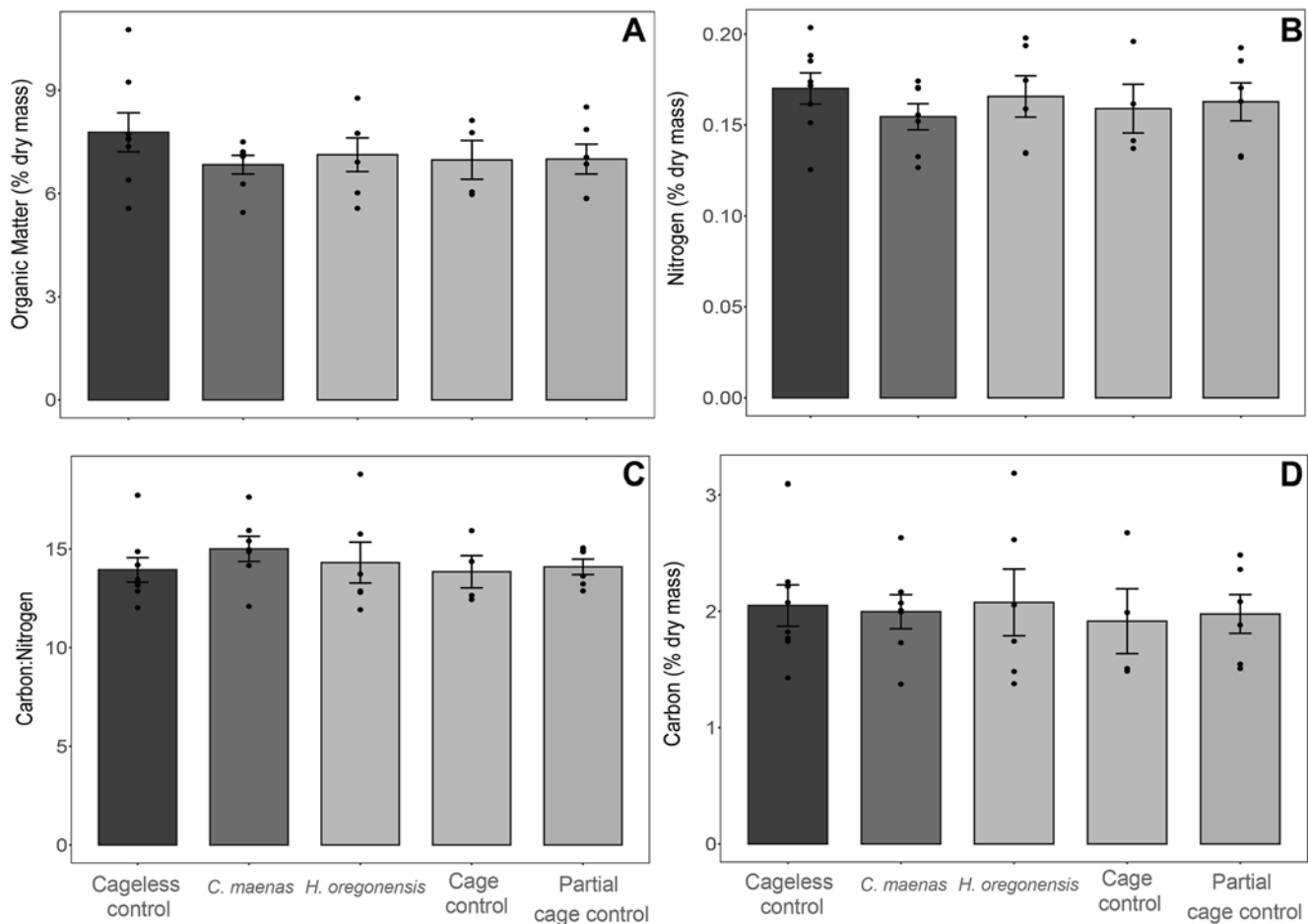


Figure 6. Bars show mean sediment (A) percent organic matter values (B) percent nitrogen (C) carbon to nitrogen ratio and (D) percent carbon by treatment derived from soil cores taken at the end of the experiment. Individual data points are presented in addition to the mean. Error bars represent \pm one standard error.

growth or advance stem loss, which complicates interpretation of crab effects on stem density. Still, we found significantly lower stem density in plots with *C. maenas* relative to all other treatments in August as well as a more substantial loss of stems over the summer growing season, which suggests that *C. maenas* reduce *S. foliosa* survival despite cage artefacts. There was no significant effect of treatment on average maximum stem height, which is consistent with previous work that found crab impacts to soil parameters manifested as a change in vegetative stem quantity rather than a change in stem size (Zhang et al. 2013).

We observed a neutral response of *S. foliosa* to *H. oregonensis* presence, in line with our predictions. Stem density in August and stem density change over time in the presence of *H. oregonensis* rarely differed from controls (Figures 3). We observed close to a twofold increase in change in stem density in the *H. oregonensis* treatment relative to the *C. maenas* treatment. It may be that *H. oregonensis* has a reduced impact on *S. foliosa* due to minimal direct disturbance to the plants and sediment relative to *C. maenas*. A crab with more intense foraging behavior like *C. maenas* may be active enough to disturb vegetative tissues and the

sediment and associated chemical and biological properties to the detriment of *S. foliosa*.

We predicted that both crabs would negatively influence benthic invertebrate abundance, with higher invertebrate depletion by *C. maenas*. However, both crabs similarly reduced overall abundance and amphipods by about 50%. Consistent with our preliminary and continuous trapping at the experimental site that found no *C. maenas* and few *H. oregonensis* within the experimental area, we found reduced individuals of crab prey species (amphipods) only in crab treatments, suggesting no ambient crab effects in uncaged plots. A cage enclosure experiment by Neira et al. (2006) reported similar invertebrate reductions in *C. maenas* enclosures located in *S. foliosa* plots. These reductions could be due to either direct consumption of the invertebrates or migration of the invertebrates to avoid predation or disturbance (Hines et al. 1997). Additionally, reduced microalgal biomass, an important food source for some benthic infauna including amphipods, can result from *C. maenas* digging activity (Neira et al. 2006) or *H. oregonensis* consumption (Knudsen 1964). Any of these mechanisms may contribute to the similarly

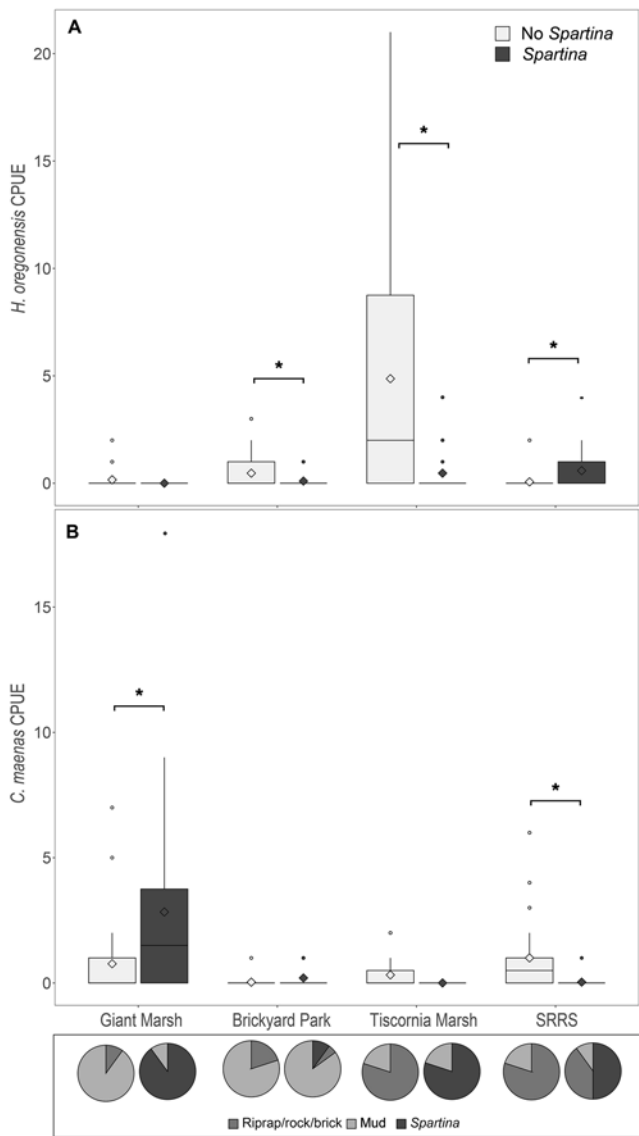


Figure 7. Boxplots show A) *H. oregonensis* catch per unit effort (CPUE, crabs/trap/day) and B) *C. maenas* CPUE at four sites in San Francisco Bay, illustrating the spread and skewness of the data. Diamonds represent the average value. Colored bars represent CPUE in areas with “no *Spartina*” (white) or “*Spartina*” (dark grey). Pie charts along the bottom represent the visual estimates of habitat substrate categorized as percent “riprap/rock/brick”, “mud”, and “*Spartina*” in each area at each site. These substrates are the same for *C. maenas* and *H. oregonensis* as traps placed in each habitat had the potential to capture both crab species.

low abundance of amphipods in both crab treatments. The invertebrate communities in both crab treatments at the end of the experiment diverged from the cageless control (significantly so for communities in *C. maenas* treatments), but not from each other. As such, reduced *S. foliosa* density with the invader present appears unlikely to be explained by predation effects alone considering the similarities in effects of the two crab species. We did not

assess annelid abundance and composition in this study due to their poor preservation, but annelids also function as bioturbators and could affect the soil chemistry and composition. Previous work attributed lower redox potential to a reduction in bioturbating annelid species within *C. maenas* enclosures, along with physical disturbance by the crab and reduced microalgae (Neira et al. 2006), which could contribute to the negative response of *S. foliosa* in *C. maenas* treatments.

We hypothesized that both crabs might lead to increased *S. foliosa* growth through deposition of wastes. Soil nitrogen and organic matter declined slightly with *C. maenas* present and was maintained with *H. oregonensis* present relative to the controls. This small difference in soil nitrogen and organic matter may partly explain the difference in *S. foliosa* stem density between the two crab treatments. Our results are similar to Zhang et al. (2013), which found no crab effects on nitrogen in plots with *Spartina*. However, this may not necessarily mean crabs are not affecting soil nitrogen. Changes in soil nitrogen from fertilization can be masked by increased nitrogen storage in belowground plant tissues (Mack et al. 2004, Zeng et al. 2010, Lu et al. 2011). *Spartina* (stem density and height) responds favorably to nitrogen additions (Boyer and Zedler 1998), and crabs may increase uptake of nitrogen in the belowground roots and rhizomes of *Spartina* species through soil oxygenation (Holdredge et al. 2010). Reduced nitrogen in soils here may be explained by lower nitrogen input in the soils in *C. maenas* treatments, potentially from less excrement, changes to infauna, and/or shallower burrowing, and/or soil oxygenation promoting nitrogen uptake by roots and rhizomes. Deeper burrowing by *H. oregonensis* could push oxygen deeper into the sediment and increase the aerobic layer of sediment, promoting nutrient cycling and increasing soil area with bioavailable nitrogen. Future studies should evaluate how the nitrogen content of soils, stems, and roots/rhizomes changes in response to both crabs to better understand interspecific differences in cordgrass response. Future work could also assess whether there are species-specific differences in excretion rates, and how redox potential and soil nitrogen content are affected by changes to bioturbating infaunal species in crab treatments, since early establishing salt marsh vegetation may rely on nutrients from infaunal invertebrate wastes as well (Holdredge et al. 2010). Organic matter decomposition rates are also increased in more oxygenated soils (Kristensen et al. 1995). Foraging activities by *C. maenas* could promote aeration of the sediment promoting uptake and resulting in lower organic matter. Decreased nitrogen and a trend towards lower sediment organic matter could develop over time.

Previous work found *C. maenas* abundances to be five times higher in *Spartina* meadows than adjacent mudflats in San Francisco Bay (mean of 3.0 crabs per trap per day versus 0.6 crabs per trap per day, E.D. Grosholz, University

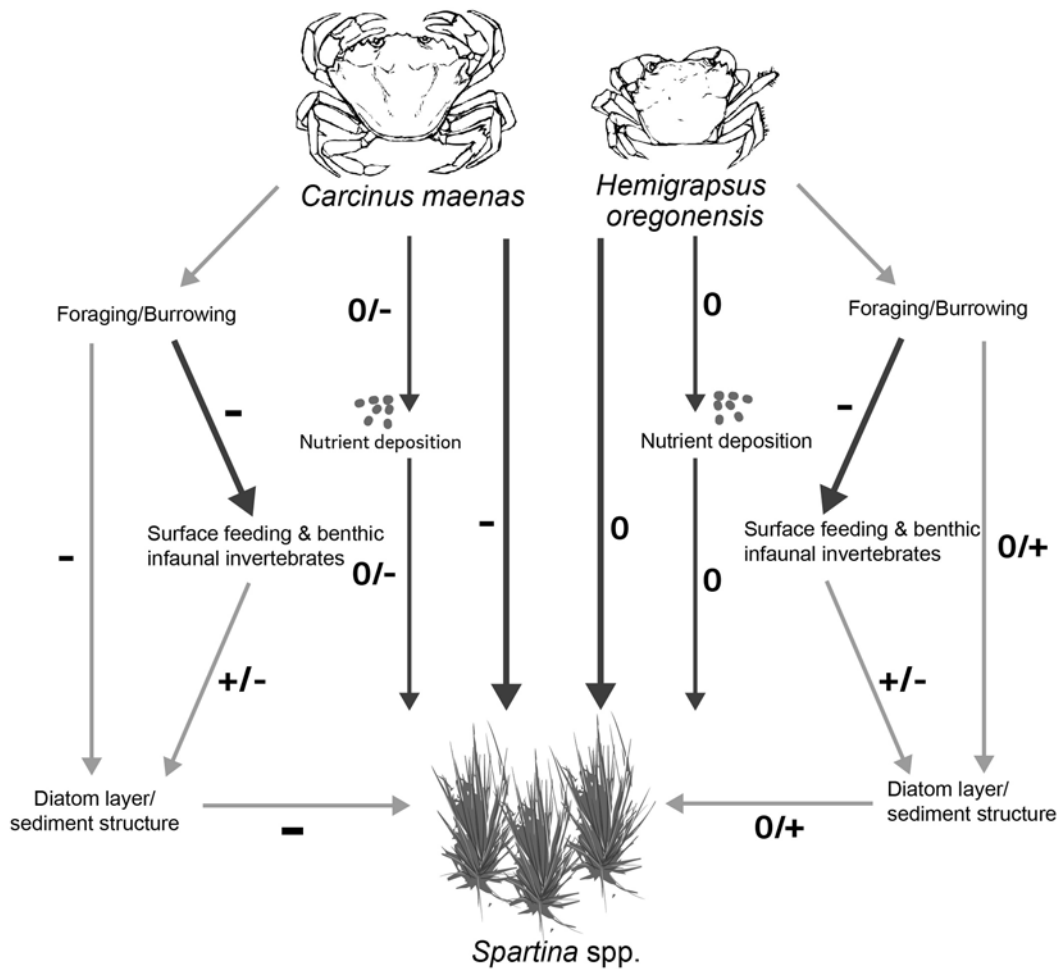


Figure 8. A diagram depicting our findings and potential interactions based on the literature. Dark grey arrows show elements that were assessed by this study and light grey arrows show other potential connections. Solid, large arrows suggest strong support based on our findings and solid, smaller arrows represent some evidence based on our findings. Positive symbols represent positive impacts, negative symbols represent negative impacts, zero symbols represent neutral impacts, and a slash in between symbols represent the potential for both types of impacts.

of California, Davis, unpublished data). Our results corroborate that finding; in Giant Marsh, where *C. maenas* was abundant (mean of ~3 crabs per trap per day), we found that *C. maenas* was found more frequently in areas with *Spartina* than areas without. In contrast, we found that in Tiscornia Marsh, where *H. oregonensis* was abundant, it was found primarily in areas of rocky structure rather than *Spartina*. In its native range, *C. maenas* is found seeking shelter from predation and desiccation under rocks and shells in the intertidal (Klein-Breteler 1976). However, on the west coast of the USA, *H. oregonensis* can outcompete *C. maenas* for refuge space in rocky habitats (Jensen et al. 2002). It may be that *H. oregonensis* excludes *C. maenas* from areas with rocky structure, causing it to seek refuge in areas with *Spartina*. This would likely increase interactions between *C. maenas* and newly planted *S. foliosa*, potentially exacerbating its impact in restoration settings. Newly planted *S. foliosa* may be more susceptible to damage

than more established cordgrass, and any impacts from *C. maenas* are likely exacerbated as the plants are establishing. Additional work is necessary to fully explore this interaction, which is likely complicated by other factors that determine crab establishment including food, predation, and recruitment patterns.

Previous studies report that invasive consumers can negatively affect restored vegetation, but few consider the indirect mechanisms by which invasive, habitat-modifying consumers can influence restoration efforts. Here we demonstrate a negative response of newly planted *S. foliosa* to *C. maenas* in the field and identify potential trophic and non-trophic factors that may contribute to negative effects of an invasive species on vegetation. We also found that when abundant, *C. maenas* is found more frequently in *Spartina* patches relative to areas without *Spartina*. Taken together, this evidence suggests that *C. maenas* has the potential to impact restored vegetation and that invasive

species like *C. maenas* should be considered in restoration planning and assessment. Habitat modifying invasive species, like crabs, may elicit a range of responses from their vegetative habitat. It may be that the net-negative impact of *C. maenas* on *S. foliosa* is due to a combination of factors, including reduced numbers of beneficial infauna, increased physical disturbance or consumption of exposed plant material, and somewhat reduced nitrogen, or perhaps other factors (Figure 8). This study focused on a limited suite of metrics to examine the effects of crabs on *S. foliosa* and its associated benthic invertebrate community, nutrients and soil structure, and these could be expanded in future studies.

A recent survey study found that respondents, associated with the Coastal and Estuarine Research Federation (CERF) and the International Coral Reef Society (ICRS), identified invasive species as being one of the top five challenges to restoration success (Hughes et al. 2020). The results of the present study support that finding and suggest that the presence of *C. maenas* can impact the establishment of *S. foliosa* and consequently restoration efforts. *Carcinus maenas* may negatively impact vegetation throughout its introduced range, and restoration practitioners should design restoration projects with this in mind and take measures to avoid sites with *C. maenas* or plan to adaptively manage should this non-native crab become a problem. Future work should explore how these effects scale with crab density. Crab surveys at restoration sites to determine crab density could aid in restoration site selection and/or active management of *C. maenas* densities in current projects (Green and Grosholz 2021). Additionally, climate-driven sea-level rise may interact synergistically with negative crab impacts and result in substantial marsh loss (Crotty et al. 2017) and future work should explore how marshes are impacted by both invasive, habitat-modifying consumers and climate change stressors like sea-level rise in tandem to inform restoration of these habitats in a changing world.

This study supplies evidence that invasive species can shift the trajectory of restoration in a way that would not have been predicted by knowing a common native crab's effects. Invasive species introduce novel contexts that may not be planned for in restoration and may impede efforts to establish habitat-forming species. The site selection process in many restoration programs has focused on ideal physical characteristics of a site that make it suitable for the plant being restored, and less so towards understanding interactions involving higher trophic levels. These system-level interactions, including those induced by invasive species, would best be considered prior to restoration implementation.

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Author Contributions

JG, KB, AC, GR conceived and designed the research; JG performed the experiment and processed samples; JG, AC analyzed the data; JG, KB contributed materials; JG wrote the manuscript and JG, KB, AC, GR edited the manuscript.

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