

An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod

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Abstract. With global increases in human impacts, invasive species have become a major threat to ecosystems worldwide. While they have been traditionally viewed as harmful, invasive species may facilitate the restoration of degraded ecosystems outside their native ranges. In New England (USA) overfishing has depleted salt marsh predators, allowing the herbivorous crab *Sesarma reticulatum* to denude hundreds of hectares of low marsh. Here, using multiple site surveys and field caging experiments, we show that the subsequent invasion of green crabs, *Carcinus maenas*, into heavily burrowed marshes partially reverses decades of cordgrass die-off. By consuming *Sesarma*, eliciting a nonlethal escape response, and evicting *Sesarma* from burrows, *Carcinus* reduces *Sesarma* herbivory and promotes cordgrass recovery. These results suggest that invasive species can contribute to restoring degraded ecosystems and underscores the potential for invasive species to return ecological functions lost to human impacts.

Key words: Cape Cod, Massachusetts, USA; *Carcinus maenas*; die-off; ecosystem recovery; habitat loss; human impacts; invasive species; nonconsumptive effects; predation; salt marsh; *Sesarma reticulatum*.

INTRODUCTION

Due to the concentration of human activities along shorelines, coastal ecosystems are among the most heavily impacted worldwide (Hassan et al. 2005, Lotze et al. 2006). These ecosystems are affected by eutrophication (Vitousek 1997), pollution (Lotze and Milewski 2004), and the overexploitation of resources, particularly high trophic level consumers (Jackson et al. 2001). Effects of consumer removal from coastal ecosystems have been well documented in coral reefs (Hughes 1994), kelp forests (Estes and Palmisano 1974), and salt marshes (Altieri et al. 2012), where the removal of predators and herbivores has had cascading, ecosystem-wide effects on basal foundation species. In the absence of keystone consumers, these systems have shifted to alternate states with reduced biodiversity (Hughes 1994) and ecosystem service provisioning (Moberg and Folke 1999).

Degraded coastal ecosystems are particularly vulnerable to species invasions (Carlton and Geller 1993), which occur in marine habitats inadvertently through shipping and transportation (Carlton 2003) and intentionally through mariculture (Ewel et al. 1999), biological control (Simberloff and Stiling 1996), and recreation (Moyle 1976). Thus, through species removals and ecosystem degradation, human impacts on coastal ecosystems facilitate species invasions. In many cases (Pimentel et al. 2005) such introductions have negative ecological and/or economic outcomes, supporting the

long-standing view of invasive species as problematic (Davis et al. 2011, Schlaepfer et al. 2012). Heavily degraded ecosystems, however, can benefit from species invasions if they return a lost ecological function (Schlaepfer et al. 2011). The potential for species to play a beneficial role outside of their native range has sparked debate on the costs and benefits of invasive species in human-impacted systems (Nuñez and Simberloff 2005, Carroll 2011, Davis et al. 2011, Schlaepfer et al. 2011, 2012, Simberloff et al. 2011, Vitule et al. 2012). In the absence of native keystone species, invasives have the potential to restore lost ecological function and drive recovery (Schlaepfer et al. 2011), but forecasting the outcomes of invasions remains largely unpredictable (Schlaepfer et al. 2012, Vitule et al. 2012).

In New England, decades of intensive recreational fishing centered on areas of dense coastal development have depleted local predator populations through trapping and hand-lining for blue crabs and rod-and-reel angling for finfish (Altieri et al. 2012). In marshes with heavy fishing pressure the depletion of native predators has resulted in a four-fold increase in the native, herbivorous marsh crab *Sesarma reticulatum*. At these densities *Sesarma* consume the cordgrass *Spartina alterniflora*, denuding hundreds of hectares of creek bank habitat (Holdrege et al. 2009). *Sesarma* herbivory is the most common driver of salt marsh die-off in the low marsh (Holdrege et al. 2009, Altieri et al. 2012, Coverdale et al. 2012), and *Sesarma* burrows increase the susceptibility of substrate to erosion and calving (Coverdale et al. 2013).

Recently, marshes on Cape Cod (Massachusetts, USA) have begun to recover from decades of consum-

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er-driven die-off (Fig. 1; Altieri et al. 2013). This recovery has coincided with the invasion of the European green crab, *Carcinus maenas*, into heavily burrowed creek banks in die-off marshes. *Carcinus*, a generalist predator introduced to North America in the early 1800s (Say 1817), is rare in healthy marshes, but common in die-off marshes where *Sesarma* burrow complexes provide refuge from physical stress and predation (Coverdale et al. 2012). Since many New England marshes no longer support historical levels of native predators (e.g., *Callinectes sapidus*, *Morone saxatilis*, *Mustelus canis*), the recent *Carcinus* invasion may reduce herbivore populations and facilitate the recovery of this heavily degraded system (Altieri et al. 2012, 2013).

New England salt marshes currently face human impacts that make them ideal for examining the potential positive role of invasive species (Schlaepfer et al. 2011). Historical human activity led to the establishment of *Carcinus*, which, in its new range, consumes and/or modifies the behavior of native snails (Trussell et al. 2004), lobsters (Rosson et al. 2006), blue crabs (MacDonald et al. 2007), and mud crabs (Miron et al. 2005), suggesting that it may interact with native salt marsh herbivores through both consumptive and nonconsumptive effects. Human impacts have also driven native predators to ecological extinction within these marshes with loss of historical ecological function (Altieri et al. 2012, Coverdale et al. 2013). Reduced predation pressure from native crustacean predators should facilitate juvenile *Carcinus* colonization, despite reports of ineffective anti-predator behavior in their nonnative range (Weis 2010). Continued predator removal also hinders native recovery and favors nonnative establishment; predator populations in heavily fished marshes have been depressed relative to unfished marshes for all years for which data are available (2009–2012; Altieri et al. 2012).

In this paper we examine the general hypothesis that *Carcinus* facilitates the recovery of New England salt marshes from die-off. Specifically we hypothesize that (1) *Carcinus* density is positively correlated with cordgrass regrowth in historical die-off marshes, (2) *Carcinus* displace *Sesarma* from refuge habitats (*Sesarma* burrows), and (3) *Carcinus* reduce *Sesarma* herbivory through consumptive and nonconsumptive effects, facilitating the regrowth of cordgrass in die-off marshes.

MATERIALS AND METHODS

Creek bank surveys

The extent of cordgrass die-off and recovery in the low marsh was quantified using field surveys at 16 marshes (11 recovering sites and 5 healthy sites) throughout Cape Cod in August 2012. Healthy and recovering sites were classified de novo based on the presence of recovery (Coverdale et al. 2013). At each site eight measurements of total cordgrass, die-off, and

recovery-zone widths were taken along six replicate 100-m permanent transects ($n = 48$ measurements/site). Cordgrass die-off from *Sesarma* grazing is easily quantified because it creates conspicuous die-off patches and is the only major source of cordgrass loss in the low marsh zone (Holdredge et al. 2009, Altieri et al. 2012, Coverdale et al. 2013). Recovery is also easily quantified because it appears as tall-form cordgrass within previously denuded die-off patches. *Sesarma* burrow density and diameter were also quantified in 25×25 cm quadrats in the low marsh zone at all sites ($n = 8$ quadrats/site).

Carcinus abundance was quantified along 10-m creek-bank transects at all sites in August 2012 ($n = 3$ banks/site). *Carcinus* were excavated by hand, measured, and released following the survey. To test the hypothesis that cordgrass recovery is correlated with burrow-dwelling *Carcinus* density, we compared *Carcinus* densities with cordgrass regrowth data from surveys (healthy sites excluded to avoid biasing analyses with multiple zero values). *Carcinus* density data were $(\log + 1)$ -transformed to meet assumptions of normality and analyzed with regression to compare *Carcinus* density and regrowth extent.

Carcinus–Sesarma burrow competition experiment

To test the hypothesis that burrow-dwelling *Carcinus* evict *Sesarma* from burrows, we performed a field burrow competition experiment. Burrow-dwelling *Carcinus* (48.3 ± 0.5 mm carapace width) and *Sesarma* (20.3 ± 0.3 mm carapace width) were collected from a single source site and randomly assigned to one of two treatments: *Sesarma* only and *Sesarma* with *Carcinus*. Crabs were placed in 1-cm-mesh hardware-cloth mesocosms ($30 \times 30 \times 30$ cm) with access to a single *Sesarma* burrow ($n = 20$ crabs/treatment). Trials were run overnight to minimize physical stress on evicted crabs. *Sesarma* location (in or out of burrow) was scored after 12 h and results were analyzed with a chi-square test.

Cordgrass recovery and consumptive vs. nonconsumptive effects

To test the hypothesis that *Carcinus* can reduce *Sesarma* herbivory and promote cordgrass recovery through both consumptive and nonconsumptive effects, we performed a fully factorial field mesocosm experiment with *Carcinus*, *Sesarma*, and cordgrass. Mesocosms were $50 \times 50 \times 50$ cm wire-mesh enclosures with shade-cloth roofs to prevent desiccation and $50 \times 50 \times 10$ cm natural peat bases installed at the upper border of the low marsh zone where both crab species are most common. Two cordgrass culms (7.31 ± 0.23 stems and 15 cm of peat with attached roots) from a single source site were transplanted into each mesocosm (see Altieri et al. 2012). *Carcinus* ($n = 1$ crab/replicate) and *Sesarma* ($n = 2$ crabs/replicate) were then released simultaneously into each mesocosm and quickly occupied available burrows (3–5 natural burrows/enclosure). Caged *Carci-*

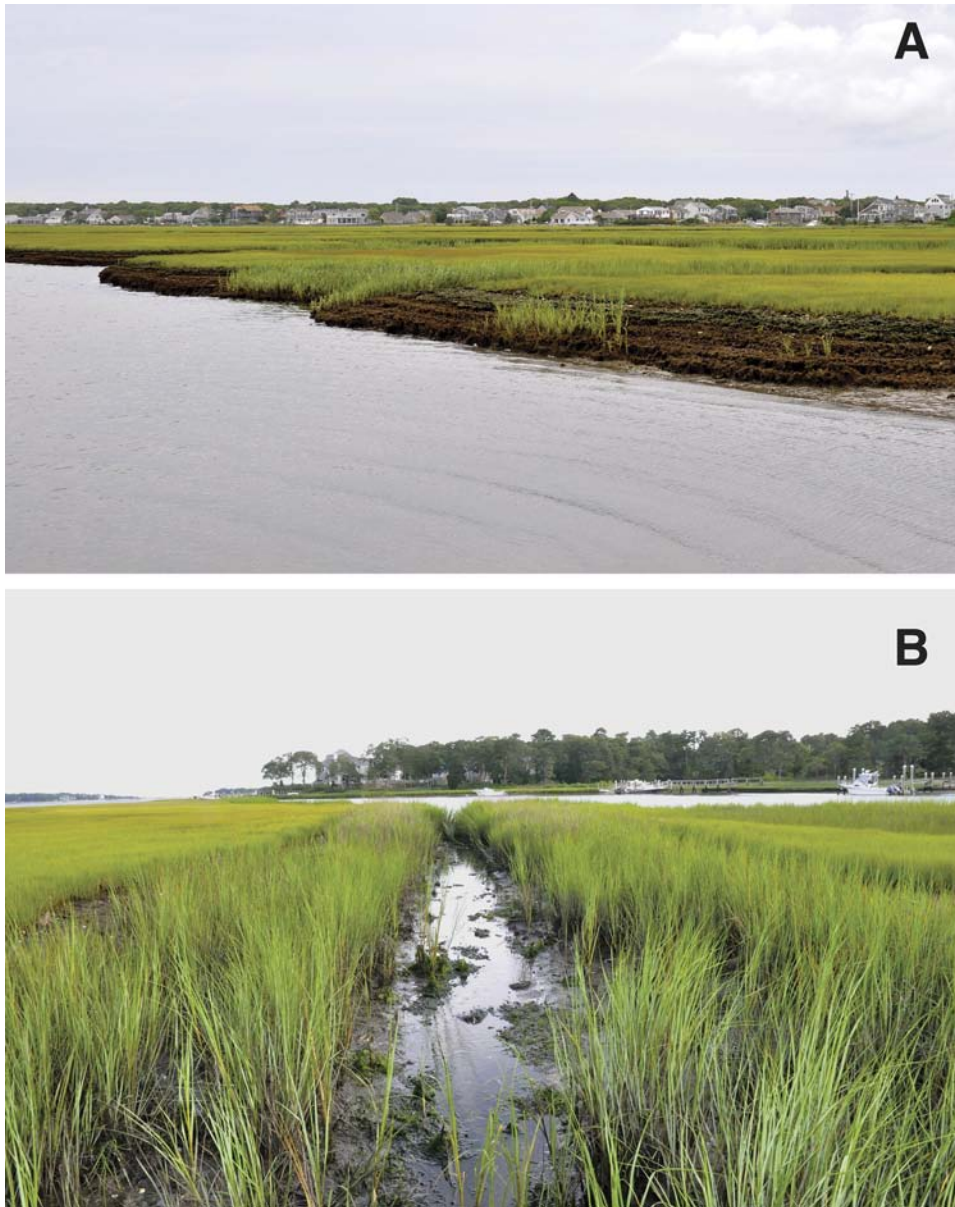


FIG. 1. (A) A representative die-off site on Cape Cod (Massachusetts, USA) with sparse cordgrass recovery in the low marsh zone. Horizontal striations are evidence of significant erosion following *Sesarma* herbivory and burrowing. (B) At many sites, cordgrass has almost fully recolonized the formerly denuded low marsh zone, with only a thin band of die-off maintained by active *Sesarma* grazing. *Carcinus* are common in *Sesarma* burrows at these sites: (A) Parker River; (B) Cotuit Marsh. Photo credits: M. Bertness, August 2012.

mus were placed in $30 \times 15 \times 15$ cm wire mesh cages in the middle of the mesocosm in nonconsumptive effects replicates. Visual and olfactory cues were transmitted through mesh cages, but caged *Carcinus* were unable to directly effect *Sesarma* survival or herbivory. After four weeks, when $>90\%$ of the cordgrass in *Sesarma*-only treatments was consumed, crabs were scored for survival and aboveground cordgrass biomass was harvested, dried, and weighed (Altieri et al. 2012). Biomass was pooled by replicate and analyzed with a single-factor ANOVA.

RESULTS

Creek bank surveys

Recovering and healthy sites differed in both the density of *Sesarma* burrow openings (110.4 ± 39.1 and 19.8 ± 11.1 [mean \pm SE] burrows/m² at recovering and healthy sites, respectively) and the number of *Carcinus* found within burrows ($F_{1,14} = 14.19$, $P = 0.0021$). *Carcinus* densities never exceeded 0.2 crabs/m at healthy sites, which lacked extensive *Sesarma* burrow complexes; at recovering sites, maximum *Carcinus* density

reached 2.8 crabs/m of creek bank. Burrows were also larger at recovering sites, likely as a result of burrow erosion (41.1 ± 1.5 and 20.1 ± 2.5 mm diameter at recovering and healthy sites, respectively). Log-transformed *Carcinus* density was positively correlated with the extent of regrowth across recovering sites and explained 37% of inter-site variation in regrowth ($P = 0.048$; Fig. 2A).

Burrow competition experiment

Carcinus were never evicted by *Sesarma* in replicates with single individuals of each species. The presence of *Carcinus*, however, significantly reduced *Sesarma* burrow use; no *Sesarma* were found in burrows when enclosed with *Carcinus* ($\chi^2 = 44.74$, $P < 0.0001$; Fig. 2B), while ~95% of *Sesarma* in enclosures without *Carcinus* occupied the single, available burrow (Fig. 2C). Fewer than 15% of *Sesarma* enclosed with *Carcinus* survived, while there was no mortality for *Carcinus* or *Sesarma* in treatments without *Carcinus*. Signs of *Carcinus* predation (broken *Sesarma* carapaces and severed limbs) were evident in all cases of *Sesarma* mortality.

Cordgrass recovery and consumptive vs. nonconsumptive effects

The presence of a single *Carcinus*, in or out of a cage, significantly reduced *Sesarma* grazing, resulting in higher final cordgrass biomass ($F_{4,38} = 27.15$, $P < 0.0001$; Fig. 3). *Sesarma* survivorship was >50% in replicates with a free-roaming *Carcinus*, and was similar in replicates with caged *Carcinus* (>75%) and without *Carcinus* (>90%). Final cordgrass biomass was an order of magnitude lower in *Sesarma*-only treatments relative to all other treatments. Cordgrass biomass did not differ between caged and uncaged *Carcinus* treatments (Fig. 3).

DISCUSSION

Our results suggest that the invasion of *Carcinus* into heavily burrowed die-off marshes on Cape Cod (Massachusetts, USA) can facilitate the recovery of cordgrass after decades of intense herbivory (Fig. 2A). *Carcinus* were most common in recovering marshes, where their presence appears to drive the recovery of cordgrass by partially restoring reduced predation pressure resulting from native predator depletion (Altieri et al. 2012). *Carcinus* are uncommon at healthy sites, likely as a result of lower burrow densities, smaller burrow openings, and higher predation rates. At die-off sites with reduced predation pressure, *Carcinus* appear to utilize larger, eroded *Sesarma* burrows for refuge from desiccation and predation, and prey on *Sesarma* while evicting resident crabs through a nonconsumptive interaction (Fig. 2B; Coverdale et al. 2012). Burrow-dwelling *Carcinus* were smaller than *Carcinus* caught in nearby subtidal habitats (57.4 ± 1.2 mm carapace width [mean \pm SE]), suggesting that refuge use by *Carcinus* is limited to smaller individuals. Average *Carcinus* ($48.0 \pm$

0.5 mm and 49.6 ± 0.5 mm at recovering and healthy sites, respectively) and *Sesarma* (21.7 ± 0.6 mm and 21.3 ± 0.8 mm at recovering and healthy sites, respectively) carapace widths, however, did not differ between healthy and recovering sites. While predation rates in small mesocosms lacking multiple refuges likely overestimate true predation rates, the results of our larger mesocosm experiment with multiple refuges suggested that both consumptive and nonconsumptive effects reduce *Sesarma* herbivory and promote cordgrass growth (Fig. 3).

Regional, ecosystem-wide effects of Carcinus invasion

Cape Cod marshes with large populations of invasive *Carcinus* have experienced widespread cordgrass recovery, with sites hosting the largest green crab populations experiencing the greatest recovery (Fig. 2A). Despite their role in reducing *Sesarma* herbivory, cordgrass recovery remains incomplete at many marshes (Fig. 1). Recent evidence of positive feedbacks, however, suggests that establishment of even sparse cordgrass stands in die-off marshes facilitates recovery and has the potential to partially restore lost ecosystem services (Altieri et al. 2013). Through belowground clonal integration and stress amelioration, cordgrass can expand from a single source to occupy wide bands of formerly denuded low marsh habitat (Altieri et al. 2013), where it rapidly reaches an aboveground size refuge from *Sesarma* herbivory, further promoting recovery (Coverdale et al. 2012).

The reduction of *Sesarma* herbivory in field enclosures with caged *Carcinus* also suggests that the multiplicative, but indirect, impacts of nonconsumptive effects may drive ecosystem-wide recovery (Fig. 3). Nonconsumptive effects have recently been recognized as important drivers of community pattern, energy flow, and prey behavior in ecosystems where direct predation was previously believed to be responsible (Trussell et al. 2004, Peckarsky et al. 2008). Consumptive and nonconsumptive effects can cause similar reductions in prey foraging, as seen here, but only nonconsumptive effects can impact multiple prey individuals simultaneously (Preisser et al. 2005). *Carcinus* has previously been shown to trigger nonconsumptive trophic cascades in rocky-shore tide pools (Trussell et al. 2004) with cascading effects on primary production. Here we show that similar effects occur in salt marshes.

The two mechanisms of cordgrass recovery described for Cape Cod marshes, the consumptive and nonconsumptive effects of *Carcinus* and the amelioration of physical stress by cordgrass, are complimentary pathways for the reestablishment of the foundation cordgrass species, *Spartina alterniflora*, in die-off marshes. By reducing *Sesarma* herbivory on vulnerable cordgrass, *Carcinus* enhance the establishment and persistence of regrowing cordgrass stands, which subsequently ameliorate physical stress and promote cordgrass expansion (Altieri et al. 2013). This combination of biotic and

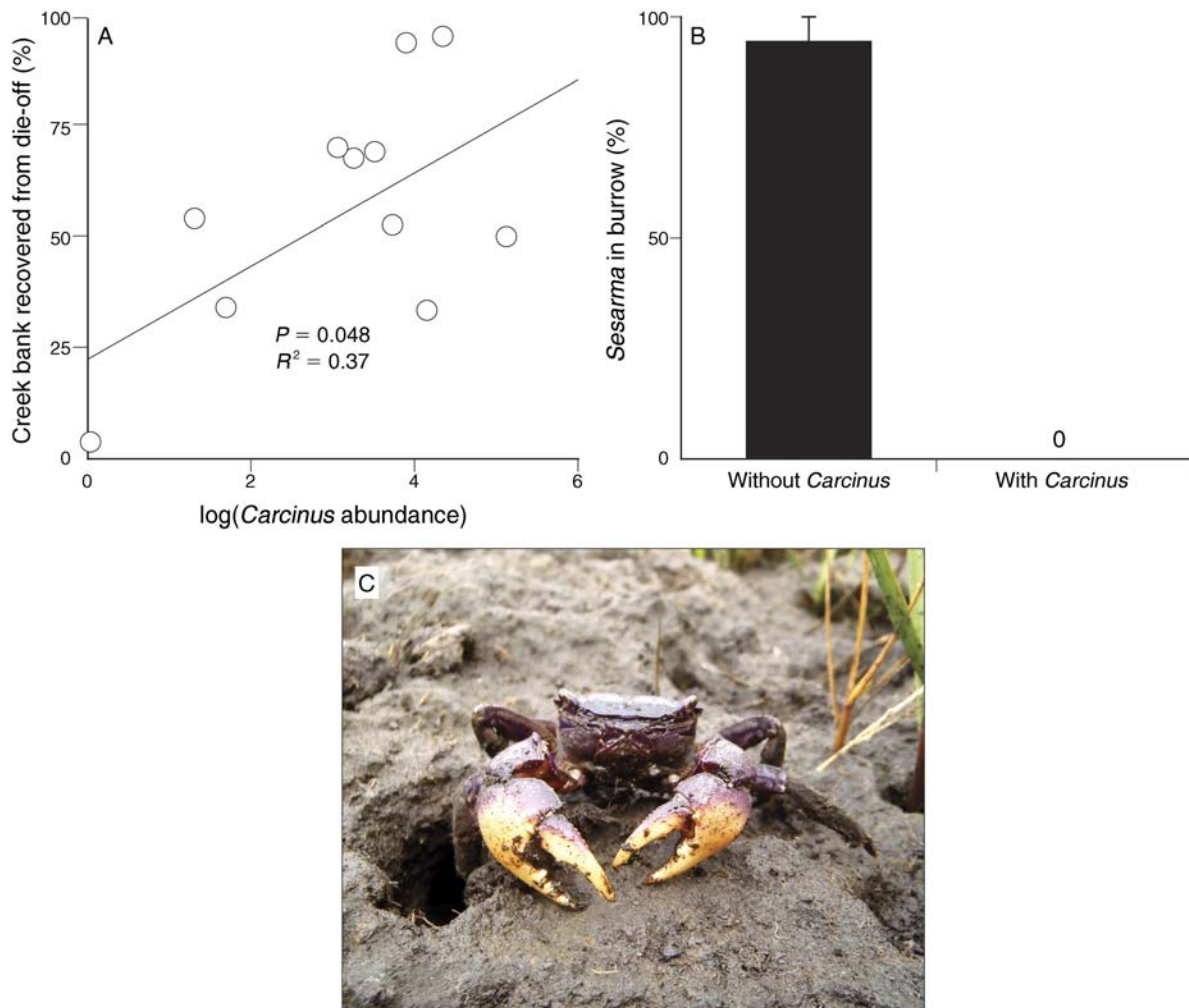


FIG. 2. (A) Regression analysis of *Carcinus* abundance and cordgrass recovery at recovering sites ($n = 11$ marshes) throughout Cape Cod. Healthy sites were excluded from analysis to avoid biasing results with multiple zero values. *Carcinus* abundance was originally measured in units of total crabs per site and was transformed to meet normality assumptions for analysis. The extent of cordgrass recovery is positively correlated with *Carcinus* abundance at recovering sites. (B) Results of *Carcinus*–*Sesarma* burrow competition experiment. The presence of *Carcinus* significantly reduced *Sesarma* burrow usage, causing *Sesarma* to remain outside of burrows where they are more vulnerable to predation and desiccation. (C) A male *Sesarma* (carapace width 24 mm) foraging near a narrow burrow opening. *Carcinus* are commonly found in eroded *Sesarma* burrows, which have wider openings as a result of erosion and active maintenance by large *Sesarma* populations. Photo credit: T. Coverdale.

abiotic factors is sufficiently powerful to overcome a ~30 yr trajectory of consistently expanding die-offs (Coverdale et al. 2013), but represents only a partial recovery of cordgrass cover, ecosystem services and ecological function (Altieri et al. 2012).

Carcinus effects on *Sesarma* survival and behavior

Carcinus have strong effects on native species in their introduced range, largely as a result of a generalist predatory nature that allows them to feed on >100 families of plants and at least 14 animal phyla (Cohen et al. 1995). In Cape Cod marshes we found that *Carcinus* fed on *Sesarma* in both burrow-competition mesocosms and field enclosures. In addition, their presence induces a behavioral change in *Sesarma* with significant fitness

costs: *Sesarma* are normally burrow dependent but are evicted by similarly sized *Carcinus*, forcing them to remain outside of burrows where they are at increased risk of desiccation and predation (Coverdale et al. 2012). In the Western Atlantic, *Carcinus* triggers similar behavioral changes in littorine snails (Trussell et al. 2004) and American lobsters (Rossong et al. 2006), suggesting that *Carcinus* has a disproportionate top-down effect on rocky shore, subtidal, and marsh ecosystems despite being a recently invasive species.

On Cape Cod, *Carcinus* are only common in heavily impacted marshes with long histories of *Sesarma*-driven die-off, reduced predator populations, and well-established burrow complexes. *Carcinus* are rare or absent from healthy marshes that host robust marine predator

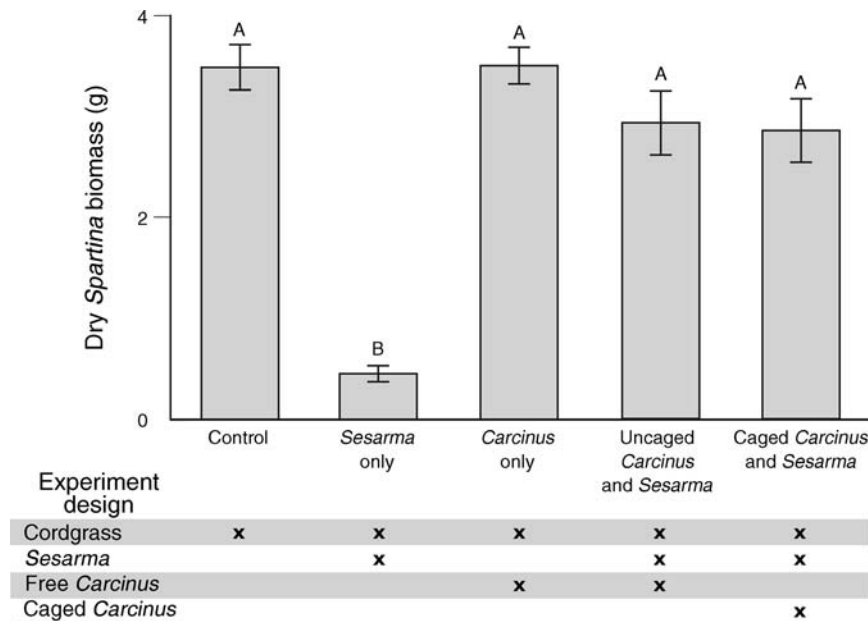


FIG. 3. Experimental design and results of a field mesocosm experiment comparing the consumptive and nonconsumptive effects of *Carcinus* on *Sesarma* herbivory. Final cordgrass biomass was significantly reduced in the *Sesarma*-only treatment, while the presence of both caged and uncaged *Carcinus* significantly reduced *Sesarma* herbivory. Final cordgrass biomass was similar in controls and all treatments with *Carcinus*. Bars with the same uppercase letters are not significantly different ($P < 0.01$); data are means \pm SE; all $n = 10$ replicates.

populations and lack eroded *Sesarma* burrow complexes, suggesting that *Carcinus*, like *Sesarma*, is dependent on the predation and desiccation refuge provided by *Sesarma* burrows for persistence in the marsh intertidal (Coverdale et al. 2012). Despite a $\sim 50\%$ reduction in predator density and $\sim 60\%$ reduction in predation rates at die-off sites (Altieri et al. 2012), *Sesarma* and small *Carcinus* remain vulnerable to predation in the intertidal and rely on burrows as refuge habitats. In addition to being generalist predators, *Carcinus* are also habitat generalists, utilizing refuge habitats in ecosystems as varied as rocky shores, cobble beaches, and subtidal mudflats in their introduced range. In many of these systems they competitively displace native species (e.g., Miron et al. 2005, Rossong et al. 2006) but, in marshes, they also appear to restore predation pressure lost to decades of recreational fishing (Altieri et al. 2012). Furthermore, since they are dependent on habitat modification by *Sesarma*, *Carcinus* are commonly found only in marshes with significantly elevated *Sesarma* populations. Our results show that, despite previous evidence of negative impacts on native species throughout its introduced range, *Carcinus* is well suited to accelerate the recovery of heavily degraded salt marsh ecosystems in New England.

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