Experimental predator removal causes rapid salt marsh die-off

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INTRODUCTION

Understanding the vulnerability and resilience of marine ecosystems to human disturbances is one of the most pressing issues of our time (Jackson et al. 2001; Lotze et al. 2006). Coastal salt marsh wetlands are among the most valuable ecosystems per capita worldwide (Costanza et al. 1997), but many have become degraded by human impacts (Lotze et al. 2006). Over the next century coastal ecosystems, such as salt marshes, are predicted to be further threatened by climate change, sea-level rise, ocean acidification and overexploitation (Jackson et al. 2001; Hoegh-Guldberg & Bruno 2010), making preservation of coastal ecosystems one of conservation biology’s greatest challenges (Biggs et al. 2009; Worm et al. 2009). Throughout the western Atlantic, salt marsh creek bank die-off, the rapid regime shift from dense monocultures of marsh grass to unvegetated eroding mud flats, has become an increasingly pervasive threat (Bertness & Silliman 2008). Historically, it was assumed that salt marshes were exclusively governed by physical factors (e.g. Teal 1962; Valiela & Teal 1974), but recent experimental field studies suggest that both bottom up and top down control can cause rapid and dramatic shifts in salt marsh ecosystem structure (Bertness et al. 2002; Silliman & Bertness 2002; Jeffries et al. 2006; Bertness & Silliman 2008). These hypotheses include: (1) eutrophication decreases plant investment into belowground biomass causing creek bank collapse (Deegan et al. 2012), (2) harsh physical conditions such as hypersaline or anoxic sediments driven by climatic extremes cause plant mortality (Alber et al. 2008), (3) increased boating activity erodes creek banks and damaged vegetation (Smith & Carullo 2007), (4) pollution and disease adversely affect plant health (Smith & Carullo 2007; Elmer et al. 2013) and/or (5) predator depletion releases herbivorous crabs from predator control (Altieri et al. 2012; Coverdale et al. 2013a). While it is likely that multiple, simultaneous threats to marsh vegetation have played a role in recent die-offs, few have been experimentally tested.

In New England, recreational overfishing has recently been hypothesised to trigger die-off by targeting and depleting large predators, releasing the herbivorous purple marsh crab Sesarma reticulatum from predator control. Excluding predators from a marsh ecosystem for a single growing season resulted in a >100% increase in herbivory and a >150% increase in unvegetated bare space compared to plots with predators. Our results confirm that marshes in this region face multiple, potentially synergistic threats.

Keywords
Trophic cascade, herbivore release, salt marsh die-off, predator depletion, experimental predator removal.

Abstract
Salt marsh habitat loss to vegetation die-offs has accelerated throughout the western Atlantic in the last four decades. Recent studies have suggested that eutrophication, pollution and/or disease may contribute to the loss of marsh habitat. In light of recent evidence that predators are important determinants of marsh health in New England, we performed a total predator exclusion experiment. Here, we provide the first experimental evidence that predator depletion can cause salt marsh die-off by releasing the herbivorous crab Sesarma reticulatum from predator control. Excluding predators from a marsh ecosystem for a single growing season resulted in a >100% increase in herbivory and a >150% increase in unvegetated bare space compared to plots with predators. Our results confirm that marshes in this region face multiple, potentially synergistic threats.
**Materials and Methods**

**Experimental setup**

This study was conducted at a marsh in North Bay, Osterville, Massachusetts bordering a marina that serves recreational fisherman and experienced severe creek bank cordgrass die-off in the early 2000s (Altieri et al. 2012). More recently, it has largely recovered from die-off (Altieri et al. 2013), potentially as a result of compensatory predation (Bertness & Coverdale 2013). Currently, creek banks at this site have only a small (<0.5 m) band of active die-off with fully recovered cordgrass above and below the remnant die-off zone. *S. reticulatum* herbivory is concentrated at the border of the high marsh, which is only inundated during monthly spring tides. Cordgrass in the low zone has reached a size refuge from herbivory (Coverdale et al. 2012) and low marsh substrate is too soft to support *S. reticulatum* burrows (Altieri et al. 2013).

We tested the impact of top predators on salt marsh vegetation with a predator exclusion experiment. Treatments included full predator exclusion cages, procedural controls and unmanipulated controls. Predator exclusion cages and cage controls measured 1.0 × 1.0 × 0.5 m (L × W × H) and were constructed of plastic coated 2 cm wire mesh. Eight replicates of each treatment were randomly assigned to plots on the terrestrial border of the low marsh where *S. reticulatum* burrowing and herbivory are concentrated. Exclusion cages were inserted 5 cm into the marsh surface, effectively preventing access to large recreationally fished predatory crabs and fish (e.g. striped bass, *Morone saxatilis*, blue crabs, *Callinectes sapidus* and smooth dogfish, *Mustelus canis*) and green crabs (*Carcinus maenas*), a compensatory predator of *S. reticulatum* (Bertness & Coverdale 2013). Exclusion cages allowed *S. reticulatum* to move in and out of cages freely via underground burrow networks. The 2-cm mesh also excluded all but the smallest juvenile predatory crabs (*C. sapidus* and *C. maenas*), which have previously been shown to be incapable of consuming adult *S. reticulatum* (Coverdale et al. 2013b). Predator exclusion cages also effectively excluded mammalian predators (e.g. raccoon, *Procyon lotor*) as well as birds (e.g. night heron, *Nycticorax nycticorax*). Cage controls were identical in dimension but lacked tops and mesh sides were elevated 15 cm over the substrate to allow predator access; access for the dominant *S. reticulatum* predators (*C. sapidus* and *C. maenas*) was not restricted by procedural control cages. Unmanipulated control plots were marked with corner posts. *S. reticulatum* burrow density, grazing pressure (per cent stems grazed) and per cent vegetation cover within each replicate plot were quantified at the initiation of the experiment to test whether starting conditions were similar across treatments. Variables were transformed when necessary to meet the assumptions of ANOVA and were analysed with a one-way ANOVA with treatment as the factor.

**Effects of *S. reticulatum* herbivory and burrowing**

To assess the effect of predator exclusion on *S. reticulatum* herbivory, we transplanted ungrazed cordgrass cores from a common source site in Narragansett Bay at the terrestrial border of each plot in May 2013. Cordgrass cores were observed weekly to ensure survival and stems were counted and scored for herbivore damage after 3 months, at which point the majority of the cordgrass had flowered. *S. reticulatum* grazing leaves characteristic rasped edges and clipped blades on cordgrass (Holdridge et al. 2008), therefore we were confident in concluding that *S. reticulatum* is the contributing grazer among potential salt marsh herbivores. The proportion of final stems grazed was analysed with a one-way ANOVA (caged vs. cage control vs. control).

To avoid disturbing enclosures, we quantified per cent bare space and *S. reticulatum* burrow density within two 0.25 m² quadrats divided into 100 5 x 5 cm sub quadrats along the top and bottom edge of all replicates after cordgrass began flowering. *S. reticulatum* burrows are easily distinguished from other crab burrows such as fiddler crabs (*Uca pugnax*) and have been previously shown to be closely associated with *S. reticulatum* abundance and herbivory (Holdridge et al. 2008; Coverdale et al. 2012, 2013b). We monitored the upper and lower halves in each replicate to quantify elevation effects, as *S. reticulatum* grazing is concentrated at the terrestrial border of the cordgrass zone. Within each zone, we also harvested cordgrass in two centrally placed 10 x 10 cm sub quadrats, and counted, dried and weighed them to quantify above-ground cordgrass biomass. All sub quadrats within the upper and lower border of the plots were pooled to yield average values for each elevation. Per cent bare space, *S. reticulatum* burrow density, and above-ground biomass were transformed to meet the assumptions of ANOVA and analysed with nested ANOVAs [elevation (plot) and treatment].

**Effects of water movement**

Previous studies suggest that wave exposure may contribute to die-off (Smith & Carullo 2007). Therefore, we tested time integrated wave exposure in each of our plots to see if there were inherent differences that might contribute to variations in die-off intensity. We deployed a magnesium calcite chalk block within the top edge of each plot to compare water movement among replicates in the first week of July (see Bertness et al. 1991). Chalk blocks were pre-weighed, glued to a hardware cloth base, pinned to the substrate with wire staples and left in the field for 5 weeks. Chalk blocks were then dried at 40 °C to a constant weight, and reweighed. Chalk loss/treatment was used as an integrated measure of wave exposure over time. Per cent chalk block dissolution was analysed with a one-way ANOVA (caged vs. cage control vs. control).

**Nutrient effects**

Previous studies suggest that eutrophication can cause large-scale marsh die-off (Deegan et al. 2012). To determine if eutrophication was a driver of small-scale variation in die-off intensity, we quantified differences in ambient nitrogen levels across treatments by transplanting an undamaged caged common source cordgrass core on the terrestrial border of each plot in mid May 2013. Cores were caged above- and
belowground with 1 cm galvanised hardware cloth to prevent herbivory (Coverdale et al. 2012). Hardware cloth cages do not influence cordgrass growth (Holdredge et al. 2008; Coverdale et al. 2012). The aboveground biomass of each core transplant was harvested, dried at 40 °C and weighed after cordgrass flowered in August.

Aboveground cordgrass transplant biomass was used to determine if cordgrass growth potential was similar across treatments; differences in growth potential may indicate local-scale pollution (Smith & Carullo 2007) or disease (Elmer et al. 2013) effects. To determine aboveground per cent leaf tissue nitrogen for each transplant core leaf tissue from each transplant core was dried in a convection oven, coarsely ground and dried at 60 °C before further grinding. Samples were analysed for per cent nitrogen using an elemental analyser (Model NC2100; ThermoQuest CE Instruments, San Jose, CA, USA). Aboveground biomass, and per cent nitrogen were analysed with separate one-way ANOVAs (caged vs. cage control vs. control).

Due to concerns about winter storm damage disturbing experimental plots, we present data from within a single growing season.

RESULTS

Initial vegetation cover, herbivory and burrow density did not differ across treatments (F2,21 = 1.02, P > 0.25; F2,21 = 1.45, P > 0.25; F2,21 = 0.30, P > 0.50 respectively).

Total predator removal from vegetated creek banks for a single growing season significantly increased S. reticulatum burrow density and bare space and decreased cordgrass abundance (Fig. 1). Final herbivory on uncaged cordgrass transplants varied across treatments: full predator exclusion plots had >100% more herbivory than cage control and control plots with predator access (F2,20 = 28.77, P < 0.0001; Fig. 2a). Aboveground cordgrass biomass mirrored differences in herbivory, with lower cordgrass biomass in high elevation subquadrats along the grazing border than in the lower elevation subquadrats (F24,21 = 3.37, P < 0.05; Fig. 2b). Overall, excluding predators led to a >60% decrease in aboveground cordgrass biomass compared to cage control and control plots (F2,21 = 23.18, P < 0.0001; Fig. 2b).

S. reticulatum burrow density and bare space also varied with visibly striking differences between control and predator exclusion plots after only 3 months (Fig. 1). S. reticulatum burrow densities were similar across elevations (F24,21 = 1.44, P > 0.10); however, predator exclusion led to a >95% overall increase in burrow density relative to cage control and control plots (F2,21 = 10.62, P < 0.001; Fig. 3a). Within replicates, the amount of bare space was higher in high elevation subquadrats along the grazing border than low elevations (F24,21 = 2.40, P < 0.05) and excluding predators led to >150% increase in bare space (F2,21 = 27.88, P < 0.0001; Fig. 3b).

The biomass and nitrogen content of caged cordgrass core transplants did not vary across treatments (F2,21 = 1.51, P > 0.05; F2,21 = 0.57, P > 0.05 respectively). There were also no differences in chalk block dissolution across treatments (F2,21 = 0.98, P > 0.25).

DISCUSSION

Our experimental predator exclusion provides substantial evidence for the potential importance of top down control in triggering rapid shifts in New England salt marshes. As pre-

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dicted by comparative studies of sites with and without preda-
tor depletion and recreational overfishing (Altieri et al. 2012),
excluding predators for a single growing season led to a
>100% increase in *S. reticulatum* herbivory (Fig. 2a), a >60%
decrease in aboveground cordgrass biomass (Fig. 2b), a >95%
increase in *S. reticulatum* substrate disturbance (Fig. 3a) and
>150% increase in unvegetated bare space relative to control
plots (Fig. 3b). We found no differences in wave exposure or
nitrogen among our plots, suggesting that neither wave expo-
sure nor nutrients contributed to the variation in experimen-
tally triggered die-off. These results suggest that predator
depletion, over the course of a single growing season, is capa-
bles of causing rapid, dramatic shifts in the biotic and abiotic
condition of New England salt marshes.

Many of the predators of *S. reticulatum* are recreationally
harvested, and depletion of these species (e.g. *M. saxatilis*,
*C. sapidus*, *M. canis*; Altieri et al. 2012) is a pressing regi-
onal conservation concern. Previous work indicates that the
biomass of non-harvested species (spider crabs, *Libinia
emarginata*, diamondback terrapins, *Malaclemys terrapin* and
mummichog fish, *Fundulus heteroclitus*) do not differ
between healthy and die-off salt marshes, suggesting that
 predator depletion in this system is the result of targeted
overfishing and not a more general fisheries decline (Altieri
et al. 2012).

Interactions between predators and *S. reticulatum* have been
shown to be both consumptive and non-consumptive in na-
ture. Non-consumptive effects have strong, cascading effects
on *S. reticulatum* behaviour, including foraging and herbivory
(Bertness & Coverdale 2013; Coverdale et al. 2013b). As a
result of perceived risk, *S. reticulatum* at our study site likely
migrated locally to the refugia provided by full predator
exclusion cages, potentially contributing significantly to the
rapid change observed in this study. Natural refugia, includ-
ing *Sesarma* burrows, have been shown to cause dense *Sesar-
ma* aggregations and localised depletion of above- and
belowground cordgrass biomass (Coverdale et al. 2012). Simi-
lar examples of non-consumptive effects in rocky shores
(Trussell et al. 2002), freshwater lakes (Peacor & Werner
1997) and terrestrial grasslands (Schmitz 1998) suggest that

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non-consumptive effects may be a ubiquitous driver of trophic cascades and that effective predator conservation is urgent (Ripple et al. 2014).

Similar predator removal experiments are rare in salt marsh ecosystems and have generally focused on the effects of intermediate predators on marsh invertebrates (e.g. Vince et al. 1976; Kneib & Stiven 1982). To our knowledge, this is the first experimental study to investigate trophic cascades initiated by top predators in salt marshes. All previous experimental studies examining the potential for trophic cascades impacting salt marsh foundation species have been comparative studies manipulating grazers at grazed and ungrazed sites (Silliman & Bertness 2002; Altieri et al. 2012; Coverdale et al. 2013a). This is in stark contrast to the abundance of experimental top predator removal studies in rocky shore (e.g. Paine 1976), soft sediment (e.g. Wilson 1991) and coral reef habitats (e.g. Hughes 1994). Such studies are critical to understanding the causes and consequences of marsh die-off throughout the western Atlantic.

The last 60 years has seen a dramatic shift in ecosystems thought to be controlled exclusively by bottom up forces. Many ecosystems, including kelp forests, coral reefs and salt marshes have been shown to shift from bottom up to top down control after human disturbance (Estes & Palmisano 1994; Hughes 1994; Jackson et al. 2001; Bertness et al. 2008). The idea that these shifts represent real responses to changing conditions and not simply an increased focus on top down processes is becoming increasingly clear.

Salt marsh die-offs resulting from dysfunctional food webs and runaway consumption have also been documented in the Canadian subarctic (Jeffries et al. 2006), and the South-eastern and Gulf Coasts of the United States (Silliman & Bertness 2002). With the mounting number of comparative and experimental studies indicating strong consumer control in salt marshes, it is imperative that the multiplicative and potentially interactive effects of both top down and bottom up forces be included in the management and conservation of salt marsh ecosystems (Costanza et al. 1997). This is particularly pressing given the environmental challenges salt marshes are predicted to face over the next century (Jackson et al. 2001; Gedan et al. 2009; Hoegh-Guldberg & Bruno 2010) and the valuable ecosystem services they provide. Furthermore, there is increasing evidence that salt marsh productivity is driven by interactions between physical factors and consumer pressure, which may operate at different spatial and temporal scales (Jeffries et al. 2006; Bertness et al. 2008; Deegan et al. 2012). While our results indicate that predator depletion can cause rapid, dramatic shifts in the biotic and abiotic condition of New England salt marshes, increasing population density and human activity in coastal areas suggests that multiple interacting threats are likely to become increasingly common (Jackson et al. 2001), with the potential to fundamentally alter ecosystems worldwide.

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AUTHORSHIP

MDB designed the project with help from CPB and TCC; all authors performed the experiments; MDB and CPB wrote the manuscript; CPB, MCB, SMC and ERS conducted the analyses; all authors edited the manuscript.

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