



Burrowing and foraging activity of marsh crabs under different inundation regimes

Katelyn Szura^a, Richard A. McKinney^{b,*}, Cathleen Wigand^b, Autumn Oczkowski^b, Alana Hanson^b, John Gurak^c, Melanie Gárate^a

^a Department of Biological Sciences, University of Rhode Island, 120 Flagg Rd, Kingston, RI 02881, USA

^b Atlantic Ecology Division, ORD-NHEERL, U.S. Environmental Protection Agency, 27 Tarzwell Dr., Narragansett, RI 02882, USA

^c The Scripps Research Institute, 10550 N Torrey Pines Rd., La Jolla, CA 92037, USA

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ABSTRACT

New England salt marshes are susceptible to degradation and habitat loss as a result of increased periods of inundation as sea levels rise. Increased inundation may exacerbate marsh degradation that can result from crab burrowing and foraging. Most studies to date have focused on how crab burrowing and foraging can impact the dominant low marsh plant species, *Spartina alterniflora*. Here we used a mesocosm experiment to examine the relationship of foraging and burrowing activity in two dominant New England crab species, *Sesarma reticulatum* and *Uca pugnator*, and the combined effect of inundation, on the dominant high marsh plant species *Spartina patens* using a 3×2 factorial design with three crab treatments (*Sesarma*, *Uca*, control) at two levels of inundation (low, high). Plants were labeled with a nitrogen (N) stable isotope tracer to estimate plant consumption by the two crab species. At both levels of inundation, we found that *S. reticulatum* had a significant negative impact on both above- and below-ground biomass by physically clipping and uprooting the plants, whereas *U. pugnator* had no significant impact. Low inundation treatments for both crab species had significantly greater aboveground biomass than high inundation. Stable N isotope tracer levels were roughly the same for both *S. reticulatum* and *U. pugnator* tissue, suggesting that the impact of *S. reticulatum* on *S. patens* was not through consumption of the plants. Overall, our results suggest the potential for *S. reticulatum* to negatively impact marsh stability, and that effects of crab foraging behavior may be heightened by increased inundation.

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1. Introduction

Salt marshes are important coastal ecosystems that provide a wide array of beneficial services: they buffer coastlines against storm events (Costanza et al., 2008), act as one of the largest sinks for greenhouse gases (McLeod et al., 2011), provide habitat for many species, and help to filter out excess nutrients from runoff (Kennish, 2001). Salt marshes in the northeastern U.S. and their associated benefits are currently at risk from a variety of stressors, as indicated by recently reported increases in areal and vegetation losses as well as overall marsh fragmentation (Kirwan and Megongial, 2013; Smith et al., 2012; Watson et al., 2014). Possible causes for marsh loss include human alterations of the marsh landscape (Bertness et al., 2002), eutrophication (Deegan et al., 2012), drought (McKee et al., 2004), disease (Elmer, 2014), and herbivory (Coverdale et al., 2012). Sea level rise is also a contributing factor and appears to be exacerbating the detrimental effects of any one, or all, of the above (Alber et al., 2008). Sea level rise in the northeastern

U.S. is particularly likely to drive marsh loss and fragmentation since it is occurring at an accelerated rate of roughly three to four times the global average (Sallenger et al., 2012).

By affecting plant biomass, herbivores may have strong impacts, both positive and negative, on saltmarsh structure and function (e.g., Alberti et al., 2011; Daleo et al., 2011; Ford et al., 2013). The extent to which herbivorous animals may affect a marsh is species-specific. Studies have shown that at high densities, geese, nutria, snails, crabs, and insects can reduce plant productivity and even cause plant mortality through foraging behavior (Evers et al., 1998; Holdredge et al., 2009; Long and Porturas, 2014; Silliman and Bertness, 2002). In addition, several herbivore species have been shown to impact marsh stability and vegetation dynamics through burrowing behavior. Burrowing herbivores are bioturbators, influencing overall plant health and substrate stability by disturbing surrounding sediment and actively consuming plant roots (Andersen, 1987). Increasing crab abundances in New England may be impacting marshes not only through their foraging behavior, but through burrowing activity as well (Coverdale et al., 2012; Neckles, 2015; Smith and Green, 2013).

In New England, several species of crabs inhabit salt marshes including *Carcinus maenas* (green crab), *Sesarma reticulatum* (purple marsh

* Corresponding author.

E-mail address: mckinney.rick@epa.gov (R.A. McKinney).

crab, hereafter *Sesarma*), and three *Uca* spp.: *Uca pugnax* (mud fiddler crab), *Uca pugilator* (sand fiddler crab), and *Uca minax* (red-jointed fiddler crab) (Williams, 1984). Most of these crabs are active burrowers that maintain individual or communal burrows, some of which can form interconnected, branching networks (Aspey, 1978; Christy, 1982; Seiple and Salmon, 1982). Several of the larger crab species (*Carcinus maenas* and *Uca minax*) are not active or extensive burrowers and instead will utilize burrows made by smaller crabs, widening them for their own use (Williams, 1984). It is the active burrowing crabs *Sesarma*, *U. pugnax*, and *U. pugilator*, which have been gaining attention recently for their potential to significantly alter marsh landscapes (Bertness et al., 2014; Coverdale et al., 2012; Smith and Green, 2013).

Sesarma and *Uca* spp. differ in their feeding and burrowing activities and thus they have the potential to impact marsh health in different ways. Excessive burrowing and bioturbation can lead to creek bank weakening, lowered plant productivity or even mortality, and increased soil erosion (Smith and Green, 2013; Wilson et al., 2012). *Sesarma* actively graze on marsh grasses both in the high and low marsh. They preferentially feed on the common low marsh grass, *Spartina alterniflora* (Seiple and Salmon, 1982), but have also been documented consuming the common high marsh species, *Spartina patens* (Smith et al., 2012, 2013). In sufficiently high densities, *Sesarma* can completely denude and weaken areas of a marsh landscape by the consumption of above- and below-ground *S. alterniflora* biomass and subsequent soil destabilization resulting from loss of plants and eventual decay of root material (Coverdale et al., 2012). In contrast, *Uca* spp. are deposit feeders and sift sediment to extract detritus, bacteria, and algae (Teal, 1958; Zeil et al., 2006). Several studies have reported positive impacts of *Uca* burrowing on marsh vegetation through bioturbation, which can help oxygenate sediment and enhance availability of organic matter (Bertness, 1985; Hughes et al., 2014; Katz, 1980). Both *Sesarma* and *Uca* spp. have the capability of moving significant volumes of sediment on the marsh landscape (Coverdale et al., 2012; Katz, 1980).

While many studies have documented the impacts of *Sesarma* and *Uca* spp. foraging on marsh vegetation, few have specifically examined burrowing activity itself, or differences in the extent of burrowing and foraging associated with level of marsh inundation. Burrowing and foraging activity may make marshes more susceptible to accelerated sea level rise and inundation by exacerbating loss of marsh substrate, changing the physical structure of soils, and through the detrimental effects of herbivory on flood intolerant plants such as *S. patens* that are already under stress from inundation. Therefore, it will be increasingly important to gain an understanding of how the activity of burrowing crabs may respond to increasing levels of inundation and hence potentially alter marsh landscapes. In this study, we used a mesocosm experiment to examine burrowing and foraging activity of *Sesarma* and *Uca pugilator* (hereafter *Uca*) over a seven week period from June through mid-August. We examined the impact of crab burrowing and foraging activity on the high marsh plant *S. patens* under two fixed marsh inundation regimes. Our objectives were to document species-specific levels of burrowing activity, and the impacts of foraging and burrowing on *S. patens* under the two inundation regimes. A nitrogen stable isotope tracer was added to the plants prior to crab exposure to test the hypothesis that crabs are consuming *S. patens* as reported in field studies (Smith et al., 2012). Our results will provide an understanding of the impacts to salt marshes from burrowing organisms as inundation increases under the current state of sea level rise.

2. Methods

2.1. Experimental design

Our experiment was conducted in a greenhouse facility in Narragansett, RI in tanks (700 L, 1.2 m diameter, 0.6 m height) that received flow-through seawater from Narragansett Bay and were linked to timers to simulate a semi-diurnal tidal regime. We used a 3 × 2 factorial design

with crab (*Uca*, *Sesarma*, control – no crabs) and inundation (low, high) as the treatments. Crab treatments were established in experimental pots (34.5 cm diameter, 24.5 cm height, 0.09 m² area) maintained at two different levels of inundation, which were typical elevations for southern New England: low, approximating 10 cm above mean high water; and high, approximating 10 cm below mean high water (Watson et al., 2014). Experimental pots were subjected to filling from low tide height to high tide height over the course of 4 h, remained at high tide over a 2-h slack period, and then drained back down to low tide followed by another 2-h slack period. Overall the experiment consisted of six replicates for each crab treatment at each inundation level, or 36 total experimental pots. The simulation of varying inundation regimes by setting experimental pots at different elevations either in a field setting or in a greenhouse has been employed by others to examine marsh system responses to single and/or multiple stressors (e.g., Hanson et al., 2016; Kirwan and Guntenspergen, 2012; Morris et al., 2013; Watson et al., 2014). In our study each experimental pot had three small plugs of the graminoid *S. patens* (Environmental Concern Inc., St. Michaels, Maryland USA) planted in the center. We placed two individual crabs (either *Uca* or *Sesarma*) into each treatment for an initial density of 22 crabs m⁻². *Sesarma* were collected using pit traps at Colt State Park in Bristol, RI (41°40'55.7"N 71°17'45.3"W) and *Uca* were collected by extracting them by hand from burrows using a shovel at Mary's Creek in Warwick, RI (41°41'18.8"N 71°27'03.1"W). Average size of *Sesarma* was 21.3 ± 2.0 mm length and 25.7 ± 2.3 mm width. *Uca* measured an average 11.8 ± 1.6 mm length and 16.6 ± 2.3 mm width. All crabs in the experiment were male. We used aluminum flashing 25.5 cm in height around the perimeter of the experimental pots and plastic mesh on the bottom drains of the pots to prevent the escape of crabs. The six experimental pots per tank were arranged in an overall circular pattern on the two different inundation platforms with three experimental pots per platform. To minimize potential stress from lack of ambient rainfall, plants were watered three times per week by pouring 167 mL of tap water over each pot using a watering can. The experiment was conducted over a total of seven weeks from 30 June 2014 to 18 August 2014.

2.2. Measurements

All response variables were measured in the experimental pots. Plant heights and densities were measured at the start of the experiment and during week four. We checked for uniformity in initial plant biomass using initial plant heights and densities and an allometric relationship between stem height and biomass for *S. patens* (K. Szura, unpublished data) and did not find any statistically significant differences between treatments. Burrow densities and diameters were measured 24 h after crabs were initially introduced, and thereafter once per week for the first six weeks of the experiment. Since *Sesarma* did not initially attempt to dig burrows and there was concern about premature mortality associated with exposure, a single refuge hole 30 mm in diameter and 50 mL in volume was artificially created in each *Sesarma* treatment. Artificially-created refuge holes were not counted or included in burrow density measurements. At the conclusion of the experiment, aboveground biomass was measured by clipping all remaining *S. patens* stems at the base and drying them to a constant weight. Below-ground biomass was measured by wet sieving roots (2 mm sieve) and then drying them to a constant weight. Macroalgae density was approximated using visual percent estimates of percent macroalgae cover in each pot.

Edaphic variables were measured from 18 randomly selected pots on 31 July 2014, during the 2 hr low slack period of the tide cycle. Soil pH was measured from a soil slurry made by homogenizing approximately 10 mL of surface soil (top 3 cm) and 15 mL of deionized water with an Orion Star A326 pH meter (Thermo Scientific, Waltham, Massachusetts, USA). Soil surface moisture content was measured using a volumetric water content sensor (Decagon Devices, Pullman, WA) inserted

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