



## A comparative assessment of salt marsh crabs (Decapoda: Brachyura) across the National Estuarine Research Reserves in New England, USA

Kenneth B. Raposa<sup>1,◉</sup>, Jason S. Goldstein<sup>2</sup>, Kristin Wilson Grimes<sup>3,◉</sup>, Jordan Mora<sup>4</sup>, Paul E. Stacey<sup>5,◉</sup>  
and Richard A. McKinney<sup>6,◉</sup>

<sup>1</sup>Narragansett Bay National Estuarine Research Reserve, Prudence Island, RI 02872, USA;

<sup>2</sup>Wells National Estuarine Research Reserve, The Maine Coastal Ecology Center, Wells, ME 04090, USA;

<sup>3</sup>University of the Virgin Islands, St. Thomas, VI 00802, USA;

<sup>4</sup>Waquoit Bay National Estuarine Research Reserve, East Falmouth, MA 02536, USA;

<sup>5</sup>Footprints In The Water LLC, Moodus, CT 06469 USA; and

<sup>6</sup>National Health and Environmental Effects Research Laboratory-Environmental Protection Agency-Office of Research and Development, Atlantic Ecology Division, Narragansett, RI 02882, USA

Correspondence: K. Raposa; email: [kenneth.raposa@dem.ri.gov](mailto:kenneth.raposa@dem.ri.gov)

(Received 9 May 2019; accepted 21 October 2019)

### ABSTRACT

Salt marsh degradation and loss is accelerating in many regions of the United States as well as worldwide. Multiple stressors are often responsible, sometimes including crab burrowing and herbivory. A recent national assessment identified stark differences in crab indicators between northern and southern New England, with the latter exhibiting intense signs of impacts by crabs, but more details on crab patterns across the entire region are needed beyond this “broad-brush” assessment. Our study used green crab (*Carcinus maenas* (Linnaeus, 1758)) traps, intensive marsh platform burrow counts, and a new multi-metric index of relative crab abundance to examine patterns in marsh crabs across four National Estuarine Research Reserves in New England. Crab indicators from the multi-metric index and burrow counts were higher in southern New England marshes; patterns from trapping of green crabs were less clear. At the marshes examined, green crabs were very abundant in Maine, lower in New Hampshire, and intermediate in southern New England. Our study confirms that abundance and impacts by crabs vary dramatically between sites in northern and southern New England, and provides improved context for managers and researchers when considering impacts to marshes from multiple crab species across New England and elsewhere.

**Key Words:** burrowing habit, crab assessment method, herbivory, multi-metric index, regional assessment, salt marsh sampling, sea-level rise

### INTRODUCTION

Research and management communities have long been focused on impacts to tidal salt marshes from physical stressors such as ditching, eutrophication, hydrologic restrictions, and accelerating sea-level rise (Burdick & Roman, 2012; Deegan *et al.*, 2012; Vincent *et al.*, 2013; Raposa *et al.*, 2017). In regions such as central California, southern New England, and the mid-Atlantic USA, concern is growing over impacts to marshes from increasing populations of crabs. Some crab species are beneficial to marsh vegetation when abundance is low (e.g. Bertness, 1985), but when populations greatly expand, they may elicit negative impacts to marshes via burrowing and/or herbivory (Holdredge *et al.*, 2009;

Vu *et al.*, 2017). New evidence suggests that growth of marsh-crab populations is sometimes linked to increasing levels of marsh inundation, which allows crabs greater access to high marsh habitats during flooding and can weaken soils and facilitate burrowing (Crotty *et al.*, 2017; Raposa *et al.*, 2018). One recent broad-scale study across US marshes revealed that crabs and their impacts are common, but not ubiquitous, across the country, with very different patterns between northern and southern New England (Wasson *et al.*, 2019). *Carcinus maenas* (Linnaeus, 1758) (green crabs, hereafter *Carcinus*) was the only species captured in northern New England, whereas species of *Uca* (marsh fiddler crabs, hereafter *Uca*), *Sesarma reticulatum* (Say, 1817) (purple marsh crab, hereafter *Sesarma*), and *Carcinus* were all abundant in southern New England.

*Carcinus* is known to consume a wide variety of benthic marine macrofauna (Mascaró & Seed, 2001) and has been implicated in declines in soft-shelled clam (*Mya arenaria* Linnaeus, 1758) populations in northern New England (e.g., Bryan *et al.*, 2015). *Carcinus* also prey upon juvenile fishes (e.g., winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792)) (Fulton *et al.*, 2013) and compete with American lobsters (*Homarus americanus* H. Milne Edwards, 1837) for space and resources (Rossong *et al.*, 2006; Williams *et al.*, 2006; Haarr & Rochette, 2012). Other work suggests that the abundance and distribution of *Carcinus* in some estuarine systems may curtail lobster catch, increase the number of antagonistic interactions with lobsters, and limit foraging and shelter use by small juvenile lobsters (Rossong *et al.*, 2011; Goldstein *et al.*, 2017; Rayner & McGaw, 2019). Surveys by the Wells National Estuarine Research Reserve (NERR), Maine have documented extremely high abundances of *Carcinus* in marshes and linked crabs to increased creekbank erosion potential via vegetation loss and reduced soil strength (Aman & Wilson Grimes, 2016).

While *Carcinus* can be common in southern New England marshes, *Sesarma* and *Uca* are more abundant and impactful. For example, many studies have documented extensive *Sesarma* burrowing and herbivory on *Spartina alterniflora* Loisel (smooth cordgrass) in marshes from Long Island Sound to Cape Cod, which can facilitate erosion and loss of seaward marsh edges (e.g., Holdredge *et al.*, 2009; Wilson *et al.*, 2012; Coverdale *et al.*, 2013a). Fiddler crab distributions, primarily *Uca pugnax* (Smith, 1870) (Atlantic marsh fiddler), have also expanded within marshes due to increased flooding from sea-level rise (Luk & Zajac, 2013). Impacts to salt marsh geomorphic integrity by *Uca* are caused by excessive burrowing, which occurs primarily along seaward edges but can extend to the upland edge (Luk & Zajac, 2013; Raposa *et al.*, 2018). The relative degree of impacts to southern New England marshes, and the extent to which these impacts co-occur, is not well known, although conditions associated with sea-level rise can benefit each species (Crotty *et al.*, 2017; Raposa *et al.*, 2018). In the Narragansett Bay NERR, Rhode Island, *U. pugnax* and its burrows are extremely abundant, and creekbank *Sesarma* grazing is also conspicuous in some areas; *Carcinus* is common but impacts are not as apparent (Raposa *et al.*, 2018). Similar conditions also occur across a limited extent of the Waquoit Bay NERR, Cape Cod, MA (KBR, unpublished data).

Crabs are clearly a concern for marshes across New England, with *Uca* and *Sesarma* populations resulting in extensive damage across southern marshes and abundant *Carcinus* populations resulting in damage to some northern marshes. Is the degree of damage caused by each particular species, or the collective stress across species, similar in the two New England sub-regions? This is difficult to answer from studies that are localized to one marsh or estuary, especially if employing different methodologies. The

use of the same or directly comparable methods in broad-scale New England marsh assessments are rare and, to our knowledge, none have been conducted during the recent period of accelerated sea-level rise and increasing crab abundance. Our goal was to provide a regional perspective by concurrently sampling crabs across four New England NERRs using multiple survey methods and sampling gears to fill the gap between crab studies localized to one estuary (e.g., Goldstein *et al.*, 2017; Raposa *et al.*, 2018) and national-scale assessments (Wasson *et al.*, 2019). Further, this design advances our understanding of relative crab impacts between northern and southern New England marshes and tests whether the sampling methods we used identify comparable distributional patterns across sites.

## MATERIALS AND METHODS

### Study sites

Crabs were sampled utilizing three distinct methods at a total of nine salt marshes (either discrete marshes or sections of larger marshes) within the four New England NERRs. These marshes include the Coggeshall and Nag marshes in Narragansett Bay, RI, three sections of the Sage Lot Pond marsh in Waquoit Bay, MA, the Great Bay Farms and Sandy Point marshes in Great Bay, NH, and two sections of marsh in the Webhannet River estuary in Wells, ME (Table 1, Fig. 1). Our initial goal was to use all three methods in all nine marshes. This was ultimately undertaken at six of the nine marshes, but only one or two of the methods was used at the remaining three marshes due to logistical or personnel constraints at some NERRs (Table 1). Despite this variability in sampling sites, each method was used in marshes stretching from RI to ME, thus providing an independent, broad-scale assessment of crabs in New England marshes.

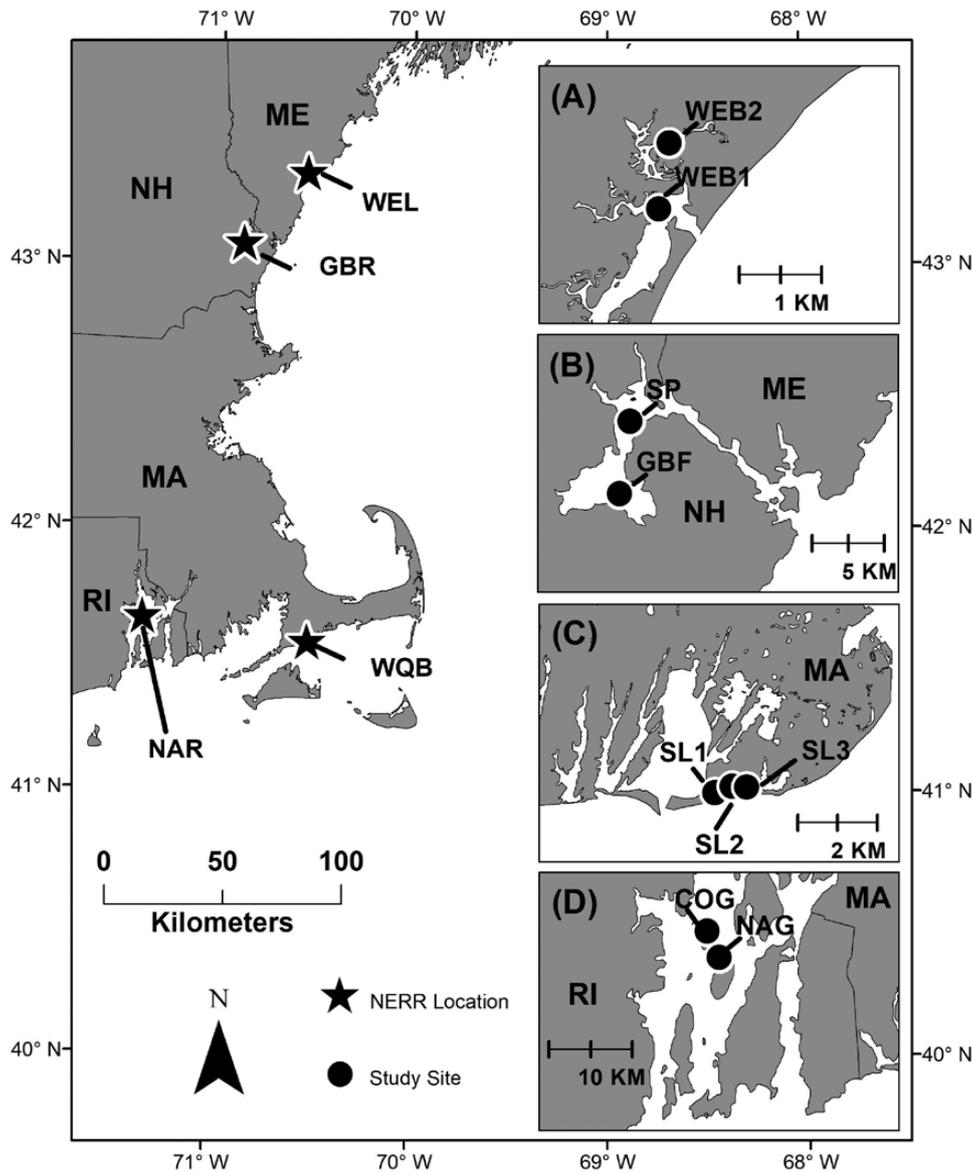
All marshes contained vegetative communities characteristic of New England marsh systems (i.e., dominated by *S. alterniflora* in lower elevation zones that are frequently flooded, and by a mix of salt meadow grasses and forbs in irregularly flooded, high elevation zones) (see Niering & Warren, 1980; Supplementary material Table S1). All marshes also comprised a mosaic of habitat types, including vegetated marsh platforms, ditches, pools, and subtidal and intertidal creeks. Hydrology, salinity, and other physical characteristics, however, varied among marshes (summarized in Table 1).

### Field sampling

We used three methods for two reasons: 1) to provide a more thorough assessment of regional crab patterns than could be obtained by a single method while avoiding inherent biases and limitations

**Table 1.** Descriptive information on each of the sampling marshes in this study. Marsh codes correspond to those shown in the maps in Figure 1. Daily tide range, temperature, salinity, and dissolved oxygen (DO) data are means during the study period from YSI sondes or Hobo dataloggers deployed with green crab traps at each marsh. Percent (%) bare is the mean cover of unvegetated marsh from burrow count sampling. Blank cells indicate that data were not collected at that marsh. “X” indicates when a sampling method was used at a marsh.

| NERR                 | Marsh name              | Code | Latitude | Longitude | Tide range (m) | Temperature (C) | Salinity (ppt) | DO (mg l <sup>-1</sup> ) | % bare | Trapping | Burrows | CAM |
|----------------------|-------------------------|------|----------|-----------|----------------|-----------------|----------------|--------------------------|--------|----------|---------|-----|
| Wells, ME            | Webhannet section 1     | WEB1 | 43.322   | -70.563   |                |                 |                |                          |        |          |         | X   |
|                      | Webhannet section 2     | WEB2 | 43.329   | -70.560   | 2.1            | 17.8            | 22.5           | 8.5                      | 0.4    | X        | X       | X   |
| Great Bay, NH        | Great Bay Farms         | GBF  | 43.061   | -70.832   |                | 24.7            | 15.3           | 7.4                      |        | X        |         | X   |
|                      | Sandy Point             | SP   | 43.056   | -70.904   |                | 18.6            | 16.5           | 7.0                      | 0.3    | X        | X       | X   |
| Narragansett Bay, RI | Coggeshall              | COG  | 41.651   | -71.342   | 1.2            | 24.7            | 28.0           | 4.4                      | 39.7   | X        | X       | X   |
|                      | Nag West                | NAG  | 41.625   | -71.325   | 0.6            | 24.4            | 29.6           | 4.3                      | 34.6   | X        | X       | X   |
| Waquoit Bay, MA      | Sage Lot Pond section 1 | SL1  | 41.553   | -70.512   |                |                 |                |                          | 44.7   |          | X       |     |
|                      | Sage Lot Pond section 2 | SL2  | 41.554   | -70.507   | 0.5            | 25.4            | 30.0           | 3.8                      | 36.3   | X        | X       | X   |
|                      | Sage Lot Pond section 3 | SL3  | 41.553   | -70.504   | 0.4            | 25.8            | 25.2           | 4.4                      | 36.4   | X        | X       | X   |



**Figure 1.** Locations of the four National Estuarine Research Reserves (NERR) sites in New England, USA studied (left) and specific marshes that were sampled within each NERR (right). Wells ME, WEL (A); Great Bay NH, GBR (B); Waquoit Bay MA, WQB (C); Narragansett Bay RI, NAR (D). Full marsh names that correspond to the codes shown here are listed in Table 1.

of single methods (Rozas & Minello, 1997) that are often designed for a specific habitat type (e.g., crab traps in creeks, pitfall traps on the marsh surface), and 2) to introduce alternate sampling methods to all reserves that previously used one or two methods or were not sampling at all, which may have obscured a clear understanding of patterns across the region. We assessed crab abundance using: 1) crab traps set in shallow subtidal marsh creeks; 2) intensive marsh platform burrow counts; and 3) a new multi-metric index of crab abundance that is referred to as the crab assessment method, or CAM index. All three methods were used during June through September 2015 to capture summer and fall conditions. Hereafter, “marsh” refers to individual marshes, and “site” to the four NERRs, which included multiple marshes as described above.

#### Crab traps

In seven of the nine NERR study marshes (Table 1), two replicate standardized *Carcinus* traps (“Blanchard”-style design, obtained from the Maine Department of Environmental Protection; 93 cm

length, 48 cm diameter, 40 cm funnel opening, 1.3 cm mesh size; see Young *et al.*, 2017) were deployed for a 24 hr period, approximately bi-weekly. One trap was set in an upstream segment of a main tidal creek and one in a lower segment of the same creek, separated by ~ 50 m between the two traps. We chose locations for trapping that were: 1) adjacent to an impacted section of marsh where there was direct evidence of crab burrowing activity; and 2) deep enough at low tide to ensure continuous submergence of the entire trap. Traps were baited with fresh-frozen herring and all traps received the same amount of bait, which was suspended in the center of the trap using a mesh lobster-bait bag. During each sampling period, we deployed either a YSI water quality datasonde (model 6600; YSI, Yellow Springs, OH, USA) or a HOBO pendant temperature logger (model UA-002-08 or U24-002-C; Onset Computer, Bourne, MA, USA) at each marsh to collect temperature and (with the YSI) other basic water quality data throughout each trap deployment. All crabs from each trap were either enumerated, sexed, and measured in the field using calipers (standard carapace width, CW, to the nearest 1 mm) or

tagged and frozen for later analysis in the laboratory. All crabs were removed and properly disposed of between sampling events following permit requirements.

### Burrow counts

Burrow density (number  $m^{-2}$ ) was quantified on one day from 20 replicate quadrats ( $0.5 \times 0.5$  m) in seven of the nine marshes (Table 1). Five quadrats were sampled in each of four different habitat types (bare creekbanks, vegetated creekbanks, marsh platform, and marsh/upland transition zone) in three marshes. Bare creekbanks were absent in the remaining four marshes, and all creekbank burrow counts were collected from vegetated creekbanks. All crab burrows greater than 3 mm diameter were counted in each quadrat.

### Crab assessment method (CAM index)

The CAM index is a new multi-metric index introduced herein that integrates field data for six metrics of crab abundance into one overall composite index score. Data for the six CAM index metrics were collected on one day along five random transects in eight of the nine study marshes (Table 1), with each transect including two sub-components arranged in a “T” pattern: a transect running parallel to a creek for 20 m along the marsh/creek edge (the “creekbank” transect sub-component), and a second transect running from the center of the creekbank transect, landward across the marsh platform to the upland edge (the “platform” transect sub-component). On each transect, 10 platform quadrats ( $0.5 \text{ m} \times 0.5 \text{ m}$ ) were spaced equidistantly from each other at distances based on overall transect length, and five creekbank quadrats were spaced 4 m apart. Four of the metrics were taken along the creekbanks: crab abundance, burrow density, % grazed stems, and % bare ground. The remaining two metrics were taken across the marsh platform: crab density and burrow density.

The creekbank crab metrics were defined as: 1) abundance as an assigned score based on the number of crabs observed while walking the 20 m creekbank length (0 = none; 1 = low [ $< 10$ ], 2 = medium [ $10\text{--}100$ ], 3 = high [ $> 100$ ]), 2) burrow density (number  $m^{-2}$ ) as the number of burrows larger than 3 mm width counted in each quadrat and multiplied by four, 3) % grazed stems is the percentage of up to 12 randomly selected *S. alterniflora* stems in each quadrat that showed clear signs of *Sesarma* grazing (Holdredge *et al.*, 2009), and 4) % bare ground is the percent cover of bare ground in each quadrat determined by the Braun-Blanquet visual method (Kent & Coker, 1992). The platform metrics were calculated as 1) crab density as the total number of crabs observed by two observers walking a 2 m wide band of platform marsh along a transect from water to upland, divided by transect area (length  $\times$  2 m wide) and 2) burrow density as described above for creekbanks.

An overall CAM index score for each marsh was calculated by 1) ranking each of the six metrics across the eight marshes where the CAM index was conducted (8 = highest marsh score for a metric, 1 = lowest score), 2) summing all the metric ranks at each marsh, 3) dividing that sum by 48 (the maximum possible total; six metrics, eight marshes), and 4) multiplying by 100. Overall marsh CAM index scores could therefore range from  $\sim 13$  to 100 with higher scores indicating higher crab abundance or impacts on marsh structure. We are using burrow density as a general indicator of crab impacts. This indicator must be considered in context because at low densities, *Uca* burrows can actually prove to be beneficial to marsh vegetation (Bertness, 1985).

### Statistical analyses

We compared *Carcinus* CPUE (mean 24 hr catch and effort for each sampling site per month, as in Young *et al.*, 2017) across NERRs using two-way ANOVA with site and month as main factors, followed by Holm-Sidak pairwise comparisons to identify significantly different

pairs of sites or months. We compared median *Carcinus* sizes across sites (pooled across months) using ANOVA on ranks and Dunn's pairwise comparisons because the data were non-normal. We did not statistically compare data from burrow counts or the CAM index across sites because each of these methods was only used once per marsh, and comparisons would have had very limited statistical power due to small sample sizes (1–3 marshes per NERR). Instead, for these methods we calculated a mean for each indicator at each marsh and averaged those across marshes within each NERR to explore patterns across the region. Spearman correlations were run comparing at the marsh level: 1) mean *Carcinus* CPUE, 2) overall burrow density (pooled across all habitats), and 3) overall CAM index scores to determine if the methods correlated with one another or if they produced different results. All statistical tests were run using SigmaPlot version 14.0 (Systat Software, San Jose, CA, USA).

## RESULTS

### Crab traps

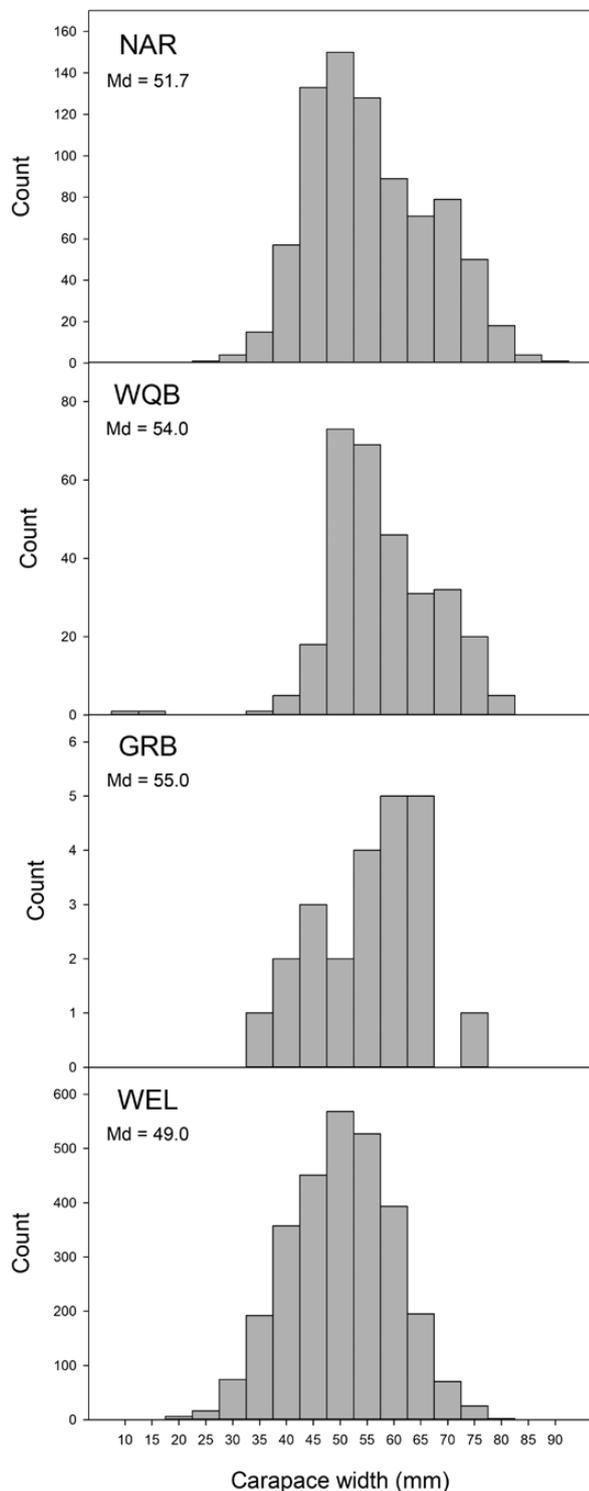
Size distributions of *Carcinus* were generally similar among the Narragansett Bay, Waquoit Bay, and Wells NERRs with a mode around 50 mm CW (ranges of 20–91 mm, 5–79 mm, and 19–76 mm at these three sites, respectively); the mode of the distribution at Great Bay was between 60–65 mm CW (range of 35–74 mm) (Fig. 2). Median *Carcinus* size was significantly different among sites (ANOVA on ranks,  $H = 215$ ,  $P < 0.001$ ), with larger crabs at Waquoit Bay compared to both Narragansett Bay and Wells (Dunn's test,  $P = 0.002$  and  $P < 0.001$ , respectively). This difference is largely due to proportionally fewer individuals smaller than 50 mm CW at Waquoit Bay compared with the other sites. *Carcinus* CPUE also varied significantly among sites (two-way ANOVA,  $F = 28$ ,  $P < 0.001$ ; no differences among months,  $F = 1$ ,  $P = 0.40$ ), with higher catches at Wells compared to all other sites (Holm-Sidak test,  $P < 0.001$  for each test); relative patterns among all sites were similar each month, although declines over time were observed in Narragansett and Waquoit Bays, likely due to disposing of crabs after each sampling session (Fig. 3). By far, most crabs in Great Bay, Waquoit Bay, and Narragansett Bay were male (70%, 75%, and 70%, respectively) but relatively more females were captured in Wells (59% males). To summarize the results from *Carcinus* trapping, *Carcinus* were largest in Waquoit Bay, but much more abundant and with more females in Wells.

### Burrow counts

Burrow densities were much higher in Narragansett Bay compared to other sites, and in southern New England marshes compared to northern sites (Fig. 4). Burrows were extremely high in bare creekbanks in Narragansett Bay (site mean = 176 burrows  $m^{-2}$ ) and decreased steadily across habitats moving towards the upland. Burrows were about equal in bare and vegetated creekbanks in Waquoit Bay and, again, lower towards the upland. Burrows were very low or absent in all habitats in northern New England marshes, and never found on the marsh platform or in the transition zone (in contrast to southern New England, where burrows were found across the entire marsh).

### Crab assessment method (CAM index)

Overall CAM index scores, and five of the six metrics included in the index, decreased steadily moving north from Narragansett Bay to Wells; the only metric without a clear regional trend was % bare along creekbanks (Fig. 5). All six metrics were by far highest in Narragansett Bay marshes, and all metrics except % bare creekbanks were very low or zero in Great Bay and Wells. Metric scores were also very low in Waquoit Bay except for platform burrow density, which was intermediate.



**Figure 2.** Size-frequency distributions and median size (carapace width in mm) of green crabs *Carcinus maenas* in the four New England National Estuarine Research Reserves (NERRS). NAR, Narragansett Bay, RI; WQB, Waquoit Bay, MA; GRB, Great Bay, NH; WEL, Wells, ME. Note the different scales of the y-axes.

#### Correlations across marshes

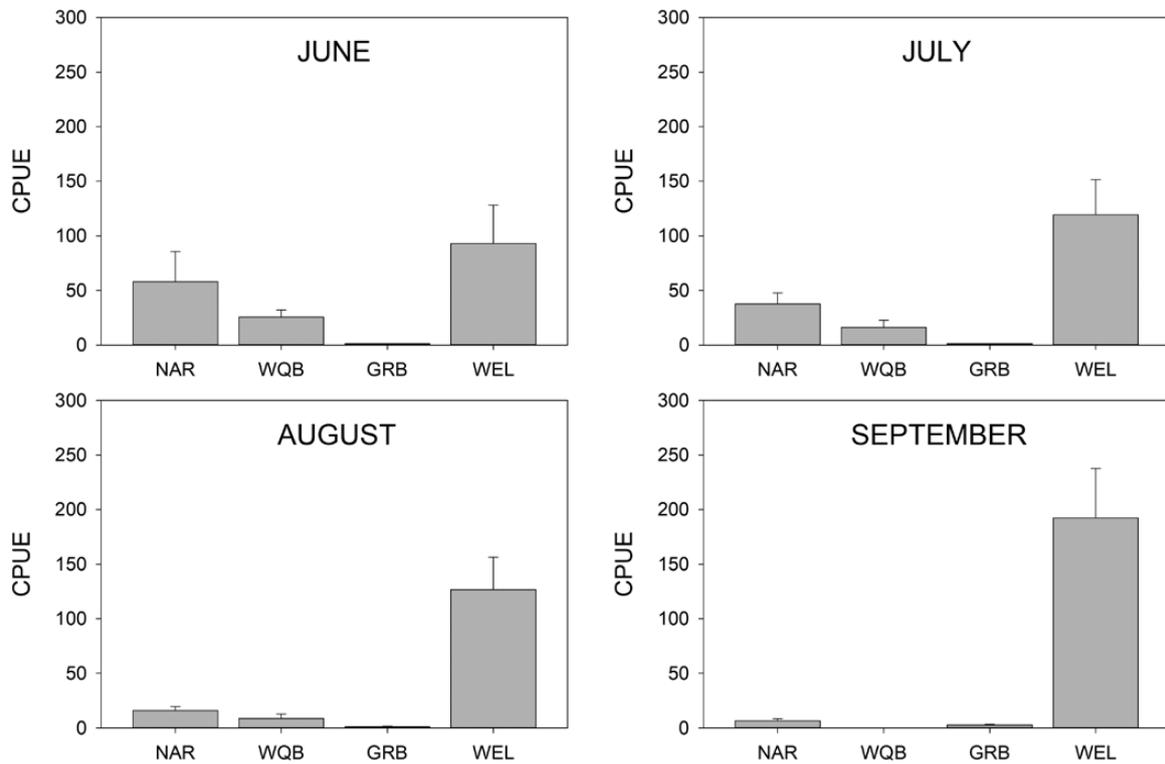
At the marsh level, burrow density and overall CAM index scores were positively correlated with each other ( $N = 6$  marshes,  $r_s = 0.94$ ,  $P = 0.02$ ), but neither was correlated with mean marsh *C. maenas* CPUE (versus burrow density,  $N = 6$ ,  $r_s = -0.03$ ,  $P = 1.0$ ; versus overall CAM index,  $N = 6$ ,  $r_s = 0.04$ ,  $P = 0.91$ ).

## DISCUSSION

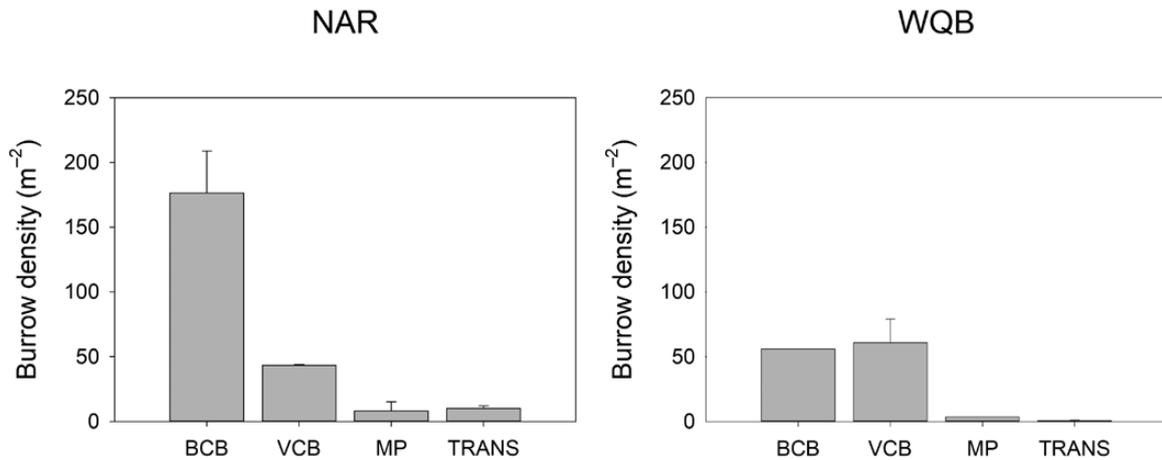
Our study corroborates a recent national-scale assessment that northern and southern sub-regions of New England exhibit stark differences in the distribution and abundance of marsh crabs (Wasson *et al.*, 2019). Crab communities in southern New England marshes are dominated by *Uca*, with *Sesarma* and *Carcinus* common but less abundant. *Carcinus* is generally the dominant species in northern New England, sometimes in great abundance, but *Uca* and *Sesarma* are rare or absent. Other studies show that northern marshes are primarily impacted by *Carcinus* burrowing along creekbanks, and southern marshes by a combination of *Uca* burrowing in multiple habitats and *Sesarma* creekbank herbivory (and to a lesser extent, burrowing) (Holdredge *et al.*, 2009; Aman & Wilson Grimes, 2016; Raposa *et al.*, 2018). In our study, however, the integrative and novel CAM index that includes multiple indicators of crab abundance and impacts across the marsh landscape clearly shows greater overall impacts to southern New England marshes, perhaps due to the presence and behavior of multiple species that were absent in the northern marshes.

Crab trapping surveys from our study documented *Carcinus* in both northern New England NERRs, but abundance varied greatly among marshes. The high CPUE in the Webhannet Marsh (Wells NERR) supports earlier work from Maine that elevated *Carcinus* abundances may impact marshes via creekbank burrowing (Aman & Wilson Grimes, 2016). This pattern, however, is not ubiquitous across even northern New England as evidenced by comparably lower catches in the Great Bay NERR marshes (although we note that seasonal fluctuations can occur and are more likely to be taken into account in studies of longer duration than ours; see Fulton *et al.* 2013). The general pattern of lower *Carcinus* abundance in Great Bay marshes compared to Wells NERR marshes in our study could be due to a wide variety of environmental factors (e.g., depth, biotic interactions, prey abundance, shelter availability, salinity) that drive the distribution of this species in these areas (reviewed in Cosham *et al.*, 2016). Great Bay is also a unique northern New England estuary in that it is expansive and deep, possibly providing numerous alternative subtidal habitats for *Carcinus* (Goldstein *et al.*, 2017) that were not included in our study area. In contrast, *Carcinus* abundance is relatively low in southern New England marshes (compared to other species, such as *Uca*), where its direct impacts to marsh morphology are relatively minimal as it can use *Sesarma* burrows rather than digging new ones (Coverdale *et al.*, 2013b). In some cases, the presence of *Carcinus* can be beneficial via competitive and predatory impacts to *Sesarma*, which allows dieback marshes to recover (Bertness & Coverdale, 2013). In summary, although *Carcinus* is pervasive across New England salt marshes, it is difficult to make broad generalizations at a regional scale because its abundance and impacts vary greatly among marshes.

Burrow counts and CAM index assessments (which include a burrow count component) revealed consistently higher crab indicators in southern than in northern New England marshes, with highest levels in RI. We caution, however, that the small number of marshes in our study may not indicate true patterns among southern New England marshes. Many studies document severe impacts to marshes across this area, including for example, in Cape Cod from intense creekbank *Sesarma* herbivory (Holdredge *et al.*, 2009), RI from both *Uca* and *Sesarma* (Bertness *et al.*, 2014; Raposa *et al.*, 2018), and CT from *Sesarma* herbivory (Schultz *et al.*, 2016). Crab impacts to an individual southern New England marsh likely depend strongly on site-specific conditions including predator abundance and the relative amount of elevation capital/inundation, resulting in high variability even among nearby marshes (Altieri *et al.*, 2012; Raposa *et al.*, 2018). We also caution that the CAM index does not capture all potential impacts from crabs to New England marshes (e.g., food web interactions); thus, the trends observed here are a conservative estimate of impacts. Our study was also limited to a single assessment, and patterns



**Figure 3.** Mean catch-per-unit-effort (CPUE) of *Carcinus maenas* captured at the four New England National Estuarine Research Reserves (NERRs). NAR, Narragansett Bay, RI; WQB, Waquoit Bay, MA; GRB, Great Bay, NH; WEL, Wells, ME. Error bars are 1 SE.

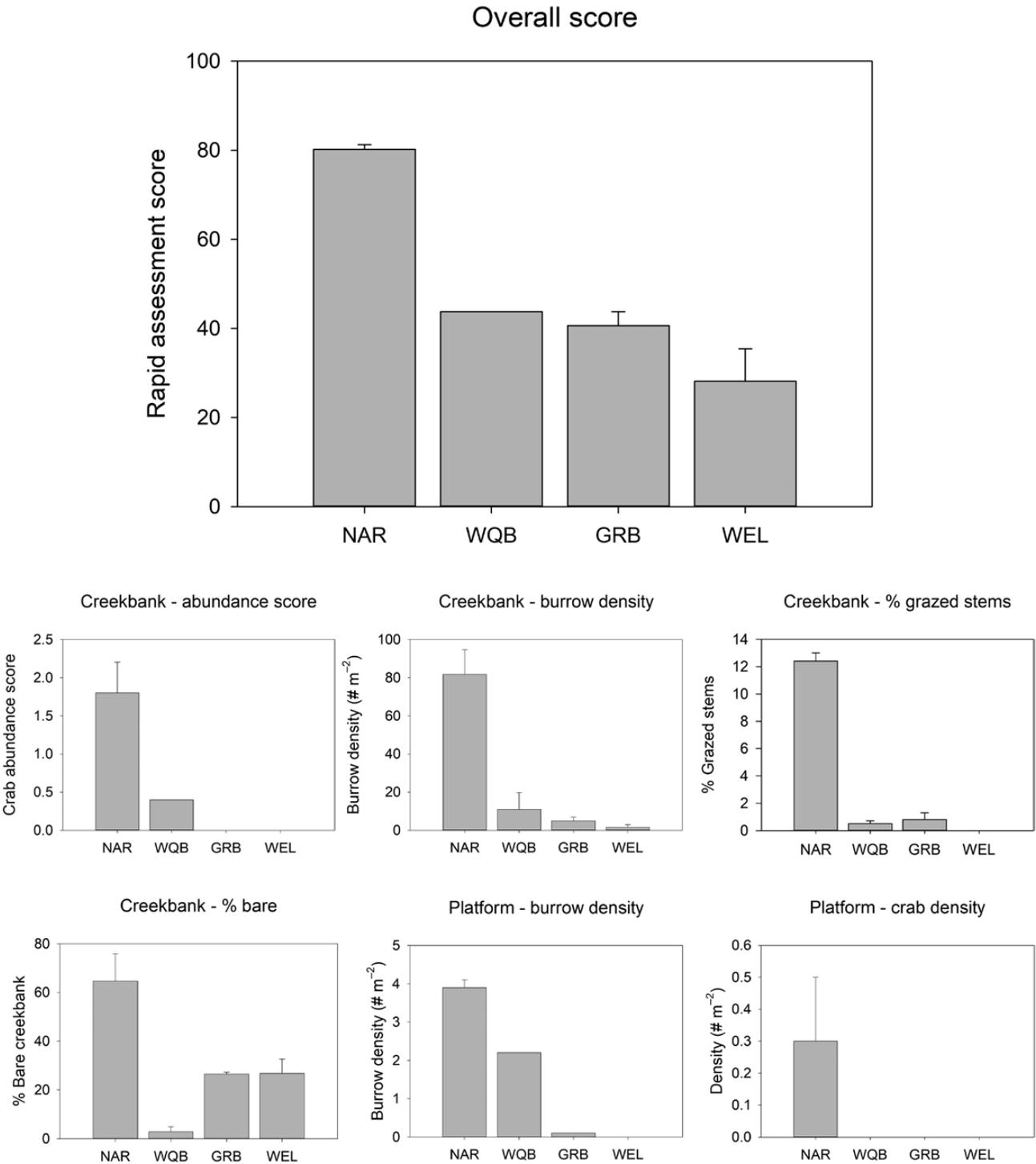


**Figure 4.** Crab burrow densities in marsh habitats at the New England National Estuarine Research Reserves (NERRs). Mean burrow densities at Great Bay, NH and Wells, ME were very low (3.6 and 0.2 burrows m<sup>-2</sup> in vegetated creekbanks in Great Bay and Wells, respectively; absent from all other habitats), and plots for these sites are not shown. BCB, bare creekbanks; VCB, vegetated creekbanks; MP, marsh platform; TRANS, marsh/upland transition; NAR, Narragansett Bay, RI; WQB, Waquoit Bay, MA. Error bars are 1 SE.

among marshes may vary in future studies (e.g., *Uca* or their burrows were not observed in Great Bay, but have since been photographically verified in the Sandy Point Marsh (PS, unpublished 2016 data)). Overall, however, crab impacts in our study were considerably higher in southern than in northern New England marshes.

Comparisons of relative crab impacts to marshes across different areas of New England is hindered by the use of different sampling gears among studies. We found a strong correlation between burrow counts and the CAM index at the marsh level, indicating that these two sampling methods produce similar data and results, but neither method correlated well with crab trapping. This is not surprising because these methods target different

species and are used in disparate habitats. Crab traps are typically set in subtidal marsh habitats such as creeks and channels to collect larger crabs, some of which may not necessarily directly use or impact the marsh platform proper. In contrast, burrow counts and the CAM index focus exclusively on crabs and their impacts to the marsh platform from creekbanks to the upland border and are not species-specific. Coastal managers are largely focused on maintaining and increasing the resilience of existing vegetated salt marsh platforms (Wigand *et al.*, 2017). From that perspective, methods that focus on vegetated habitats such as burrow counts or the CAM index may be more appropriate for gauging crab impacts to southern New England marshes compared to trapping in creeks. In northern New England, where *Carcinus* impacts to



**Figure 5.** Results from the crab assessment method (CAM) index. The overall multi-metric index score, pooled across marshes within each National Estuarine Research Reserve (NERR) site, is shown at top; below are scores for each individual metric within the CAM index, by NERR. NAR, Narragansett Bay, RI; WQB, Waquoit Bay, MA; GRB, Great Bay, NH; WEL, Wells, ME. Error bars are 1 SE.

creekbanks is the current focus, crab traps in creeks may still be more appropriate.

Of the two methods we used on the marsh platform, we recommend the CAM index because it provides more information on a variety of crab indicators for approximately the same effort as conducting more extensive burrow counts. As with other multi-metric indices for marshes (e.g., Raposa *et al.*, 2016), the CAM index we present here can easily be modified in future assessments to include other metrics of crab abundance and impacts. A future

version of the CAM index could include an additional crab trapping component to provide crab metrics from subtidal creek, creekbank, and marsh platform habitats for an even more comprehensive assessment. If assessed across multiple dates, the CAM index could also be used to document and track ecosystem change over time, which may be of interest to managers.

Our study compared data from three different crab-sampling methods, but many more are available, and each can provide data specific to different habitats. Examples include: 1) enclosure traps

with high capture efficiencies that produce estimates of densities in shallow aquatic habitats such as creeks and pools (Raposa *et al.*, 2003) or on the marsh surface (Roman *et al.*, 2002); 2) pitfall traps to estimate relative abundance of different species on the marsh platform (Bertness *et al.*, 2014; Raposa *et al.*, 2018); and 3) cameras to capture time-series photographs or videos (e.g., Hemmi & Zeil, 2003; Bergshoeff *et al.*, 2018). The variety of crab-sampling methods is advantageous because one or more should be appropriate for addressing most questions, but caution is advised because each gear has inherent biases and produces diverse types of data, which may be interpretively inconsistent (Rozas & Minello, 1997; Young *et al.*, 2017), making comparisons challenging.

Concern over crab impacts to New England marshes is growing, and with it a need for accurate and efficient crab-sampling methods that effectively assess impacts to help guide management. To our knowledge, aside from perhaps crab trapping (see Young *et al.*, 2017) and some enclosure traps (Raposa *et al.*, 2003), most marsh-crabs sampling methods have unfortunately not been adequately evaluated and cannot yet be recommended for large-scale or long-term monitoring as well as for inter-comparisons. Pitfall traps, for example, may be a good choice because they are easy to deploy, inexpensive, can be readily standardized, and provide relevant data on community composition, abundance, size and habitat use. But in terrestrial habitats, pitfall traps have been repeatedly shown to be highly biased and inefficient (e.g., Topping & Sunderland, 1992; Spence & Niemela, 1994, and references therein). If this is also true in marsh habitats, pitfall traps may not be a good choice for monitoring. We therefore recommend an increased emphasis on evaluating multiple marsh crab-sampling methods to improve guidance on gear selection for both localized and larger-scale studies.

With many southern New England marshes already on a trajectory towards submergence (Watson *et al.*, 2017), crab abundance and impacts in this region are unlikely to increase further and may even decline as marshes are lost to drowning (Raposa *et al.*, 2018). We expect impacts to increase in northern marshes over time, however, as burrowing and herbivorous species extend their range north (Johnson, 2014) and become more abundant in marshes that should eventually experience net reductions in elevation capital as inundation increases with sea-level rise. Our results therefore represent a quantitative baseline to which future marsh crab assessments might be compared to document responses to climate change, sea-level rise, and other stressors. Future work should nevertheless sample additional sites having larger sample sizes.

## SUPPLEMENTARY MATERIAL

S1 Table. Vegetation in New England National Estuarine Research Reserve (NERR) marshes.

## ACKNOWLEDGEMENTS

We would like to thank Jake Aman, Laura Byergo, Michele Condon, Molly Dennett, Tim Dubay, Amelie Jensen, Jeremy Miller, Annie Procaccini, and Katelyn Szura for field assistance and help with some of the data compilation. This work was supported by grants to all participating reserves from National Oceanic and Atmospheric Administration (NOAA) Office for Coastal Management. This report, Tracking Number ORD-020684, has been reviewed technically by the U.S. Environmental Protection Agency (EPA) Office of Research and Development, National Health and Environmental Effects Research Laboratory, Atlantic Ecology Division, Narragansett, RI, USA and approved for publication. Approval does not signify the contents necessarily reflect the views and policies of the EPA. This article is contribution no. 210

from the Center for Marine & Environmental Studies, University of the Virgin Islands. We also thank the helpful suggestions and comments from two anonymous reviewers, which greatly improved the manuscript.

## REFERENCES

- Altieri, A.H., Bertness, M.D., Coverdale, T.C., Herrmann, N.C. & Angelini, C. 2012. A trophic cascade triggers collapse of a salt marsh ecosystem with intensive recreational fishing. *Ecology*, **93**: 1402–1410.
- Aman, J. & Wilson Grimes, K. 2016. *Measuring impacts of invasive European green crabs on Maine salt marshes: a novel approach*. Report to the Maine Outdoor Heritage Fund, Wells National Estuarine Research Reserve, Wells, ME, USA.
- Bergshoeff, J.A., McKenzie, C.H., Best, K., Zargarpour, N. & Favaro, B. 2018. Using underwater video to evaluate the performance of the Fukui trap as a mitigation tool for the invasive European green crab (*Carcinus maenas*) in Newfoundland, Canada. *PeerJ*, **6**: e4223 [doi: 10.7717/peerj.4223].
- Bertness, M.D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, **66**: 1042–1055.
- Bertness, M.D. & Coverdale, T.C. 2013. An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. *Ecology*, **94**: 1937–1943.
- Bertness, M.D., Brisson, C.P., Bevil, M.C. & Crotty, S.M. 2014. Herbivory drives the spread of salt marsh die-off. *PLoS ONE*, **9**(3): e92916 [doi: 10.1371/journal.pone.0092916].
- Bryan, E., Tan, P. & Beal, B.F. 2015. Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA. *Journal of Experimental Marine Biology and Ecology*, **462**: 62–73.
- Burdick, D.M. & Roman, C.T. 2012. Salt marsh responses to tidal restriction and restoration: a summary of experiences. In: *Tidal marsh restoration: a synthesis of science and management* (C.T. Roman & D.M. Burdick, eds.), pp. 373–382. Island Press, Washington, DC, USA.
- Cosham, J., Beazley, K.F. & McCarthy, C. 2016. Environmental factors influencing local distributions of European green crab (*Carcinus maenas*) for modeling and management applications. *Environmental Reviews*, **24**: 244–252.
- Coverdale, T.C., Axelman, E.E., Brisson, C.P., Young, E.W., Altieri, A.H. & Bertness, M.D. 2013b. New England salt marsh recovery: opportunistic colonization of an invasive species and its non-consumptive effects. *PLoS ONE*, **8**(8): e73823 [doi: 10.1371/journal.pone.0073823].
- Coverdale, T.C., Bertness, M.D. & Altieri, A.H. 2013a. Regional ontogeny of New England salt marsh die-off. *Conservation Biology*, **27**: 1041–1048.
- Crotty, S.M., Angelini, C. & Bertness, M.D. 2017. Multiple stressors and the potential for synergistic loss of New England salt marshes. *PLoS ONE*, **12**(8): e0183058 [doi: 10.1371/journal.pone.0183058].
- Deegan, L.A., Johnson, D.S., Warren, R.S., Peterson, B.J., Fleeger, J.W., Fagherazzi, S. & Wollheim, W.M. 2012. Coastal eutrophication as a driver of salt marsh loss. *Nature*, **490**: 388–392.
- Fulton, B.A., Fairchild, E.A. & Warner, R. 2013. The green crab *Carcinus maenas* in two New Hampshire estuaries. Part 1: Spatial and temporal distribution, sex ratio, average size, and mass. *Journal of Crustacean Biology*, **33**: 25–35.
- Goldstein, J.S., Morrissey, E.M., Moretti, E.D. & Watson, W.H. III. 2017. A comparison of the distribution and abundance of European green crabs and American lobsters in Great Bay Estuary, New Hampshire, USA. *Fisheries Research*, **189**: 10–17.
- Haarr, M.L. & Rochette, R. 2012. The effect of geographic origin on interactions between adult invasive green crabs *Carcinus maenas* and juvenile American lobsters *Homarus americanus* in Atlantic Canada. *Journal of Experimental Marine Biology and Ecology*, **422–423**: 88–100.
- Hemmi, J.M. & Zeil, J. 2003. Burrow surveillance in fiddler crabs I. Description of behavior. *Journal of Experimental Biology*, **206**: 3935–3950.
- Holdredge, C., Bertness, M.D. & Altieri, A.H. 2009. Role of crab herbivory, in die-off of New England salt marshes. *Conservation Biology*, **23**: 672–679.
- Johnson, D.S. 2014. Fiddler on the roof: a northern range extension for the marsh fiddler crab *Uca pugnax*. *Journal of Crustacean Biology*, **34**: 671–673.
- Kent, M. & Coker, P. 1992. *Vegetation description and analysis: A practical approach*. John Wiley and Sons, Chichester, UK.

- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. **Vol. 1**, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].
- Luk, Y.C. & Zajac, R.N. 2013. Spatial ecology of fiddler crabs, *Uca pugnax*, in southern New England salt marsh landscapes: potential habitat expansion in relation to salt marsh change. *Northeastern Naturalist*, **20**: 255–274.
- Mascaró, M. & Seed, R. 2001. Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L. *Marine Biology*, **139**: 1135–1145.
- Milne Edwards, H. 1837. *Histoire naturelle des Crustacés comprenant l'anatomie la physiologie et la classification de ces animaux*. **Vol. 2**. Librairie Encyclopédique de Roret, Paris.
- Niering, W.A. & Warren, R.S. 1980. Vegetation patterns and processes in New England salt marshes. *BioScience*, **30**: 301–307.
- Raposa, K.B., Roman, C.T. & Heltshe, J.F. 2003. Monitoring nekton as a bioindicator in shallow estuarine habitats. *Environmental Monitoring and Assessment*, **81**: 239–255.
- Raposa, K.B., Mckinney, R.A., Wigand, C., Hollister, J.W., Lovall, C., Szura, K., Gurak, J.A., McNamee, J., Raithe, C. & Watson, E.B. 2018. Top-down and bottom-up controls on southern New England salt marsh crab populations. *PeerJ*, **6**: e4876 [doi: 10.7717/peerj.4876].
- Raposa, K.B., Wasson, K., Smith, E., Crooks, J.A., Delgado, P., Fernald, S.H., Ferner, M.C., Helms, A., Hice, L.A., Mora, J.W., Puckett, B., Sanger, D., Shull, S., Spurrier, L., Stevens, R. & Lerberg, S. 2016. Assessing tidal marsh resilience to sea-level rise at broad geographic scales with multi-metric indices. *Biological Conservation*, **204**: 263–275.
- Raposa, K.B., Weber, R.L.J., Ekberg, M.C. & Ferguson, W. 2017. Vegetation dynamics in Rhode Island salt marshes during a period of accelerating sea level rise and extreme sea level events. *Estuaries and Coasts*, **40**: 640–650.
- Rayner, G., & McGaw, I.J. 2019. Effects of the invasive green crab (*Carcinus maenas*) on American lobster (*Homarus americanus*): Food acquisition and trapping behaviour. *Journal of Sea Research*, **144**: 95–104.
- Roman, C.T., Raposa, K.B., Adamowicz, S.C., James-Pirri, M.J. & Catena, J.C. 2002. Quantifying vegetation and nekton response to tidal restoration of a New England salt marsh. *Restoration Ecology*, **10**: 450–460.
- Rossong, M.A., Quijon, P.A., Williams, P.J. & Snelgrove, P.V.R. 2011. Foraging and shelter behavior of juvenile American lobster (*Homarus americanus*): the influence of a non-indigenous crab. *Journal of Experimental Marine Biology and Ecology*, **403**: 75–80.
- Rossong, M.A., Williams, P.J., Comeau, M., Mitchell, S.C. & Apaloo, J. 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). *Journal of Experimental Marine Biology and Ecology*, **329**: 281–288.
- Rozas, L.P. & Minello, T.J. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries*, **20**: 199–213.
- Say, T. 1817. An account of the Crustacea of the United States (continued). *Journal of the Academy of Natural Sciences at Philadelphia*, **1**: 155–169.
- Schultz, R.A., Anisfeld, S.C. & Hill, T.D. 2016. Submergence and herbivory as divergent causes of marsh loss in Long Island Sound. *Estuaries and Coasts*, **39**: 1367–1375.
- Smith, S.I. 1870. Notes on American Crustacea. No. I. Ocyropoidea. *Transactions of the Connecticut Academy of Arts and Sciences*, **2**: 113–176.
- Spence, J.R. & Niemela, J.K. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist*, **126**: 881–894.
- Topping, C.J. & Sunderland, K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, **29**: 485–491.
- Vincent, R.E., Burdick, D.M. & Dionne, M. 2013. Ditching and ditch-plugging in New England salt marshes: effects on hydrology, elevation, and soil characteristics. *Estuaries and Coasts*, **36**: 610–625.
- Vu, H.D., Wieski, K. & Pennings, S.C. 2017. Ecosystem engineers drive creek formation in salt marshes. *Ecology*, **98**: 162–174.
- Wasson, K.W., Raposa, K., Almeida, M., Beheshti, K., Crooks, J.A., Deck, A., Dix, N., Garvey, C., Goldstein, J., Johnson, D.S., Lerberg, S., Marcum, P., Peter, C., Puckett, B., Schmitt, J., Smith, E., St. Laurent, K., Swanson, K., Tyrrell, M. & Guy, R. 2019. Pattern and scale: evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale. *Ecology*, **100**: e02813 [doi: 10.1002/ecy.2813].
- Watson, E.B., Raposa, K.B., Carey, J.C., Wigand, C., & Warren, R.S. 2017. Anthropocene survival of southern New England's salt marshes. *Estuaries and Coasts*, **40**: 617–625.
- Wigand, C., Ardito, T., Chaffee, C., Ferguson, W., Paton, S., Raposa, K., Vandemoer, C. & Watson, E. 2017. A climate change adaptation strategy for management of coastal marsh systems. *Estuaries and Coasts*, **40**: 682–693.
- Williams, P.J., Floyd, T.A. & Rossong, M.A. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). *Journal of Experimental Marine Biology and Ecology*, **329**: 66–74.
- Wilson, C.A., Hughes, Z.J. & FitzGerald, D.M. 2012. The effects of crab bioturbation on mid-Atlantic saltmarsh tidal creek extension: geotechnical and geochemical changes. *Estuarine, Coastal and Shelf Science*, **106**: 33–44.
- Young, A.M., Elliott, J.A., Incatasciato, J.M. & Taylor, M.L. 2017. Seasonal catch, size, color, and assessment of trapping variables for the European green crab *Carcinus maenas* (Linnaeus, 1758) (Brachyura: Portunoidea: Carcinidae), a nonindigenous species in Massachusetts, USA. *Journal of Crustacean Biology*, **37**: 556–570.