# The fiddler crab *Minuca pugnax* (Smith, 1870) (Decapoda: Brachyura: Ocypodidae) reduces saltmarsh algae in its expanded range

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## ABSTRACT

It is well known that species across the world are expanding or shifting their ranges because of climate change. Yet, we know little about their impact on the habitats they colonize. In an observational study, we examined the effect of the fiddler crab *Minuca pugnax* (Smith, 1870) on benthic microalgal biomass in salt marshes in its expanded range (northeastern Massachusetts, USA). We found that plots with *M. pugnax* had, on average, 74% lower diatom biomass and 77% lower cyanobacteria biomass than plots without *M. pugnax*. Our results indicate that this climate migrant can impact saltmarsh functioning by limiting benthic microalgal biomass.

**Key Words:** climate change, microphytobenthos, range expansion, range shift, top-down control, *Uca pugnax*

## INTRODUCTION

Climate migrants are populations within a species that colonize a new habitat or range due to the climate-driven range expansions or shifts of that species (Johnson *et al.*, 2020). Ecologists and biogeographers have identified thousands of climate migrants, from fishes to insects to crabs (Parmesan & Yohe, 2003; Sorte *et al.*, 2010; Johnson, 2015; Hale *et al.*, 2017). Yet, we know little about how climate migrants influence the functioning of the ecosystems that they colonize. Fiddler crabs are excellent species to examine the impact of climate migrants because they are found in intertidal habitats throughout the world (Rosenberg, 2020), they can strongly influence ecosystem functioning (Katz, 1980; Moore, 2019), and poleward range expansions due to ocean warming have been documented for some species (Johnson, 2014; Peer *et al.*, 2015; Rosenberg, 2018; Truchet *et al.*, 2019).

The fiddler crab, *Minuca pugnax* (Smith, 1870) (formerly *Uca pugnax*), has expanded its range north of its historical northern limit of Cape Cod, Massachusetts (MA) to Maine, USA (Johnson, 2014; Rosenberg, 2020; DSJ, unpublished data). It lives in salt marshes, which are intertidal grasslands. As a burrowing ecosystem engineer (*sensu* Jones *et al.*, 1994), *M. pugnax* has a strong influence on saltmarsh functioning, physical structure, and biodiversity (Katz, 1980; DePatra & Levin 1989; Gittman & Keller, 2013). While many researchers have focused on the role of *M. pugnax* as an ecosystem engineer in salt marshes (e.g., Gittman & Keller, 2013; Moore, 2019), its role as a consumer has been

overlooked. *Minuca pugnax* is a deposit feeder and like most species of fiddler crabs, it grazes benthic microalgae (also known as "microphytobenthos" (e.g., MacIntyre *et al.*, 1996)) mostly diatoms and cyanobacteria, from the sediment surface (Shanholtzer, 1973; Haines & Montague, 1979; Bursey, 1985). To our knowledge, no one has explicitly tested the impact of *M. pugnax* on benthic microalgae in either its historical or expanded range. Darley *et al.* (1981) saw chlorophyll *a* biomass increases when they excluded fiddler crabs in a Georgia (USA) salt marsh. Because three species of fiddler crabs (*M. pugnax*, the red-jointed fiddler crab *M. minax* (Le Conte, 1885), and the sand fiddler crab *Leptuca pugilator* (Bosc, 1802)) co-exist in this marsh (Teal, 1958), their experiment likely shows the impact of the fiddler crab community, not of a single species.

There are several reasons that salt marshes found in the expanded range of *M. pugnax* (i.e., north of Cape Cod, MA, USA) are excellent living laboratories to test the effects of this climate migrant on benthic microalgal biomass. First, the grazing impacts of fiddler crabs on benthic microalgae can be isolated to a single species, *M. pugnax*, because it is the only fiddler crab present in this part of its range (Johnson, 2014; Wasson *et al.* 2019; Rosenberg, 2020). Second, the distribution of *M. pugnax* colonies in the expanded range is patchy with tens of meters between colonies (Martínez-Soto & Johnson, 2020). Finally, unlike *M. pugnax* in the historical range, individuals of *M. pugnax* in the expanded range remain close to their burrows and do

not appear to drove, where high-density scuttles of crabs move through the marsh to graze (DSJ, personal observation). This restricted movement likely results in patches of saltmarsh benthos between the colonies untouched by crabs. This allowed us to compare benthic microalgal biomass between patches with and without *M. pugnax*. We hypothesized that the biomass of benthic microalgae would be lower in patches with *M. pugnax* compared to those without *M. pugnax*.

## MATERIALS AND METHODS

### Site description

This study was conducted in the salt marshes flooded by West Creek in the Plum Island Estuary in Rowley, MA, USA (42°44′16.0″N, 70°50′53.2″W) (Fig. 1). These salt marshes are part of the Great Marsh, which is the largest expanse of salt marshes in the northeastern USA. The estuary is mesotidal with mean tides ~2.6 m and spring tides of 3 m (Johnson *et al.*, 2007). The expansive marshes are largely above mean high water (so-called "high marsh"), which is dominated by salt hay, *Spartina patens* ((Aiton) Muhl, 1817) (~45 cm shoot height), and punctuated by isolated patches of stunted *Spartina alterniflora* (Loisel, 1807) (~40 cm shoot height). The low marsh (below mean high water) is a 1–3 m wide band of tall-form *S. alterniflora* (up to 150 cm shoot height; Johnson *et al.*, 2016). Unlike marshes found in the historical range (i.e., south of Cape Cod, MA, USA), where *M. pugnax* can inhabit both *S. patens* and *S. alterniflora* habitats (Luk & Zajac, 2013; Wasson *et al.*, 2019),

*M. pugnax* is found exclusively in the low marsh in the expanded range (Johnson 2014; Martínez-Soto & Johnson, 2020).

Other burrowing species present in the tall-form *S. alterniflora* zone in the Great Marsh include infaunal polychaetes and amphipods with burrows ≤ 1 mm in diameter (Johnson *et al.*, 2007). Burrowing crabs found in salt marshes in the historical range, such as the red-jointed fiddler crab *M. minax*, the sand fiddler crab *L. pugilator*, and the purple marsh crab *Sesarma reticulatum* (Say, 1817), are absent from these marshes (Johnson, 2014; Wasson *et al.*, 2019; Rosenberg, 2020). As a result, it is easy to distinguish *M. pugnax* burrows from those of other species.

### Data collection

To test the hypothesis that *M. pugnax* reduced benthic microalgal biomass, we selected ten plots (0.0625 m²) with fiddler crabs present (determined by the presence of burrows and either feeding pellets or crabs) and counted burrows within the plot. Each crab plot was paired with a reference plot (lacking burrows, feeding pellets, or crabs) that was 1–2 m away, for a total of 20 plots. Plot pairs were at least 10 m apart from each other due to the patchiness of *M. pugnax* colonies. We estimated the biomass of benthic microalgal functional groups (diatoms, cyanobacteria, and green algae) on the sediment surface with a handheld fluorometer (BenthoTorch, BBe Moldaenke, Germany) in duplicate samples within each plot. Measurements within crab plots were taken adjacent to crab burrows, but not over them. Data were collected at low tide on a sunny afternoon on 22 August 2019.



**Figure 1.** Sampling location. Measurements were taken along the marsh edge in the area defined by the white box. This figure is available in color at *Journal of Crustacean Biology* online.

## Statistical analysis

To determine if there was a statistical difference for the biomass of diatom and cyanobacteria between plots with and without fiddler crabs, we conducted a two-tailed paired t-test for unequal variances in R version 4.0.0 (R Core Team 2020). Green algae were not detected in any plot. Prior to analysis, the duplicate samples from each plot were averaged.

## RESULTS

On average, diatom biomass was 64% lower and cyanobacteria biomass was 77% lower in plots with *M. pugnax* burrows than in plots without burrows ($P \leq 0.02$) (Fig. 2). Burrow densities in plots with *M. pugnax* ranged from 16–96 m$^{-2}$.

## DISCUSSION

Our results demonstrate that the fiddler crab *M. pugnax* in its expanded range lowers the biomass of benthic microalgae in salt marshes. Similar results have been found for other species of fiddler crabs. For instance, the sand fiddler *L. pugilator* can reduce sediment biomass of chlorophyll *a* (a proxy of benthic microalgae) by 20–70% on beaches on the east coast of the USA during a single low tide (Robertson *et al.*, 1980; Reinsel, 2004). Based on a mesocosm study in Australia, Kristensen & Alongi (2006) found that the calling fiddler crab *Gelasimus vocans* (Linnaeus, 1758) reduced sediment chlorophyll *a* by 75% at the surface (0–1 cm), but
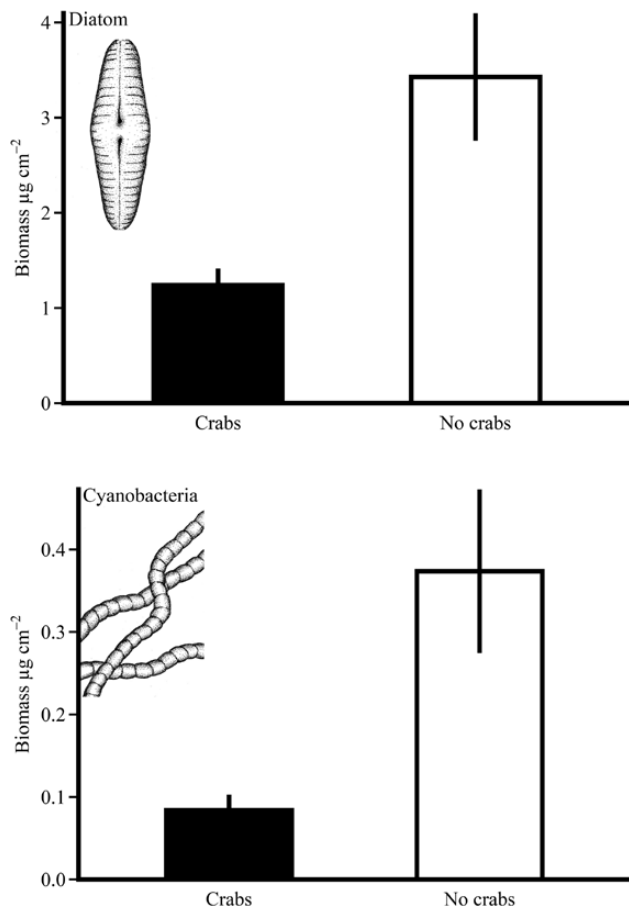


**Figure 2.** Mean biomass of benthic diatoms and cyanobacteria in the presence ("Crabs") and absence ("No crabs") of the fiddler crab, *Minuca pugnax*. Error bars represent standard error of the mean ($N = 10$).

had no impact on deeper layers. This is consistent with feeding in fiddler crabs, which occurs on the top 1–2 cm of sediment (Wolfrath, 1992).

*Minuca pugnax* reduces benthic microalgal biomass in salt marshes, and as a result it may have indirect effects on the functioning and food webs of salt marshes. Other saltmarsh animals, including polychaetes, gastropods, copepods, and amphipods, rely on benthic microalgae for food (Galván *et al.*, 2008, 2011; Pascal *et al.*, 2013). *Minuca pugnax* may indirectly influence the small-scale (as measured in meters) distribution of these animals through exploitative competition for benthic microalgae. Further, diatoms and cyanobacteria excrete extracellular polymeric substances that create biofilms on the sediment surface (Decho, 2000). These biofilms can stabilize sediments and reduce tidal erosion (Paterson, 1989; Fagherazzi *et al.*, 2013). Fiddler crabs may enhance erosion, not only through burrow construction and maintenance (Smith & Green, 2015), but also by grazing benthic microalgae, a sediment stabilizer. Lastly, benthic microalgae are important sinks for water-column nitrogen and can mitigate the impacts of nitrogen pollution (Drake *et al.*, 2009; Hope *et al.*, 2020; Oakes *et al.*, 2020). By reducing benthic microalgae, fiddler crabs may impact the metabolism of the ecosystem and limit the ability of the marsh to uptake excess nitrogen. *Minuca pugnax* may also enhance nitrogen uptake by the marsh by stimulating algal production through grazing and converting nitrogen into secondary (i.e., crab) production.

Our results should be interpreted within the limitations of our study. We found that benthic microalgal biomass was lower in plots with *M. pugnax versus* plots without *M. pugnax* during a single low tide. Our sampling does not account for temporal dynamics of benthic microalgae production. For instance, in a salt marsh in Argentina, Ribeiro & Iribarne (2011) found that during flooding tides, benthic microalgae could replenish up to 100% of its biomass within a day of feeding by the Uruguayan fiddler crab *Leptuca uruguayensis* (Nobili, 1901). In a 12-day experiment in South African mangroves, Peer *et al.* (2019) found that selective grazing by the fiddler crab *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016) lowered diatom and cyanobacteria biomass, which allowed green algae to flourish and resulted in no overall net effect on the grazing by fiddler crabs on benthic microalgal biomass. That said, Spivak & Ossolinki (2016), found that the average turnover of benthic microalgae (measured as the biomass to production ratio) was 59 days in August for the habitats we sampled. This slow turnover time suggests that the effect of *M. pugnax* on benthic microalgal biomass in this marsh will persist for days.

Individuals of *M. pugnax* may have greater per-capita grazing on benthic microalgal biomass in the expanded range than in the historical range because individuals are larger in the expanded range than in the historical range (Johnson *et al.*, 2019). The population-level impacts of *M. pugnax* on benthic microalgal biomass in the expanded range, however, are likely small relative to populations in the historical range. The densities of the burrows of *M. pugnax* in the expanded range average fewer than 10 burrows m$^{-2}$ (Martínez-Soto & Johnson, 2020), whereas, burrow densities in the historical range can be as high as 300 burrows m$^{-2}$ (McCraith *et al.*, 2003). Although *M. pugnax* populations are currently small in the expanded range, they are growing (Martínez-Soto & Johnson, 2020). Our results suggest that as *M. pugnax* populations grow in their expanded range, so too will their impact on benthic microalgae.

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