[Research article: FINAL JCB-2370]

Running head: JOHNSON *ET AL*: FIDDLER CRABS REDUCE ALGAE

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

David Samuel Johnson, Kayla S. Martínez-Soto, Manisha Pant, Serina Sebilian Wittyngham and Emily M. Goetz

[1]*Virginia Institute of Marine Science, William & Mary, P.O. Box 1346, Gloucester Point, Virginia 23062, USA*

Correspondence: D.S. Johnson; e-mail: dsjohnson@vims.edu

(Received 21 July 2020; accepted 27 August 2020)

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of its historical northern limit of Cape Cod, Massachusetts (MA) to Maine, USA (Johnson, 2014; Rosenberg, 2020; DSJ, unpublished data).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).

<*Fig. 1*>

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 m^2) 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.

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}.

<*Fig. 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 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

159 by the marsh by stimulating algal production through grazing and converting nitrogen into
160 secondary (i.e., crab) production.

161 Our results should be interpreted within the limitations of our study. We found that
162 benthic microalgal biomass was lower in plots with *M. pugnax versus* plots without *M. pugnax*
163 during a single low tide. Our sampling does not account for temporal dynamics of benthic
164 microalgae production. For instance, in a salt marsh in Argentina, Ribeiro & Iribarne (2011)
165 found that during flooding tides, benthic microalgae could replenish up to 100% of its biomass
166 within a day of feeding by the Uruguayan fiddler crab *Leptuca uruguayensis* (Nobili, 1901). In a
167 12-day experiment in South African mangroves, Peer *et al.* (2019) found that selective grazing
168 by the fiddler crab *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016) lowered diatom and
169 cyanobacteria biomass, which allowed green algae to flourish and resulted in no overall net
170 effect on the grazing by fiddler crabs on benthic microalgal biomass. That said, Spivak &
171 Ossolinki (2016), found that the average turnover of benthic microalgae (measured as the
172 biomass to production ratio) was 59 days in August for the habitats we sampled. This slow
173 turnover time suggests that the effect of *M. pugnax* on benthic microalgal biomass in this marsh
174 will persist for days.

175 Individuals of *M. pugnax* may have greater per-capita grazing on benthic microalgal
176 biomass in the expanded range than in the historical range because individuals are larger in the
177 expanded range than in the historical range (Johnson *et al.*, 2019). The population-level impacts
178 of *M. pugnax* on benthic microalgal biomass in the expanded range, however, are likely small
179 relative to populations in the historical range. The densities of the burrows of *M. pugnax* in the
180 expanded range average fewer than 10 burrows m^{-2} (Martínez-Soto & Johnson, 2020), whereas,
181 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.

ACKNOWLEDGEMENTS

We thank T. Doyle for letting us use his handheld fluoroprobe, A.C. Hyman for his illustrations of the diatom and cyanobacteria, and three anonymous reviewers and the Editor-in-Chief for their helpful comments. This is contribution 3933 from the Virginia Institute of Marine Science. This work was supported by the National Science Foundation under grants 1902712, 1637630, 1754259, 1832221. The authors declare no conflicts of interest.

LITERATURE CITED

Bosc, L.A.G. 1802. *Histoire naturelle des crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature*, **Vol. 1**. Déterville, Paris.

Bursey, C.R. 1985. Diet overlap in the marsh crabs *Sesarma reticulatum* (Decapoda: Grapsidae) and *Uca pugnax* (Decapoda: Ocypodidae). *Proceedings of the Pennsylvania Academy of Science*, **59**: 38–40.

Darley, W.M., Montague, C.L., Plumley, F.G., Sage, W.W. & Psalidas, A.T. 1981. Factors limiting edaphic algal biomass and productivity in a Georgia salt marsh. *Journal of Phycology*, **17**: 122–128.

DePatra, K.D. & Levin, L.A. 1989. Evidence of the passive deposition of meiofauna into fiddler crab burrows. *Journal of Experimental Marine Biology and Ecology*, **125**: 173–192.

204 Decho, A.W. 2000. Microbial biofilms in intertidal systems: an overview. *Continental Shelf*
205 *Research,* **20**: 1257–1273.
206 Drake, D.C., Peterson, B.J., Galván, K.A., Deegan, L.A., Fleeger, J.W., Hopkinson, C., Johnson,
207 J.M., Koop-Jakobsen, K., Lemay, L.E., Miller, E.E., Picard, C. & Warren, R.S. 2009.
208 Salt marsh ecosystem biogeochemical responses to nutrient enrichment: a paired
209 15N tracer study. *Ecology,* **90**: 2535–2546.
210 Fagherazzi, S., FitzGerald, D.M., Fulweiler, R., Hughes, Z., Wiberg, P.L., McGlathery, K.L.,
211 Morris, J.T., Tolhurst, T.J., Deegan, L.A. & Johnson, D.S. 2013. Ecogeomorphology of
212 tidal tlats. In*: Treatise on geomorphology*, **Vol. 12**, *Ecogeomorphology* (J.F. Shroder, ed.),
213 pp. 182–200. Academic Press, San Diego, CA, USA.
214 Galván, K., Fleeger, J.W. & Fry, B. 2008. Stable isotope addition reveals dietary importance of
215 phytoplankton and microphytobenthos to saltmarsh infauna. *Marine Ecology Progress*
216 *Series*, **359**: 37–49.
217 Galván, K., Fleeger, J.W., Peterson, B., Drake, D., Deegan, L.A. & Johnson, D.S. 2011. Natural
218 abundance stable isotopes and dual tracer additions help resolve resources supporting a salt
219 marsh food web. *Journal of Experimental Marine Biology and Ecology,* **410**: 1–11.
220 Gittman, R.K. & Keller, D.A. 2013. Fiddler crabs facilitate *Spartina alterniflora* growth,
221 mitigating periwinkle overgrazing of marsh habitat. *Ecology* **94**: 2709–2718.
222 Haines, E.B. & Montague, C.L. 1979. Food sources of estuarine invertebrates analyzed using
223 $^{13}C/^{12}C$ ratios. *Ecology*, **60**: 48–56.
224 Hale, S.S., Buffum, H.W., Kiddon, J.A. & Hughes, M.M. 2017. Subtidal benthic invertebrates
225 shifting northward along the US Atlantic Coast. *Estuaries and Coasts*, **40**: 1744–1756.

226 Hope, J.A., Paterson, D.M. & Thrush, S.F. 2020. The role of microphytobenthos in soft-sediment
227 ecological networks and their contribution to the delivery of multiple ecosystem services.
228 *Journal of Ecology* [doi: 10.1111/1365-2745.13322].
229 Johnson, D.S. 2014. Fiddler on the roof: a northern range extension for the marsh fiddler crab
230 *Uca pugnax*. *Journal of Crustacean Biology*, **34**: 671–673.
231 Johnson, D.S. 2015. The savory swimmer swims north: A northern range extension of the blue
232 crab *Callinectes sapidus*? *Journal of Crustacean Biology*, **35**: 105–110.
233 Johnson, D.S., Crowley, C., Longmire, Nelson, J., Williams, B. & Wittyngham, S. 2019. The
234 fiddler crab, *Minuca pugnax*, follows Bergmann's rule. *Ecology and Evolution*, **9** [doi:
235 10.1002/ece3.5883].
236 Johnson, D.S., Fleeger, J.W., Galván, K.A. & Moser, E.B. 2007. Worm holes and their space-
237 time continuum: spatial and temporal variability of macroinfaunal annelids in a northern
238 New England salt marsh. *Estuaries and Coasts*, **30**: 226–237.
239 Johnson, D.S., Shields, J.D., Doucette, D. & Heard, R. 2020. A climate migrant escapes its
240 parasites. *Marine Ecology Progress Series*, **641**: 111–121.
241 Johnson, D.S., Warren, R.S., Deegan, L.A. & Mozdzer, T.J. 2016. Saltmarsh plant responses to
242 eutrophication. *Ecological Applications*, **26**: 2647–2659.
243 Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, **69**:
244 373–386.
245 Katz, L.C. 1980. Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). *Estuarine and*
246 *Coastal Marine Science*, **11**: 233–237.

247 Kristensen, E. & Alongi, D.M. 2006. Control by fiddler crabs (*Uca vocans*) and plant roots
248 (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment.
249 *Limnology and Oceanography*, **51**: 1557–1571.
250 Le Conte, J. 1855. On a new species of *Gelasimus*. *Proceedings of the Academy of Natural*
251 *Sciences of Philadelphia*, **7**: 402–403.
252 Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines,*
253 *Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* **Vol. 1**, Edn. 10.
254 Reformata. Laurentii Salvii, Holmiae [= Stockholm].
255 Luk, Y.C. & Zajac, R.N. 2013. Spatial ecology of fiddler crabs, *Uca pugnax*, in southern New
256 England salt marsh landscapes: Potential habitat expansion in relation to salt marsh change.
257 *Northeastern Naturalist*, **20**: 255–274.
258 MacIntyre, H.L., Geider, R.J. & Miller, D.C. 1996. Microphytobenthos: The ecological role of
259 the "secret garden" of unvegetated shallow-water marine habitats. I. Distribution,
260 abundance and primary production. *Estuaries*, **19**: 186–201.
261 Martínez-Soto, K.S. & Johnson, D.S. 2020. The density of the Atlantic marsh fiddler crab
262 (*Minuca pugnax*, Smith, 1870) (Decapoda: Brachyura: Ocypodidae) in its expanded range
263 in the Gulf of Maine, USA. *Journal of Crustacean Biology*, **40**: [doi:
264 10.1093/jcbiol/ruaa049].
265 McCraith, B.J., Gardner, L.R., Wethey, D. S. & Moore, W.S. 2003. The effect of fiddler crab
266 burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a
267 southeastern salt marsh. *Journal of Marine Research*, **61**: 359–390.
268 Moore, A. 2019. What is the role of ecosystem engineers in New England salt marshes? A
269 mesocosm study of the fiddler crab and the purple marsh crab. *Wetlands*, **39**: 371–379.

Naderloo, R., Schubart, C.D. & Shih, H.T. 2016. Genetic and morphological separation of *Uca occidentalis*, a new East African fiddler crab species, from *Uca annulipes* (H. Milne Edward, 1837) (Crustacea: Decapoda: Brachyura: Ocypodidae). *Zoologischer Anzeiger - A Journal of Comparative Zoology*, **262**: 10–19.

Nobili, G. 1901. Decapodi raccolti dal Dr. Filippo Silvestri nell'America meridionale. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino*, **16**: 1–16.

Oakes, J.M., Riekenberg, P.M. & Eyre, B.D. 2020. Assimilation and short-term processing of microphytobenthos nitrogen in intertidal sediments. *Limnology and Oceanography* [doi: 10.1002/lno.11459].

Pascal, P.Y., Fleeger, J.W., Boschker, H.T.S., Mitwally, H.M. & Johnson, D.S. 2013. Response of the benthic food web to short-term and long-term nutrient enrichment in saltmarsh mudflats. *Marine Ecology Progress Series*, **474**: 27–41.

Paterson, D.M. 1989. Short-term changes in erodibility of intertidal cohesive sediments related to the migratory behaviour of epipelic diatoms. *Limnology and Oceanography,* **34**: 223–234.

Peer, N., Miranda, N.A.F. & Perissinotto, R. 2015. A review of fiddler crabs (genus *Uca* Leach, 1814) in South Africa. *African Zoology*, **50**: 187–204.

Peer, N., Miranda, N.A.F. & Perissinotto, R. 2019. Impact of fiddler crab activity on microphytobenthic communities in a South African mangrove forest. *Estuarine, Coastal and Shelf Science*, **227** [doi: 10.1016/j.ecss.2019.106332].

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing (v.4.0.0, “Arbor Day”), Vienna, Austria [https://www.R-project.org/].

292 Reinsel, K.A. 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat:
293 season-dependent effects in one tidal cycle. *Journal of Experimental Marine Biology and*
294 *Ecology*, **313**: 1–17.
295 Ribeiro, P.D. & Iribarne, O.O. 2011. Coupling between microphytobenthic biomass and fiddler
296 crab feeding. *Journal of Experimental Marine Biology and Ecology*, **407**: 147–154.
297 Robertson, J.R., Bancroft, K., Vermeer, G. & Plaisier, K., 1980. Experimental studies on the
298 foraging behavior of the sand fiddler crab *Uca pugilator* (Bosc, 1802). *Journal of*
299 *Experimental Marine Biology and Ecology*, **44**: 67–83.
300 Rosenberg, M.S. 2018. New record and range extension of the fiddler crab *Uca princeps* (Smith,
301 1870) from California, USA. *Journal of Crustacean Biology*, **38**: 823–824.
302 Rosenberg, M.S. 2020. A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda:
303 Brachyura: Ocypodidae). Part 2: Biogeography. *Journal of Crustacean Biology*, **40**:
304 [doi:10.1093/jcbiol/ruaa029].
305 Shanholtzer, S.F. 1973. Energy flow, food habitats and population dynamics of *Uca pugnax* in a
306 salt marsh system. Ph.D. thesis, University of Georgia, Athens, GA, USA.
307 Say, T. 1822. Description of univalve terrestrial and fluviatile shells of the United States. *Journal*
308 *of the Academy of Natural Sciences of Philadelphia*, **2**: 370–381.
309 Smith, S. I. 1870. Notes on American Crustacea. No. I. Ocypodoidea. *Transactions of the*
310 *Connecticut Academy of Arts and Sciences*, **2**: 113–176.
311 Smith, S.M. & Green, C.W. 2015. Sediment suspension and elevation loss triggered by Atlantic
312 mud fiddler crab (*Uca pugnax*) bioturbation in salt marsh dieback areas of southern New
313 England. *Journal of Coastal Research*, **31**: 88–94.

314 Sorte, C.J.B., Williams, S.L. & Carlton, J.T. 2010. Marine range shifts and species introductions:
315 comparative spread rates and community impacts: Range shifts and non-native species
316 introductions. *Global Ecology and Biogeography* **19**: 303–316.
317 Spivak, A.C. & Ossolinki, J. 2016. Limited effects of nutrient enrichment on bacterial carbon
318 sources in salt marsh tidal creek sediments. *Marine Ecology Progress Series*, **544**: 107–
319 130.
320 Teal, J.M. 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology*, **39**: 186–193.
321 Truchet, D.M., Buzzi, N.S., Carcedo, M.C. & Marcovecchio, J.E. 2019. First record of the
322 fiddler crab *Leptuca* (=*Uca*) *uruguayensis* in the Bahía Blanca Estuary (Buenos Aires,
323 Argentina) with comments on its biology in South America. *Regional Studies in Marine*
324 *Science*, **27**: 100539 [doi: 10.1016/j.rsma.2019.100539].
325 Wasson, K., Raposa, K., Almeida, M., Beheshti, K., Crooks, J.A., Deck, A., Dix, N., Garvey, C.,
326 Goldstein, J., Johnson, D.S., Lerberg, S., Marcum, P., Peter, C., Puckett, B., Schmitt, J.,
327 Smith, E., St. Laurent, K., Swanson, K., Tyrell, M. & Guy, R. 2019. Pattern and scale:
328 Evaluating generalities in crab distributions and marsh dynamics from small plots to a
329 national scale. *Ecology*, **100** [doi: 10.1002/ecy.2813].
330 Wolfrath, B. 1992. Field experiments on feeding of the European fiddler crab *Uca tangeri*.
331 *Marine Ecology Progress Series*, **90**: 39–43.
332

333 FIGURE CAPTIONS

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

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 ($N = 10$).