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LETTER

A physical-biogeochemical mechanism for negative feedback between marsh crabs and carbon storage

Julia A Guimond[1], Angelia L Seyfferth[1,2], Kevan B Moffett[3] and Holly A Michael[1,4]

[1] Department of Geological Sciences, University of Delaware, Newark DE 19716, United States of America
[2] Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19716, United States of America
[3] School of the Environment, Washington State University, Vancouver, WA 98686, United States of America
[4] Department of Civil & Environmental Engineering, University of Delaware, Newark DE 19716, United States of America

E-mail: hmichael@udel.edu

Abstract

Tidal marshes are valuable global carbon sinks, yet large uncertainties in coastal marsh carbon budgets and mediating mechanisms limit our ability to estimate fluxes and predict feedbacks with global change. To improve mechanistic understanding, we assess how net carbon storage is influenced by interactions between crab activity, water movement, and biogeochemistry. We show that crab burrows enhance carbon loss from tidal marsh sediments by physical and chemical feedback processes. Burrows increase near-creek sediment permeability in the summer by an order of magnitude compared to the winter crab dormancy period, promoting carbon-rich fluid exchange between the marsh and creek. Burrows also enhance vertical exchange by increasing the depth of the strongly carbon-oxidizing zone and reducing the capacity for carbon sequestration. Results reveal the mechanism through which crab burrows mediate the movement of carbon through tidal wetlands and highlight the importance of considering burrowing activity when making budget projections across temporal and spatial scales.

1. Introduction

As atmospheric carbon dioxide concentrations climb, attention has turned to fast-action mitigation to complement long-term reduction strategies (Molina *et al* 2009, Rogelj *et al* 2018). Conserving terrestrial forests with high carbon uptake capacities has traction as one such fast-action strategy to boost Earth's carbon sequestration (Canadell and Raupach 2008, Molina *et al* 2009). Vegetated coastal ecosystems also sequester a disproportionately large amount of carbon relative to their fraction of global land area (Mcleod *et al* 2011, Duarte *et al* 2013) but unlike terrestrial forests, the ability of coastal wetlands to continuously build vertically prevents them from reaching a storage ceiling. High rates of primary productivity by dense vegetation and slow decomposition in anoxic soils enable marshes to store carbon for centuries and longer.

Despite their importance, the carbon budgets of saline and brackish tidal wetlands (herein referred to as tidal/coastal wetlands or marshes) are poorly constrained. Much uncertainty stems from the complexity of interacting plant, water, soil, nutrient, fauna, microbe, and even climate ecosystem components. A particularly under-constrained influence on coastal wetland net carbon sequestration is the role of burrowing, or bioturbating, animal species.

In marshes around the globe, crabs such as *Uca* spp. and *Sesarma* spp. construct burrows of varying shapes and sizes (Wolf et al 1975, Hughes *et al* 1998, Koo *et al* 2005, Morgan *et al* 2006, Wang *et al* 2010). During burrow construction, sediment and stored organic matter are excavated to the marsh surface, increasing the potential for erosive carbon export (Montague 1982) particularly near creeks, where most burrow activity occurs (Teal 1958, Katz 1980, McCraith *et al* 2003, Wasson *et al* 2019). Burrows
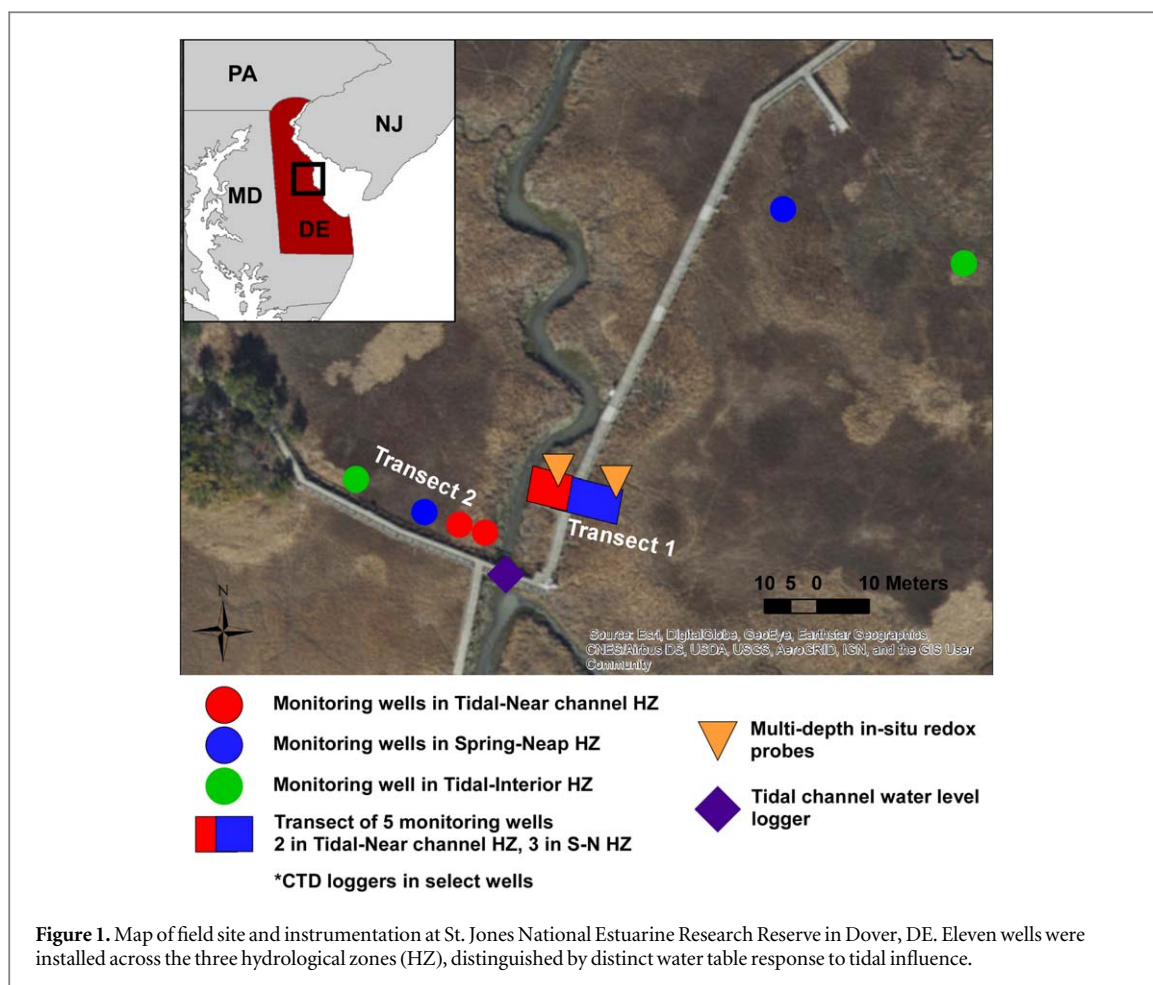
Figure 1. Map of field site and instrumentation at St. Jones National Estuarine Research Reserve in Dover, DE. Eleven wells were installed across the three hydrological zones (HZ), distinguished by distinct water table response to tidal influence.

increase the area of sediment air/water interface, enhancing carbon emissions (Lee 2008) and act as macropores, or conduits of preferential water flow, increasing exchange between surface water and groundwater (Xin *et al* 2009, Stahl *et al* 2014, Xiao *et al* 2019). Aeration increases the subsurface reduction-oxidation (redox) potential (Thomas and Blum 2010) and carbon oxidation rates (Kostka *et al* 2002a, Kostka *et al* 2002b), and decreases carbon stock of the sediment (Montague 1982, Thomas and Blum 2010, Wilson *et al* 2012, Thomson *et al* 2019). Gaseous emission measurements over burrows show higher CO_2 efflux compared to non-bioturbated areas (Montague 1982, Kristensen *et al* 2008, Penha-Lopes *et al* 2010, Pülmanns *et al* 2014, Ouyang *et al* 2017), but these measurements themselves cannot identify mechanisms driving the increase. Seasonal changes in crab behavior are another unknown that may further complicate the impact of crabs on carbon budgets in high latitudes, because burrows are maintained only during warm periods (i.e. summer) when crabs are most active (Knopf 1966, Krebs and Valiela 1978, Katz 1980).

Understanding of the mechanisms, magnitudes, and timing by which crab burrows influence tidal wetland carbon fluxes is limited, reducing our ability to predict coastal carbon dynamics and feedbacks with climate change. Here we quantify the effects of crab burrows on tidal marsh hydrology and geochemistry via changes in sediment permeability and redox potential and link these to changes in carbon oxidation rates.

2. Study site and field measurements

This study was conducted at St. Jones National Estuarine Research Reserve (NERR) in Dover, Delaware (figure 1). The brackish marsh is *Spartina*-dominated (*S. alterniflora, S. cynosuroides, and S. patens*), and characteristic of brackish marshes on the United States' Southeast Atlantic Coast with a levee and ponded water marsh area (Wiegert *et al* 1990). Based on our observations and pitfall traps assessments by Wasson *et al* (2019), *Uca minax*, the brackish-water fiddler crab, was the most prominent crab species and responsible for most burrows. *Uca pugilator* and *Sesarma reticulatum* were also observed.

Water level fluctuations were measured using pressure sensors (Solinst, Canada) recording data continuously at fifteen-minute intervals in eleven shallow monitoring wells (figure 1; Text S1). Wells were installed 1.2 m deep with sand-pack around the screens in different vegetation zones and at different distances from the creek. Wells were constructed using 3.175 cm schedule 40 PVC with 91 cm of slotted well screen. Air

pressure was also recorded continuously every fifteen minutes, approximately 1 m above the marsh surface in the middle of the well transect and used to barometrically correct the absolute pressure readings.

The marsh was divided into three hydrologic zones (HZs), tidal-near channel, spring-neap, and tidal-interior, distinguished by and named for their hydrological characteristics. The complexity of marsh hydrology inhibits use of generalized naming schemes such as high/low marsh that overlook the unique hydrology within each zone. For example, the high levee in this marsh exhibits groundwater table dynamics similar to traditionally designated high marsh areas but falls within the low marsh zone. Our zones roughly correspond to vegetation zonations proposed by Wilson *et al* (2015) and support the concept of ecohydrologic zonations developed by Moffett *et al* (2012). However, given our emphasis on hydro-redox linkages presented in this paper, our zonations are named to reflect the hydrologic conditions. The tidal-near channel HZ had large diurnal water table elevation fluctuations within approximately 7 m of the creek and high primary productivity. The spring-neap HZ encompassed high elevation areas, such as the levee, where the water table fluctuated with spring-neap tidal harmonics, reflecting the inundation frequency. *Phragmites* and *S. cynosuroides* colonized this zone. The tidal-interior HZ encompassed the lower elevation, frequently saturated marsh where tidal water table fluctuations occurred but the water table remained close to the marsh platform, typical of ponded water marshes (Wiegert *et al* 1990) (see Text S2 available online at stacks.iop.org/ERL/15/034024/mmedia for further discussion of these zones and a discussion of their relation to the vegetation zones of Wilson *et al* (2015)). Four wells were located in the tidal-near channel HZ with two located less than 0.75 m from the creek bank, five wells were located in the spring-neap HZ, and two wells were located in the tidal-interior HZ. Wells were arranged in two transects, one of five wells and one of four wells, spanning the tidal channel to the marsh interior (figure 1). Two wells were located in the marsh interior disconnected from the tidal channel-marsh interior transects.

Two falling head slug tests were conducted monthly from February 2017 to February 2018 in each well using a 5.28×10^{-4} m³ slug. Hydraulic conductivity (K) was calculated using the Bouwer–Rice equation and average K from the two tests was reported each month at each well (Bouwer and Rice 1976). To assess differences between sites and bioturbated and non-bioturbated periods, ANOVA and Single Factor Tukey post-hoc tests were performed (see Text S1). Water table elevation data from a tidal-near channel HZ well and water level data from the tidal channel were used to calculate the hydraulic gradient between the marsh platform and tidal channel at fifteen minute intervals for each season. Periods when flow was from the channel to the marsh (i.e. negative) were not

included in the calculation. To calculate the porewater exchange between the marsh platform and tidal channel, Darcy's Law was used with our seasonally variable measured K and hydraulic gradient. Each of the 15 min outflow fluxes were averaged for an entire season to get the average flux per day into the tidal channel during that season.

Burrow density was measured monthly in each hydrologic zone (HZ) (tidal-near channel, spring-neap, and tidal-interior). Three locations within each zone were randomly selected and burrows counted within a 1×1 m PVC square. Statistical analyses were conducted to assess differences in macropore counts between sites. The depth and volume of the burrows were determined from *in situ* Plaster of Paris burrow casts created at low-neap tide (figure S3, Text S1). 14–25 random burrows from each HZ were chosen (49 total); casts were excavated and measured for length, depth, and circumference at the top, middle, and bottom. Depths represented portions of burrows above the water table, below which plaster did not solidify.

Multi-level *in situ* redox sensors (Paleo Terra, Amsterdam, Netherlands) were installed near the creek and in the high marsh, within 3 m of a monitoring well, and connected to a datalogger (Campbell Scientific, CR1000). Probes were constructed of epoxy tubes reinforced with fiberglass and were 103 cm long and 16 mm in diameter. Sensor depths were customized to correspond to stratigraphy determined from sediment cores (Bothfeld 2016). In the spring-neap HZ, a 10-level probe had sensors at 4, 7, 16, 29, 39, 49, 59, 69, 79, and 94 cm depths. In the tidal-near channel HZ, a 9-level probe had sensors at 10, 13, 22, 35, 50, 60, 75, 85, and 100 cm depths. A Calomel reference electrode (Fisher Scientific) placed in saturated KCl was also connected to the datalogger (CR1000) and used to establish a reference potential. Probes were calibrated before and after deployment in calibration solution or DI water.

Sippers (1/4 inch aluminum sampler with 2 inch screen; M.H.E. Products) were used to collect porewater at depths of 10, 25, and 75 cm in each HZ at high-neap and low-neap tide in the summer (1 August 2017) and winter (24 January 2018), and in the tidal channel. Depths were chosen to span the root zone and below and capture oxidized and reduced zones based on Eh collected earlier in summer 2017. Porewater was immediately filtered and aliquoted into vials for analyses (see Text S1). Total carbon (TC) and dissolved inorganic carbon (DIC) were measured by combustion. Dissolved organic carbon (DOC) was calculated by difference (Elementar Vario-Cube).

3. Results

Crab burrow density was spatially and temporally variable (figure 2). Burrows appeared in February and increased in number through August, reaching a
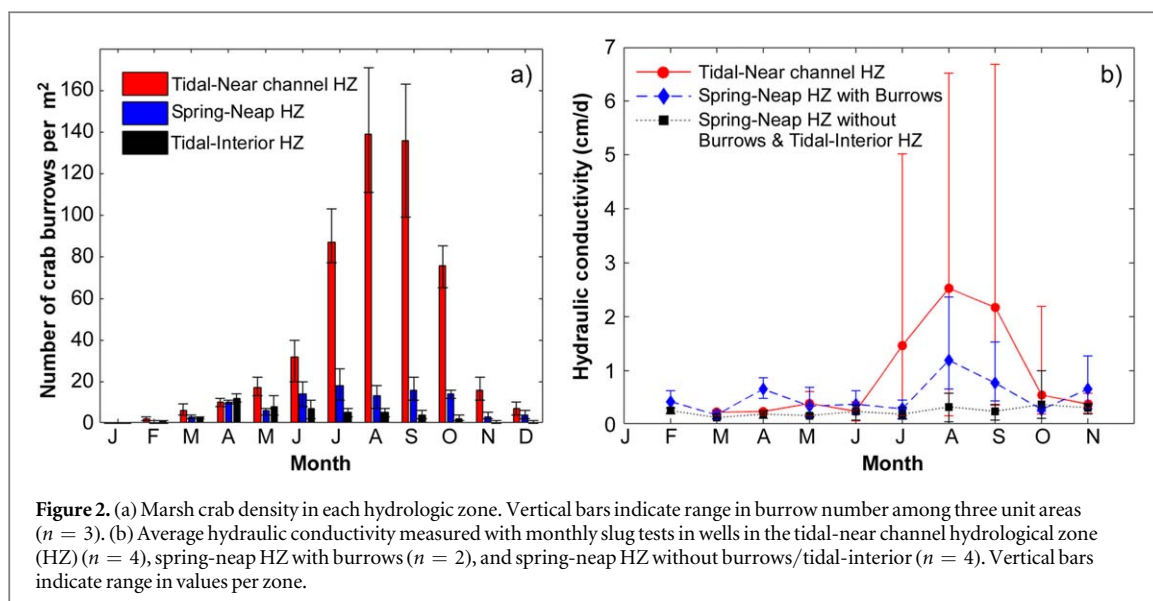
Figure 2. (a) Marsh crab density in each hydrologic zone. Vertical bars indicate range in burrow number among three unit areas ($n = 3$). (b) Average hydraulic conductivity measured with monthly slug tests in wells in the tidal-near channel hydrological zone (HZ) ($n = 4$), spring-neap HZ with burrows ($n = 2$), and spring-neap HZ without burrows/tidal-interior ($n = 4$). Vertical bars indicate range in values per zone.

maximum density of 171 burrows per m² (figure 2(a)). The highest density in the tidal-near channel HZ occurred in August and September, when densities were 275% of June levels and were on average 10 times more abundant than in the spring-neap HZ and 30 times in the tidal-interior HZ. During burrowing periods, the average number of burrows was statistically significantly different between the tidal-near channel HZ and both tidal-interior and spring-neap HZs, but not between the tidal-interior and spring-neap HZ (table S2). In contrast, during non-burrowing periods, there was no statistically significant difference in burrow density between any of the HZs (table S2). Burrow casts showed depths from 3.1 to 37.5 cm with an average of 17.2 cm. Burrows were interconnected, had multiple offshoots and entry holes, and visibly connected the marsh platform to tidal channel (figure S2).
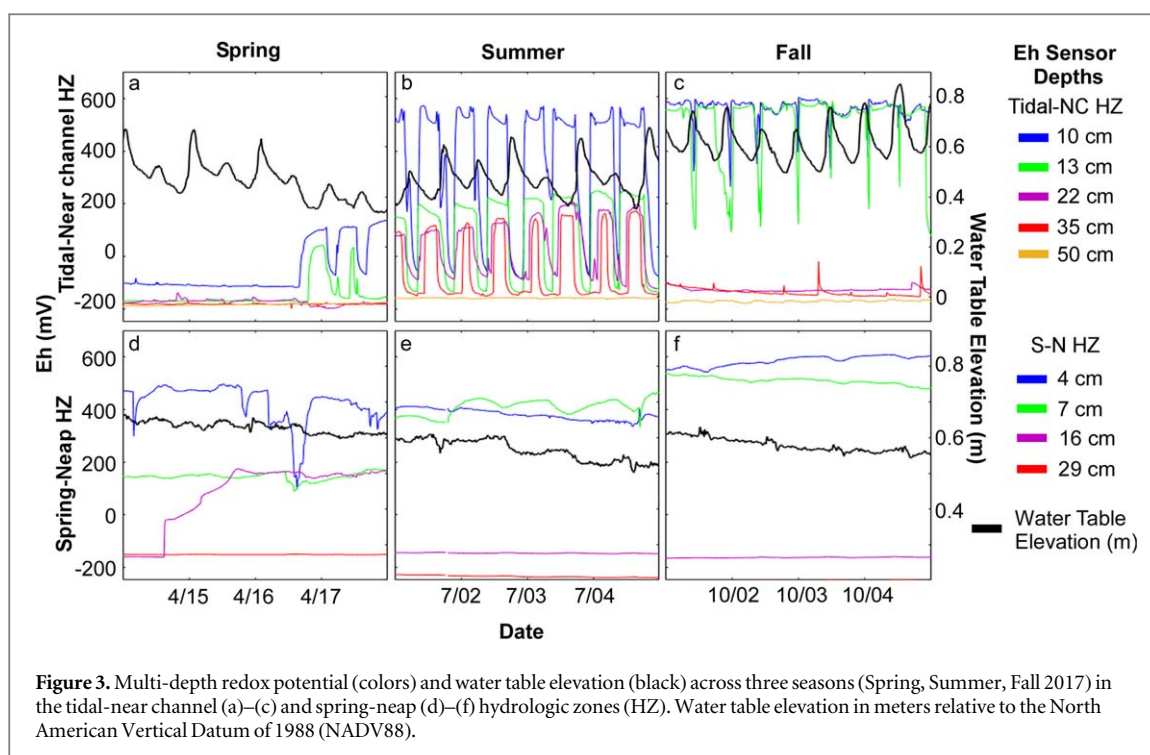
The hydraulic conductivity (K) of the marsh platform increased by an order of magnitude from winter to summer (figures 2(b), S3). Between February and November, K ranged from 0.051 to 6.7 cm/d. The 10-well average was highest in August at 1.4 cm/d, compared to 0.16 cm/d in March. The increase in K from winter/spring to summer was most prominent within the tidal-near channel HZ, where burrows were most abundant and, in some cases, connected to the bank of the channel. Slug test results from the tidal-near channel HZ were corroborated by the hydraulic head amplitude attenuation factor (AAF: ratio of tidal amplitude in tidal-near channel HZ well to the creek (Rotzoll *et al* 2013)), an indicator of the average K between the creek and well. AAF was greater in summer (0.4–0.6) than winter (<0.3; figure S4, Text S3). Inter-zone variability in slug tests may be due to burrow presence or absence within the effective radius of the slug test. However, the AAF integrates the volume between well and tidal channel, capturing the bulk average K. Average K in the spring-neap HZ showed seasonal variation only

in wells with burrows observed in the immediate area (figure 2(b)), where average K increased from 0.17 cm/d in March to 1.2 cm/d in August. In the spring-neap HZ wells without nearby burrows and tidal-interior HZ well, K was consistently low, ~0.1–0.4 cm/d.

The summer increase in K in the tidal-near channel HZ was attributed to the seasonal emergence of high burrow densities; however, the relationship was nonlinear. The less than two-fold increase in tidal-near channel HZ burrow numbers between July and August and the corresponding ten-fold increase in K suggests there is a burrow density threshold above which burrows connect, producing a step increase in permeability. While belowground ecological productivity (i.e. roots) may impact permeability, the increase in multiple wells during periods that correspond to high bioturbation suggests that bioturbation is the main driver increasing permeability.

An elevated summer K resulted in a greater exchange of tidal-near channel HZ porewater between the marsh platform and tidal channel in the summer compared to fall and spring. Using the calculated seasonally averaged positive hydraulic gradient between the tidal-near channel HZ and creek, a temporally variable K (spring/fall = 0.25 cm/d; summer = 2.5 cm/d), and Darcy's Law, we calculated a daily volumetric discharge to the tidal channel approximately 10-times greater in summer than in spring or fall.

Concurrently with seasonal changes in marsh permeability and fluid exchange, there were pronounced changes in the magnitude of marsh sediment redox potentials (Eh) and both the amplitude and depth of tidal Eh oscillations (figure 3). High Eh values indicate geochemical conditions that promote faster carbon loss by oxidation. In the spring, Eh in the tidal-near channel HZ was low and oscillated only in shallow sediments and during neap tides when water table elevations in the marsh were lowest. Eh at 10 cm and 13 cm depths increased from ~−200 to ~150 mV

Figure 3. Multi-depth redox potential (colors) and water table elevation (black) across three seasons (Spring, Summer, Fall 2017) in the tidal-near channel (a)–(c) and spring-neap (d)–(f) hydrologic zones (HZ). Water table elevation in meters relative to the North American Vertical Datum of 1988 (NADV88).
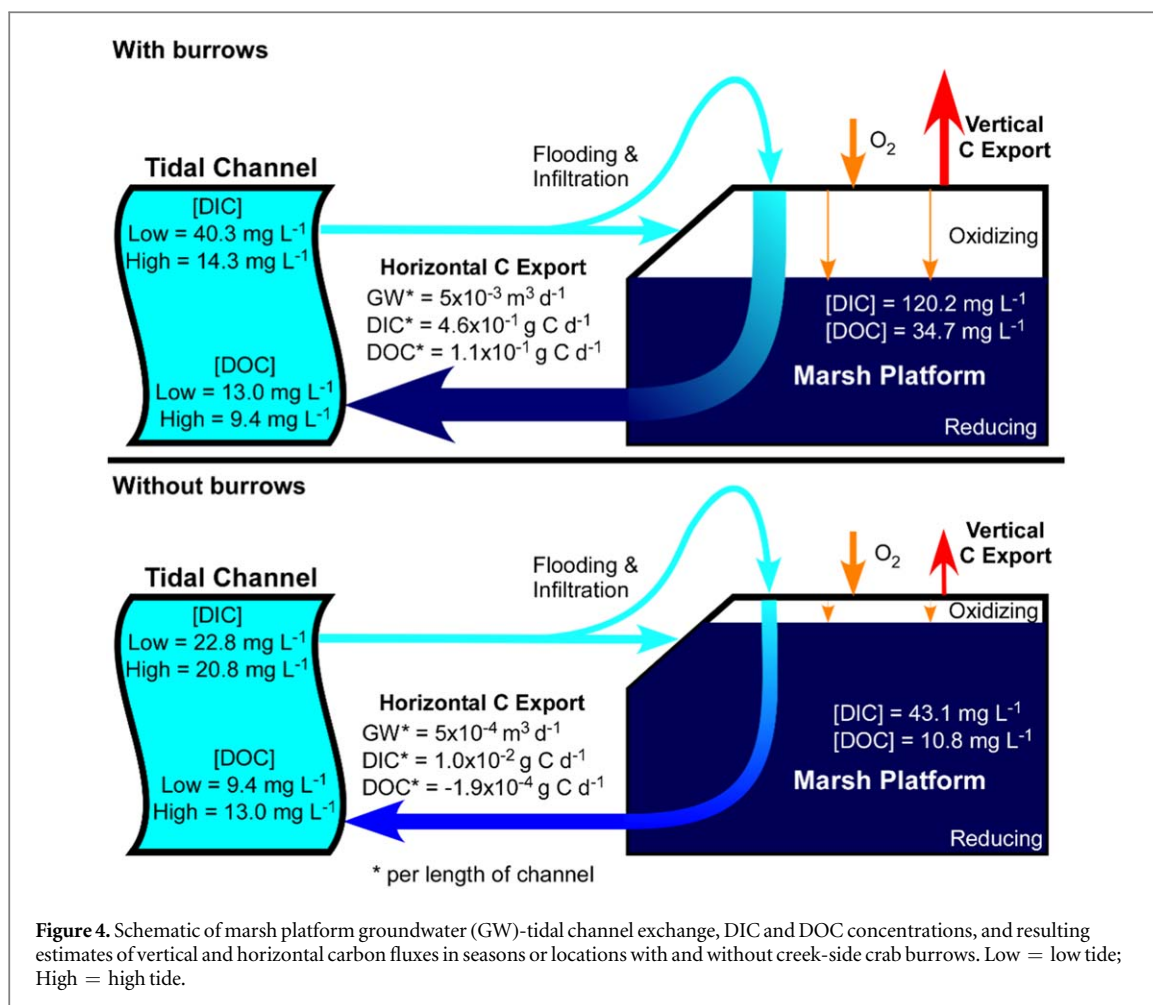
from higher spring to lower neap conditions (figures 3(a) and S5a). Eh deeper than 13 cm remained constant and low at approximately −200 mV. When burrow density peaked in the summer, Eh oscillations occurred with each diurnal tide throughout an entire spring-neap cycle and reached depths of at least 35 cm (figures 3(b), S5b). Eh ranged from −150 to >500 mV over a single diurnal tidal cycle in the summer. In the fall, oscillations only occurred in the top 13 cm of sediment and ranged from 100 to 600 mV (figures 3(c), S5c). Unlike redox potential in the tidal-near channel HZ, the spring-neap HZ did not show large variation in Eh (figures 3(d)–(f), S6) but sustained a strong vertical gradient in Eh over time. In the tidal-interior HZ, Eh was uniformly low.

Burrow-induced hydrological and redox changes were concurrent with measured changes in porewater DOC and DIC. On the seasonal time scale, tidally-averaged porewater DOC and DIC concentrations in the tidal-near channel HZ were greater in summer than winter (figure S7(c), (d), whereas DOC and DIC concentrations in the spring-neap and tidal-interior HZs were seasonally more uniform (figure S7(e)–(h)). On the tidal time scale, tidal-near channel HZ porewater DIC concentrations were notably different between high and low tides in the summer (figure S7(c); along with Eh fluctuations, figure 3 and S5). In non-bioturbated areas (spring-neap and tidal-interior HZ) and in the tidal-near channel HZ during the winter, DIC and DOC concentrations at low and high tide showed small changes in concentration (figure S7(c)–(h)).

The increase in dissolved carbon may be attributed to elevated temperature, plant activity, or an enhanced

supply of carbon (i.e. plant exudates) during the summer when plants are actively growing or due to physical dynamics such as advection of groundwater into macropores, which were not measured in this study. However, seasonal temperature changes are uniform across the marsh platform and belowground net primary production is similar between tall *S. alterniflora* (tidal-near channel HZ) and *S. cynosuroides* (spring-neap HZ) (Schubauer and Hopkinson 1984) (figure S7(e), (g)). Therefore, the seasonal increase and tidal variability in dissolved carbon, particularly DIC, in the tidal-near channel HZ compared to more consistent concentrations in the spring-neap and tidal-interior HZs, suggests attribution to more rapid oxidation due to burrow-enhanced porewater flushing and large Eh oscillations. While the linked influences between crab burrows, marsh hydrology, redox potential, and porewater dissolved carbon concentrations suggest that burrows are important to the net marsh carbon balance, we are unable to elucidate the relative importance of plant activity.

Like the sediments, tidal channels showed important fluctuations in carbon content and export. In general, salt marsh porewater drains to tidal creeks during low tide (Wilson and Gardner 2006, Moffett *et al* 2012), reflected in concentrated, more porewater-like chemistry of low-tide creek waters (Zhang *et al* 2014, Moffett and Gorelick 2016). Besides allowing greater oxygen penetration, crab burrows further enhance drainage of carbon-enriched marsh porewater (figure S8) to the tidal creeks during low tide, when the hydraulic gradient is greatest. DOC and DIC concentrations in the creek support the observed summer increase in oxidized carbon export from the marsh,

Figure 4. Schematic of marsh platform groundwater (GW)-tidal channel exchange, DIC and DOC concentrations, and resulting estimates of vertical and horizontal carbon fluxes in seasons or locations with and without creek-side crab burrows. Low = low tide; High = high tide.

with summer creek DIC (but not DOC) concentrations higher at low tide (40.3 mg l^{-1}) than high tide (14.3 mg l^{-1}) (table S1, figure S7). In contrast, in the winter, the differences between low and high tide creek water DIC and DOC concentrations were small (2.0 mg l^{-1}) (figure S7).

Using season-specific excess porewater DOC and DIC concentrations and season-specific Darcy fluxes for the tidal-near channel HZ, we calculated the excess horizontal carbon flux between the marsh platform and tidal channel during the bioturbated summer and non-bioturbated winter periods (figure 4). High dissolved carbon concentrations in the marsh porewater in the summer coupled with enhanced marsh-creek fluid exchange facilitated by dense crab burrowing resulted in an order-of-magnitude increase in the horizontal flux of carbon from marsh to creek (i.e. marsh carbon loss).

4. Discussion

This study is the first to quantify how hydrology, crab activity, and redox potential are linked through space and time and together affect the marsh carbon balance. We identify and quantify two mechanisms that mediate carbon fluxes and transformation. First, a temporally and spatially dynamic hydro-biological

mechanism impacts the magnitude of lateral water exchange and, in turn, carbon exchange via crab-mediated physical changes in the near-channel sediment. We show that in the summer, crabs excavate burrows which increase marsh permeability in heavily bioturbated areas. More permeable sediments conduct greater fluxes of oxygen and reactant-rich water into the marsh by aeration and flood-infiltration, enhancing the creek-bank water exchange. Recent work has identified this lateral exchange of water and dissolved carbon between the marsh platform and tidal channel to be an important component of coastal carbon budgets (Bauer *et al* 2013, Wang *et al* 2016, Najjar *et al* 2018). However, the magnitude of and mechanisms driving lateral carbon export are not well understood.

The linkages between hydrology, crab activity, and redox potential also suggest a hydro-biogeochemical mechanism through which burrows increase lateral carbon exchange with the tidal channel (through increased DIC concentrations), as well as vertical carbon exchange to the atmosphere (through increased CO_2 production and evasion). The burrow-mediated increase in the depth and (positive) magnitude of Eh in heavily bioturbated areas impacts the rates and quantity of carbon oxidation. By increasing the volume of the high-Eh zone, the region of aerobic and higher-yield anaerobic oxidation (i.e. NO_3^- or Fe-reduction)

increases (Thomas and Blum 2010), decreasing carbon storage through faster rates of carbon oxidation (figure 4). In non-bioturbated sediment, studies show that carbon oxidation rates are high in the top 0–10 cm, ranging from 2.4–4.8 $g\,C\,m^{-2}\,d^{-1}$, but rapidly decrease below the top 10 cm of sediments to about 0.54 g C m^{-2} d^{-1} (Middelburg *et al* 1996, Kristensen 2000, Kostka *et al* 2002b), resulting in a depth integrated carbon oxidation rate for the top 35 cm of sediment of 6.8 $g\,C\,m^{-2}\,d^{-1}$.

In bioturbated sediments, high Eh at depth would allow for faster oxidation rates to penetrate deeper in the marsh sediment (Kostka *et al* 2002b). In the bioturbated tidal-near channel HZ, the maximum depth of sediments diurnally reaching high (oxidative) Eh values coinciding with low tides was 35 cm in the summer. Assuming a gradual decrease from 2.4 $g\,C\,m^{-2}\,d^{-1}$ at the surface to 0.54 $g\,C\,m^{-2}\,d^{-1}$ to at least 35 cm (instead of 10 cm as before) (Kristensen 2000, Kostka *et al* 2002b), this would result in a depth-integrated oxidation rate for the top 35 cm of 13.1 g C m^{-2} d^{-1}, 1.9 times that if crab bioturbation were absent.

Our conservative estimates of depth-integrated carbon oxidation fall within the range of CO_2 emissions from tidal wetlands reported in the literature, yet these studies do not necessarily consider the partitioning of oxidized carbon between vertical (gaseous) and lateral (aqueous) export (Morris and Whiting 1986, Magenheimer *et al* 1996, Middelburg *et al* 1996, Abril and Borges 2004). For example, some of the oxidized carbon is converted to DIC, further increasing the lateral carbon exchange. Our measured porewater DIC concentrations in bioturbated sediments in the summer were consistent with this inferred burrow-induced increased carbon oxidation rate based on field Eh measurements. However, this elevated carbon oxidation was transient and spatially variable, only occurring in the tidal-near channel HZ and in summer, and to a lesser extent fall, when burrows are most abundant and when microbes are expected to be more active because of freshly deposited organic carbon from plant root exudates and warmer temperatures.

Were the findings of this study generalized to all marshes likely to have similar crab burrowing activity, the total effect of this burrow-enhanced carbon oxidation could be a non-negligible component of the global marsh carbon cycle. We roughly estimate as a thought experiment to place our findings in context, that the crab burrow-enhanced oxidation effects described herein could reduce global marsh gross carbon sequestration by about 0.35 Tg C yr^{-1}. This estimate was based on our observed 1.9-fold increase in carbon oxidation in bioturbated areas, an estimation that 0.4% of marsh area within current crab habitat is inhabited by crabs, and an assumed average crab activity period of 90 d (Katz 1980; see Text S1 for more detailed methods). We acknowledge that this estimate involves broad assumptions and glosses over very many details. However, carbon storage and accumulation

in salt marshes has been shown to be relatively insensitive to latitude and mean temperature (Chmura *et al* 2003), supporting the notion of calculating and roughly assessing the oxidation portion of the marsh carbon balance with similar latitudinal extrapolation. According to Ouyang and Lee (2014), the net global carbon sequestration rate in salt marshes is approximately 10.1 Tg yr-1. This suggests that approximately 3.5% of gross carbon sequestration may be re-oxidized by the processes investigated in this paper. With warming, crabs are expected to expand their habitat range (Walther *et al* 2002, Johnson 2014, Brodie *et al* 2017), which could increase the oxidation—by sheer habitat expansion, not any temperature effect—to 0.44 T g C yr-1. However, with SLR and coastal marsh inundation, crabs could also see a decrease in their habitat area. Therefore, the positive and negative feedbacks of climate change on these important processes should be further explored. These calculations are highly uncertain due to variability in the magnitude and extent of heavy bioturbation, number of active days, percent of area bioturbated, changes in marsh area, and future crab population dynamics, among other factors. However, they illustrate that this process has the potential to be globally significant.

5. Conclusions

In this work, we observationally identify and quantify mechanistic feedbacks between biology, hydrology, and biogeochemistry that will improve understanding of the role of tidal saline marshes in the global carbon cycle. Our analysis shows that crab burrowing activity mediates carbon fluxes in coastal marshes through physical and biogeochemical processes. Crab burrows increase the exchange of carbon-rich fluid between the marsh platform and tidal channel via changes in near-creek sediment permeability. Crab burrows also increase the depth and (positive) magnitude of Eh in areas of greatest bioturbation, which increases the rate and quantity of carbon oxidation. While there is large uncertainty in crab habitat due to future climate variability, the processes identified in this study suggest that changes in their habitat have the potential to be globally important. Thus, we suggest that crabs are important biogeochemical engineers and that their populations should be considered in assessments of the marsh carbon storage system.

Data availability

Data are available in supporting information and will be uploaded to a public repository on acceptance. The data that support the findings of this study are openly available at https://doi.org/10.4211/hs.8f0b5599b871457ebb47f0bac898f156.

References

Abril G and Borges A V 2004 Carbon dioxide and methane emissions from estuaries *Greenhouse Gas Emissions: Fluxes and Processes, Hydroelectrics Resevoirs and Natural Environments (Environ. Sci. Ser.)* ed A L Tremblay *et al* (Berlin: Springer) pp 187–207

Bauer J E, Cai W-J, Raymond P A, Bianchi T S, Hopkinson C S and Regnier P A G 2013 The changing carbon cycle of the coastal ocean *Nature* **504** 61–70

Bothfeld F 2016 Spatial and temporal heterogeneity of methane and carbon dioxide production and flux in a temperate tidal salt marsh *Masters Thesis* University of Delaware

Bouwer H and Rice R C 1976 A slug test for determining hydraulic conductivity of unconfined aquifers with completely or partially penetrating wells *Water Resour. Res.* **12** 423–8

Brodie R J, Roberts B, Espinosa J I, Heilman K, Borgianini S A, Welch J M and Reinsel K A 2017 Seasonal and latitudinal variations in the energy reserves of the mud fiddler crab Uca pugnax : implications for the response to climate change *Aquatic Biol.* **26** 113–23

Canadell J G and Raupach M R 2008 Managing forests for climate change mitigation *Science* **320** 1456–8

Chmura G L, Anisfeld S C, Cahoon D R and Lynch J C 2003 Global carbon sequestration in tidal, saline wetland soils *Glob. Biogeochem. Cycles* **17** 12

Duarte C M, Losada I J, Hendriks I E, Mazarrasa I and Marbà N 2013 The role of coastal plant communities for climate change mitigation and adaptation *Nat. Clim. Change* **3** 961–8

Hughes C E, Binning P and Willgoose G R 1998 Characterisation of the hydrology of an estuarine wetland *J. Hydrol.* **211** 34–49

Johnson D S 2014 Fiddler on the roof: a northern range extension for the marsh fiddler crab Uca pugnax *J. Crustacean Biol.* **34** 671–3

Katz L C 1980 Effects of burrowing by the fiddler crab, Uca pugnax (Smith) *Estuarine Coast. Mar. Sci.* **11** 233–7

Knopf G N 1966 Observations on behavioral ecology of the fiddler crab, Uca pugilator (Bosc) *Crustaceana* **11** 302–5

Koo B J, Kwon K K and Hyun J-H 2005 The sediment-water interface increment due to the complex burrows of macrofauna in a tidal flat *Ocean Sci. J.* **40** 221–7

Kostka J E, Gribsholt B, Petrie E, Dalton D, Skelton H and Kristensen E 2002a The rates and pathways of carbon oxidation in bioturbated saltmarsh sediments *Limnol. Oceanogr.* **47** 230–40

Kostka J E, Roychoudhury A and Van Cappellen P 2002b Rates and controls of anaerobic microbial respiration across spatial and temporal gradients in saltmarsh sediments *Biogeochem.* **60** 49–76

Krebs C T and Valiela I 1978 Effect of experimentally applied chlorinated hydrocarbons on the biomass of the fiddler crab, Uca pugnax (Smith) *Estuarine Coast. Mar. Sci.* **6** 375–86

Kristensen E 2000 Organic matter diagenesis at the oxic/anoxic interfacein coastal marine sediments, with emphasis on the role of burrowing animals *Hydrobiologia* **426** 1–24

Kristensen E, Flindt M R, Ulomi S, Borges A V, Abril G and Bouillon S 2008 Emission of CO_2 and CH_4 to the atmosphere by sediments and open waters in two Tanzanian mangrove forests *Mar. Ecol. Prog. Ser.* **370** 53–67

Lee S Y 2008 Mangrove macrobenthos: assemblages, services, and linkages *J. Sea Res.* **59** 16–29

Magenheimer J F, Moore T R, Chmura G L and Daoust R J 1996 Methane and carbon dioxide flux from a macrotidal salt marsh, Bay of Fundy *Estuaries* **19** 139–45

McCraith B J, Leonard R G, Wethey D S and Moore W S 2003 The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh *J. Mar. Res.* **61** 359–90

Mcleod E, Chmura G L, Bouillon S, Salm R, Björk M, Duarte C M and Silliman B R 2011 A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2 *Frontiers Ecol. Environ.* **9** 552–60

Middelburg J J, Klaver G, Nieuwenhuize J, Wielemaker A, De Haas W, Vlug T and Van Der Nat J F W A 1996 Organic matter mineralization in intertidal sediments along an estuarine gradient *Mar. Ecol. Prog. Ser.* **132** 157–68

Moffett K B and Gorelick S M 2016 Relating salt marsh pore water geochemistry patterns to vegetation zones and hydrologic influences *Water Resour. Res.* **52** 1729–45

Moffett K B, Gorelick S M, McLaren R G and Sudicky E A 2012 Salt marsh ecohydrological zonation due to heterogeneous vegetation-groundwater-surface water interactions *Water Resour. Res.* **48** W02516

Molina M, Zaelke D, Madhava Sarma K, Andersen S O, Ramanathan V and Kaniaru D 2009 Reducing abrupt climate change risk using the Montreal Protocol and other regulatory actions to complement cuts in CO_2 emissions *Proc. Natl Acad. Sci.* **106** 20616LP-20621

Montague C L 1982 The influence of fiddler crab burrows and burrowing on metabolic processes in salt marsh sediments *Estuarine Comparisons* ed V S Kennedy (New York: Academic) pp 283–301

Morgan S G, Spilseth S A, Page H M, Brooks A J and Grosholz E D 2006 Spatial and temporal movement of the lined shore crab pachygrapsus crassipes in salt marshes and its utility as an indicator of habitat condition *Mar. Ecol. Prog. Ser.* **314** 271–81

Morris J T and Whiting G J 1986 Emission of gaseous carbon dioxide from salt-marsh sediments and its relation to other carbon losses *Coast. Estuarine Res. Fed.* **9** 9–19

NOAA National Estuarine Research Reserve System (NERRS) System-wide Monitoring Program. Data accessed from the NOAA NERRS Centralized Data Management Office

Najjar R G *et al* 2018 Carbon budget of tidal wetlands, estuaries, and shelf waters of Eastern North America *Glob. Biogeochem. Cycles* **32** 389–416

Ouyang X and Lee S Y 2014 Updated estimates of carbon accumulation rates in coastal marsh sediments *Biogeosciences* **11** 5057–71

Ouyang X, Lee S Y and Connolly R M 2017 Structural equation modelling reveals factors regulating surface sediment organic carbon content and CO_2 efflux in a subtropical mangrove *Sci. Total Environ.* **578** 513–22 Elsevier B.V.

Penha-Lopes G, Kristensen E, Flindt M, Mangion P, Bouillon S and Paula. J 2010 The role of biogenic structures on the biogeochemical functioning of mangrove constructed wetlands sediments-a mesocosm approach *Mar. Pollut. Bull.* **60** 560–72

Pülmanns N, Diele K, Mehlig U and Nordhaus I 2014 Burrows of the semi-terrestrial crab ucides cordatus enhance CO_2 release in a north brazilian mangrove forest *PLoS One* **9** e109532

Rogelj J *et al* 2018 Mitigation pathways compatible with 1.5 °C in the context of sustainable development *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* ed V Masson-Delmotte *et al* accepted (https://ipcc.ch/sr15/)

Rotzoll K, Gingerich S B, Jenson J W and El-Kadi A I 2013 Estimating hydraulic properties from tidal attenuation in the Northern Guam Lens Aquifer, territory of Guam, USA *Hydrol. J.* **21** 643–54

Schubauer J P and Hopkinson C S 1984 Above- and belowground emergen macrophyte production and turnover in a coastal marsh ecosystem, Georgia *Limnol. Oceanogr.* **29** 1052–65

Stahl M O, Tarek M H, Yeo D C J, Badruzzaman A B M and Harvey C F 2014 Crab burrows as conduits for groundwater-surface water exchange in Bangladesh *Geophys. Res. Lett.* **41** 8342–7

Teal J M 1958 Distribution of fiddler crabs in georgia salt marshes *Ecology* **39** 185–93

Thomas C R and Blum L K 2010 Importance of the fiddler crab Uca pugnax to salt marsh soil organic matter accumulation *Mar. Ecol. Prog. Ser.* **414** 167–77

Thomson A C G, Trevathan-Tackett S M, Maher D T, Ralph P J and Macreadie P I 2019 Bioturbator-stimulated loss of seagrass sediment carbon stocks *Limnol. Oceanogr.* **64** 342–56

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee T J C and Bairlein F 2002 Ecological responses to recent climate change *Nature* **416** 389–95

Wang J Q, Zhang X D, Jiang L F, Bertness M D, Fang C M, Chen J K, Hara T and Li B 2010 Bioturbation of burrowing crabs promotes sediment turnover and carbon and nitrogen movements in an estuarine salt marsh *Ecosystems* **13** 586–99

Wang Z A, Kroeger K D, Ganju N K, Gonneea M E and Chu S N 2016 Intertidal salt marshes as an important source of inorganic carbon to the coastal ocean *Limnol. Oceanogr.* **2** 1916–31

Wasson K *et al* 2019 Pattern and scale: evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale *Ecology* **100** e02813

Wiegert R G and Freeman B J 1990 Tidal salt marshes of the Southeast Atlantic Coast: a community profile (Washington, DC: US Department of the Interior, Fish and Wildlife Service)

Wilson A M, Evans T, Moore W, Schutte C A, Joye S B, Hughes A H and Anderson J L 2015 Groundwater controls ecological zonation of salt marsh macrophytes *Ecology* **96** 840–9

Wilson A M and Gardner L R 2006 Tidally driven groundwater flow and solute exchange in a marsh: numerical simulations *Water Resour. Res.* **42** 1–9

Wilson C A, Hughes Z J and FitzGerald D M 2012 The effects of crab bioturbation on Mid-Atlantic saltmarsh tidal creek extension: geotechnical and geochemical changes *Estuarine Coast. Shelf Sci.* **106** 33–44

Wolf P L, Sheryl F S and Reimold R J 1975 Population estimates for Uca Pugnax (Smith, 1870) on the duplin estuary marsh, Georgia, USA (Decapoda Brachyura, Ocypodidae) *Crustaceana* **29** 79–91

Xiao K, Wilson A M, Li H and Ryan C 2019 Crab burrows as preferential flow conduits for groundwater flow and transport in salt marshes: a modeling study *Adv. Water Res.* **132** 103408

Xin P, Jin G, Li L and Barry D A 2009 Effects of crab burrows on pore water flows in salt marshes *Adv. Water Res.* **32** 439–49

Zhang H, Moffett K B, Windham-Myers L and Gorelick S M 2014 Hydrological controls on methylmercury distribution and flux in a tidal marsh *Environ. Sci. Technol.* **48** 6795–804