

RESEARCH ARTICLE

Responses of a tidal freshwater marsh plant community to chronic and pulsed saline intrusion

Fan Li¹ | Christine Angelini² | James E. Byers³ | Christopher Craft⁴ | Steven C. Pennings¹¹Department of Biology and Biochemistry, University of Houston, Houston, Texas, USA²Environmental Engineering Sciences, University of Florida, Gainesville, Florida, USA³Odum School of Ecology, University of Georgia, Athens, Georgia, USA⁴School of Public and Environmental Affairs, Indiana University, Bloomington, Indiana, USA

Correspondence

Steven C. Pennings

Email: scpennin@central.uh.edu

Funding information

National Science Foundation, Grant/Award Number: OCE-1237140 and OCE-1832178; University of Georgia Marine Institute

Handling Editor: D. Edmead

Abstract

1. Climate change causes both chronic and pulsed environmental changes to ecosystems. In estuaries, tidal freshwater marshes experience both extended and episodic periods of elevated salinities due to sea level rise, reduced river discharge during drought and storm surge, but most research has focused on extended (press) perturbations.
2. Over a 4-year period, we added diluted seawater to replicated plots in a tidal freshwater marsh in Georgia, USA to raise porewater salinities from freshwater to oligohaline. We assessed the ecosystem effects of press (continuous) and pulse (2 months per year) changes in salinity by measuring the responses of dominant angiosperms, benthic microalgae and dominant macro-invertebrates (fiddler crabs). We transplanted angiosperms typical of oligohaline and mesohaline conditions into plots as bioindicators (phytometers) to assess potential for vegetation changes over longer time periods.
3. In the press treatment, the cover of all common plant species decreased. *Ludwigia repens* almost disappeared within the first month; *Polygonum hydropiperoides* nearly disappeared within the first growing season; *Pontederia cordata* and *Zizaniopsis miliacea* declined over the 4 years but did not completely disappear. The decline in the four most dominant plant species decreased total above-ground plant biomass, leading to an increase in light penetration and increased densities of benthic diatoms and cyanobacteria. The density of fiddler crab burrows was not significantly affected by the treatments, but was positively related to above-ground plant biomass across all replicates. Transplant experiments indicated that plants typical of higher salinity conditions (e.g. *Schoenoplectus* sp.) performed well under conditions prevalent in the press plots.
4. In the pulse treatment, only *L. repens* declined, and there was no effect on community-level above-ground biomass or other community variables.
5. **Synthesis.** Our results indicate that tidal freshwater marsh plant and animal communities are vulnerable to extended periods of salinization but resilient to short saline pulses. Although saline pulses did not impair most ecosystem functions,

the decline in a single species (*L. repens*) in the pulse treatment was associated with reduced marsh accretion and no elevation gain—factors which must be positive for wetland survival in an era of rising seas. Thus, periodic salinization may threaten the long-term persistence of freshwater wetlands even before dramatic changes in community structure occurs.

KEYWORDS

brackish marsh, climate change, press, pulse, salinity, salinization, sea level rise, tidal freshwater marsh

1 | INTRODUCTION

Predicting ecosystem responses to environmental change is an important goal of ecological research in a time of rapid anthropogenic change. One extreme scenario of environmental change is a chronic alteration in a variable, or a 'press' (Smith et al., 2009). Many studies have explored the consequences of potential environmental changes by using the press treatments of, for example, sea level rise (Langley et al., 2013) or elevated CO₂ (Pastore et al., 2016). Presses should cause a sequence of events starting with physiological responses, changes in community structure and finally species loss and immigration of species tolerant of the new conditions (Smith et al., 2009). In nature, however, ecosystems typically experience fluctuating disturbances rather than persistent press changes (Donohue et al., 2016). Intermittent or 'pulsed' disturbances may also cause individual mortality and changes in community structure and ecosystem function (Ciais et al., 2005; Thibault & Brown, 2008); however, they may not cause permanent 'state' changes because their short-term nature may allow the ecosystem to recover in between pulses to its previous composition and function (Ratajczak et al., 2017; Smith, 2011).

In coastal habitats, climate change, storms and anthropogenic factors are predicted to cause both press and pulse changes to the environment (Parkyn & Collier, 2004). Climate change is expected to affect temperature and precipitation patterns; in many areas, this may result in altered freshwater delivery to coastal habitats (Nijssen et al., 2001). In addition, anthropogenic activities may reduce freshwater delivery through diversion of freshwater for irrigation, household use and industry (Cloern & Jassby, 2012; Enright & Culbertson, 2009). Mean sea level is variable among years, but is expected to increase between 0.38 and 2 m during the coming century (Church & White, 2011; Horton et al., 2014). Higher sea levels will force saline water upstream within estuaries and tidal rivers into lower salinity habitats, changing salinity gradients along estuaries (Knighton et al., 1991; Wood & Harrington, 2015). Similarly, storm surges can push saline water upstream as pulse events (Middleton, 2016).

Situated in the upper estuary, tidal freshwater marshes are characterized by high macrophyte diversity, productivity and nutrient retention (Costanza et al., 1998; Craft, 2007; Loomis & Craft, 2010; Van de Broek et al., 2016; Więski et al., 2010). Tidal freshwater

marsh plants are usually competitively dominant over plants tolerant of more saline conditions (Crain et al., 2004; Guo & Pennings, 2012), but their downstream distribution is constrained by their limited tolerance to salinity (Guo & Pennings, 2012; Li & Pennings, 2018; Wetzel et al., 2004). If elevated salinity occurs in a tidal freshwater marsh, as might happen due to drought, storm surge or high sea levels, growth of freshwater plants may decrease through osmotic effects and the accumulation of toxic ions (Adam, 1990), driving shifts in the composition of plant communities (Knighton et al., 1991; McKee & Mendelssohn, 1989; Sharpe & Baldwin, 2012; Sutter et al., 2015). Given long-term projections of sea level rise, freshwater marshes may be replaced by vegetation typical of brackish or salt marshes downstream (Craft et al., 2009). If salinization is only temporary, however, as might occur due to decreased freshwater inflows during a drought, freshwater plants may be resilient to saline pulses and able to recover once the pulse is withdrawn (Flynn et al., 1995; Goodman et al., 2010; Howard & Mendelssohn, 1999).

The effects of saltwater intrusion on foundation species, such as marsh-building plants, are likely to cascade and affect many other taxa in the community (McFarlin et al., 2015). The loss of marsh macrophytes is likely to facilitate benthic microalgae by increasing light and nutrient availability (Sullivan & Currin, 2002). The loss of marsh macrophytes is also likely to affect marsh invertebrates, because both vascular plants and microalgae are food for fiddler crabs, other invertebrates and fish (Bertness et al., 2014; Holdredge et al., 2009; Silliman & Bertness, 2002; Sullivan & Moncreiff, 1990), and because plants provide structural support for burrows and refuge from predators (Bertness & Miller, 1984; Bortolus et al., 2002; Nomann & Pennings, 1998; Wang et al., 2015). Thus, understanding effects on plants as a basal resource and structure provides a basis from which to predict how press and pulse saltwater intrusion will affect the entire ecosystem.

We conducted a 4-year field experiment to determine the responses of a tidal freshwater marsh community to presses and pulses of saline water addition in coastal Georgia. Previous findings from this experiment revealed that the press treatment altered porewater biogeochemistry (increased chloride, sulphate, sulphide, ammonium, nitrate and phosphorus); reduced above- and below-ground macrophyte biomass; decreased microbial diversity and function; decreased net ecosystem exchange, ecosystem respiration and CH₄

emissions; and decreased surface elevation (Herbert et al., 2018; Mobilian et al., 2020; Solohin et al., 2020; Widney et al., 2019) (Table S1). The pulse treatment produced transient increases in chloride and sulphate that rapidly returned to baseline conditions, and prevented vertical accretion of the marsh platform due to the loss of roots and rhizomes in the soil, while other ecosystem properties and processes were largely unaffected (Table S1). Here, we build on these findings by reporting effects on vascular plants, benthic microalgae and macro-invertebrates.

We tested four hypotheses. (1) Both presses and pulses of saline water will suppress the performance and abundance of individual plant species; however, (2) communities experiencing saline pulses will recover once the pulses are withdrawn. Moreover, because saline treatments (and consequent thinning of vegetation) will alter light penetration and the above- and below-ground structure provided by marsh plants, (3) benthic microalgae will increase in treatments where macrophytes decrease, and (4) fiddler crab densities will change in treatments where macrophytes decrease, either increasing in response to more food (benthic microalgae) or decreasing in response to reduced physical structure (e.g. roots) to support burrows.

2 | MATERIALS AND METHODS

2.1 | Site description

We conducted the experiment, part of the Georgia Coastal Ecosystem Long Term Ecological Research program (<https://gce-iter.marsci.uga.edu/>), in a tidal freshwater marsh (latitude 31.3394, longitude -81.4666) on the Altamaha River, Georgia, USA. Work was approved by the Coastal Resources Division of the Georgia Department of Natural Resources. The marsh contained a mixture of emergent herbaceous species with four dominant species: *Ludwigia repens*, *Polygonum hydropiperoides*, *Pontederia cordata* and *Zizaniopsis miliacea*. *L. repens* (creeping primrose-willow) is a mat-forming perennial herb, typically <15 cm tall, with creeping stems, and its roots grow from nodes which lie on the soil. *P. hydropiperoides* (swamp smartweed) and *P. cordata* (pickerelweed) are understory perennials that grow up to ~1 m in height. *Z. miliacea* (wild rice), the dominant species, is a perennial grass growing from large rhizomes with stems up to ~3 m tall, and represented the majority of the plant biomass.

2.2 | Experimental design

The experiment consisted of 30 experimental plots, each 2.5 m × 2.5 m, established at the site in December 2012. We measured plot elevation using real-time kinematic GPS. Plots had an average elevation of 0.718 m relative to NAVD88 and were flooded twice daily by the tides, with an average flooding depth of ~25 cm at high tide (Mobilian et al., 2020; Widney et al., 2019). We briefly describe the plots and treatments below; additional methodological

details are provided in previous publications resulting from the experiment that have focused on porewater and soil chemistry (Widney et al., 2019), carbon cycling (Herbert et al., 2018; Widney et al., 2019) and soil microbial communities (Mobilian et al., 2020).

In March 2013, a polycarbonate frame was inserted ~15 cm into the soil to define the perimeter of each plot, except for the control plots described below. The frame extended an additional ~15 cm above the soil surface. The purpose of the frames was to minimize lateral movement of treatment water that was added to the plots at low tide so that it would infiltrate into the plot rather than flowing across the soil surface out of the plots. Two features of the frame minimized effects on normal tidal flooding, that is, allowing natural flooding and draining of the plots. First, the top of the frame was submerged at ~70% of high tides (Widney et al., 2019), allowing flow over the top of the frame. Second, the frames had two holes (~2 cm diameter) in the sides just above the soil surface that were plugged when we watered the plots, but otherwise were open to allow the exchange of tidal water. There was no evidence that the frame affected clonal growth of the dominant plants in the area: *L. repens* spread over the top of the frame, *P. hydropiperoides* and *Zizaniopsis miliacea* readily spread by rhizomes beneath it and other species recruited into the plots by seed (authors personal observations).

Plots were assigned one of the five treatments: press of saline water addition, press of freshwater addition and pulse of saline water addition, control and control with frame. The saline press treatment was intended to simulate chronic saltwater intrusion. The saline pulse treatment was intended to mimic saltwater intrusion that occurs during seasonal periods of low river flow (Figure S1). The freshwater press treatment was intended to control for the effects of increased additions of water to the plots. The control treatment (no frame) served as an unmanipulated comparison for the experimental treatments. Finally, the control with frame treatment was included as a methodological control to assess any effects of the frame (we found none).

We monitored the plots without imposing treatments in 2013 to collect baseline data, then initiated the treatments on 14 April 2014 at which time we began to collect seawater (~22 PSU) from Hudson Creek at Meridian Landing (latitude 31.4335, longitude -81.3627) and freshwater (<0.5 PSU) from the Altamaha River near the study site and mixed them on site to create brackish water of ~15 PSU. Plots were dosed three to four times each week at low tide. The saline press plots received additions of brackish water, with the goal and result of elevating porewater salinity to 2–5 PSU. Pulse plots received brackish water during September and October, when low flow conditions in the Altamaha River typically occur. For the rest of the year, pulse plots received fresh river water. The freshwater treatment plots received additions of river water. All treated plots were dosed on the same days and each received the same volume of water (~265 L). Typically, the treatment additions infiltrated into the soil within 30 min after addition. The volume of water that we added to the plots at low tide was ~5% of that added by natural tidal flooding (Herbert et al., 2018).

Once treatments began, we collected porewater samples from shallow (10–35 cm) wells weekly from a subsample of the plots (each plot was sampled at least monthly) and measured salinity using a handheld refractometer to monitor the efficacy of the treatments over time. Five plots (two control with frame plots, one freshwater addition plot and two press of saline water addition plots) did not match the porewater salinity goals because of leakage out of plots. We therefore changed the treatment designations of these five plots beginning in January 2015, 9 months after treatments were initiated, to better match treatment goals. Because these switched plots had a shorter treatment duration (3 instead of 4 years), this change was conservative with respect to identifying treatment effects. Porewater data from this study are available online (Craft, 2017).

2.3 | Vegetation measurements

We measured stem density and height within a permanent 0.83 m × 0.83 m subplot inside each plot. We made the measurements three to six times during each growing season from 2013 through 2017 (1 year pre-treatment and 4 years of treatment, Table S2). We measured the height of all stems of *Z. miliacea* and *P. hydropiperoides*, and all leaves of *P. cordata*. The fourth common species, *L. repens*, has a creeping morphology for which height measurements were not appropriate. We visually estimated the per cent cover of the four most abundant plant species, *L. repens*, *P. hydropiperoides*, *P. cordata* and *Z. miliacea*, in each entire 2.5 m × 2.5 m plot (Dethier et al., 1993), except that the cover of *L. repens* was not measured in 2013. We deliberately focused our analyses on the four dominant plant species that made up the vast majority of the biomass and cover in the plots. Other plant species were so rare (often present as single small individuals in one or two plots) that they were unlikely to have measurable impacts on plant cover or biomass; we took notes on these but do not formally present data. The total canopy cover often summed to >100% because the foliage of the different species overlapped. We measured leaf-level photosynthetic rates (2013–2016) of the tallest individuals in each plot of *Z. miliacea*, *P. hydropiperoides* and *P. cordata* three to six times each growing season using an LCi photosynthesis system (ADC BioScientific Ltd., Hoddesdon, UK). Plant data from this study are available online (Li, 2017).

To non-destructively estimate above-ground biomass in the experimental plots, we collected 50 *Z. miliacea* stems (50–235 cm), 54 *P. hydropiperoides* stems (30–123 cm) and 95 *P. cordata* leaves (30–120 cm) from a marsh adjacent to the study site in July 2016. The heights of the stems or leaves were measured on site, and then the plant material was dried at 60°C to constant mass. We created allometric relationships between biomass and height for these species (Table S3) and used these relationships to estimate above-ground biomass from the non-destructive height measurements that we took in the 0.83 m × 0.83 m subplots over the course of the experiment. Allometric data from this study are available online (Li, 2017).

2.4 | PAR, microalgae and fiddler crabs

We measured the photosynthetically active radiation (PAR) above the plant canopy and 10 cm above the soil in each plot using a SunScan Canopy Analysis System (Delta-T Devices Ltd.) on 1–6 dates during each growing season from 2013 to 2017 (Table S2) and calculated the proportion of light penetrating the canopy. PAR data from this study are available online (Li, 2017). We estimated the abundance of green algae, diatoms and cyanobacteria using an *in situ* fluorimetric probe (bbe-Moldaenke GmbH BenthosTorch, Schwentinental, Germany). Measurements were taken monthly from February 2016 to December 2017 (Table S2). The probe uses spectral analysis to estimate the abundance of these three microalgal groups in surface sediments (Echenique-Subiabre et al., 2016). We averaged four readings from each plot to give a single value per plot per date. Microalgal data from this study are available online (Craft, 2015). The only abundant benthic macro-invertebrate at the study site was the fiddler crab *Minuca minax* (= *Uca minax*). We counted fiddler crab burrows (>0.5 cm in diameter) in a 0.75 by 0.5 m² quadrat in each plot in spring and fall of 2014, 2015 and 2016 (Table S2). Burrows are a good non-destructive proxy for crab abundance (Angelini et al., 2015). Fiddler crab burrow data from this study are available online (Angelini, 2018).

2.5 | Transplant (Phytometer) experiment

Because the experimental site was in the middle of an extensive tidal fresh marsh and physically isolated from brackish marshes, which were several kilometres downstream, brackish marsh plants were essentially unable to recruit naturally to the experiment due to distance. We therefore transplanted two species of brackish marsh plants into the plots in 2017 as phytometers, or indicator transplants, to quantify how well they would perform if they had been able to recruit, with the expectation that they would do well in the saline treatments. We collected culms of *Juncus roemerianus* and *Schoenoplectus* sp. (likely *Schoenoplectus americanus*) from a brackish marsh ~5 km downstream of the study site (GCE site 8, Latitude 31.3126, Longitude -81.4209) on 7 March 2017, watered them with freshwater for 3 days to minimize transplant shock and planted a single culm of each species into each plot on 10 March 2017. We collected individual culms at least 1 m apart to minimize the likelihood of collecting genetically identical individuals. When transplanted, *J. roemerianus* culms had ~10 leaves and *Schoenoplectus* sp. culms had ~2 shoots. *Schoenoplectus* sp. transplants grew quickly in some treatments, so we harvested them on 25 July 2017 to prevent them from becoming so abundant that they might affect conditions in the plots. *J. roemerianus* transplants grew slowly, and we waited until 15 October 2017 to harvest them. We excavated the transplants, dried above- and below-ground biomass at 60°C for 3 days and weighed it. Phytometer data from this study are available online (Li, 2017).

2.6 | Statistical analyses

We used repeated-measures analysis of variance (ANOVA) to identify treatment-related differences in estimated above-ground biomass and cover (for individual species and total), proportion of light penetrating the canopy, benthic microalgae and fiddler crab burrows with plot elevation as a covariate to account for variation in elevation among plots. We confined our repeated-measures analysis to the period after the five treatment plots were re-designated (2015 and forward). To minimize the effects of the annual growth cycle on the results, we limited statistical analyses of the plant responses to data collected in June, July and August when above-ground biomass was at its seasonal peak, but we show all data in the figures to illustrate the seasonal growth patterns of the plants, which justify this approach. The phytometer data were analysed using a one-way ANOVA. The analyses of above-ground, below-ground and total biomass gave similar statistical results, so we report only results for total biomass.

To examine the effects of light availability on benthic microalgae, we used linear regression to relate microalgae abundance to light penetration measured at the same approximate time (November 2016). We also used linear regression to explore relationships between fiddler crabs (burrows), light availability and above-ground biomass measured in fall (September–November 2016). We chose to focus on this date because it was late in the experiment and during a warm time of the year when the crabs would have been active and

the pulse treatment was either in effect or had just been completed. Analyses were conducted using Statistical Analysis Systems, SAS Institute Inc.

3 | RESULTS

3.1 | Porewater salinity

The treatments were effective at achieving desired salinity goals. Within a few weeks after saline water additions began, porewater salinity in the press treatment rose to oligohaline (0.5–5) conditions (Figure 1a). It decreased thereafter, averaging 2.18 ± 0.05 (SE) over the duration of the entire treatment period. The porewater salinity in the pulse plots increased to oligohaline conditions during each treatment period, with an average during the treatment period of 1.28 ± 0.15 in 2014, 1.40 ± 0.16 in 2015, 1.55 ± 0.15 in 2016 and 0.79 ± 0.15 in 2017 (Figure 1b). Porewater salinity in the pulse plots rapidly fell to ambient conditions when the saline pulse was discontinued. The control, control with frame and freshwater addition plots had porewater salinity typical of the tidal freshwater zone at this site (<0.5), with averages over the entire experiment of 0.25 ± 0.01 , 0.22 ± 0.01 and 0.22 ± 0.01 respectively (Figure 1c–e). These last three treatments often showed small salinity peaks in the fall during the time of low seasonal river discharge that caused high seasonal salinity in the river water (Figure 1; Figure S1).

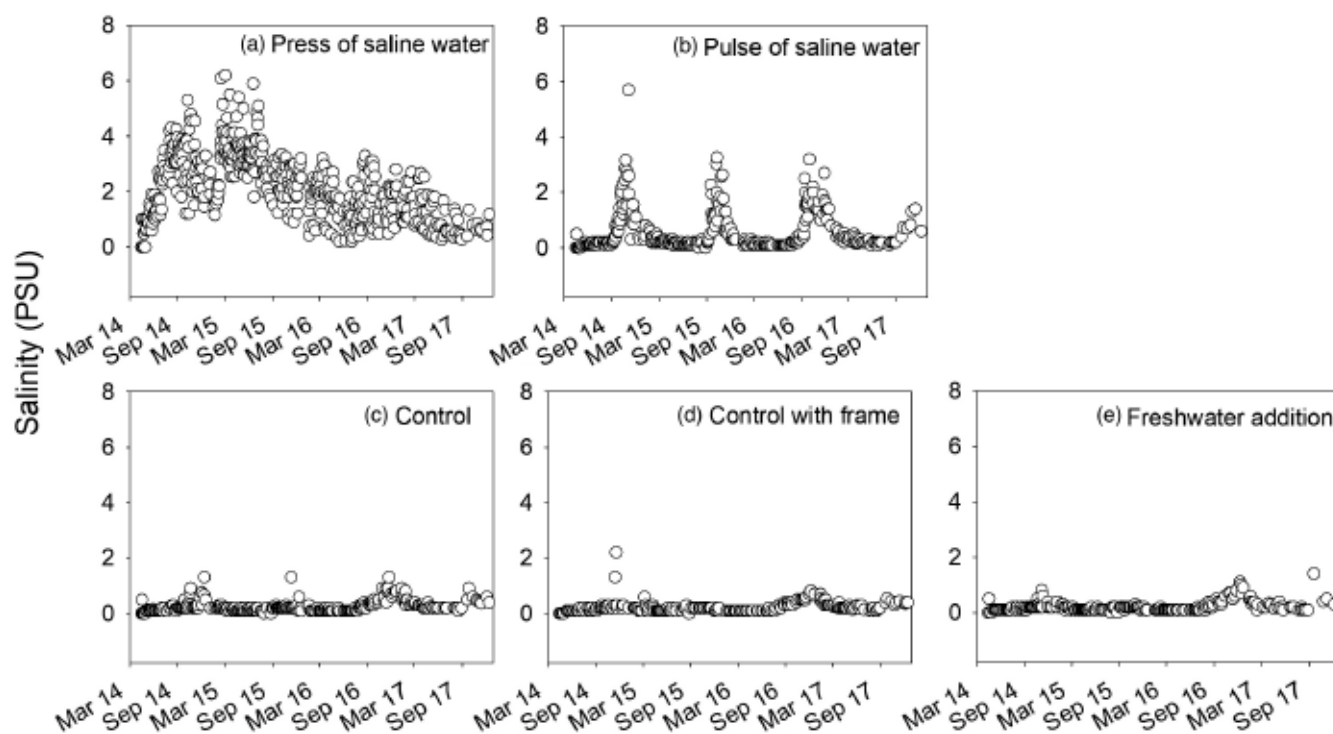


FIGURE 1 Porewater salinity in experimental plots throughout the duration of the experimental treatments (14 April 2014 to 15 December 2017)

3.2 | Vegetation biomass and cover

The press treatment reduced biomass of all plant species, with some responding faster than others. There was a significant effect of treatment on above-ground biomass of *Z. miliacea* ($p < 0.01$) and significant effects of treatment and treatment by date on *P. hydropiperoides* ($p < 0.001$) (Table 1). Above-ground biomass of *P. hydropiperoides* was reduced by ~75% in the press treatment relative to the control as early as July 2014 after only 3 months of saline water additions (Figure 2a). *P. hydropiperoides* continued to decline in the press treatment and disappeared from the press treatment in 2015. Above-ground biomass of *Z. miliacea* was unaffected by treatments in 2014 but was reduced compared to control and fresh treatments beginning in July 2015 and it was reduced by ~70% in the press treatment relative to the control in following years (Figure 2c). Above-ground biomass of *P. cordata* was highly variable but was reduced by ~80% in the press treatment relative to the control beginning in 2015 and in following years (Figure 2b, date $\times$ treatment $p = 0.05$). Total above-ground biomass (the sum of these three species) responded similar to *Z. miliacea*, the dominant species. Beginning in July 2015, total above-ground biomass was reduced (ultimately by >50%) in the press treatment compared to the other treatments (Figure 5a).

Plots varied in elevation by up to 15 cm. Elevation as a covariate explained a significant amount of variability in *Zizaniopsis* biomass and total above-ground biomass (Tables 1 and 2), and the ability to detect treatment differences was strengthened by the addition of the covariate to the model. *Z. miliacea* and total above-ground biomass were greater at lower elevations ($r = -0.26$, $p < 0.001$ and $r = -0.24$, $p < 0.001$ respectively).

The press treatment reduced the cover of all plant species, with some responding faster than others, but only one species was affected by the pulse treatment. Per cent cover of *L. repens* was affected by treatment ($p < 0.001$) and, for *P. hydropiperoides*, *P. cordata* and *Z. miliacea*, the interaction of treatment and date ($p < 0.05$; Table 1). The cover of *L. repens* was reduced by ~95% in the press treatment relative to the control within 1 month after saline water addition began in April 2014, and it remained at low levels in the press treatment thereafter (Figure 3a). The per cent cover of *L. repens* was reduced by ~70% in the pulse treatment relative to the control

by October 2014, and by May 2015, both pulse and press treatments contained almost no *L. repens*. The cover of *L. repens* increased in the pulse treatment early in each year following the decline the previous autumn, but it never attained more than 11% cover, well below its abundance in the control and fresh treatments, which varied over time but was usually >40%. The cover of *P. hydropiperoides* was reduced in the press treatment compared to the other treatments after 1 month, and was reduced to almost zero in the press treatment by the end of 2014 (Figure 3b). The cover of *Z. miliacea* was reduced in the press treatment (63%) relative to the control and fresh treatments (>90%) by October 2014 and continued to decrease in the press treatment in the following years (Figure 3d). The cover of *P. cordata* was not affected by the treatments in 2014 but was strongly reduced in the press treatment in following years (Figure 3c).

The per cent cover of *L. repens* was positively related to elevation (Table 1), whereas the cover of *Z. miliacea*, like above-ground biomass, decreased with increasing elevation. Above-ground biomass of *P. hydropiperoides*, *P. cordata* and *Z. miliacea* in the plots was low in March, relatively high in May–August and low again in October (Figure 2) matching previous descriptions of seasonal dynamics for *P. cordata* and *Z. miliacea* (Birch & Cooley, 1982; Heisey & Antoni, 1982; Li et al., 2018).

We observed only a few effects of the treatments on plant photosynthetic rates (Figure S2). The photosynthetic rate of *P. hydropiperoides* was not affected by the treatments in 2014. In 2015 and 2016, *P. hydropiperoides* disappeared from the press treatment plots, and so it could not be examined further. The photosynthetic rate of *P. cordata* did not differ among treatments throughout the study period, while the photosynthetic rate of *Z. miliacea* declined in the press treatment in 2014, with the strongest differences among treatments in August 2014 (Figure S2c). In later years, *Z. miliacea* was absent from some press plots, reducing the power of these comparisons. We did not measure plant photosynthetic rates in 2017.

As plant biomass decreased in the press treatment, a few plants typical of brackish conditions invaded the plots, but were rare and did not occur in all replicates, likely because the experiment was several kilometres upstream from potential seed sources. The phytometers (transplanted plants), however, gave us a standardized way

TABLE 1 Repeated-measure analysis of covariance (ANOVA) results (F and p-values) for estimated above-ground biomass and per cent cover in June, July and August 2015, 2016 and 2017 using elevation as a covariate. For the continuous variable of elevation, + and – denote the directionality of the effect. We did not estimate above-ground biomass for *Ludwigia repens*

Variable	Effect (df)	<i>Polygonum hydropiperoides</i>	<i>Pontederia cordata</i>	<i>Zizaniopsis miliacea</i>	<i>Ludwigia repens</i>
Above-ground biomass	Treatment (1, 24)	11.46, $p < 0.0001$	1.99, ns	4.75, $p < 0.01$	NA
	Date (8, 192)	1.38, ns	1.10, ns	0.83, ns	NA
	Date $\times$ Trt (32, 192)	3.62, $p < 0.0001$	1.56, $p = 0.05$	1.38, ns	NA
	Elevation (1)	0.44, ns	2.34, ns	6.67, $p < 0.05$ (–)	NA
Per cent cover	Treatment (1, 24)	21.63, $p < 0.0001$	4.23, $p < 0.01$	12.16, $p < 0.0001$	7.56, $p < 0.001$
	Date (8)	2.54, $p < 0.05$	0.59, ns	1.71 ns	2.32, $p < 0.05$
	Date $\times$ Trt (32, 192)	2.95, $p < 0.0001$	1.69, $p < 0.05$	1.82, $p < 0.01$	1.36, ns
	Elevation (1)	0.81, ns	3.14, ns	8.26, $p < 0.01$ (–)	5.24, $p < 0.05$ (+)

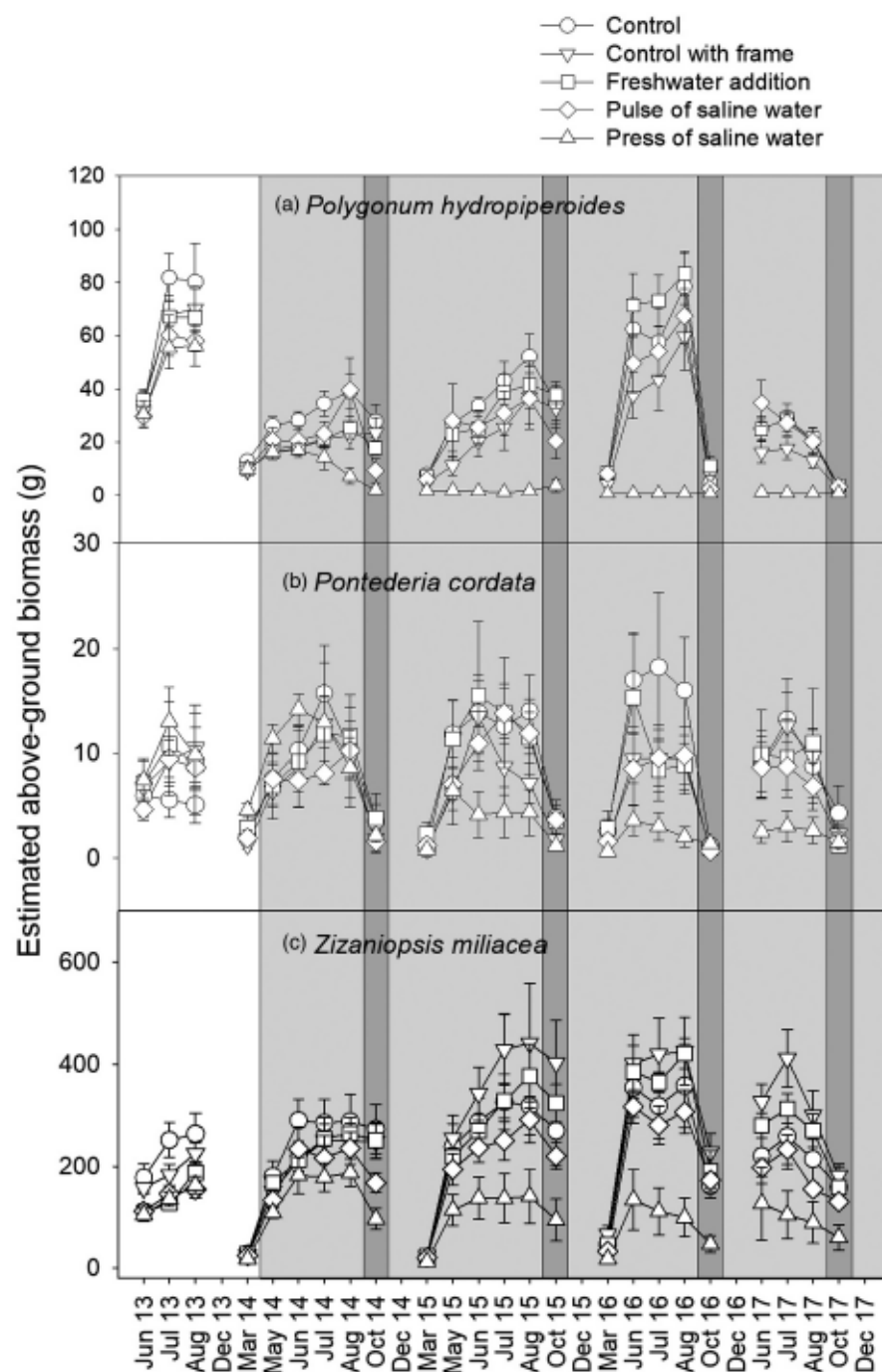


FIGURE 2 Estimated above-ground biomass (0.83×0.83 m subplot) ($\pm$ SE) of *Polygonum hydropiperoides*, *Pontederia cordata* and *Zizaniopsis miliacea* from 2013 through 2017. The light grey areas indicate the press treatment periods, and the dark grey areas indicate the pulse treatment periods

Effect (df) ^a	Total above-ground biomass ^a	Proportion of light penetrating the canopy	Fiddler crab burrow number
Treatment (4, 24)	7.25, $p < 0.001$	9.00, $p < 0.0001$	2.15, $p < 0.10$
Date (9, 216) ^b (4, 96) ^c	1.04, ns	2.44, $p < 0.05$	2.49, $p < 0.5$
Date $\times$ Trt (36, 216) ^b (15, 96) ^c	1.96, $p < 0.05$	2.39, $p < 0.001$	1.47, ns
Elevation (1)	6.46, $p < 0.05$ (-)	6.32, $p < 0.05$ (+)	0.27, ns

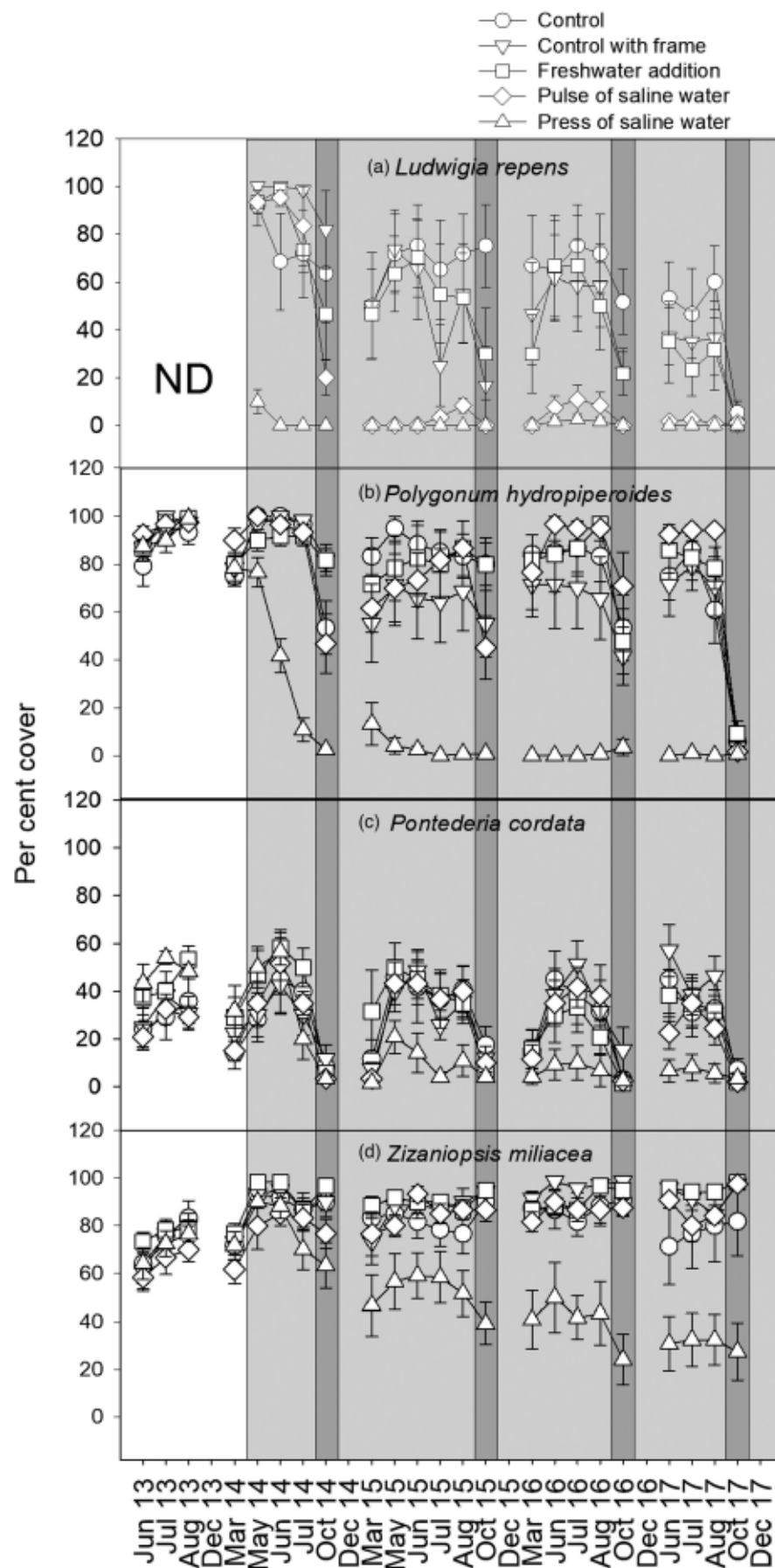
^aDegrees of freedom for biomass are the same as in Table 1.

^bDegrees of freedom for light.

^cDegrees of freedom for crabs.

TABLE 2 Repeated-measure analysis of covariance (ANOVA) results (F and p-values) for total above-ground biomass, proportion of light penetrating the canopy in June, July and August (2015 through 2017) and fiddler crab burrow number (spring and fall 2015 through 2017) using elevation as a covariate. For the continuous variable of elevation, +a nd denote the directionality of the effect

FIGURE 3 Per cent cover ($\pm$ SE) of *Ludwigia repens*, *Polygonum hydropiperoides*, *Pontederia cordata* and *Zizaniopsis miliacea* from 2013 through 2017. The cover of *Ludwigia repens* was not measured before May 2014. The light grey areas indicate the press treatment periods, and the dark grey areas indicate the pulse treatment periods



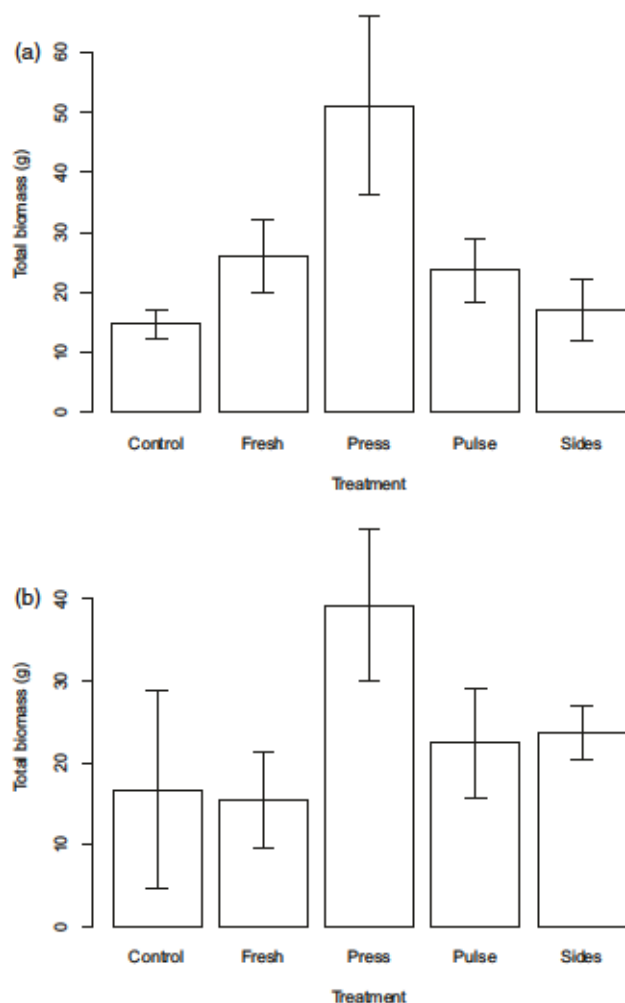


FIGURE 4 Total (above- plus below-ground) biomass of (a) *Schoenoplectus sp.* and (b) *Juncus roemerianus* plants transplanted into experimental plots

to assess plot suitability for the brackish species, *Schoenoplectus sp.* and *J. roemerianus*. *Schoenoplectus sp.* transplants grew twice as large in the press treatment as in the other treatments ($F_{4,26} = 3.42$, $P = 0.02$) (Figure 4a). *J. roemerianus* transplants showed a similar pattern, but results were more variable and not significant ($F_{4,21} = 1.79$, $p = 0.17$) (Figure 4b).

3.3 | Light availability, benthic microalgae and fiddler crabs

The press treatment increased light availability and stimulated benthic microalgae. By 2015, as above-ground biomass in the press plots decreased, the proportion of light penetrating the canopy increased in the press treatment to values of ~50% compared to ~20% in all other treatments (one-way ANOVA, $p < 0.01$) (Table 2, Figure 5b). With increased light availability, there was a significant effect of the treatments on the benthic microalgae community (Table 3). Cyanobacteria and diatoms were most abundant in the press

treatment (Figure 6b,c), whereas green microalgae, the least abundant taxa, were least abundant in the press treatment (Figure 6a, Table 3). Diatoms, the most abundant microalgae overall, showed a strong seasonal pattern of abundance (Figure 6c), with a peak in the winter (November–February) when plant biomass is naturally low.

Fiddler crab burrows were marginally less abundant in the press and pulse (42–43 m⁻²) treatments than the other treatments (51–61 m⁻²) ($p = 0.10$; Table 2). There was no effect of elevation on fiddler crab density ($p = 0.61$).

As hypothesized, the treatment-induced changes in plant cover and composition that had occurred by fall 2016 cascaded to affect physical conditions (sunlight), microalgae and fauna through multiple pathways (Figure 7e). As above-ground biomass of plants decreased, light penetration through the canopy increased and fiddler crab burrow density decreased (Figure 7a,b). The abundance of both cyanobacteria and diatoms was positively related to the proportion of light penetrating the canopy (Figure 7c–d). The abundance of green microalgae, however, was not related to changes in light penetration ($p = 0.78$). Because of the design of the experiment, in which plant abundance was only suppressed in the press treatment, replication of the low biomass conditions was ineluctably limited. This argues for some caution in interpreting the results; however, we believe that these points are biologically credible rather than 'outliers'.

4 | DISCUSSION

Global change is likely to affect ecosystems through a complicated mixture of pulse, ramp and press changes (Donohue et al., 2016). Thus, there is a need to move beyond simple press experiments that compare ecosystem responses to different levels of global change drivers, and to incorporate additional global change treatments that emphasize variability. For example, experiments in terrestrial grasslands that vary the timing and magnitude of rainfall pulses have been as informative as previous experiments that altered total annual rainfall (Wang et al., 2021). Here, we took a similar approach to examining salinization of coastal wetlands by comparing press and pulse salinization treatments.

Climate change is predicted to cause both presses and pulses of saline water intrusion into tidal freshwater marshes (Herbert et al., 2015; White & Alber, 2009; Wood & Harrington, 2015). We examined the effects of a saline press and pulse in a field experiment for a 4-year period. We are aware of only one similar multi-year study of salinization in emergent wetland plant communities that was conducted in the field (Neubauer, 2013), but it focused on C cycling, not species effects, and did not include a saline pulse treatment. Otherwise, studies examining the effects of salinity on freshwater marsh plants have been conducted in the greenhouse over relatively short periods of time (8 weeks to 1 year), and none compared press and pulse treatments simultaneously in a field experiment (Howard & Mendelsohn, 2000; Sharpe & Baldwin, 2012; Spalding & Hester, 2007; Sutter et al., 2015; Woo & Takekawa, 2012).

FIGURE 5 Estimated total (sum of *Polygonum hydropiperoides*, *Pontederia cordata* and *Zizaniopsis miliacea*) above-ground biomass (0.83×0.83 m subplot) ($\pm$ SE) and proportion of light penetrating the canopy ($\pm$ SE) in all treatments from 2013 to 2017. Light penetration was not measured before March 2014. The light grey areas indicate the press treatment periods, and the dark grey areas indicate the pulse treatment periods

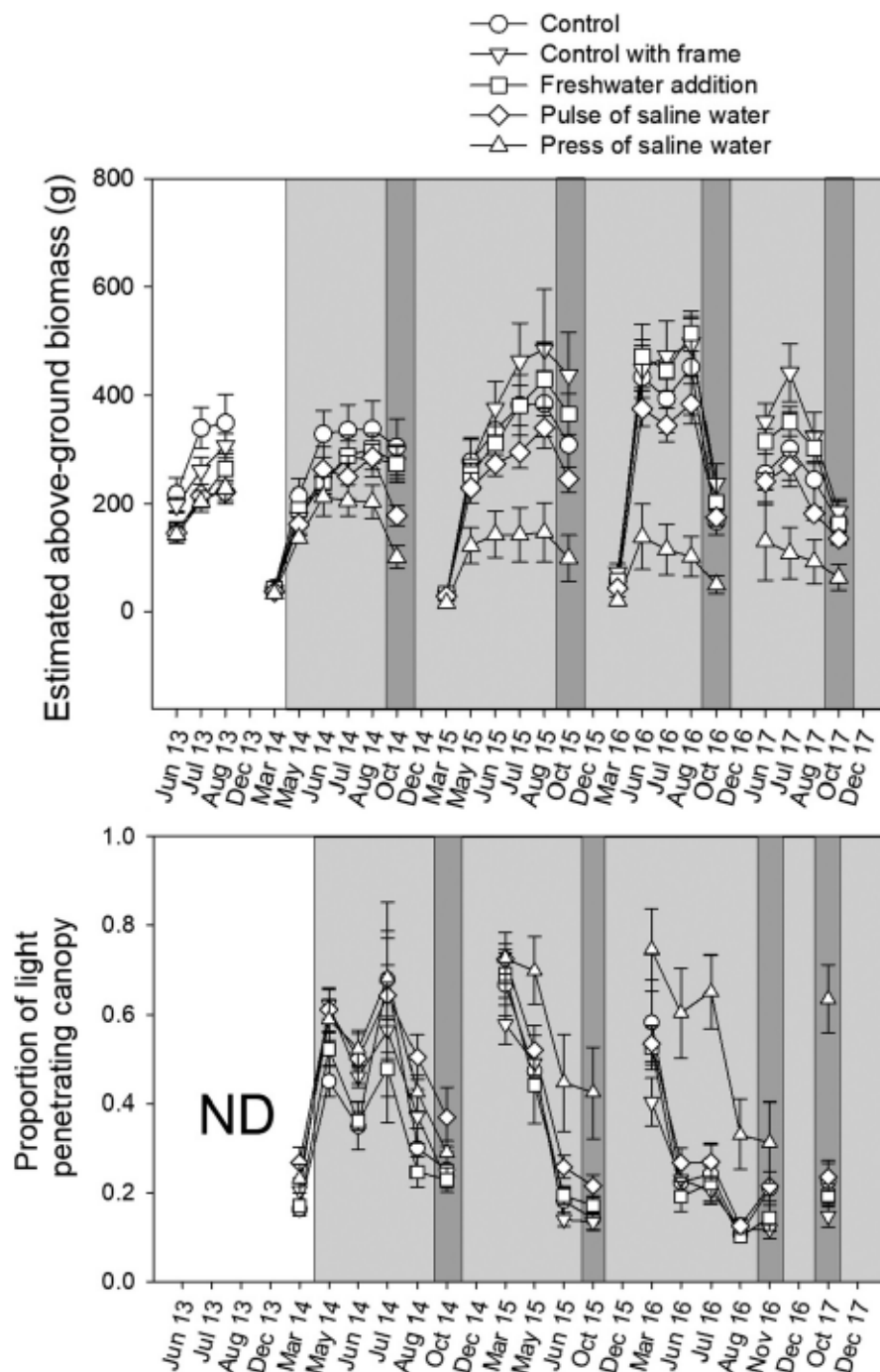


TABLE 3 Repeated-measure analysis of covariance (ANOVA) results (F and p-values) for the abundance of benthic microalgae (green algae, cyanobacteria and diatoms) measured monthly using elevation as a covariate for the years 2016 (February–December) and 2017 (January–December). For the continuous variable of elevation, + and – denote the directionality of the effect

Effect (df)	Abundance of green algae	Abundance of cyanobacteria	Abundance of diatoms
Treatment (4, 24)	8.73, $p < 0.001$	3.62, $p < 0.05$	5.05, $p < 0.01$
Date (22, 528)	2.07, $p < 0.01$	1.00, ns	2.59, $p < 0.0001$
Date $\times$ Treatment (88, 528)	1.92, $p < 0.0001$	2.15, $p < 0.0001$	1.42, $p < 0.05$
Elevation (1)	9.98, $p < 0.01$ (+)	1.59, ns	2.27, ns

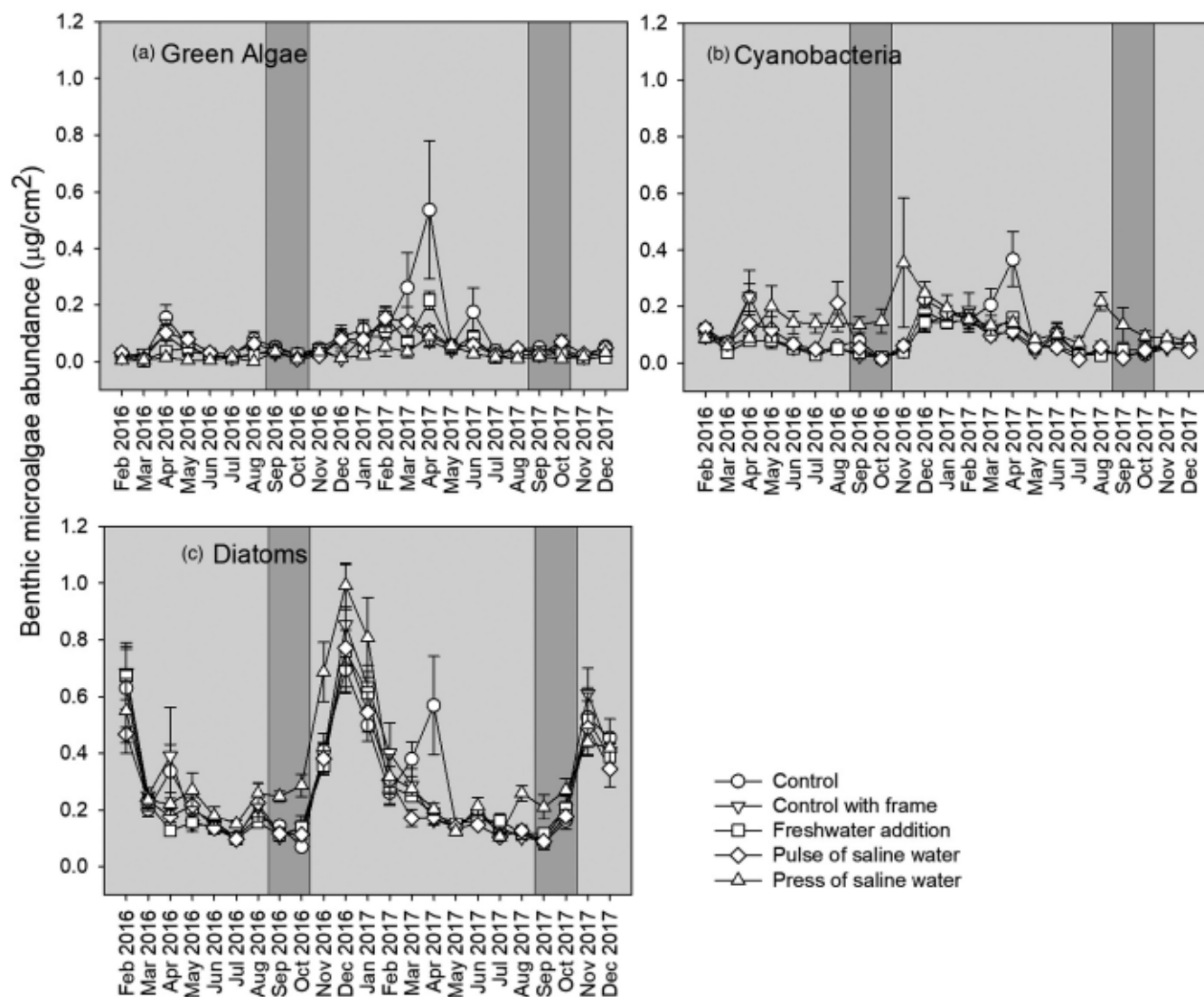


FIGURE 6 The abundance of (a) green algae, (b) cyanobacteria and (c) diatoms ($\pm$ SE) in all treatments from February 2016 to December 2017. The light grey areas indicate the press treatment periods, and the dark grey areas indicate the pulse treatment periods

We believe that our approach, using a multi-year field experiment, provides much more realistic insights into the effects of coastal salinization.

Our results supported the first hypothesis that both press and pulsed salinization would suppress the performance of individual plant species; however, effects varied among the four plant species that dominate the community. *L. repens* largely disappeared from both press and pulse plots after salinity additions began. *P. hypodiploides* was also sensitive to salinity and declined in cover and productivity in the press treatment starting in the first year of saline water addition. *Z. miliacea* and *P. cordata* were less sensitive, but both species gradually declined in the press treatment as the experiment progressed. This is consistent with previous mesocosm experiments that identified these latter two species as relatively salt tolerant (Li & Pennings, 2018, 2019). The suppression of all four dominant species in the press treatment was consistent with the general finding that plants typical of low-salinity habitats cannot

tolerate the abiotic stress of higher salinities (Crain et al., 2004; Guo & Pennings, 2012).

In addition to expecting that presses and pulses of saline water would suppress the performance of individual plant species, we also expected hierarchical responses to the treatments, with relatively fast physiological changes followed by species reordering, and then finally by species loss (Smith et al., 2009). This idea was not supported. In general, the treatments did not affect plant photosynthetic rates. Other studies have found that photosynthetic rate per unit leaf area remained unchanged in the face of elevated salinities because elevated salinity increased chloroplast density per unit leaf area (Munns & Tester, 2008), suggesting that physiological effects of salinity may be manifested in other variables, such as increased respiration, that we did not measure.

Although both presses and pulses of saline water addition caused plant community composition to shift away from that of the controls, results of press and pulse treatments differed markedly.

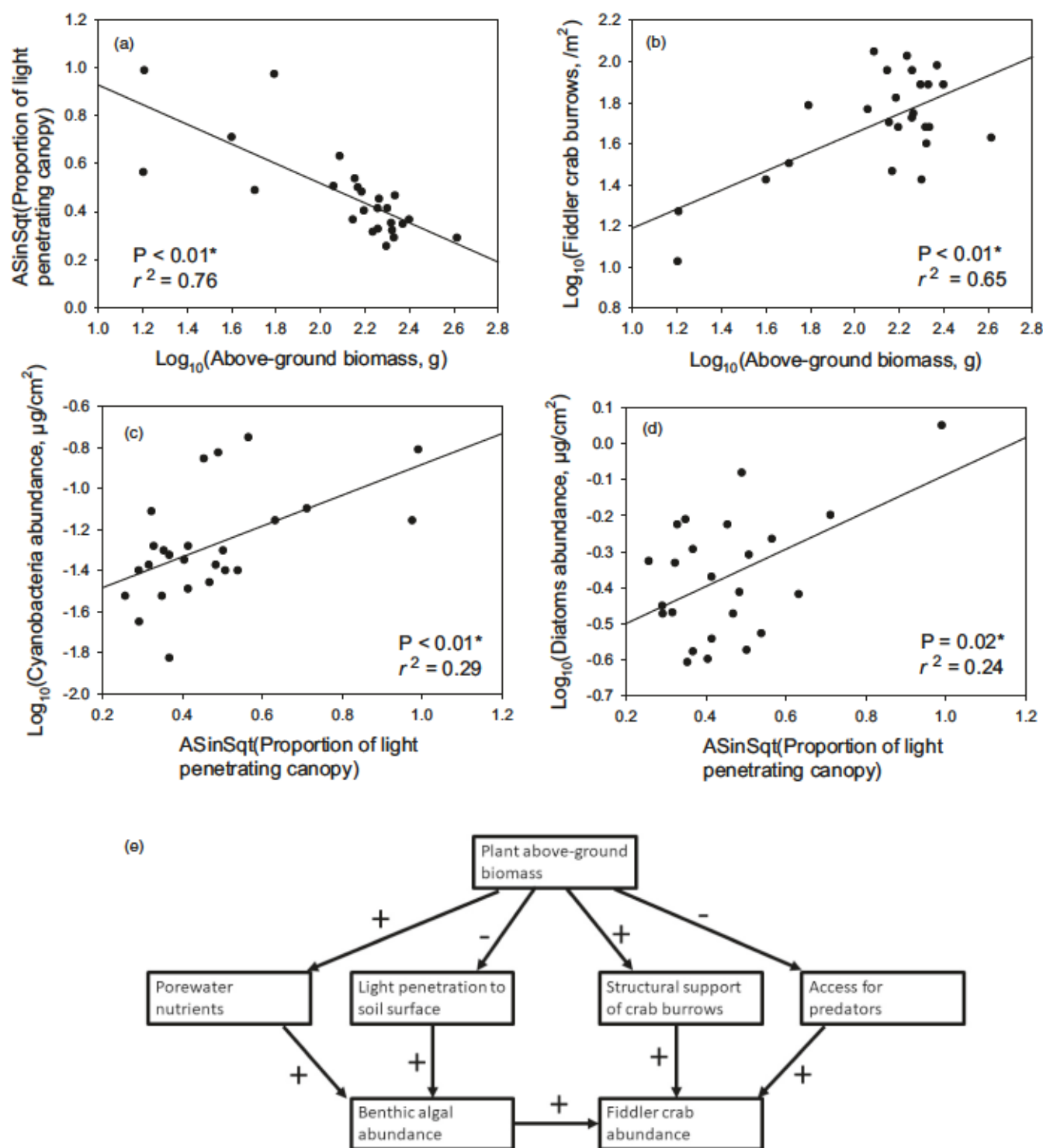


FIGURE 7 Cascading effects of treatments on benthic microalgae and fiddler crabs include the effects of plant above-ground biomass on (a) proportion of light penetrating the canopy and (b) fiddler crab burrow density, and the effects of proportion of light penetrating the canopy on (c) abundance of cyanobacteria and (d) abundance of diatoms. Data were from fall (September to November) 2016. The relationship between green microalgae abundance and proportion of light penetrating the canopy was not significant ($p = 0.78$), and therefore was not shown. Additional hypothesized mechanisms linking plant above-ground biomass to benthic algae and fiddler crab abundance include (e) effects on porewater nutrients, structural support for crab burrows and access for predators

With presses of saline water, two species almost disappeared in the first year, and all species declined in per cent cover in the second year. With pulses of saline water, the main effect was the

suppression of a single plant species (*L. repens*) beginning in the second year of the project. This finding is consistent with a mesocosm experiment containing many of the same plant species, in which the

duration of salinity pulses was just as important as their level of salinity in affecting plant community structure (Li & Pennings, 2019). Consequently, the important insight from comparing the press and pulse treatments is that periodic pulses of saline water will exclude only some species from the local community, even if all would be excluded by a sustained press.

Our second hypothesis, that community structure in the pulse treatment would recover once the saline pulses were withdrawn, was not supported, as *L. repens* declined in the pulse treatment and did not recover between pulse events. Many tidal freshwater marsh plants have some ability to recover after saline pulses (Flynn et al., 1995; Howard & Mendelssohn, 1999; Li & Pennings, 2019; Sutter et al., 2014). If saline pulses are severe enough or frequent enough, however, they will cause persistent changes in the plant community. For example, in a mesocosm experiment conducted in Louisiana, *S. lancifolia* recovered after exposure to saline water of 12 g/L for 1 month, but failed to recover after the community was exposed to 12 g/L (PSU) saline water for 3 months, resulting in a shift to a monospecific *S. americanus* stand (Howard & Mendelssohn, 2000). This illustrates the general point that even brief pulses of global change drivers may have important effects on natural communities.

Although repeated saline pulses caused one plant species to be lost from the pulse treatment, total above-ground biomass was maintained at levels similar to those in the controls because the dominant species were unaffected by the short-duration pulse. Most other measured parameters such as porewater chemistry, net ecosystem exchange (NEE) and CO₂ and CH₄ emissions also were not affected by the pulse treatment (Herbert et al., 2018; Solohin et al., 2020; Widney et al., 2019). The press treatment, on the other hand, caused a dramatic reduction in plant above-ground biomass along with reduced NEE and CO₂ and CH₄ emissions (Herbert et al., 2018) as all species either declined or disappeared. The loss of vegetation also led to persistent increases in porewater NH₄ and PO₄ (Widney et al., 2019). Thus, long-term saltwater intrusion might reduce primary production, C cycling, and N and P retention of tidal freshwater marshes for an extended period of time if immigration of brackish water vegetation is slow. This result is consistent with the idea that the loss of minor species from a community will not strongly affect community function, because compensatory responses of the most abundant, 'dominant' or 'foundation' species maintain community function (Dayton, 1972; Grime, 1998).

Decreased productivity is expected to decrease the ability of a marsh to accumulate sediment (Morris et al., 2002), and thereby threaten persistence of the intertidal habitat. In our experiment, the press plots experienced an elevation loss of ~3 cm compared to the control plots over a 3.5-year period, which was mostly due to reduced root inputs and loss of below-ground plant biomass (Solohin et al., 2020). The pulse treatment neither gained nor lost elevation after 3.5 years while, at the same time, the control and fresh treatments gained 2–3 cm of elevation (Solohin et al., 2020). One possible explanation for the lack of elevation gain in the pulse treatment is the near absence of *L. repens* from these plots. *L. repens* declined dramatically in the pulse treatment and was extirpated from the press

treatment, and its presence was positively correlated with elevation gain after 3.5 years ($R = 0.54$, $p < 0.01$, July 2017). Although *L. repens* did not represent a large proportion of biomass in the plots, its mat-like growth form may have led to a disproportionate impact on sediment accumulation and retention. These findings suggest that the loss of a single species, in this case *L. repens*, may impair marsh elevation gain while other ecosystem properties and processes are unaffected (Table S1). This function might ultimately be replaced by a more salt-tolerant species that could immigrate from downstream, but that did not happen during the duration of our experiment because our plots were located far from brackish marsh habitat. Although a link between *L. repens* and elevation gain in this habitat is plausible, additional experiments are required to confirm that this, and not some other, unmeasured difference between treatments was the mechanism. If it is correct, however, it supports the view that at least some ecosystem functions can be affected by the loss of single species, even if not the most abundant members of the community (Lyons & Schwartz, 2001).

In our experiment, we did not observe differences in plant performance in the freshwater addition treatment relative to the controls, nor did we observe effects of the freshwater addition treatment on other measured variables including porewater chemistry (Herbert et al., 2018; Solohin et al., 2020; Widney et al., 2019). Thus, we attribute the responses that we observed in the press and pulse treatments to salinity, not to additional flooding per se. In a previous saline water addition experiment in South Carolina, plant biomass in a *Z. miliacea*-dominated marsh was also reduced in the saline press treatment (Neubauer, 2013). In that experiment, however, the freshwater addition treatment increased ecosystem primary production, CO₂ emissions and net ecosystem production, indicating that freshwater addition alone could affect ecosystem processes. The difference in results from freshwater addition among the two experiments deserves further attention, but could have been caused by our experiment being located in a wetter habitat than was the case for the previous study.

Macrophyte biomass is likely to affect microalgal abundance and invertebrate densities through multiple pathways (Figure 7e). Our third hypothesis, that benthic microalgae would increase in treatments where macrophytes decreased, was largely supported. We observed increased abundance of cyanobacteria and diatoms in the press treatment. Green microalgae, which were less abundant, decreased instead, perhaps due to competition from other benthic microalgae. The loss of marsh vegetation allowed more sunlight to reach the sediment, and this likely was one mechanism explaining increases in benthic microalgae (Sullivan & Currin, 2002; Whitcraft & Levin, 2007). In addition, porewater ammonium, nitrate and phosphate increased in the press plots as the added salinity desorbed cations (NH₄) from soil cation exchange sites and/or increased mineralization of organic matter (Jun et al., 2013), and uptake of N and P by vascular plants was reduced (Herbert et al., 2018; Widney et al., 2019); these increases in nutrients might also have benefited benthic microalgae (Sin et al., 2007). Regardless of the mechanism, decreased in abundance (and thus presumably production)

by vascular plants were partially compensated for by increases in abundance (and likely production) of microalgae. Because benthic microalgae are an important carbon source for estuarine food webs (Sullivan & Moncreiff, 1990), increases in microalgae production are likely to benefit other species, although with the exception of fiddler crabs, these effects were not measured here. In nature, any increase in microalgal production caused by a salinization event that killed tidal fresh marsh plants would likely be temporary, because brackish marsh plants would eventually invade the site. However, until brackish marsh plants did invade, this change from vascular to algal primary producers might be important for the estuarine food web.

Our fourth hypothesis, that fiddler crab densities would change in treatments where macrophytes decreased, was marginally supported. Crab burrow density declined in press plots where vegetation was nearly absent but the differences among treatments was only marginally significant ($p < 0.10$). The presence of vegetation in wetlands affects the distribution of crab burrows through three different mechanisms (Figure 7e). First, in soft sediments, plant rhizomes and roots provide structural support for crab burrows (Bertness, 1985). For example, the mud fiddler crab *Uca pugnax* preferentially burrows close to underground parts of *Spartina alterniflora* in low salt marsh habitats to gain structural support for its burrows (Bertness & Miller, 1984). Second, the presence of vegetation may reduce the exposure of marsh crabs to predators, such as wading birds or raccoons. In experiments, the number of fiddler crab burrows increased with artificial shading that likely provided a refuge from predators in clearings (Nomann & Pennings, 1998). Third, as shown above, vascular plants suppress benthic microalgae, which are a food source for deposit-feeding crabs. Because this third mechanism predicts a negative relationship between crabs and macrophyte abundance, it has little support from our data since we found that crab burrows decreased with decreasing plant biomass and increased light penetration. Although the first two mechanisms act in the same direction as our experimental results (highlighting their plausibility in explaining the fiddler crab response to our treatments), a more detailed study is needed to untangle the various effects of freshwater macrophytes on fiddler crabs.

Our study focused on the effects of increased salinity that might be expected due to climate change, sea level rise and freshwater withdrawal from rivers. Some of these factors, such as sea level rise, would also affect flooding of tidal fresh marshes. How these systems will respond to the combination of increased salinity and increased flooding is outside the scope of our study, but deserves future study. Similarly, although we studied press and pulse variation separately, these are likely to be combined in nature (Donohue et al., 2016)—for example, a storm or drought might occur after a period of sea level rise—and these combinations also merit future study using more complicated experimental designs.

In our experiment, two plant species from brackish marshes performed well in the press plots when transplanted there. These species, however, did not colonize the press plots naturally, likely because the experimental site was too far away from a suitable propagule source. In nature, salinization events that kill plants in

tidal freshwater marshes are most likely to occur close to brackish marsh habitats, and propagule supply may not be limited. However, in extreme cases, transplantation of brackish marsh plants or seeds to an affected site by habitat managers might be useful in facilitating rapid accommodation of the ecosystem to higher salinities.

Our findings from the press treatment indicate that extended salinization, such as would occur following rapid sea level rise, drought or large withdrawals of freshwater from rivers, will result in widespread loss of the plant species that dominate tidal fresh marshes until vegetation typical of higher salinity habitats can colonize. In addition, our results illustrate that pulsed changes, even if they do not have dramatic effects on the most dominant species in a community, nevertheless can affect species composition, and that the loss of a single secondary species, *L. repens*, may affect wetland elevation gain/loss. This last finding is particularly important, because it illustrates that without immigration of compensatory species, changes that may threaten the ability of tidal freshwater marshes to keep pace with sea level rise can occur even while the dominant plants and animals are unaffected. More generally, our results illustrate that short pulses of global change drivers can affect ecosystems, but results will likely differ from the findings of press experiments, which in some cases are less realistic mimics of how global change will occur. Ultimately, forecasting both the short- and long-term future states of ecosystems will require studies that combine an understanding of the effects of ongoing pulses with that of the effects of long-term press changes.

ACKNOWLEDGEMENTS

This material is based on the work supported by the National Science Foundation through the Georgia Coastal Ecosystems Long Term Ecological Research program under Grants No. OCE-1237140 and OCE-OCE-1832178. The authors thank Ellen Herbert, Dontreice Smith, Jacob Shalack, Caroline Reddy, Timothy Montgomery, Nicole DeSha, Sasha Greenspan, Ashby Nix, Robin Wei, Shanze Li, Eric Weingarten, Narissa Turner, Jonathan Adams, Sean Sharp, Julie Blaze, Jeff Beauvais, IU Wetland Biogeochemistry Laboratory students, GCE-LTER Schoolyard participants and others who helped in the field. This is contribution number 1100 of the University of Georgia Marine Institute.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

C.C. and S.C.P. conceived the ideas and designed the methodology; All authors but especially F.L. collected and analysed the data; F.L. and S.C.P. led the writing of the manuscript; C.A., J.E.B. and C.C. contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data presented in the manuscript are archived at the Environmental Data Initiative as follows. Fiddler crab data: <https://>

doi.org/10.6073/pasta/b3d8f5e01ebba0da8fd3a2a78671c0ce (Angelini, 2018); Microalgal data: <https://doi.org/10.6073/pasta/7464fe6528c4cb2d04fb99642f19a433> (Craft, 2015); Porewater data: <https://doi.org/10.6073/pasta/dadbaa37af67d97c76552d0700eab16a> (Craft, 2017); Plant and PAR data: <https://doi.org/10.6073/pasta/335d605abdcd984713006fbcd86c9f97> (Li, 2017).

ORCID

Fan Li  <https://orcid.org/0000-0003-4386-2543>

Christine Angelini  <https://orcid.org/0000-0002-6669-5269>

James E. Byers  <https://orcid.org/0000-0001-9240-0287>

Christopher Craft  <https://orcid.org/0000-0003-3345-6592>

Steven C. Pennings  <https://orcid.org/0000-0003-4757-7125>

REFERENCES

- Adam, P. (1990). *Saltmarsh ecology*. Cambridge University Press.
- Angelini, C. (2018). Effect of salt water intrusion on the distribution of invertebrates in a GA tidal freshwater marshes from the GCE Seawater Addition Long-Term Experiment (SALTEX) project. Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/b3d8f5e01ebba0da8fd3a2a78671c0ce>.
- Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P. M., Smolders, A. J. P., & Silliman, B. R. (2015). Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150421.
- Bertness, M. D. (1985). Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, 66, 1042–1055.
- 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, e92916.
- Bertness, M. D., & Miller, T. (1984). The distribution and dynamics of *Uca pugnax* (Smith) burrows in a new England salt marsh. *Journal of Experimental Marine Biology and Ecology*, 83, 211–237.
- Birch, J. B., & Cooley, J. L. (1982). Production and standing crop patterns of giant cutgrass (*Zizaniopsis miliacea*) in a freshwater tidal marsh. *Oecologia*, 52, 230–235.
- Bortolus, A., Schwindt, E., & Iribarne, O. (2002). Positive plant-animal interactions in the high marsh of an Argentinean coastal lagoon. *Ecology*, 83, 733–742.
- Church, J. A., & White, N. J. (2011). Sea-level rise from the late 19th to the early 21st century. *Surveys in Geophysics*, 32, 585–602.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., ... Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437, 529–533.
- Cloern, J. E., & Jassby, A. D. (2012). Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, 50, RG4001. <https://doi.org/10.1029/2012RG000397>
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1998). The value of the world's ecosystem services and natural capital. *Ecological Economics*, 25, 3–15.
- Craft, C. (2007). Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and U.S. tidal marshes. *Limnology and Oceanography*, 52, 1220–1230.
- Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H., & Machmuller, M. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, 7, 73–78.
- Craft, C. B. (2015). Green algae, cyanobacteria and diatom concentrations from the GCE-LTER Seawater Addition Long-Term Experiment (SALTEX) Project. Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/7464fe6528c4cb2d04fb99642f19a433>.
- Craft, C. B. (2017). Daily porewater salinity, conductivity, and temperature measurements from the GCE-LTER Seawater Addition Long-Term Experiment (SALTEX) Project. Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/dadbaa37af67d97c76552d0700eab16a>.
- Crain, C. M., Silliman, B. R., Bertness, S. L., & Bertness, M. D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology*, 85, 2539–2549.
- Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In B. Parker (Ed.), *Proceedings of the colloquium on conservation problems in Antarctica* (pp. 81–96). Allen Press.
- Dethier, M. N., Graham, E. S., Cohen, S., & Tear, L. M. (1993). Visual versus random-point percent cover estimations: 'objective' is not always better. *Marine Ecology Progress Series*, 96, 93–100.
- Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19, 1172–1185.
- Echenique-Subiabre, I., Dalle, C., Duval, C., Heath, M. W., Couté, A., Wood, S. A., Humbert, J.-F., & Quiblier, C. (2016). Application of a spectrofluorimetric tool (bbe BenthosTorch) for monitoring potentially toxic benthic cyanobacteria in rivers. *Water Research*, 101, 341–350.
- Enright, C., & Culbertson, S. D. (2009). Salinity trends, variability, and control in the northern reach of the San Francisco Estuary. *San Francisco Estuary and Watershed Science*, 7. <https://doi.org/10.15447/sfews.2009v7iss2art3>
- Flynn, K. M., McKee, K. L., & Mendelsohn, I. A. (1995). Recovery of freshwater marsh vegetation after a saltwater intrusion event. *Oecologia*, 103, 63–72.
- Goodman, A. M., Ganf, G. G., Dandy, G. C., Maier, H. R., & Gibbs, M. S. (2010). The response of freshwater plants to salinity pulses. *Aquatic Botany*, 93, 59–67.
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86, 902–910.
- Guo, H., & Pennings, S. C. (2012). Mechanisms mediating plant distributions across estuarine landscapes in a low-latitude tidal estuary. *Ecology*, 93, 90–100.
- Heisey, R. M., & Antoni, W. H. D. (1982). Biomass and production of *Pontederia cordata* and *Potamogeton epihydrus* in three Connecticut rivers. *American Journal of Botany*, 69, 855–864.
- Herbert, E. R., Boon, P., Burgin, A. J., Neubauer, S. C., Franklin, R. B., Ardón, M., Hopfensperger, K. N., Lamers, L. P. M., & Gell, P. (2015). A global perspective on wetland salinization: Ecological consequences of a growing threat to freshwater wetlands. *Ecosphere*, 6, 1–43.
- Herbert, E. R., Schubauer-Berigan, J. P., & Craft, C. B. (2018). Differential effects of chronic and acute simulated seawater intrusion on tidal freshwater marsh carbon cycling. *Biogeochemistry*, 138, 137–154.
- 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.

- Horton, B. P., Rahmstorf, S., Engelhart, S. E., & Kemp, A. C. (2014). Expert assessment of sea-level rise by AD 2100 and AD 2300. *Quaternary Science Reviews*, 84, 1–6.
- Howard, R. J., & Mendelssohn, I. A. (1999). Salinity as a constraint on growth of oligohaline marsh macrophytes. II. Salt pulses and recovery potential. *American Journal of Botany*, 86, 795–806.
- Howard, R. J., & Mendelssohn, I. A. (2000). Structure and composition of oligohaline marsh plant communities exposed to salinity pulses. *Aquatic Botany*, 68, 143–164.
- Jun, M., Altor, A. E., & Craft, C. B. (2013). Effects of increased salinity and inundation on inorganic nitrogen exchange and phosphorus sorption by tidal freshwater floodplain forest soils, Georgia (USA). *Estuaries and Coasts*, 36(3), 508–518.
- Knighton, A. D., Mills, K., & Woodroffe, C. D. (1991). Tidal-creek extension and saltwater intrusion in northern Australia. *Geology*, 19, 831–834.
- Langley, A. J., Mozdzer, T. J., Shepard, K. A., Hagerty, S. B., & Patrick Megonigal, J. (2013). Tidal marsh plant responses to elevated CO₂, nitrogen fertilization, and sea level rise. *Global Change Biology*, 19, 1495–1503.
- Li, F. (2017). Plant Responses to the GCE-LTER Seawater Addition Long Term Experiment (SALTEx) from 2013 to 2016. Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network. <https://doi.org/10.6073/pasta/335d605abdcd984713006fbcd86c9f97>.
- Li, F., & Pennings, S. C. (2018). Responses of tidal freshwater and brackish marsh macrophytes to pulses of saline water simulating sea level rise and reduced discharge. *Wetlands*, 38, 885–891.
- Li, F., & Pennings, S. C. (2019). Response and recovery of low-salinity marsh plant communities to presses and pulses of elevated salinity. *Estuaries and Coasts*, 42, 708–718.
- Li, S., Hopkinson, C. S., Schubauer-Berigan, J. P., & Pennings, S. C. (2018). Climate drivers of *Zizaniopsis miliacea* biomass in a Georgia, U.S.A. tidal fresh marsh. *Limnology and Oceanography*, 63, 2266–2276.
- Loomis, M. J., & Craft, C. B. (2010). Carbon sequestration and nutrient (nitrogen, phosphorus) accumulation in river-dominated tidal marshes, Georgia, USA. *Soil Science Society of America Journal*, 74, 1028–1036.
- Lyons, K. G., & Schwartz, M. W. (2001). Rare species loss alters ecosystem function—invader resistance. *Ecology Letters*, 4, 358–365.
- McFarlin, C. R., Bishop, T. D., Hester, M., & Alber, M. (2015). Context-dependent effects of the loss of *Spartina alterniflora* on salt marsh invertebrate communities. *Estuarine, Coastal and Shelf Science*, 163, 218–230.
- McKee, K. L., & Mendelssohn, I. A. (1989). Response of a freshwater marsh plant community to increased salinity and increased water level. *Aquatic Botany*, 34, 301–316.
- Middleton, B. A. (2016). Differences in impacts of Hurricane Sandy on freshwater swamps on the Delmarva Peninsula, Mid-Atlantic Coast, USA. *Ecological Engineering*, 87, 62–70.
- Mobilian, C., Wisnoski, N. I., Lennon, J. T., Alber, M., Widney, S., & Craft, C. B. (2020). Differential effects of press vs. pulse seawater intrusion on microbial communities of a tidal freshwater marsh. *Limnology and Oceanography Letters*. <https://doi.org/10.1002/lol2.10171>
- Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. *Ecology*, 83, 2869–2877.
- Munns, R., & Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 59, 651–681.
- Neubauer, S. (2013). Ecosystem responses of a tidal freshwater marsh experiencing saltwater intrusion and altered hydrology. *Estuaries and Coasts*, 36, 491–507.
- Nijssen, B., O'Donnell, G. M., Hamlet, A. F., & Lettenmaier, D. P. (2001). Hydrologic sensitivity of global rivers to climate change. *Climatic Change*, 50, 143–175.
- Nomann, B. E., & Pennings, S. C. (1998). Fiddler crab–vegetation interactions in hypersaline habitats. *Journal of Experimental Marine Biology and Ecology*, 225, 53–68.
- Parkyn, S. M., & Collier, K. J. (2004). Interaction of press and pulse disturbance on crayfish populations: Flood impacts in nature and forest streams. *Hydrobiologia*, 527, 113–124.
- Pastore, M. A., Megonigal, J. P., & Langley, J. A. (2016). Elevated CO₂ promotes long-term nitrogen accumulation only in combination with nitrogen addition. *Global Change Biology*, 22, 391–403.
- Ratajczak, Z., D'Odorico, P., Collins, S. L., Bestelmeyer, B. T., Isbell, F. I., & Nippert, J. B. (2017). The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs*, 87(2), 198–218.
- Sharpe, P. J., & Baldwin, A. H. (2012). Tidal marsh plant community response to sea-level rise: A mesocosm study. *Aquatic Botany*, 101, 34–40.
- Silliman, B. R., & Bertness, M. D. (2002). A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 10500–10505.
- Sin, Y., Sigleo, A. C., & Song, E. (2007). Nutrient fluxes in the microalgal-dominated intertidal regions of the Lower Yaquina Estuary, Oregon (USA). *Northwest Science*, 81, 50–61.
- Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, 99, 656–663.
- Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90, 3279–3289.
- Solohin, E., Widney, S. E., & Craft, C. B. (2020). Declines in plant productivity drive loss of soil elevation in a tidal freshwater marsh exposed to saltwater intrusion. *Ecology*, 101, e03148.
- Spalding, E. A., & Hester, M. W. (2007). Interactive effects of hydrology and salinity on oligohaline plant species productivity: Implications of relative sea-level rise. *Estuaries and Coasts*, 30, 214–225.
- Sullivan, M. J., & Currin, C. A. (2002). Community structure and functional dynamics of benthic microalgae in salt marshes. In M. P. Weinstein, & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 81–106). Springer.
- Sullivan, M. J., & Moncreiff, C. A. (1990). Edaphic algae are an important component of salt marsh food-webs: Evidence from multiple stable isotope analyses. *Marine ecology progress series. Oldendorf*, 62, 149–159.
- Sutter, L. A., Chambers, R. M., & Perry, J. E. (2015). Seawater intrusion mediates species transition in low salinity, tidal marsh vegetation. *Aquatic Botany*, 122, 32–39.
- Sutter, L. A., Perry, J. E., & Chambers, R. M. (2014). Tidal freshwater marsh plant responses to low level salinity increases. *Wetlands*, 34, 167–175.
- Thibault, K. M., & Brown, J. H. (2008). Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 3410–3415.
- Van de Broek, M., Temmerman, S., Merckx, R., & Govers, G. (2016). Controls on soil organic carbon stocks in tidal marshes along an estuarine salinity gradient. *Biogeosciences*, 13, 6611–6624.
- Wang, J., Bertness, M. D., Li, B., Chen, J., & Lü, W. (2015). Plant effects on burrowing crab morphology in a Chinese salt marsh: Native vs. exotic plants. *Ecological Engineering*, 74, 376–384.
- Wang, J., Tian, D., Knapp, A. K., Chen, H. Y. H., Luo, Y., Li, Z., Hou, E., Huang, X., Jiang, L., & Niu, S. (2021). Precipitation manipulation and terrestrial carbon cycling: The roles of treatment magnitude, experimental duration and local climate. *Global Ecology and Biogeography*, 30, 1909–1921.
- Wetzel, P. R., Kitchens, W. M., Brush, J. M., & Dusek, M. L. (2004). Use of a reciprocal transplant study to measure the rate of plant community change in a tidal marsh along a salinity gradient. *Wetlands*, 24, 879–890.
- Whitcraft, C. R., & Levin, L. A. (2007). Regulation of benthic algal and animal communities by salt marsh plants: Impact of shading. *Ecology*, 88, 904–917.
- White, S., & Alber, M. (2009). Drought-associated shifts in *Spartina alterniflora* and *S. cynosuroides* in the Altamaha River estuary. *Wetlands*, 29, 215–224.

- Widney, S. E., Smith, D., Herbert, E. R., Schubauer-Berigan, J. P., Li, F., Pennings, S. C., & Craft, C. B. (2019). Chronic but not acute saltwater intrusion leads to large release of inorganic N in a tidal freshwater marsh. *Science of the Total Environment*, 695, 133779.
- Więski, K., Guo, H., Craft, C., & Pennings, S. (2010). Ecosystem functions of tidal fresh, brackish, and salt marshes on the Georgia coast. *Estuaries and Coasts*, 33, 161–169.
- Woo, I., & Takekawa, J. Y. (2012). Will inundation and salinity levels associated with projected sea level rise reduce the survival, growth, and reproductive capacity of *Sarcocornia pacifica* (pickleweed)? *Aquatic Botany*, 102, 8–14.
- Wood, C., & Harrington, G. A. (2015). Influence of seasonal variations in sea level on the salinity regime of a coastal groundwater-fed wetland. *Groundwater*, 53, 90–98.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Li, F., Angelini, C., Byers, J. E., Craft, C. & Pennings, S. C. (2022). Responses of a tidal freshwater marsh plant community to chronic and pulsed saline intrusion. *Journal of Ecology*, 110, 1508–1524. <https://doi.org/10.1111/1365-2745.13885>