

Stress and subsidy effects of seagrass wrack duration, frequency, and magnitude on salt marsh community structure

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Abstract. Environmental perturbations can strongly affect community processes and ecosystem functions by acting primarily as a subsidy that increases productivity, a stress that decreases productivity, or both, with the predominant effect potentially shifting from subsidy to stress as the overall intensity of the perturbation increases. While perturbations are often considered along a single axis of intensity, they consist of multiple components (e.g., magnitude, frequency, and duration) that may not have equivalent stress and/or subsidy effects. Thus, different combinations of perturbation components may elicit community and ecosystem responses that differ in strength and/or direction (i.e., stress or subsidy) even if they reflect a similar overall perturbation intensity. To assess the independent and interactive effects of perturbation components, we experimentally manipulated the magnitude, frequency, and duration of wrack deposition, a common stress-subsidy in a variety of coastal systems. The effects of wrack perturbation on salt marsh community and ecosystem properties were assessed both in the short-term (at the end of a 12-week experimental manipulation) and long-term (6 months after the end of the experiment). In the short-term, plants and associated benthic invertebrates exhibited primarily stress-based responses to wrack perturbation. The extent of these stress effects on density of the dominant plant *Spartina alterniflora*, total plant percent cover, invertebrate abundance, and sediment oxygen availability were largely determined by perturbation duration. Yet, higher nitrogen content of *Spartina*, which indicates a subsidy effect of wrack, was influenced primarily by perturbation magnitude in the short-term. In the longer term, perturbation magnitude determined the extent of both stress and subsidy effects of wrack perturbation, with lower subordinate plant percent cover and snail density, and higher *Spartina* nitrogen content in high wrack biomass treatments. However, stress effects on the marsh community were generally less pronounced 6 months after the wrack perturbation, indicating capacity for recovery. Our results demonstrate that individual perturbation components can determine the degree to which its effects on the community elicit primarily stress- and/or subsidy-based responses. Further, the nature and extent of stress-subsidy effects can change over time, depending on species' relative ability to tolerate and/or recover from perturbation.

Key words: *allochthonous input; disturbance; duration; frequency; intensity; magnitude; marine subsidy; perturbation; salt marsh; Spartina alterniflora; wrack.*

INTRODUCTION

A rich tradition of ecological research includes examining the effects of environmental perturbations on population, community, and ecosystem processes (e.g., Connell 1978, Huston 1979, Odum et al. 1979, Sousa 1979, Polis et al. 1997, Wootton 1998, Mackey and Currie 2001, Yang et al. 2008). As they increase in overall intensity, perturbations can shift from a subsidy that increases ecosystem functions such as productivity and stability to a stress that decreases and/or destabilizes ecosystem functioning, resulting in a predicted unimodal performance curve with increasing perturbation in natural systems (Odum et al. 1979). For example, low to moderate levels of perturbation, such as seasonal flooding, may subsidize

a system, while moderate to high levels of perturbation, such as sustained or continuous flooding, may stress a system (Odum et al. 1979, Poff 2002, Wright et al. 2015). Although perturbations are often viewed along a single axis, they can vary in multiple components, including magnitude, frequency, and duration, which may not have equivalent effects on population, community, and ecosystem processes (Shea et al. 2004). For instance, flood duration strongly influences the abundance of flood-tolerant vs. flood-intolerant species, whereas flood magnitude strongly influences sediment transport and plant recruitment (Poff et al. 1997). However, predicting the response of riverine communities to changing duration of a low flow vs. a high flow flood event requires a clear understanding of the combined effects of duration and magnitude. Relatively little is known about how these components may independently and interactively determine whether a perturbation operates predominantly as a subsidy or a stress.

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Where a perturbation falls along the subsidy-stress spectrum will also likely vary across population, community, and ecosystem responses (Yang et al. 2008, Yee and Juliano 2012), with species identity and trophic level affecting the strength and direction of perturbation effects, depending on the independent and interactive effects of perturbation components. For example, resource pulses in the form of species migrations (Sinclair 2003, Moore and Schindler 2008, Walters et al. 2009), flooding (Poff et al. 1997, Poff 2002, Wright et al. 2015), or anthropogenic activities vary in magnitude, duration, and frequency, with differential effects on producers and consumers that potentially alter species interactions. In a wetland, nutrient enrichment increased quality (subsidy effect – greater phosphorus availability) but decreased quantity (stress effect – increased competition with macrophytes) of periphyton, whereas total macroinvertebrate community biomass exhibited a unimodal response to a gradient of phosphorus addition (King and Richardson 2007). Similarly, stable isotope analysis revealed that marine-derived nitrogen from the annual migration of anadromous alewife was quickly incorporated into multiple trophic levels of the stream community, but the effects of this nutrient influx on stream ecosystem functions such as primary production and decomposition rate were negligible (Walters et al. 2009), possibly as a result of simultaneous stress effects on the system.

Further, perturbations can alter the horizontal and/or vertical diversity of food webs (i.e., diversity within and across trophic levels; Hughes et al. 2007) and the length of food chains (McHugh et al. 2010). Given the influence of numerically dominant plant species (i.e., foundation species) on community diversity and ecosystem stability, examining perturbation effects on these primary producers is a valuable approach for clarifying how environmental perturbations affect species interactions, community composition, and ultimately productivity and diversity, particularly in communities where these same species serve as habitat providers (Armesto and Pickett 1985, Petraitis et al. 1989, Collins et al. 2001). For example, seaweed deposited by tides and storms (i.e., wrack) is a common environmental perturbation in coastal habitats, including salt marshes and terrestrial islands, that causes a direct physical stress for foundation species and other existing vegetation (Bertness and Ellison 1987, Pennings and Richards 1998). However, its consequent effects on the abundance and diversity of the associated invertebrate community (Bishop and Kelaher 2007) and rates of herbivory (Piovia-Scott et al. 2013) depend on whether it decreases (e.g., by destroying vegetation or altering plant species composition) or increases (e.g., by providing shade/shelter and/or improving plant nutrient content) the quality of existing habitat and resources for each associated species. Further, the coincident allochthonous input of nutrients and invertebrate prey from wrack deposition is also a potentially valuable resource subsidy to multiple

trophic levels on terrestrial islands (Spiller et al. 2010, Piovia-Scott et al. 2011) and in estuarine habitats (Pennings and Richards 1998, Newton and Thornber 2013).

The short-term vs. long-term effects of individual perturbation components, as well as their combined impact, may also differ, possibly shifting from primarily stress-based to primarily subsidy-based (or vice versa; Odum et al. 1979, Moore and Schindler 2008, Yang et al. 2008, Wright et al. 2013), or varying in the predominant mechanism underlying the response (Piovia-Scott et al. 2013). For example, the migration of anadromous and semelparous fish like salmon can alter stream ecosystems via multiple pathways, including subsidy effects of marine-derived nutrient loading and stress effects of nest building and habitat disturbance. Immediately following a migration event, water nutrient concentrations were strongly positively correlated with spawning density (i.e., magnitude), but subsidy effects quickly attenuated, with no relationship between water chemistry and perturbation magnitude in the next season (Rinella et al. 2013). Similarly, perturbation magnitude and time since the event shape the stress effects of salmon on algal and invertebrate populations: while algal biomass quickly recovered from initial stress effects regardless of perturbation magnitude, the recovery (or lack thereof) of invertebrate populations to pre-salmon levels in the next season strongly depended on spawning density (i.e., magnitude; Moore and Schindler 2008, Harding and Reynolds 2014). Likewise, seaweed wrack can fundamentally alter coastal ecosystems through multiple subsidy-stress pathways that operate on different time scales (Spiller et al. 2010, Piovia-Scott et al. 2011, 2013, Wright et al. 2013). In the short-term, wrack shades and smothers existing vegetation (Bertness and Ellison 1987, Pennings and Richards 1998), but it can also provide alternative resources to island ecosystems (Spiller et al. 2010, Piovia-Scott et al. 2011) and ameliorate existing environmental stress in salt marshes (Pennings and Richards 1998). Over the longer-term, wrack increases nutrient availability (Newton and Thornber 2013, Piovia-Scott et al. 2013), but its negative effects on the plant community can also decrease sediment organic carbon content and thus impact the capacity of salt marshes to act as blue carbon sinks (Macreadie et al. 2013). Thus, studies seeking to quantify perturbation effects also need to consider time since the event as a factor in predicting the extent of stress- and subsidy-based responses.

The goals of our study were to assess the independent and interactive effects of perturbation components on foundation species population dynamics, community structure, and ecosystem function in both the short-term (i.e., immediately after the event) and longer-term (i.e., 6 months after the event). To address these questions, we conducted a 12-week field experiment manipulating the magnitude, frequency, and duration of seagrass wrack addition to a salt marsh – a system that frequently experiences wrack deposition (Bertness and Ellison 1987, Pennings and Richards 1998, Macreadie et al. 2013). We

focused on the response of the foundation plant species *Spartina alterniflora*, as well as associated plant species abundance, benthic invertebrate densities, plant tissue nutrient content, sediment organic matter, and oxygen availability to assess the relative effects of each perturbation component on community and ecosystem properties at the end of the wrack manipulation (i.e., in the short-term). We again measured the full suite of responses 6 months after the end of the wrack manipulation to assess the longer-term effects of wrack deposition on the salt marsh community and to determine the most persistent components of this environmental perturbation. Finally, we calculated “realized perturbation” for each of our treatments to facilitate the comparison of perturbation regimes that consist of different perturbation components. This metric is comparable to previously published metrics like disturbance rate (a measure of magnitude \times frequency in units of cm^2/week ; e.g., Svensson et al. 2009). By combining the effects of perturbation magnitude, frequency, and duration (Svensson et al. 2009, Miller et al. 2011), realized perturbation allowed us to examine the effects of wrack deposition on a single axis and thus to test the subsidy-stress hypothesis and the predicted unimodal performance curve (Odum et al. 1979) for each of our response variables.

METHODS

We conducted our field experiment in a salt marsh in St. Joseph Bay, FL (29.715181, -85.305860), a site with dense subtidal seagrass beds adjacent to salt marshes. In September 2012, we established 96 1 m \times 2 m plots in six rows (i.e., blocks) of 16 plots each, with each plot enclosed in a 4' plastic mesh safety fence (Uline) secured to rebar at each corner. Each block ran parallel

to the shoreline approximately 0.5–1 ft above mean lower low water (MLLW) and contained 16 randomly assigned plots – including four control plots and 12 experimental plots, with each of the 12 unique wrack treatments (see Table 1 for a summary) included in each block ($N = 6$ for each experimental treatment and $N = 24$ for the control treatment). The magnitude manipulation included a low (average 4 kg/m^2) and a high (average 14 kg/m^2) biomass addition, which is representative of the typical range of wrack deposition in St. Joseph Bay ($3\text{--}30 \text{ kg/m}^2$, A. R. Hughes *unpublished data*). Wrack is typically deposited in the high marsh in the late summer and fall on the extreme tides (new and full moon), which occur twice monthly, and remains until the next tide of sufficient height removes it. Thus, the duration of wrack deposition depends on relative location in the marsh: lower elevations of the high marsh can have wrack deposited or removed during biweekly tidal events, while higher elevations experience wrack deposition and removal only at the most extreme 4-week tidal events. We mimicked these dynamics by testing two levels of perturbation duration (2- and 4-weeks), crossed with two levels of perturbation frequency (once or twice). For the high frequency (twice) perturbation, we also manipulated “interpulse”, or the time between wrack perturbation events, including 2- and 4-week periods between wrack addition (see Table 1 for a summary) that represent observed dynamics of wrack movement as a result of tidal cycles. Because time since wrack and our metric of “realized perturbation” (see *Statistical analysis* for details) effectively capture differences in interpulse duration and allow comparisons across all treatment combinations, we focus on these components of wrack rather than interpulse duration in the results.

TABLE 1. Summary of 12 wrack treatment combinations used in the Fall 2012 field experiment.

Treatment ID	Duration	Frequency	Magnitude	Interpulse duration	Time since wrack	Realized perturbation
Control	NA	NA	NA	NA	NA	0
2-1-Low	2	1	Low	NA	11	0.73
4-1-Low	4	1	Low	NA	9	1.78
2-2-Low (2)	2	2	Low	2	7	2.29
2-1-High	2	1	High	NA	11	2.55
2-2-Low (4)	2	2	Low	4	5	3.20
4-1-High	4	1	High	NA	9	6.22
2-2-High (2)	2	2	High	2	7	8.00
4-2-Low (2)	4	2	Low	2	3	10.67
2-2-High (4)	2	2	High	4	5	11.20
4-2-Low (4)	4	2	Low	4	1	32.00
4-2-High (2)	4	2	High	2	3	37.33
4-2-High (4)	4	2	High	4	1	112.00

Notes: Duration reflects the length of time (in weeks) that each wrack addition remained on the plot; frequency refers to the number of times wrack was added to each plot; low and high magnitude wrack treatments received an average of 4 and 14 kg/m^2 of wrack with each application, respectively; interpulse duration refers to the time (in weeks) between wrack addition in treatments with frequency >1 ; time since wrack is the number of weeks since wrack removal to the final sampling at the end of the experimental manipulation; and realized perturbation is calculated as [(wrack biomass \times perturbation frequency \times pulse duration)/time since wrack].

We collected fresh seagrass wrack from a nearby site in St. Joseph Bay, FL; wrack consisted predominantly of *Thalassia testudinum*, and composition was consistent throughout the experiment. We filled mesh bags with wrack, soaked them in freshwater for 5 min to ensure a consistent wet mass and remove associated animal species, manually spun them to remove most of the water, weighed them, and then combined them in larger bags to create low and high magnitude treatments for transport to the field site. Wrack was distributed evenly across plots, and at the end of each perturbation period (i.e., after 2 or 4 weeks), wrack was removed from the plots by hand.

We measured the following response variables at the beginning of the experiment (prior to wrack addition) in September 2012 and at the end of the 12-week wrack manipulation in December 2012: stem density (live and dead), stem height (height of six randomly selected stems), and percent cover of the dominant plant species *Spartina alterniflora* (hereafter, *Spartina*); percent cover of all subordinate plant species, including sea lavender *Limonium carolineanum* (hereafter, *Limonium*), pickleweed *Salicornia sp.* (hereafter, *Salicornia*), saltgrass *Distichlis spicata*, and turtleweed *Batis maritima*; plant species richness; density of the snail *Littoraria irrorata*; and the number of burrows of the fiddler crab *Uca pugnator*. In each plot, plant percent cover, height, and species richness, as well as fiddler burrow density were measured in two randomly placed 0.5 × 0.5 m quadrats, whereas *Spartina* stem density and snail abundance were measured in two randomly placed 0.25 × 0.25 m quadrats. Of the subordinate plant species, only *Limonium* and *Salicornia* were found consistently across plots, so we focused on them in our single species analyses. At the end of the wrack manipulation, we also collected sediment cores to determine sediment organic matter (SOM), sampled *Spartina* leaf tissue to measure carbon (C) and nitrogen (N) content as a proxy for nutrient availability, and measured sediment oxygen availability (i.e., redox) and temperature at a depth of 5 cm using an Orion Star™ A321 portable pH meter (Thermo Fisher Scientific, Waltham, Massachusetts, USA). To measure SOM, a sediment core (5 cm length × 2 cm diameter) was collected from the center of each plot, stored at −20°C prior to analysis, dried for 24–48 h at 60°C to get initial dry weight, combusted at 525°C for 3 h, and weighed to determine organic matter content. To determine *Spartina* leaf tissue C:N, a portion of the second leaf from a randomly selected stem was clipped and stored at −20°C prior to analysis, rinsed with deionized water and dried for 24–48 h at 60°C, homogenized using a Retsch MM400 mixer mill, and %C and %N were measured on a Flash EA 1,112 elemental analyzer (Thermo Finnigan Fisher Scientific, Waltham, Massachusetts, USA).

To examine the persistence of wrack effects in the salt marsh, we also measured the full suite of response variables in 60 randomly selected plots (including all treatment combinations) 6 months after the end of the wrack manipulation in July 2013.

Statistical analysis

First, to examine the relative and interactive effects of each perturbation component on the salt marsh community in the short-term, we excluded the control treatment and ran linear mixed effects models on responses at the end of the 12-week wrack manipulation with a three-way interaction between the categorical variables magnitude, frequency, and duration, including initial (i.e., pre-perturbation) condition as a covariate and row (i.e., block) as a random effect. Second, to evaluate the long-term effects of wrack perturbation on the salt marsh community, we used the same model structure to assess the effects of wrack on the same response variables 6 months after the wrack manipulation.

Because the effects of wrack strongly depended on the components (i.e., magnitude, frequency, and duration) of perturbation (see *Results*), as well as time since wrack (see Appendix S1 for details), we also calculated “realized perturbation” for each of our treatments, with realized perturbation being equal to [(wrack magnitude × perturbation frequency × pulse duration)/time since wrack], in units of kg/m² [(wrack biomass per area in kg/m² × number of events × length of event(s) in weeks)/time since event in weeks], which allowed us to examine the effects of wrack perturbation on a single axis. Time since wrack was a strong predictor of plant performance and invertebrate abundance (Appendix S1: Fig. S1), with both negative, stress effects and positive, subsidy effects decreasing linearly with increasing time since perturbation (Appendix S1: Fig. S1). However, the slope of this relationship often differed depending on the magnitude of the perturbation (significant time since wrack × magnitude interaction), indicating that a metric like realized perturbation that incorporates both the overall intensity of the event (i.e., magnitude × frequency × duration) and time since the event is necessary for comparisons of species responses along a single axis.

We used a mixed effects model to assess the effects of realized perturbation (log-transformed, linear and quadratic fit) on each response variable, with block as a random effect and initial condition as a covariate. If the best model included a quadratic term, then we used Davies test (Davies 2002) to test the null hypothesis of a constant slope across the range of the predictor variable, followed by piecewise regression to estimate the breakpoint if applicable. The identification of a perturbation breakpoint for each response, and subsequent comparison of threshold effects across the salt marsh community, can greatly inform management practices and activities (Brenden et al. 2008). If no breakpoint was identified, we present the results of the mixed effects model with a quadratic fit.

All analyses were conducted in RStudio (version 0.98.1102), using the lme4 and lmerTest packages with the Satterthwaite approximation for degrees of freedom to generate *F* and *P*-values for linear mixed effects models, and the segmented package for Davies test and piecewise regression.

RESULTS

Short-term perturbation effects of wrack

Plant productivity and richness.—The impacts of wrack magnitude, duration, and frequency on the dominant plant *Spartina* depended on the measure of plant production (see Appendix S2: Table S1 for details). Increasing wrack duration had a significant negative effect on *Spartina* stem density ($F_{1,63} = 16.96$, $P < 0.001$; Fig. 1A) and percent cover ($F_{1,63} = 13.91$, $P < 0.001$). Similarly, greater wrack frequency had a negative effect on *Spartina* percent cover ($F_{1,63} = 4.67$, $P = 0.035$). The magnitude and frequency of wrack perturbation also had an interactive effect on *Spartina* stem density ($F_{1,63} = 8.28$, $P = 0.005$): increasing the frequency of a low magnitude (i.e., low biomass) wrack event had little effect, but increasing the frequency of a high magnitude wrack event had a strong negative effect on *Spartina* stem density (Fig. 1B). In contrast, the effects of wrack addition on *Spartina* height

depended on magnitude ($F_{1,63} = 14.37$, $P < 0.001$, Fig. 1C): *Spartina* height declined less in the low biomass treatment than in the control (i.e., no wrack) and high biomass treatments.

The effects of wrack addition on the subordinate plant species were generally negative, though the extent of the effect depended on individual perturbation component(s). Only wrack duration significantly affected *Salicornia* percent cover ($F_{1,57} = 6.08$, $P = 0.017$, Fig. 1D), whereas the interaction of magnitude \times duration ($F_{1,58} = 8.04$, $P = 0.006$; Fig. 1E) and of duration \times frequency ($F_{1,58} = 5.22$, $P = 0.026$; Fig. 1F) both influenced *Limonium* percent cover. Increasing the duration of a high magnitude, but not low magnitude, wrack perturbation significantly decreased *Limonium* abundance, reducing percent cover by $>30\%$ compared to the control (Fig. 1E). Similarly, increasing the duration of a one-time wrack deposition event (i.e., frequency = 1) had a minimal effect on *Limonium* percent cover compared to the control, whereas increasing the duration of multiple perturbations

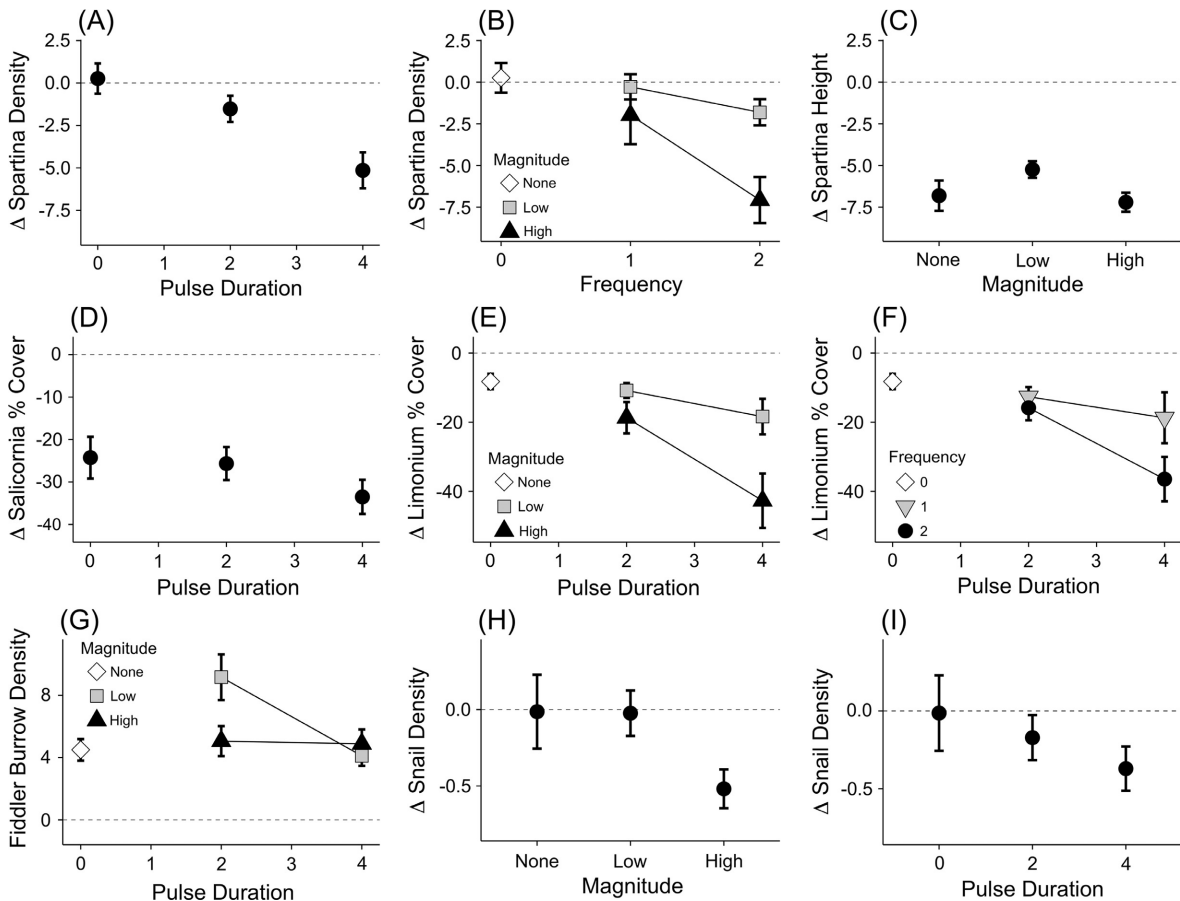


FIG. 1. Components of wrack treatment (duration, frequency, and magnitude) that affected *Spartina* stem density (per 0.0625 m^2 quadrat; A, B) and height (C); percent cover of *Salicornia* (D) and *Limonium* (E–F); and density of fiddler crabs (per 0.25 m^2 quadrat; G) and snails (per 0.0625 m^2 quadrat; H, I) at the end of the wrack manipulation (mean \pm SE). D–F represent plant percent cover per 0.25 m^2 quadrat. In the analyses, initial measurements were included as a covariate in the model (see *Methods*). If initial density, height, and/or percent cover was significant, figures represent change (Δ) from the beginning of the experiment to the end of the experiment; if not, figures present only the final measurements.

(i.e., frequency = 2) had a strong negative effect on *Limonium* abundance, reducing percent cover by >25% compared to the control (Fig. 1F).

Despite effects on individual plant species, wrack had little effect on overall marsh plant species richness: the average number of species per plot changed <0.75 across treatments during the experiment, and there were no significant independent or interactive effects of wrack components on richness (Appendix S2: Table S1).

Invertebrate abundance.—The interaction of wrack duration × magnitude affected fiddler crab burrow density ($F_{1,58} = 4.63, P = 0.036$); in the high biomass wrack treatment, burrow density was consistently low, regardless of duration, whereas there was a significant increase in burrow density after a short duration (i.e., 2-week), low biomass wrack event, but little change in burrow density after a long duration (i.e., 4-week), low biomass wrack event (Fig. 1G). Magnitude ($F_{1,58} = 15.59, P < 0.001$) and duration ($F_{1,58} = 4.49, P = 0.038$) of wrack addition also affected density of snail abundance, though additively: *Littoraria* density was lowest in the high biomass or long duration wrack treatments (Fig. 1H, I).

Nutrient availability and plant stoichiometry.—There was no effect of wrack addition on surface or subsurface SOM ($P > 0.24$). However, wrack duration negatively affected sediment oxygen availability, with redox lowest after a 4-week wrack exposure compared to the control or a 2-week wrack exposure (Fig. 2A). In addition, duration, frequency, and magnitude of wrack addition each significantly affected *Spartina* C:N (duration: $F_{1,64} = 10.84, P < 0.001$; frequency: $F_{1,64} = 15.84, P < 0.001$; magnitude: $F_{1,64} = 35.41, P < 0.001$): plant C:N was lower in the longer duration, higher frequency, and greater magnitude treatments, potentially indicating increased tissue quality in these treatments (Fig. 2B–D). Changes in *Spartina* C:N were due to changes in plant %N, not changes in plant %C; there was no effect of any component of disturbance on plant %C ($P > 0.25$). However, the interaction of duration × magnitude, and of frequency × magnitude, both significantly affected plant %N. Increasing the duration or frequency of wrack deposition only significantly increased *Spartina* %N in the high biomass treatment (25% and 30% increase, respectively), not the low biomass treatment (Fig. 2E, F).

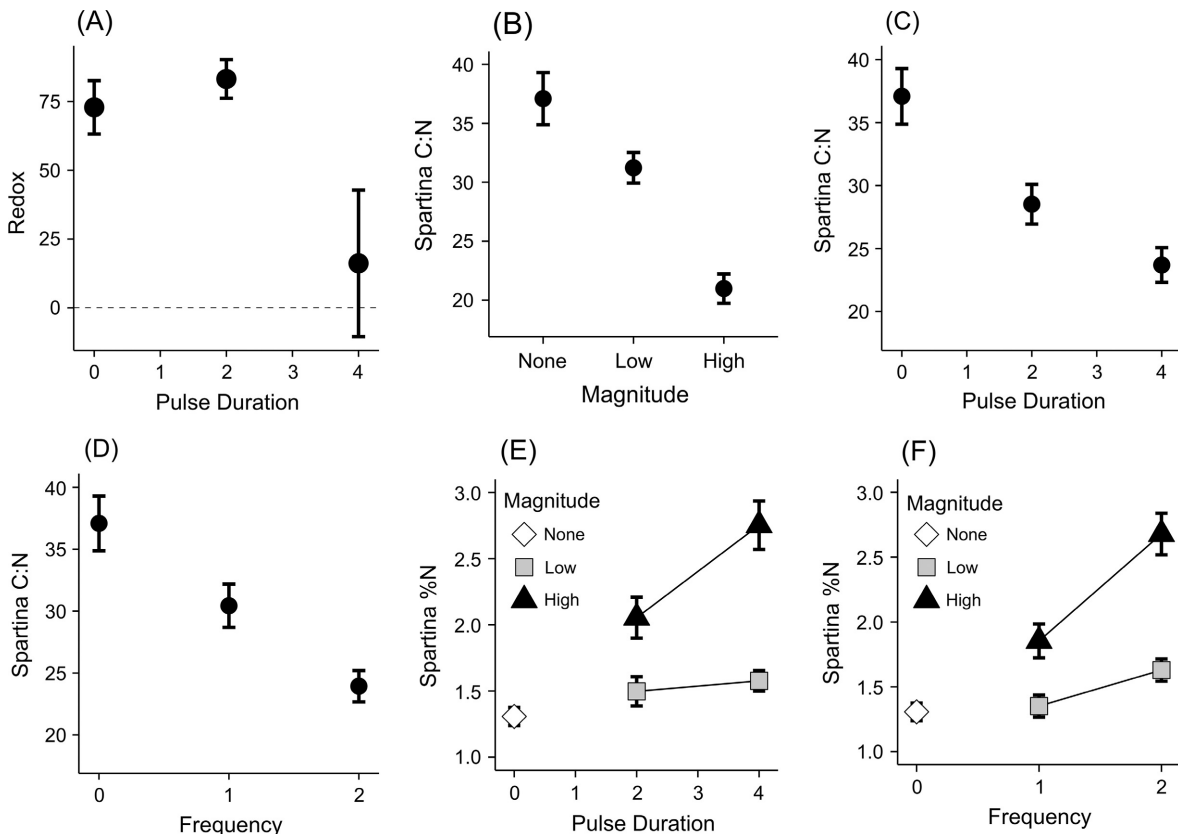


FIG. 2. Short-term effects of wrack (A) duration on sediment oxygen availability (i.e., redox; measured in mV), and of wrack (B) magnitude, (C) duration, and (D) frequency on *Spartina* tissue carbon:nitrogen ratio, and (E) duration × magnitude and (F) frequency × magnitude on *Spartina* tissue nitrogen content at the end of the wrack manipulation (mean ± SE).

Long-term perturbation effects of wrack

The longer-term effects of wrack (i.e., 6 months after the wrack manipulation) on the marsh plant community were relatively minimal (see Appendix S3: Table S1 for details), with no effect of any perturbation component on *Spartina* or *Salicornia* responses in July 2013. However, the interactive effect of magnitude \times duration on *Limonium* percent cover persisted 6 months after the experiment (Fig. 3A). In addition, the interaction of magnitude \times frequency affected *Limonium* percent cover in

the longer term (Fig. 3B). Invertebrate abundance also varied over the longer term, with magnitude having a persistent negative effect on snail density (Fig. 3C) and the interaction of duration \times frequency affecting fiddler burrow density 6 months after the wrack manipulation (Fig. 3D). The effects of wrack on sediment oxygen availability and plant stoichiometry were also detectable in the longer term; the interaction of magnitude \times duration affected redox (Fig. 3E), while the magnitude of the perturbation increased *Spartina* %N (Fig. 3F) and decreased *Spartina* C:N 6 months after wrack removal.

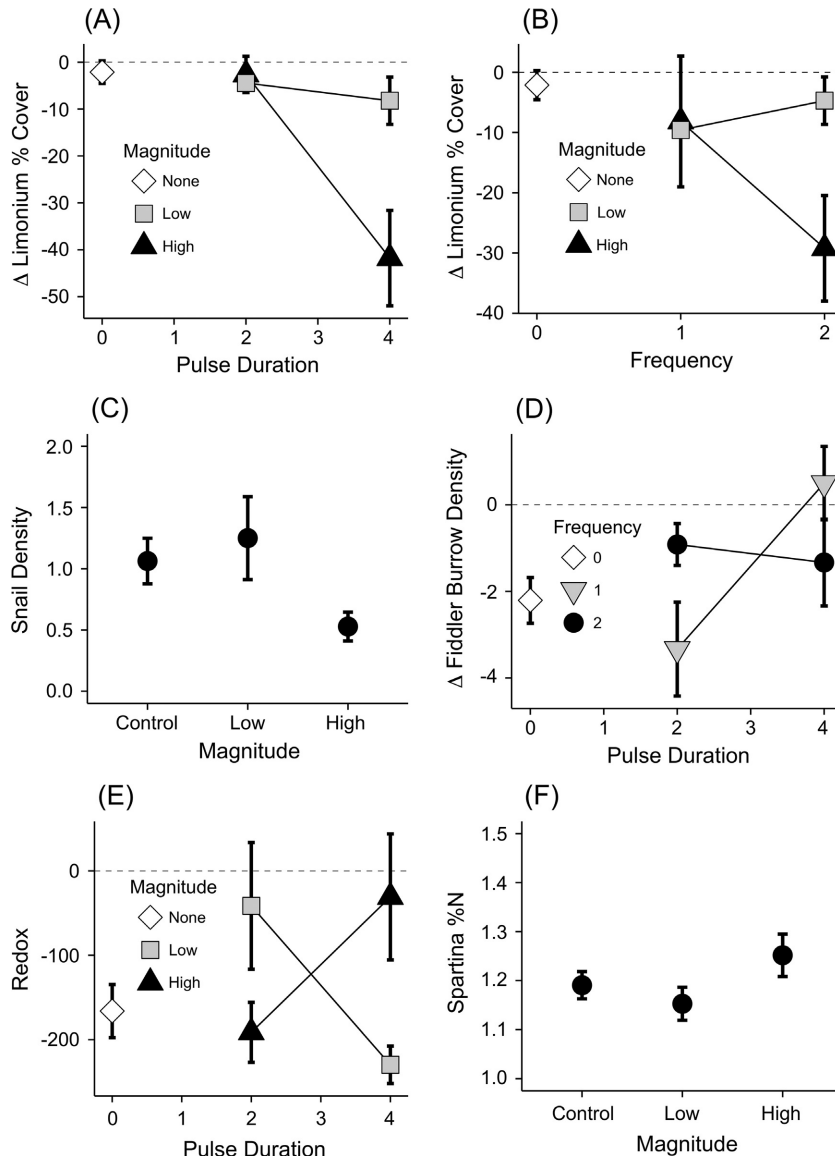


FIG. 3. Effects of magnitude, duration, and frequency of wrack addition on the salt marsh community (mean \pm SE) in the longer term (i.e., six months after the wrack manipulation). Effects of wrack (A) duration \times magnitude and (B) frequency \times magnitude on *Limonium* percent cover per 0.25 m² quadrat (Δ : change from the beginning of the experiment to six months after the end of the experiment), of wrack (C) magnitude on snail density (per 0.0625 m² quadrat), (D) duration \times frequency on fiddler burrow density (per 0.25 m² quadrat), (E) duration \times magnitude on sediment oxygen availability (i.e., redox; measured in mV), and (F) magnitude on *Spartina* tissue nitrogen content.

Realized perturbation effects of wrack

“Realized perturbation” was a strong predictor of wrack effects on the salt marsh community (Table 2), yet plant and invertebrate responses, as well as ecosystem properties, rarely showed a unimodal performance curve with increasing perturbation. For instance, the dominant plant species *Spartina*, exhibited a breakpoint in the regression slope for both measures of *Spartina*

TABLE 2. Regression of plant and invertebrate responses, nutrient availability, and ecosystem properties on linear and quadratic rates of realized perturbation (see *Methods* for details).

Response	F	P
Plant species richness		
Rate	0.665	0.417
Rate ²	3.219	0.076
<i>Spartina</i> stem density (Breakpoint = 0.06)		
Below breakpoint	0.939	0.343
Above breakpoint	24.087	<0.001
<i>Spartina</i> stem height		
Rate	0.029	0.864
Rate ²	2.232	0.139
<i>Spartina</i> percent cover (Breakpoint = 0.36)		
Below breakpoint	2.398	0.131
Above breakpoint	12.705	<0.001
<i>Limonium</i> percent cover (Breakpoint = 0.39)		
Below breakpoint	0.436	0.514
Above breakpoint	10.570	0.002
<i>Salicornia</i> percent cover		
Rate	4.417	0.038
Rate ²	0.022	0.882
Fiddler burrow density		
Rate	1.201	0.276
Rate ²	9.998	0.002
Snail density		
Rate	17.133	<0.001
Rate ²	0.274	0.602
<i>Spartina</i> C:N		
Rate	32.837	<0.001
Rate ²	1.631	0.205
<i>Spartina</i> %C		
Rate	1.008	0.318
Rate ²	0.107	0.744
<i>Spartina</i> %N (Breakpoint = 0.01)		
Below breakpoint	0.215	0.647
Above breakpoint	35.041	<0.001
Sediment SOM		
Rate	2.199	0.142
Rate ²	0.288	0.593
Redox (Breakpoint = 1.15)		
Below breakpoint	0.225	0.637
Above breakpoint	2.404	0.165

Note: For non-linear responses, if a Davies test identified a breakpoint in the regression slope, the results of linear mixed effects models conducted above and below the estimated breakpoint are presented (bold denotes $P < 0.05$; italics denotes $0.05 < P < 0.1$).

production (Davies test: stem density, $P = 0.04$; percent cover, $P = 0.004$), with little effect of a low intensity (i.e., magnitude \times frequency \times duration) wrack event that occurred >7 weeks prior to the end of the experiment (i.e., low realized disturbance), but above a threshold (breakpoint: 0.06 for stem density; 0.37 for percent cover), there was a significant decline in *Spartina* production as realized perturbation increased (Fig. 4A, B). Percent cover of the subordinate plant species *Limonium* also showed a threshold response (Davies test: $P = 0.04$, breakpoint = 0.39; Fig. 4C). In contrast, the subordinate plant species *Salicornia* declined linearly with increasing realized perturbation (Fig. 4D), and there was no relationship between realized perturbation and *Spartina* stem height.

The realized perturbation effects of wrack also strongly predicted invertebrate responses: fiddler crab (*Uca*) burrow density showed the only unimodal performance curve, with densities peaking at intermediate realized effects of wrack (Fig. 4F), whereas snail (*Littoraria*) abundance decreased linearly as realized perturbation increased (Fig. 4E). Wrack also affected plant elemental composition, but these results reflected a threshold response to realized perturbation: there was little effect of a low intensity wrack event that occurred 11 weeks earlier on *Spartina* %N, but above a threshold (Davies test: $P = 0.003$, breakpoint 0.01), *Spartina* %N increased linearly with both increasing wrack intensity and decreasing time since wrack (Fig. 4G). The wrack effects on ecosystem properties also reflected a threshold response to realized perturbation: above a threshold (Davies test: $P < 0.001$, breakpoint 1.15), redox declined linearly with increasing realized perturbation in plots exposed to high intensity treatments and sampled ≤ 3 weeks after wrack removal (Fig. 4H). In contrast, there was no relationship between sediment organic matter (SOM) and wrack realized perturbation.

DISCUSSION

Wrack perturbation significantly affected the salt marsh community and ecosystem in the short-term, with pervasive stress effects on plant density, invertebrate abundance, and sediment oxygen availability, as well as a subsidy effect on nutrient availability (i.e., *Spartina* N content) (Fig. 4). The short-term stress effects of wrack depended primarily on wrack duration, with perturbation length negatively affecting the plant community at the end of the wrack manipulation. *Spartina* stem density and *Salicornia* percent cover were substantially lower in the longer duration treatments than in the shorter duration treatments (Fig. 1A, D). Similarly, the effects of wrack on *Limonium* percent cover depended on the interactive effects of duration \times magnitude, and of duration \times frequency (Fig. 1E, F). The negative effects of increasing duration were not limited to the plant community, but also negatively influenced snail density (Fig. 1I), though these effects on invertebrates

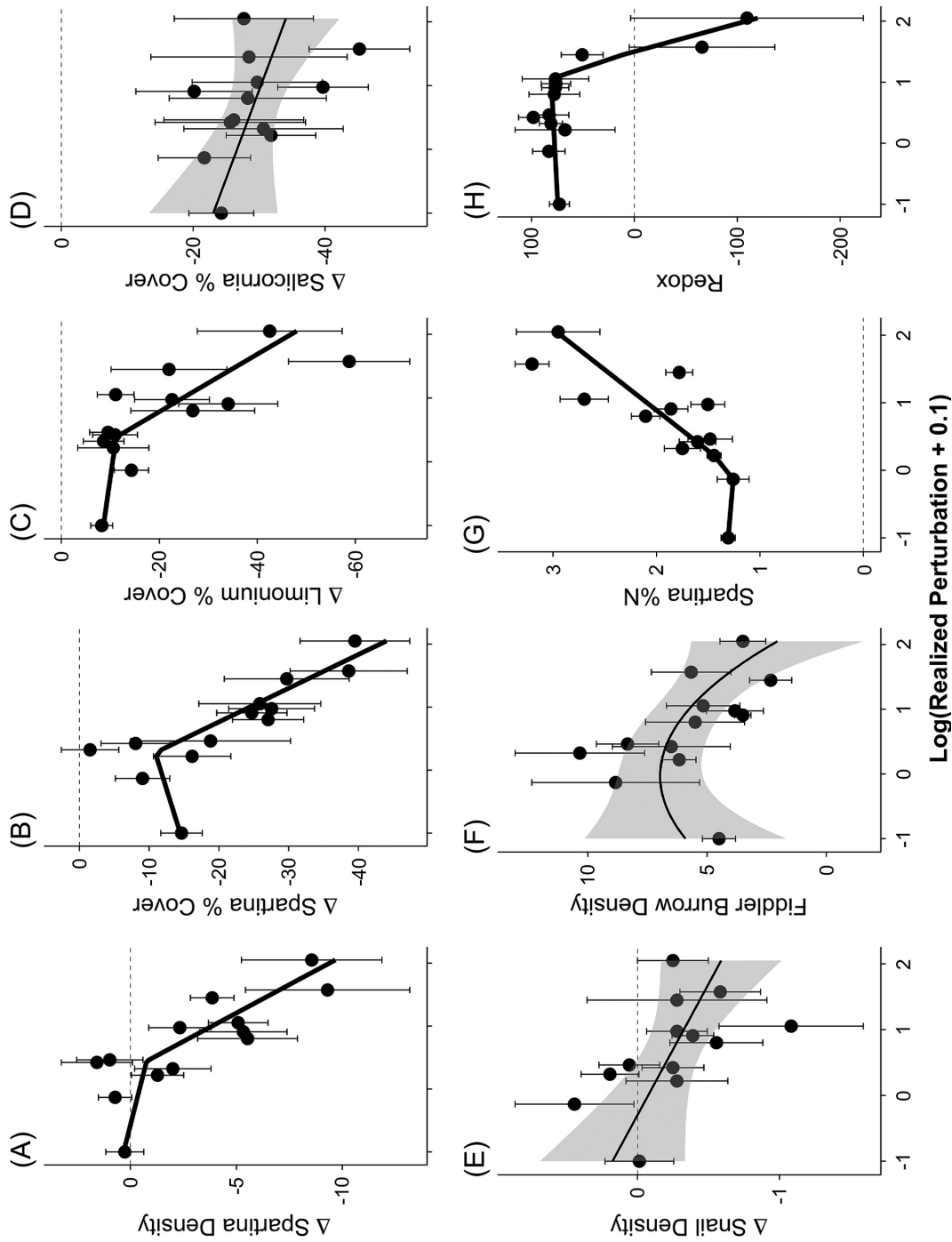


FIG. 4. Relationship (linear or quadratic fit $\pm 95\%$ CI; mean \pm SE) between wrack realized perturbation (log-transformed; see *Methods* for details) and (A) change in *Spartina* stem density (per 0.0625 m² quadrat) from the beginning to the end of the wrack manipulation (September–December 2012); (B) change in *Spartina* percent cover (per 0.25 m² quadrat); (C) change in *Limonium* percent cover (per 0.25 m² quadrat); (D) change in *Salicornia* percent cover (per 0.25 m² quadrat); (E) change in snail density (per 0.0625 m² quadrat); (F) fiddler burrow density at the end of the wrack manipulation (per 0.25 m² quadrat); (G) *Spartina* tissue N content; and (H) sediment oxygen availability (i.e., redox; measured in mV).

were generally weaker than on plants. In addition, duration of wrack perturbation also negatively affected sediment characteristics, with substantially lower oxygen availability in the longer duration treatments (Fig. 2A). Thus, our results suggest that the duration of a perturbation like wrack that physically shades and smothers existing vegetation (Bertness and Ellison 1987, Pennings and Richards 1998) plays a strong role, both independently and interactively, in determining the degree of stress experienced by the salt marsh community in the short-term.

In contrast to the predominant stress effects of wrack, the short-term subsidy effects of wrack perturbation were less pronounced and depended primarily on the magnitude of the event, with high magnitude treatments consistently increasing *Spartina* tissue %N relative to the low magnitude treatments. Further, increasing the duration or frequency of a high magnitude perturbation had a much greater effect on *Spartina* %N (~30% increase) than increasing the duration or frequency of a low magnitude perturbation (~10% increase) (Fig. 2E, F). These changes in plant N content may reflect a substantial increase in sediment nutrient availability (Bishop and Kelaher 2007, Newton and Thornber 2013), which can affect growth rates in the short-term and plant-plant interactions in the long-term, though shading effects of wrack may also have contributed to changes in tissue composition (Kephart and Buxton 1993, Treydte et al. 2007). However, any benefits of nutrient subsidy from wrack perturbation did not offset the extensive costs of physical stress in the short-term, particularly in higher magnitude, longer duration, and/or greater frequency wrack perturbations, as *Spartina* stem density and percent cover generally decreased more in the presence of wrack than in its absence (Fig. 1A, B).

Six months after the wrack perturbation (i.e., in the longer-term), stress effects on the salt marsh community were less pronounced, indicating capacity for recovery. Subsidy effects also persisted, though to a lesser extent. Wrack duration still played a role in determining the strength of perturbation effects on the salt marsh community, through both independent and interactive effects with magnitude and frequency (Fig. 3A, D, E). However, perturbation magnitude also figured prominently in both the stress and subsidy effects of wrack in the longer term (Fig. 3A, B, C, E), suggesting that the relative importance of individual components in predicting the effects of a perturbation in the short-term (i.e., weeks to months) vs. long-term (i.e., months to years) may be different. In addition, the degree to which each species experiences a perturbation as a stress vs. a subsidy depends on a variety of species traits, including morphology, life history, phenology, and competitive ability (Haddad et al. 2008), as well as the intensity (i.e., magnitude \times duration \times frequency) of the perturbation. For example, wrack perturbation represented a (weak) stress on snail density, with magnitude playing a key role in both the short- and long-term. These stress effects likely resulted from negative

impacts on *Spartina*, which snails use as a refuge from inundation and predation, as well as for foraging (Silliman and Newell 2003, Hughes 2012, Kimbro 2012, Hughes et al. 2015). In contrast, wrack represented both a stress and a subsidy for fiddler burrow density, with positive and negative effects of wrack addition depending on individual perturbation components and overall intensity. A short duration, low magnitude wrack perturbation may have benefitted fiddler crabs by increasing shelter availability, soil moisture, and/or nutrient availability, or by decreasing temperature, but high magnitude and/or long duration perturbation events appear to outweigh any subsidy effects with the increased stress of reduced mobility and/or difficulty burrowing.

Plant community responses also differed in the short- and long-term as a function of species identity. For instance, while wrack addition reduced *Spartina* stem density in the short-term (Fig. 1A, B), there were no residual effects of wrack on *Spartina* density or percent cover in the longer term, indicating that the dominant plant species is relatively tolerant of wrack perturbation (Bertness and Ellison 1987) and/or has a high capacity for recovery from disturbance (Angelini and Silliman 2012). Further, while we did not measure sediment nutrient availability directly in this experiment, potential subsidy effects of wrack in the shorter-term, such as increased N (Bishop and Kelaher 2007, Newton and Thornber 2013), may also have facilitated the recovery of *Spartina* in the longer-term. The long-term effects of wrack on *Salicornia* percent cover were similarly negligible, but even the short-term effects of wrack on this opportunistic species, which frequently colonizes bare patches in the salt marsh (Ellison 1987), were relatively small. In contrast, the negative effects of wrack deposition on the competitively inferior species *Limonium* persisted six months after the experiment (Fig. 3A, B); while its capacity for recovery from disturbance relative to other plant species is unknown, the negative effects of wrack on *Limonium* percent cover in the short-term were much more extensive than those on either *Spartina* or *Salicornia* (Fig. 1), at least partially explaining why the long-term stress effects of wrack were most pronounced for *Limonium*. Because the effects of wrack vary among species and over time, the components (i.e., magnitude, duration, and frequency) of stress-subsidy perturbations may shift plant-plant interactions from competitive to facilitative by increasing the degree of physical stress experienced by each species (Bertness and Shumway 1993) and/or altering nutrient availability (Bishop and Kelaher 2007, Newton and Thornber 2013).

Our “realized perturbation” index, which takes into consideration both total intensity of wrack deposition and time since wrack removal, allowed a test of the predicted unimodal performance curve across a single integrated metric of perturbation (Odum et al. 1979, Fig. 4). We found a unimodal performance curve for only one of our response variables, with fiddler burrow density peaking at low to intermediate levels of wrack

perturbation, but then decreasing at higher levels of realized perturbation (Fig. 4F). In contrast, we found a threshold effect of wrack on measures of both stress (i.e., decreasing plant stem density and percent cover; Fig. 4A–C) and subsidy (i.e., increasing plant N content; Fig. 4G). A recent meta-analysis found that studies manipulating resource fluxes had smaller effect sizes than observational studies of resource fluxes in the field (Allen and Wesner 2016); thus, the effects of naturally occurring wrack deposition, in particular the subsidy component, may potentially be greater and/or persist longer. The timing of a resource subsidy can also determine the strength and direction of the effects on the recipient community; for example, an early season resource pulse in streams increased consumer growth rate and population biomass, with cascading effects on prey abundance, decomposition rate, and nutrient cycling, whereas a late season resource pulse (analogous to ours) did not affect the recipient community (Sato et al. 2016). Similarly, the relatively small effects of our experimental wrack additions on invertebrates may be due to decreased activity of snails and fiddler crabs during the late fall and winter. Thus, the natural timing of wrack events in this system may limit their effects.

In many cases, environmental perturbations like wrack deposition (this study), flooding (Wright et al. 2015), and species migrations (e.g., salmon: Moore and Schindler 2008, wildebeest: Sinclair 2003) simultaneously represent both a stress and a subsidy to the impacted community and ecosystem, but whether and to what degree a resource flux mediates the stress effects of perturbation likely depends on the magnitude, frequency, and/or duration of the event, as well as time since the event and the extent of nutrient limitation in the recipient ecosystem (Newton and Thornber 2013). In our study, perturbation duration played a key role in determining the stress effects of wrack, whereas perturbation magnitude strongly affected the subsidy effects of wrack in the short-term; the consistency of these effects across perturbation events and diverse communities merits further investigation. In addition, consideration of overall intensity of the event relative to time since perturbation (i.e., realized perturbation) may facilitate the identification of key disturbance thresholds and aid in management activities and restoration planning as environmental perturbations continue to increase in magnitude, frequency, and duration (Brenden et al. 2008). Further, while the co-occurrence of a stress and a subsidy may have relatively little effect on species richness (this study, Fischer et al. 2016), the benefits of greater resource availability may offset the costs of a disturbance, leading to an increase in productivity but a decrease in stability, particularly in high diversity communities (Wright et al. 2015, Fischer et al. 2016). Explicitly contrasting the stress-subsidy effects of perturbations on relatively low diversity communities (such as the salt marsh community in this study) with effects on high diversity communities may further clarify the relative importance of perturbation components, and the

implications for population and community responses across ecosystems.

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