Supporting Online Material for

Drought, Snails, and Large-Scale Die-off of Southern U.S. Salt Marshes

Brian R. Silliman,* Johan van de Koppel, Mark D. Bertness, Lee Stanton, Irving A. Mendelssohn

*To whom correspondence should be addressed. E-mail: brian_silliman@brown.edu

Published 16 December 2005, Science 310, 1803 (2005) DOI: 10.1126/science.1118229

This PDF file includes:

Materials and Methods
Fig. S1
References
Materials and Methods

Site description and drought effects on marsh soils. Because marsh die-off has been most severe in LA and GA (S1-4), we focused our experimental work on two dieback areas (Lighthouse and Airport Marshes) on Sapelo Island, GA, at the University of Georgia Marine Institute, and two in LA, near the Louisiana Universities Marine Consortium in Port Fourchon, LA. All four sites occur at mid-marsh elevations in intermediate height Spartina (.5-1.5 m tall) zones in areas that are typically flooded either once daily (LA) or twice daily (GA). In GA the tidal amplitude is ~ 3m and, in LA it is ~ .35 m. Despite frequent flooding of marsh soils, which would seem, intuitively, to make them relatively immune to drought stress, intense heat and drastically reduced rainfall in the southeast from 1999-2001 still led to significant increases in edaphic stressors in marsh soils (Table 1). In both states, state climatologists have declared the period 1999-2001 a 100-year drought (J. Grymes, Louisiana State Climatologist, Dr. David Stooksbury, Georgia State Climatologist, S1-4); total annual rainfall was reduced in both states by 25-35% (Table 1). Extensive field monitoring and lab experiments indicate that these drought-driven increases in soil stressors were likely due to a combination of high evaporation rates, low freshwater input from rain and groundwater flow and, at times, low river discharge and low estuarine water levels, especially in the Gulf where tidal amplitude is extremely small (S1). At the GA and LA die-off sites, inundation lasts ~1-3 hours on each flood tide. In GA, this was consistent over the entire drought cycle, 1999-2001. In LA, however, in the summer of 1999, near-record low discharge out of the Mississippi River (second lowest on record) combined with near-record low water levels in the Gulf of Mexico (lowest 15% percentile since 1950) are thought to have reduced inundation of LA marshes at a time when rainfall was coincidently minimal and the heat indexed elevated (S1). This combination of stressors then is thought to have led to drying of marsh soils and increased interstitial soil acidity and metal toxicity; coincident elevated salinities (Table 1) are thought to have exacerbated these drought effects (S1). In GA, although water levels did not affect flooding regimes significantly, salinities in the estuarine waters flooding marshes on Sapelo Island increased ~ 50% from a normal 18-23ppt to 28-32ppt during drought years (Table 1) and interstitial salinities in mid-elevation marshes near die-off sites rose ~ 75% from a range of 25-33ppt to 45-55ppt - levels that severely stress Spartina growth and stimulate top-down control by snails (see results of salt x snail experiment; Table 2).

Caging experiments. At each site, caging experiments were begun in July 2002. Experimental treatments (n=3) consisted of: (1) fenced snail removal plots, (2) unmanipulated control plots, and (3) partially-caged control plots (S5). Porewater redox and salinity were measured at low tide during the day once each season in each treatment (S5). Measuring salinity during low tide is a conservative measurement of soil stressors, because differences between unvegetated and vegetated sediments should be greatest at this time, yet we found no differences in values among treatments (see below). Importantly, results from our seasonal survey of edaphic factors did not differ significantly from soil measurements taken monthly at the same sites by separate research groups (S1).
Soil redox and salinity levels in caging experiment. At die-off sites in both LA and GA, there were no treatment effects on redox potential and salinity (p= 0.32, ANOVA, all cases), and both physical factors never reached levels known to be lethal to Spartina (10). For LA site 1, redox = -235 +/- 42.8 mv, salinity = 18.4 +/- 2.1 ppt; for LA site 2, redox = -253 +/- 64.3 mv, salinity = 18.8 +/- 1.9 ppt; for GA site 1, redox = -325 +/- 67 mv, salinity = 34.3 +/- 3.7 ppt; for GA site 2, redox = -286 +/- 87 mv, salinity = 33.6 +/- 2.9 ppt. This caging experiment, however, took place in 2002 as drought conditions were subsiding; thus, our readings of normal levels of physical stress in marsh soils, like those in other die-off studies (8-11), do not preclude grazer interactions with drought-induced soil stress in 1999 and 2000 and 2001, during peak drought years. Indeed, data in Table 1 clearly show that intense drought occurred in these areas and that marsh soil stressors (i.e., salinity) that are known to negatively affect Spartina growth (S1) were concomitantly elevated in the years just prior to die-off.

Grazing impacts of snail fronts. To test the hypothesis that the expansion rate of marsh die-off increases with increasing snail density, at each site, we marked 15-25, 3-m stretches of die-off border (stretches separated by > 10m) and monitored border movement and snail densities over 1 year (Fig. 1). To determine the relative impact of snail grazing on extent of marsh die-off, we divided total amount of area cleared by snails during the experiment (= total length of high density borders x average net loss of grass along those borders) by total area of die-off at the beginning of the study (determined with measuring tape).

Salt x grazer experiment. To determine if sub-lethal salt stress intensifies snail grazing, we added ocean salt to 1x1 m sections of healthy, intermediate-form Spartina marsh with and without experimental snail removal in Airport Marsh, GA. Salt was delivered monthly (March-October) to sediments in 50-ml plastic centrifuge tubes with holes drilled into the sides (S5). In total, 900 g of salt/ m² were added. Porewater salinity was monitored monthly (S5). After eight months, mean plant biomass for: no salt+snails=12.87+/-1.04; no salt-snails=15.63+/- .97; salt+snails 2.43+/-.58; salt-snails 8.5+/- .93; for main effect of salt and grazers, P<0.001, two-way ANOVA, and for salt x grazer interaction, P=0.03, two-way ANOVA. Increased top-down control on salt stressed plants seems to be due to a combination of increased snail grazing and fungal growth per unit area of leaf on those plants (B.R. Silliman unpub. data), which perhaps resulted from salt stress weakening plant defenses against snail grazing (reduced lignin in leaves) and fungal infection (reduced antibody production).

Snail movement experiment. We placed 200 painted (paint=finger nail polish, which has no detectable affect on snail movement patterns – B. R. Silliman unpub. data) snails along the mudflat-Spartina interface, approximately 2m into the mudflat, and monitored snail movement over two hours. Within one hour, 96% of snails (P<0.001, chi square) had moved 2m across the mudflat into the healthy marsh and attached to live stems. This result was expected given Littoraria’s characteristic behaviors of (1) always being associated with Spartina stems (because stems provide access to their preferred food source – fungi and escape from swimming predators at high tide) as opposed to exposed mudflats, and (2) not moving significantly in the horizontal plane unless they are placed on exposed mudflats, underwater, or in the presence of blue crabs or other predators. In these cases, their movements change from ~25 cm/ hour in the vegetated marsh up to ~16m/ hour (B.R. Silliman unpublished data).
Reconstruction of snail densities. We estimated snail densities prior to marsh die-off at our experimental sites to compare with those found in, and adjacent to, snail fronts on die-off borders. To do this, we quantified snail densities in adjacent healthy marsh areas (~ 250 m away) using the methods previously described (n=50 quadrats). This is likely an accurate and conservative estimate technique given that *Littoraria* rarely moves more than 5m horizontally over a year (S5) when cordgrass is healthy and because *Littoraria* tends to disperse in relatively equal densities over short distances in the same *Spartina* height zones (100-400m). At all sites, snail densities in adjacent, healthy marsh areas were significantly lower than those found in concentrated fronts on die-off borders (p< 0.0001, t-test).

Marsh recovery and snail movements. To date, recovery of die-off areas throughout the southeast has been patchy (S1-4). In LA, the study sites have now almost fully recovered due to successful seed recruitment. In GA, sites are slowly recovering from the edges through clonal growth, but only along edges where snail fronts did not establish (Fig. 3). Because snails in fronts will continue to move toward cordgrass and not back into mudflats (see movement study above), primary space-holders in this system are provided with a behaviorally-driven refuge for recovery. This spatial disconnect between areas of intensified top-down control and areas of plant recovery, should contribute to system resilience from complete collapse and should persist until grazer densities become so high that snail waves do not dissipate after disturbance, and snails in fronts have no choice but to turn back onto mudflats and recovering areas after reaching limits of marsh plant distribution (e.g., creekbanks).

Potential interactions with season. In colder climates (e.g., New Jersey, Virginia, North Carolina), snails typically stop grazing and move to high marsh habitats in the winter and “hibernate”. This seasonal-cessation of snail grazing has the potential to disrupt the snail front propagation and mitigate runaway community collapse, especially in more seasonal climates. In GA and LA, however, where winter temperatures are typically mild, snails continue to graze throughout winter, unless cold temperatures set in (B.R. Silliman, pers. obs.). During these cold snaps, snails typically hibernate not in the higher marsh but at the base of *Spartina* upon which they have been grazing. Once temperatures rise, they begin grazing again. Thus, in more southern marshes, colder temperatures will likely slow propagation, but not completely dissipate snail fronts, while in climates with extended cold winters, the change of seasons will likely buffer the system from further runaway consumption when grazer fronts form.

A model of consumer front formation

Below, we develop a model of the *Spartina*-snail interaction to investigate whether the mechanisms uncovered by the experiments presented in the paper have the potential to explain the formation of consumer fronts. We apply a minimal modelling approach in that we only include in the model those aspects of the ecology of the snail-*Spartina* interaction that seem most relevant to front formation. The model describes changes in local plant standing crop and snail density by the following partial differential equations
interaction along a 1D domain. The model results support our hypothesis that the
causing localized vegetation loss, on the spatial dynamics of the snail-cordgrass
investigate whether the proposed interactions can produce fronts
in our observations.

A concentration.

The model assumes logistic growth for Spartina, multiplied by a term
(P+AB)/(P+B) to include the effect edaphic stress on plant growth (S6, S7). The effects of
dedaphic stress $A$ are ameliorated by increased plant standing crop (e.g., by shading the
soil, reducing salinity, and increasing oxygen penetration into the soil via the roots),
which is supported by a number of experimental studies in U.S. salt marshes (S8). When
$P$ is close to zero, the term reduces to $A$, and hence growth is reduced by this factor,
reflecting the direct effect of salt stress on plant growth. If $P$ is high, the term reduces to
1, and there is no effect of edaphic stress on plant growth due to the ameliorating effects
of plant biomass on edaphic stress. If $A < 0$, plant growth on bare soil is negative, and
plant establishment is precluded by edaphic stress. When $A > 0$, plant growth is positive,
and does not limit establishment. Snail movement is assumed to consist of a directional
component (i.e., always towards healthy grass and off of mudflats), dependent on local
gradient of plant standing crop $\partial P/\partial x$ (taxis), and a random component that is modelled
by a diffusion approximation to simulate movement of snails away from high conspecific
concentrations. We furthermore do not explicitly include the indirect effects of fungal-
farming by snails. Rather, we include snail-damaging effects directly using saturating
relation between snail damage and plant standing crop.

We obtained parameter values from the result of our experiments and personal
observations. The parameter values used for the model analysis were: $R=0.1, K=4000,$
$A=-0.3, B=1333, C=0.1, F=8000, E=0.1, D=0.001, V=4*10^{-10},$ and $W=2*10^{-7}.$ An
estimate of $R$ was found in literature (S9). $K$ was based on the maximal Spartina biomass
found in our experiments (S10). The value of $C$ was derived from the observation that it
takes 1000 snail approximately two-three weeks to empty a 2000 g/m$^2$ stand of Spartina
(B. Silliman, personal observation). The value of $D$ was based on an estimated snail life
span of in between 1 and 5 years ($D = 0.1$ percent per day corresponds to a life span of
about 3 years). The remaining parameter values were common-sense estimates. Note that
our model does not aim to produce accurate predictions of front dynamics, as our model
leaves out many aspects determining snail-Spartina dynamics. We solely aim to
investigate whether the proposed interactions can produce fronts per se.

Model dynamics. We used the model to study the effect of physical disturbance,
causin localized vegetation loss, on the spatial dynamics of the snail-cordgrass
interaction along a 1D domain. The model results support our hypothesis that the

\[
\frac{\partial P}{\partial T} = RP\left(1 - \frac{P}{K}\right)\left(\frac{P + AB}{P + B}\right) - C \frac{P}{P + F} S,
\]

\[
\frac{\partial S}{\partial T} = \left(EC - \frac{P}{P + F} - D\right) S - \frac{\partial VS}{\partial X} S + W \frac{\partial^2 S}{\partial X^2}.
\]

Here $P$ is Spartina standing crop (g m$^{-2}$), $S$ is snail density (individuals m$^{-2}$), $R$ is the
intrinsic growth rate of Spartina (d$^{-1}$), $K$ is the maximum standing crop of Spartina (g m$^{-2}$), $A$ is the proportional reduction in Spartina growth in bare environments, $B$ is the
standing crop where environmental stress is reduced by half (g m$^{-2}$), $C$ is the maximal
damaging effect of a snail on Spartina (d$^{-1}$), $F$ is the saturation constant for snail grazing
(g m$^{-2}$), $E$ is the relation between grazing damage and snail growth, $D$ is the mortality rate
of the snails (d$^{-1}$), $V$ is the taxis constant (m$^4$g$^{-1}$d$^{-1}$), and $W$ is the diffusion constant of
snails (m$^2$ d$^{-1}$).
interaction between stress induced die-off and directional consumer movement can induce a persistent, traveling wave of consumers (Fig S1A). At the start of the simulation, both snails and cordgrass are at a temporal equilibrium. At t = 0, we decreased Spartina biomass to zero at the left end of the simulated domain, creating a steep gradient of standing crop, to simulate localized dieback due to drought conditions (Fig S1A). Subsequent model simulation predicts a front of high snail density to form at the edge of the die-off area. This front in turn induces further marsh degradation, invoking a spatial feedback between movement of snail front and loss of vegetation at the disturbance edge (Fig S1A). Whether this front persists in time depends critically on the density of snails in the undisturbed vegetation, as the front only continues to perpetuate through the vegetation if snail density in the matrix vegetation is sufficiently high to fuel further perpetuation as snails are naturally lost from the front due to migration away from high conspecific densities.

Front formation depends critically on the interaction of local feedback processes and directional movement by snails towards dense vegetation. A non-spatial version of this model behaves qualitatively similar to the classical predator-prey model of Rosenzweig (S11) if $A > 0$. If $A < 0$, two attractors may occur, a boundary equilibrium at $P, S = 0, 0$ and an internal equilibrium. A non-spatial model that is structurally similar to the one described in this paper, including the effects of deteriorating growth conditions in bare soils, is analyzed in Van de Koppel and Rietkerk (S12). We also analyzed a version of the above model which only includes random snail movements (e.g., only a diffusion term). This model does not exhibit front formation.

**Sensitivity analysis.** Our empirical results point to two forces that have the potential to strongly affect health of southeast U.S. marshes: elevated soil salinity, caused by extended periods of drought, and decreased snail mortality rates, possibly resulting from recent declines of blue crabs (40-85% - 29), a major predator of Littoraria (S10). To investigate how system dynamics may be affected by these changes, we analyzed the model’s sensitivity to changes in stress-induced growth reduction and consumer mortality rate. To focus on those parameters that are critical in determining models behaviour, we derived a non-dimensional version of the model:

$$\frac{∂p}{∂t} = p\left(1 - p\right)\left(\frac{p + ab}{p + b}\right) - \frac{p}{p + f} s,$$

$$\frac{∂s}{∂t} = \left(e \frac{p}{p + f} - d\right) s - \frac{∂vs}{∂x} \frac{∂p}{∂x} + \frac{∂^2 s}{∂x^2}.$$  

Here $p = P/K$, $s = S \cdot C/K/R$, $t = R \cdot T$, $x = \sqrt{(C/K \cdot W) \cdot X}$, $a = A$, $b = B/K$, $f = F/K$, $e = E \cdot C/K$, $d = D/R$, $v = V/W \cdot K$. Hence, the model has six essential parameters, four of which are species characteristics ($b, f, e,$ and $v$), and are not directly under human influence. We analysed the model for its sensitivity to changes in the (standardized) reduction of plant growth by edaphic stress $a$, and the (standardized) mortality rate of the snails $d$, as these parameters have the potential to be affected by climate change and food web manipulation. The analysis revealed that the $a-d$ parameter plane of edaphic stress and background snail density is divided into three zones (Fig. S1C). When background snail density is low (e.g., at high snail mortality levels), a localized disturbance only induces local collapse of vegetation, and snail fronts quickly dissipate, as observed in LA
marshes (Fig. 3). At intermediate snail densities (the grey zone in figure S1C), the disturbance invokes a sustained moving front of snails that perpetuates through the landscape, leading to protracted travelling consumer waves and vegetation loss, similar to that seen in GA (Fig. 3). When snail densities are increased even further (at near zero mortality rates), the extreme grazing intensity leads to collapse of vegetation due to overgrazing, even in the absence of edaphic stress, a scenario not yet demonstrated in the field.

This analysis reveals strong interactive effects between increasing edaphic stress, due to heightened climatic extremes, and increased snail densities, through lowered mortality. Both edaphic stress and snail mortality can be decreased quite significantly in isolation before overgrazing and vegetation die-off occurs (figure S1B, arrows A&B). If, however, both environmental stress and background snail densities are increased (e.g., low plant growth in bare soil and low snail mortality), the system enters a region in parameter space where local, small scale disturbances lead to emergence of traveling waves of snails, radiating away from the initial disturbance, and resulting in die-off of vegetation at extensive scales (figure S1B, arrow C). Together, these results underline the importance of the interactive effects of increasing environmental extremes and changes in food web structure in determining the potential for runaway vegetation loss in the snail-cordgrass system.
Figure S1. (A) Temporal development of the spatial snail-cordgrass system, following a disturbance from equilibrium conditions at $t = 0$, on the left side of the Figure (cordgrass: solid grey line, snails: dashed grey line). The system responds to the disturbance by forming a snail front (solid line), which perpetuates through the simulated domain. (B) Parameter space depicting the qualitative dynamics of the snail-cordgrass system as a function of snail mortality rate $d$ and stress-induced reduction of growth $a$. In the right region, disturbances do not generate persistent fronts. In the left region, the grazing system is unstable, and the snails will overgraze the cordgrass vegetation. In the grey region in between, snail fronts are formed. Note that the region exhibiting snail fronts increases in size as the edaphic environment becomes more stressful.
Snail Mortality

Growth reduction factor $a = -0.3, -0.2, -0.1, 0.0, 0.1, 0.2, 0.3$

Distance (m) 0 5 10 15 20 25

Snail density (#/m$^2$) 0 500 1000 1500 2000 2500 3000

Plant standing crop (%) 0 1000 2000 3000 4000 5000

A: Snail front formation

B: Bifurcation analysis

Increasing edaphic stress

Increasing snail densities
References