

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

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Salt marshes in the southeastern United States have recently experienced massive die-off, one of many examples of widespread degradation in marine and coastal ecosystems. Although intense drought is thought to be the primary cause of this die-off, we found snail grazing to be a major contributing factor. Survey of marsh die-off areas in three states revealed high-density fronts of snails on die-off edges at 11 of 12 sites. Exclusion experiments demonstrated that snails actively converted marshes to exposed mudflats. Salt addition and comparative field studies suggest that drought-induced stress and grazers acted synergistically and to varying degrees to cause initial plant death. After these disturbances, snail fronts formed on die-off edges and subsequently propagated through healthy marsh, leading to cascading vegetation loss. These results, combined with model analyses, reveal strong interactions between increasing climatic stress and grazer pressure, both potentially related to human environmental impacts, which amplify the likelihood and intensity of runaway collapse in these coastal systems.

Degradation of coastal ecosystems is occurring worldwide (1). Large-scale eutrophication, food web alteration, runaway consumer effects, climate change, habitat destruction, and disease have all been implicated as causes of extensive loss of key coastal ecosystems including kelp forests, mangroves, oyster reefs, seagrass beds, and coral reefs (2–7). These threats rarely occur in isolation from one another, and the realized damage we observe may well be exaggerated by synergistic interactions (as opposed to simply additive stress). Failure to understand these synergies will lead to further loss of important ecosystem services including shoreline buffering, nutrient and sediment filtering, and critical nursery and adult habitat for fisheries and shorebirds (1). Because near-shore communities generate >\$150 billion in benefits per year through the tourism, aquaculture, and fishery industries, elucidating the complex causes of marine ecosystem degradation is one of the most pressing ecological issues of our times (1).

Over the past 6 years, salt marshes along the southeastern and gulf coasts of the United States experienced unprecedented die-off, with affected areas ranging in size from 100 m² to 3 km², totaling >250,000 acres, and oc-

curing along >1500 km of coastline (8–11). These systems are the most ecologically and economically important shoreline communities along the eastern and gulf U.S. seaboard (12). The key to protecting these critical habitats is to understand the factors that affect marsh community structure and how those factors may be changing. For nearly 60 years, the paradigm of salt marsh ecology has been that bottom-up factors (e.g., nutrients, soil salinity) are the primary forces controlling growth of the dominant habitat-forming plant in the community, *Spartina alterniflora* (cordgrass) (12). Accordingly, investigations of die-off of

this grass have focused on the role of physical stressors such as salinity and soil moisture-related factors (8–11).

Recent experimental evidence, however, has shown that grazing is also important in regulating grass production (13–16). Manipulation of the most abundant marsh grazer, the periwinkle snail (*Littoraria irrorata*), revealed these gastropod consumers damage live *Spartina* when grazing their fungal food (14, 15). Subsequent facilitation of fungal infection in leaf tissue via snail radular activity leads to drastic reductions in aboveground plant production (16) and, at high densities, grazing by fungal-farming snails destroys the marsh canopy (15). Although both edaphic (i.e., soil-related) stresses and grazing can potentially harm salt marsh vegetation, there is currently no consensus on the relative importance of these factors in explaining marsh dieback. Extreme physical stressors [e.g., decreased soil moisture, elevated salinities in marsh soils and estuarine waters, increased soil acidity; see Table 1 (8–11, 17)] generated by a severe drought from ~1999 to 2001 in the southern United States [Table 1, recurrence interval ~100 years (17)] and biotic interactions with fungal pathogens [*Fusarium* spp. (11)] have been considered as plausible causal factors (8–11). However, no studies have examined experimentally the role of grazers in either contributing to or expanding initial dieback areas.

To examine the extent and intensity of grazer impacts at marsh die-off sites, we quantified snail abundance at 12 randomly chosen die-off sites that spanned 1200 km of shoreline and experimentally investigated the relative contribution of these consumers to marsh loss at two sites in Georgia and two in Louisiana

Table 1. Rainfall levels, Palmer Drought Severity Index (PDSI) values, and salinities in Sapelo Island, Georgia (for Airport Marsh and Marsh Landing Creek) and Louisiana coastal marsh ecosystems during the peak of a 100-year drought (~1999 to 2001) event that immediately preceded marsh die-off in both states. For Georgia, drought rainfall data are for 2000 and 2001 and for predrought years from 1958 to 1999. The PDSI, which is a meteorological drought index based on precipitation, temperature, and available water content of the soil, ranges from 4.0 or more for extremely wet conditions to -4.0 or less for extreme drought and covered the same time periods as for rainfall. For salinities, data are averages of monthly (soil salinity) and daily (estuarine salinity) measurements taken at the same location on Sapelo Island, Georgia, from June to September in 2000 and 2001 and for nondrought years from June to September in 2003 and 2004 (mean 2003–2004 rainfall = 134.4 cm). For Louisiana, drought rainfall is for 1999 and 2000 and for predrought years from 1950 to 1998. The PDSI is provided for the same time periods as for rainfall. Estuarine salinities before the drought were for the period from 1961 to 1998; drought estuarine salinities were for 1999 and 2000. For Louisiana, data are averages of monthly means. Data are means ± SD.

Drought indicator	Georgia		Louisiana*	
	Drought	Predrought/ nondrought	Drought	Predrought
Yearly rainfall (cm)	93 ± 7.5	131 ± 21	102 ± 76	132 ± 74
PDSI	-2.71 ± 0.57	0.18 ± 1.56	-2.85 ± 1.27†	0.11 ± 2.02†
Estuarine salinities (ppt)	30.5 ± 1.41	20.8 ± 3.54	25.5 ± 0.6	20.6 ± 5.6
Marsh soil salinities (ppt)	48.6 ± 4.27	27.3 ± 2.58	†	†

*Data modified from (22). †Grand Terre, LA. Although interstitial salinities before and after the drought are not available for Louisiana, interstitial salinities collected in June 2000 at a dieback site at Bay Junon ranged from 27 to 32 ppt; salinity was 23 ppt in an adjacent nondieback site (8).

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Table 2. Snail densities (individuals/m²) at 12 marsh die-off sites in the southeastern United States. In the summer of 2002, at each site, 10 quadrats (50 cm by 50 cm) were randomly placed (i) along the two types of die-off border (i.e., the exposed mudflat-healthy marsh interface) typically

encountered at each site—that is, borders with high snail densities and those with low densities; (ii) on exposed mudflats; and (iii) in adjacent healthy marsh areas. Lengths of high-density snail fronts are in parentheses. Data are means ± SD.

Site	Snail density			
	Exposed mudflat	Die-off border with low snail density	Die-off border with high snail density	Healthy marsh
Bourbon Field Marsh, Sapelo Island, GA	0	223 ± 96	1076 ± 243 (98 m)	176 ± 59
Airport Marsh, Sapelo Island, GA	0	564 ± 132	2175 ± 675 (68 m)	487 ± 92
Dean Creek, Sapelo Island, GA	1.2 ± 2.3	48 ± 26	416 ± 45 (24 m)	185 ± 67
Lighthouse Marsh, Sapelo Island, GA	0	834 ± 112	2634 ± 456 (128 m)	558 ± 121
South Marsh, Ossabaw Island, GA	0	114 ± 43	457 ± 167 (32 m)	78 ± 17
Jerico River, Bryan County, GA	0	3 ± 3	15 ± 9	1.4 ± 0.8
South Marsh, Talahi Island, GA	0	128 ± 87	412 ± 254 (14 m)	68 ± 11
Exp. Site 1, Fort Fourchon, LA	0	67 ± 32	1356 ± 387 (212 m)	82.2 ± 12.6
Exp. Site 2, Fort Fourchon, LA	0.2 ± 0.1	45 ± 29	1067 ± 365 (185 m)	68.4 ± 14.6
Watch Tower Marsh, Bell Buruch, SC	0	38 ± 16	225 ± 112 (13 m)	49 ± 15
Inlet Marsh, Bell Buruch, SC	0	63 ± 31	315 ± 96 (13 m)	56 ± 17
Charleston, SC	0	32 ± 18	402 ± 167 (22 m)	96 ± 37

(17). An initial survey of dieback sites revealed extreme densities of plant-grazing snails, commonly 500 to 2000 individuals/m², aggregated in extensive fronts on die-off borders. Snail density was near zero on exposed mudflats, peaked on the die-off/healthy marsh border, and dropped off considerably within healthy marsh (Table 2).

To test the hypothesis that *Littoraria* grazing expands marsh dieback areas, we placed 1-m by 1-m wire-mesh enclosures in July 2002 (i) just ahead of fronts of snails on die-off borders, and (ii) in remnant *Spartina* patches inside die-off areas. We monitored the effects of snail removal on cordgrass biomass and soil physical conditions for ~14 months until September 2003 (17). We also examined the effects of snail density on expansion of die-off border and quantified the total vegetated area cleared by moving consumer fronts (17). Finally, to examine the relationship between both consumer front persistence and propagation and snail density in adjacent healthy areas, we set up permanent 50-cm by 50-cm plots along line transects running perpendicular to die-off borders (–5 m, inside die-off area on exposed mudflats; 0 m, on border; 5 m, within healthy areas; 10 m; and 20 m) and monitored snail densities and *Spartina* biomass in those plots over a 1-year period starting in July 2002 (17).

Recent studies have suggested that top-down control by fungal-farming snails intensifies when *Spartina* is either stressed or receives nutrient enhancement, because facilitated, facultative pathogenic fungi growing in grazer wounds on live leaves experience enhanced growth (14–16). To test whether sublethal drought stress observed in marsh soils and estuarine waters throughout the Southeast (8–11, 17) (Table 1) could have acted together with grazing to generate initial die-off areas, we experimentally elevated salt con-

centrations in marsh soils with and without snails at one healthy marsh site in Georgia (434 ± 54 snails/m²) from March to October 2002 (17).

Experimental manipulation of *Littoraria* on high-density borders and in remnant *Spartina* patches supports our hypothesis that snail grazing contributes to expanding dieback in southern U.S. salt marshes (Fig. 1). In both Georgia and Louisiana marshes, snail removal increased *Spartina* biomass by more than three orders of magnitude, whereas continued snail access to *Spartina* in control plots resulted in heavy overgrazing, destruction of marsh canopy, and conversion of healthy salt marsh cordgrass to exposed mudflat both along die-off borders and on edges of remnant *Spartina* patches (Figs. 1 and 2). The primary mechanism by which snails killed *Spartina* was likely through facilitation of pathogenic fungi during farming activities—an indirect pathway of control, as has been shown in past studies (14, 16)—and not through consumption of live plant material. In all plots, there was no evidence that physical stress negatively affected *Spartina* health (17), as caged, isolated patches of cordgrass on mudflats (Fig. 2) were dense, robust, and green in the absence of intense snail grazing. This observation of minimal soil stress during our caging study (July 2002 to July 2003) is consistent with the cessation of drought conditions in Georgia and Louisiana marshes in 2002 (Table 1). Combined with results from snail exclusion experiments (Fig. 1), these findings imply that runaway consumption can carry on the process of vegetation loss in the absence of drought-induced effects.

After moving through control plots, snail fronts maintained structure and continued to eliminate healthy marsh (Fig. 1). As concentrated waves of consumers passed over vegetated areas, *Spartina* grass disappeared and

exposed mudflats remained (Figs. 2 and 3). How far and how long these fronts propagated, however, was strongly dependent on snail density both in the front itself and at the experimental sites before die-off (17). When snail density in consumer fronts was high (>1000 individuals/m²), front propagation from initially marked areas through healthy marsh was extensive, reaching a maximum of 14 m in Louisiana and 31 m in Georgia, whereas at lower densities (100 to 400 individuals/m²) front effects were significantly diminished (Fig. 1). From a temporal perspective, when snail densities before marsh die-off and outside of fronts were low, as in Louisiana (78 ± 33 individuals/m²), snail fronts broke up in <8 months. In contrast, at Georgia sites, where snail densities outside of fronts and before die-off were high (485 ± 124 individuals/m²), front propagation lasted >1 year (Fig. 3). The tendency for consumer fronts to break up and for snails to spread out likely occurs because *Littoraria* experience intense intraspecific competition at high densities (14–16).

The total extent of marsh destroyed by snails (17) tracked background snail density and front persistence. Snail grazing in two Louisiana marshes resulted in relatively small but significant expansion of die-off areas (an 11% increase, from 22,980 m² to 25,320 m²). In Georgia, long-lived snail fronts converted extensive marsh habitat into exposed mudflat, increasing original die-off areas by at least 185% (from 2230 m² to 6456 m²; because snail fronts were already formed when we arrived, total impact estimates are underestimations). Thus, when grazer density is high, marsh systems become more susceptible to runaway grazing, and top-down forces can be responsible for significantly larger proportions of marsh die-off. Our survey of 12 marshes in the southeastern United

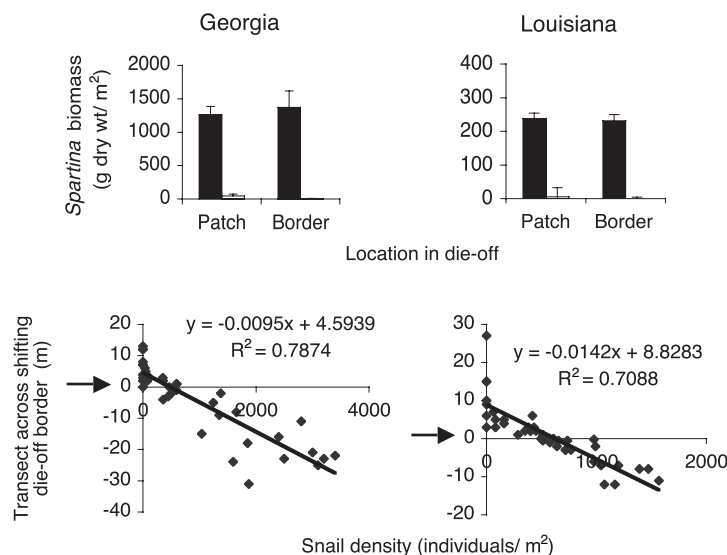


Fig. 1. Effects of snail exclusions on *Spartina* biomass in interior (i.e., remnant patches of live cordgrass) and on border of marsh die-off sites in Georgia (left) and Louisiana (right), and least squares linear regression of mean *Littoraria* density on 5-m sections of die-off border and net movement of that border over 1 year in Georgia and Louisiana ($n = 39$ for Georgia, $n = 44$ for Louisiana). In the lower panels, 0 m on the line of the abscissa indicates original position of die-off border and is denoted by a horizontal arrow; negative numbers close to the current 0-m position indicate further marsh loss and expansion of mudflats, whereas positive numbers indicate community recovery and grass growth into die-off areas. For the caging experiment, data for each state were separately analyzed using a two-way (treatment \times site) analysis of variance (ANOVA). Data either exhibited homogeneity of variance and were normally distributed or were transformed using log transformations for assumption conformity. Only linear contrasts were compared, using Tukey's post hoc test. Because we found no significant effect of site ($P > 0.43$, both cases), data from replicate sites were pooled. Solid bars (left) indicate snail exclusion treatments; open bars (right) indicate uncaged controls. Error bars indicate SE.

States (Table 2) revealed snail fronts at 11 of 12 die-off areas, which suggests that consumer wave propagation was an important, yet overlooked (8–11), contributing factor to the expansion of dieback throughout the Southeast.

Reconstruction of snail densities before marsh die-off and severe drought conditions from 1999 to 2001 (Table 1) (8–11) indicate that snail grazing alone did not initiate marsh die-off in Louisiana or Georgia. In Louisiana, snail densities [78 individuals/m² (14, 15)] were well below levels needed to completely denude vegetated marsh under nonstressful conditions, and all evidence to date points to drought-induced soil moisture stress and related edaphic factors (e.g., salinity, acidification, and metal toxicity) as the primary initiating factors (Table 1) (8–11, 17). However, only nonlethal physical conditions were observed in the field, both during die-off events in Louisiana and Georgia (Table 1) and afterward (8–11). These data suggest that less intense, sublethal drought stress interacting with snail grazing could also have caused or contributed to initial marsh die-off in some instances. In Georgia, die-off occurred extensively at many locations with low snail density (Jerico River marsh, Table 2) (9, 10), but at many sites in Georgia snail densities were high enough (100 to 600 individuals/m², Table 2) to strongly suppress *Spartina* growth (14, 15) and potentially

interact synergistically with drought-induced stress.

Our experimental simulation of drought-induced salt stress supports this prediction and reveals that elevated salinities intensify top-down control by snails. Experimentally increasing dissolved salt concentrations in the soil to approximate drought conditions [from 35.33 ± 2.63 parts per thousand (ppt) to 56.83 ± 6.24 ppt; see Table 1 for comparisons] in the absence of snails reduced grass growth by 45%, whereas in the presence of snails, high salt levels had a significantly greater negative effect (84% biomass reduction), resulting in near-complete mortality of *Spartina* (17). Thus, although drought stress was likely the overwhelming cause of initial die-off when snail densities were low [most Louisiana marshes; Table 2 (8–11)], our experimental results and surveys indicate that climate-induced stress and consumer pressure acted together at many other sites (i.e., in marshes with high snail density in Georgia) to generate original die-off disturbances.

On the basis of this analysis and our experimental results, we hypothesize that extensive die-off in southern marshes was caused by the following sequence of interacting events: (i) Protracted and intense drought (3 to 4 years) resulted in stressful soil conditions, which acted either alone or in combination with plant-grazing snails to cause rapid community

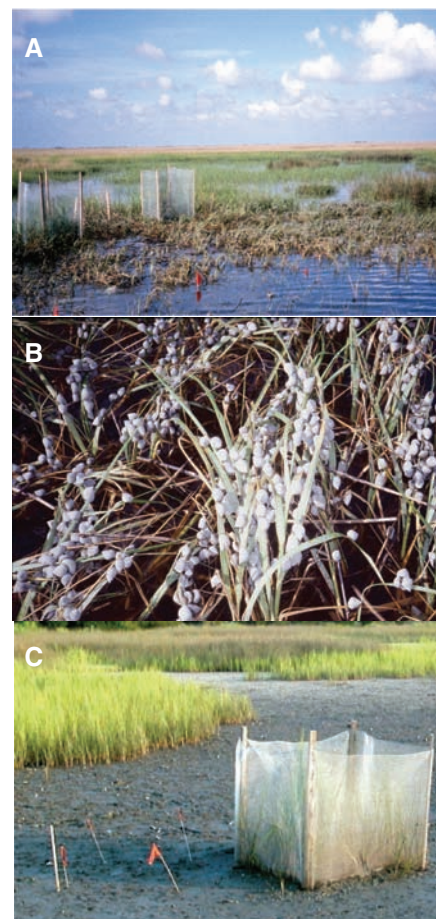


Fig. 2. (A) Snail front enclosures (wrapped in hardware cloth) installed on die-off border at one site in Louisiana. Gray area in front of cages is a snail front. (B) Representative extreme snail densities found in snail front pictured in (A). (C) Effect of exclusion cage on *S. alterniflora* biomass on die-off border at the Lighthouse Marsh in Georgia.

die-off in well-defined, distinct areas. (ii) After these areas were denuded by grazers and natural processes, predictable, behaviorally driven snail movement toward live *Spartina* (17) led to snails concentrating on die-off borders, forming consumer fronts. (iii) Run-away grazing and density-dependent propagation of snail fronts, which persisted >1 year after drought impacts subsided, carried on the process of vegetation loss to expand the total area of marsh degradation. After drought stress subsided in 2002, some die-off areas began to recover in 2003 via vegetative growth from adjacent healthy marsh (17), but only along borders without snail fronts (Fig. 1). To date, most die-off areas have yet to fully recover (17), but the trend for marsh plants to recolonize exposed mudflats and for consumer fronts to break up shows that vegetation loss in this system is not unidirectional for the observed levels of grazer density and drought-induced stress.

We developed a spatially explicit model that supports our experimental findings, indi-

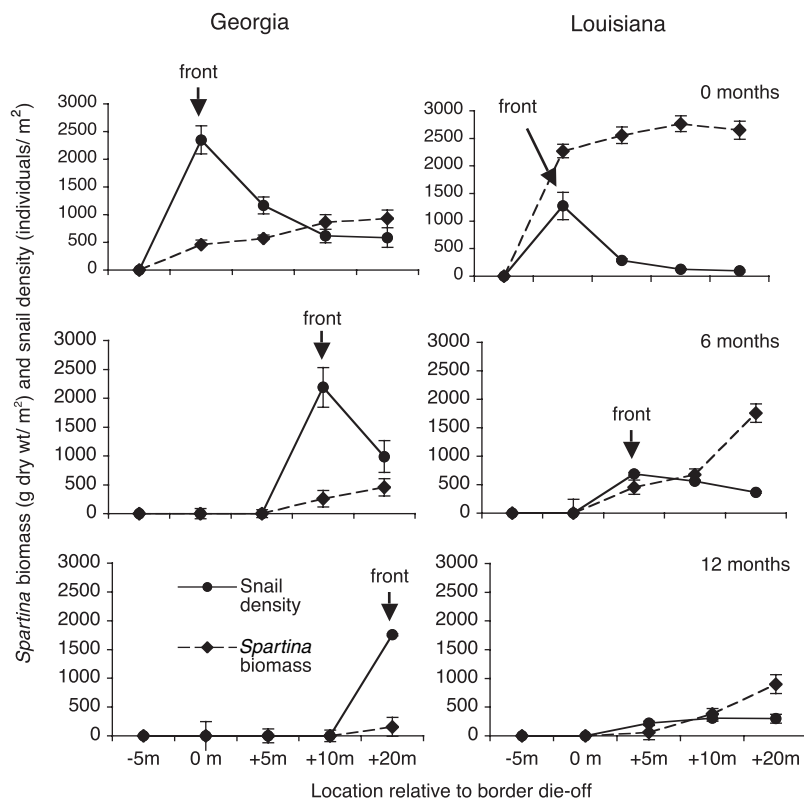


Fig. 3. Change in *Littoraria* density and *Spartina* biomass over 6 to 12 months on die-off mudflat (–5 m), original border at time zero (0 m), and 5, 10, and 20 m into live marsh at two die-off sites in Georgia (left) and Louisiana (right). For each distance at each site, $n = 5$. In Georgia and Louisiana, readings were taken at time zero (July 2002), ~6 months later, and after ~1 year. Differences in snail density and *Spartina* biomass were assessed separately for each state and date using a two-way (distance \times site) ANOVA. We did not use repeated-measures analysis or Bonferroni adjustments because we had a priori hypotheses about each date (i.e., snail fronts would be moving toward grass, dissipating and mowing down *Spartina*). Because there was no site effect ($P > 0.16$), we pooled data from replicate sites for one analysis per state per date. For snail densities, there was a significant effect of distance in all cases ($P < 0.02$). For *Spartina* biomass, there was a significant effect of distance at time zero and after 6 and 12 months in Louisiana ($P < 0.04$) and for time zero and after 6 months in Georgia ($P < 0.001$).

ating that (i) the interaction of drought stress, grazing, and directional snail movements can lead to formation of traveling consumer waves (17) (fig. S1A), and (ii) consumer fronts form only when both edaphic stress and snail densities are high, but not when either of these factors occurs in isolation (fig. S1B). In addition, model analyses point to the multiplicative effects of two forces that have the potential to strongly affect the health of southeastern U.S. marshes: (i) increased incidence of intense drought, caused by increasing climatic extremes [see discussion in (8)], and (ii) decreased snail mortality rates, which have the potential to occur as a result of recent population declines in blue crabs [40 to 85% (18)], a major predator of *Littoraria* (15). Occurring simultaneously, these factors could act synergistically to increase system susceptibility to even more intense and prolonged vegetation loss and, potentially, unidirectional large-scale collapse. Increased drought stress lowers the threshold grazer density needed to generate consumer fronts and runaway con-

sumption of *Spartina*, as we have shown, while decreased snail predation may allow that critical threshold to be crossed even faster. Although decreased predation by blue crabs could lead to lowered snail mortality rates, more study is required to clarify the sources of snail predation and human influence on top-down control in this system.

Our experimental results provide definitive field evidence that the interplay between physicochemical stressors and trophic interactions plays an important role in die-off of coastal salt marshes in the southern United States. Drought-induced soil stress can amplify top-down control by grazers and initiate marsh plant die-off in localized intertidal areas. These disturbances then stimulate the formation of consumer fronts, leading to waves of salt marsh destruction resulting from runaway consumption. These findings stress that interactions between food web dynamics and climate must be considered when investigating community collapse in coastal systems. Despite similar observations of consumer fronts leading to habitat

collapse in kelp beds [sea urchins (2)], arctic salt marshes [snow geese (19)], and coral reefs [sea stars (20)]—all initially in response to human alteration of food web structure or nutrient regimes [but see (21) for evidence of emerging climatic feedbacks in arctic marshes]—there is relatively little understanding of how the potential for runaway consumption will interact with climate change–induced weather extremes to affect system stability and persistence. Recognition of the interactive, nonlinear processes by which such effects are manifested is paramount for successful management of ecosystems that face anthropogenic impacts through multiple stressors.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/310/5755/1803/DC1

Materials and Methods

Fig. S1

References

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