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TITLE: The perfect storm: Extreme weather drives and predation maintains phase shift in dominant Chesapeake Bay bivalve

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RUNNING PAGE HEAD: Storm-driven phase shift

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SUMMARY

Extreme weather events are expected to increase in frequency, duration, and severity due to anthropogenic climate change, and they have been implicated in ecosystem phase shifts in terrestrial and marine systems[1,2]. As these events become more severe, it is critical to understand how they alter ecosystems. Tropical Storm Agnes in 1972 was a “100-year storm” that lowered salinity and increased sedimentation throughout Chesapeake Bay[3,4], and was suspected of altering long-term ecosystem dynamics[5]. Here we show that Tropical Storm Agnes resulted in a phase shift to a low-density state for the soft-shell clam *Mya arenaria*, which was once a biomass dominant in Chesapeake Bay. The storm caused massive mortality of bivalves, including *M. arenaria*[6]. This storm also altered predator-prey dynamics between *M. arenaria* and the blue crab *Callinectes sapidus*, shifting from a system controlled from the bottom-up by prey resources, to a system controlled from the top-down by predation pressure on bivalves. Predation by *C. sapidus* is sufficient to maintain the low-density steady state where *M. arenaria* densities hover 40 y later. Two species may exhibit nonlinear dynamics that result in phase shifts[2], and extreme weather events may serve as a natural pulse stressor, triggering the phase shift[7]. Considering the increasing frequency of stochastic storm events[8] and the preponderance of multispecies interactions exhibiting nonlinear dynamics, phase shifts are likely to become more common in the future. Hence, identification of species that are most at risk to shifts in state under extreme climate events should be a priority for marine ecosystem conservation.

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TEXT

Extreme weather events are costly, and are likely to become even more common with predicted increases in the intensity and frequency of extreme events due to anthropogenic climate change[8]. In the U.S. alone, there were 30 climate disasters exceeding $1 billion U.S.D. between January 2016 and October 2017, including hurricanes Harvey, Irma, and Maria which impacted the southeastern U.S. and Caribbean territories in the summer of 2017[9]. When examining the cost of extreme weather, ecological impacts are rarely considered, even though the impacts of such events on the ecosystem may be severe[10]. Traditionally, the impacts of these ecosystem changes have been hard to quantify, though when quantified they illustrate the value of ecosystem services for humanity[11].

Understanding the impacts of extreme climate events on ecosystems is essential to make predictions for the future, and to prevent unwanted ecological surprises[1]. Biotic interactions such as predator-prey dynamics contain nonlinearities that result in complex and often unpredictable ecosystem responses[2]. Shifts in predator-prey interactions may occur due to differences between predators and prey in their tolerance to stressors[12]. When strong or frequent extreme weather events occur, they may cause mass mortality of one or a few species with low resistance or resilience[13]. Such declines in abundance of one or a few species may lead to an alternative stable state[7,14]. Multiple stable states occur when the relative abundances of species within a community are altered and persist under the same environmental conditions; this change in abundance occurs due to a perturbation, but persists after the perturbation ends[2].

Tropical Storm Agnes, which reached and remained in the Chesapeake Bay watershed 21-23 June 1972, has long been suspected of resulting in long-term changes for the Bay[5].

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Tropical Storm Agnes was a “100-year storm” that caused sustained, extremely low salinities (Figure 1) and increased sedimentation throughout Chesapeake Bay[3,4]. This storm has been blamed for the loss of seagrass in certain areas of Chesapeake Bay[5], high mortality rates and recruitment failure in oysters *Crassostrea virginica*[15], and declines in abundance of the soft-shell clam *Mya arenaria*, which suffered a mass mortality after the storm[6].

Mya arenaria was abundant enough to support a major commercial fishery throughout Chesapeake Bay prior to 1972[16]. When the population declined abruptly after Tropical Storm Agnes, the fishery never recovered in lower Chesapeake Bay (Virginia) [17]. Attempts to revive a commercial fishery in Virginia waters were never realized after the storm’s passage. The commercial fishery for soft-shell clams in the Maryland portion of the Bay is characterized by variable and low harvest[18]; the fishery declined by 89% after the storm and has been near collapse since[19].

The failure of *M. arenaria* to recover from storm-related declines has been attributed to predation, habitat loss, disease, rising temperatures, and overfishing[17]. The Virginia and Maryland portions of Chesapeake Bay have different habitats, disease dynamics, climates, and fishing pressure; therefore, these factors are unlikely to explain the inability of *M. arenaria* to recover from low density in both regions[17,18]. More recently, disease has been blamed for an added minor decline in *M. arenaria*[18]; however, there is no evidence that disease prevalence or intensity are correlated with *M. arenaria* density[17].

Experimental evidence suggests that on a local scale, interactions between *M. arenaria* and their major predator, the blue crab *Callinectes sapidus*[20], are capable of keeping clams at low densities[21,22]. *Mya arenaria* burrow deeply in sediments, and when clams are at low densities, crabs are unable to detect their presence[21]. The result is a low-density refuge for *M. arenaria*,

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driven by disproportionately low predation, which is characteristic of a type III functional response[21,22]. Given this evidence regarding a potential mechanism for the decline in *M. arenaria* and maintenance of the population at low density, this study examines the effects of Tropical Storm Agnes and predator-prey interactions on basin-scale population dynamics of *M. arenaria*.

We show that Tropical Storm Agnes in 1972 resulted in a phase shift for *M. arenaria*, which was maintained at low abundance likely due to predation by the blue crab *C. sapidus*. An abrupt shift in clam abundance was identified in 1972, the year of Tropical Storm Agnes (Figure 2). Before the storm, crab abundance was positively correlated with clam abundance at a lag of 1 y ($r = 0.66$, $p = 0.01$), indicating that each year, clams were prey for juvenile crabs that recruited to the fishery at one year of age (Figure 3a). After the storm, clam abundance was negatively correlated with crab abundance with a lag of 1 y ($r = -0.48$, $p = 0.04$), indicating that each year, crabs were consuming juvenile clams that would have recruited to the fishery a year later (Figure 3b). This is consistent with a phase shift from a system controlled from the bottom-up by prey resources, to a system controlled from the top-down by predation pressure on bivalves.

Predator-prey modeling confirmed the presence of high-density (at carrying capacity) and low-density (at 1.41 clams m^{-2}) steady states separated by an unstable steady state at 20.93 clams m^{-2} (Figure 4). We propose that *M. arenaria* existed in Chesapeake Bay at high density until perturbed past the unstable steady state in 1972 by Tropical Storm Agnes. Thereafter, it was able to persist at low abundance due to the low-density refuge from blue crab predation[21,22], rather than collapsing to local extinction. Unfortunately, *M. arenaria* is unlikely to rebound to high abundance without a beneficial disturbance, such as a considerable recruitment episode or substantial reduction in predation pressure, which propels it above the unstable steady state (Figure 4) and concurrently allows it to overcome the exacerbated disease burden.

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Predator-prey models with these two species alone was capable of reproducing observations of clam densities and mortality rates, consistent with the idea that blue crabs are a major driver of *M. arenaria* population dynamics [20–22]. The low-density steady state predicted by the predator-prey model is similar to observed densities of *M. arenaria* in Chesapeake Bay. *Mya arenaria* persist in the lower Chesapeake Bay at average densities of 0.4 – 1.73 m^{-2} (95% CI), despite episodes of high recruitment[17]. In the field, juvenile *M. arenaria* exposed to predators suffered 76.3% higher mortality as compared to caged individuals[23]. Predator exclusion treatments confirmed that blue crabs were responsible for most of the mortality of juvenile *M. arenaria*[23], and mortality rates observed in the field were comparable to mortality rates predicted by the model for blue crab density 4.8 m^{-2}, which is a typical density for juvenile crabs in the summer months in Chesapeake Bay[24].

The observations, theory, and mechanistic basis indicate that *M. arenaria* was subjected to a storm-driven phase shift to low abundance, which has been maintained by blue crab predation. As extreme weather events become more common with climate change, it is essential to examine the potential for such perturbations to produce phase shifts that may permanently change basin-scale trophic dynamics. Evidence for storm-driven phase shifts in coral reefs[14], kelp ecosystems[7], and now soft-sediment communities (current study) suggests that management of these ecosystems should include an examination of nonlinear interactions and the potential for phase shifts. Identification of species that are most at risk to shifts in state will help to preserve communities that are sensitive to extreme weather events, minimizing ecological and economic losses.

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METHODS

Changepoint analysis of time series was conducted in R statistical software[25] on *Mya arenaria* landings[26] and adult female *Callinectes sapidus* abundance (VIMS trawl survey) in the Chesapeake Bay from 1955-1994, with an AIC penalty and using the segment neighbor algorithm[27,28]. This time period was chosen for analysis because it begins when *M. arenaria* landings data first became available and ends before the slow decline in landings post-1994 due to fisheries collapse.

Predator-prey ordinary differential equation (ODE) models were modified with a type III functional response:

$$N(t) = rN\left(1 - \frac{N}{K}\right) - f(N)P$$

where N is the density of prey, P is the density of predators, r is the intrinsic per capita growth rate, K is the carrying capacity, and $f(N)$ takes the form of a type III functional response:

$$\text{Type III: } f(N) = \frac{N^2 bT}{1 + cN + bT_h N^2}$$

where T is the time available for foraging, T_h is handling time, and b and c are components of the attack rate in a type III response [29,30].

Models were parameterized using data from the literature as follows: P = 0.06 m^{-2} [31], r = 1.75 y^{-1} [32], K = 200 m^{-2} [33], T = 1 y, T_h = 0.001483 y [21], b = 26.29743 y^{-1} [21], and c = 0.143 [21].

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Models were analyzed for steady states. To examine mortality rates, we solved the equation for number consumed:

$$N_E = N - f(N)\,P$$

where N_E = the number of clams eaten calculated for a period of 8 d (0.02192 y) at an initial density of N = 48 m^{-2} to match the field predation experiments[23]. We then calculated mortality as:

$$M = \frac{N - N_E}{N} * 100\ \%$$

where M = percent mortality. Density of predators P was allowed to vary to achieve M = 76.3% [23], and the resultant predator density that achieved observed mortality rates of juvenile *M. arenaria* was compared to published juvenile blue crab densities for Chesapeake Bay.

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AUTHOR CONTRIBUTIONS

CNG performed the analysis and wrote the manuscript. CNG, RDS, and RNL contributed substantially to study conception and design, interpretation of the data, and manuscript revisions.

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FIGURES

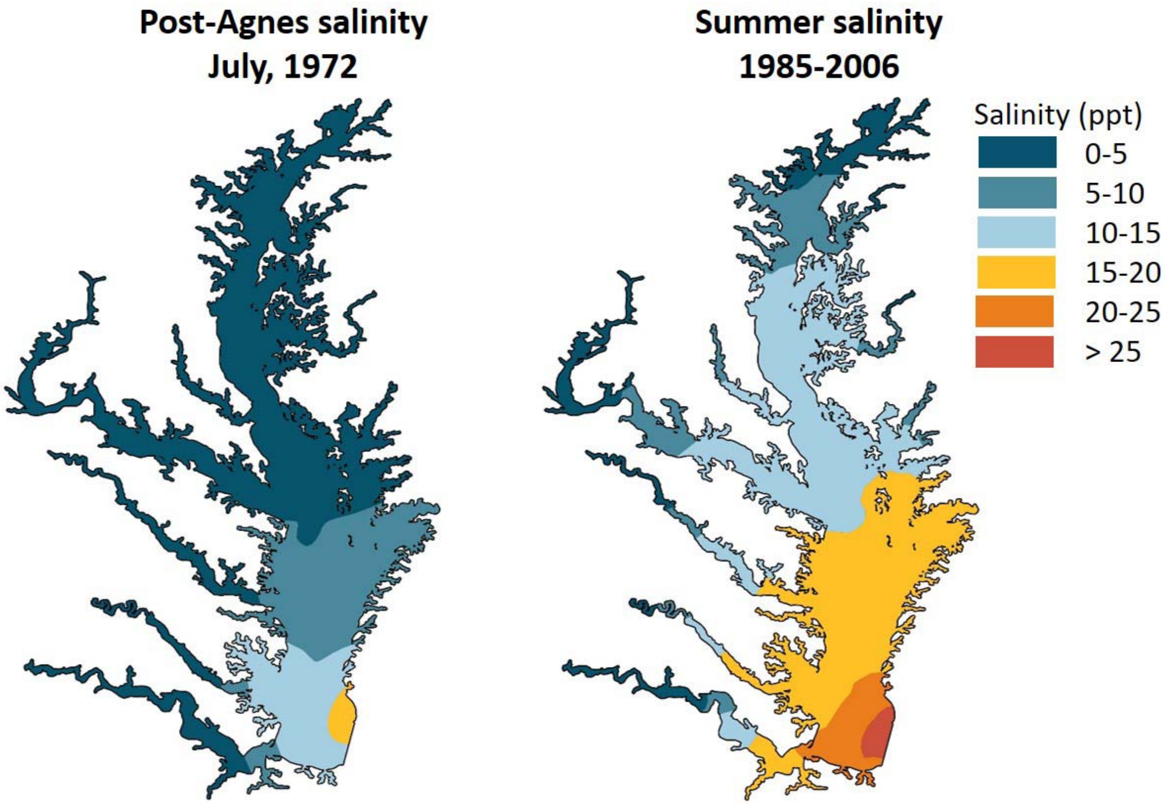

Figure 1. Salinity profiles for post-Agnes (left) and average summer (right) conditions. Post-Agnes salinity was measured over the period June 29 – July 3, 1972 [4]. The summer salinity profile (right) is average surface salinity for 1985-2006 [34].

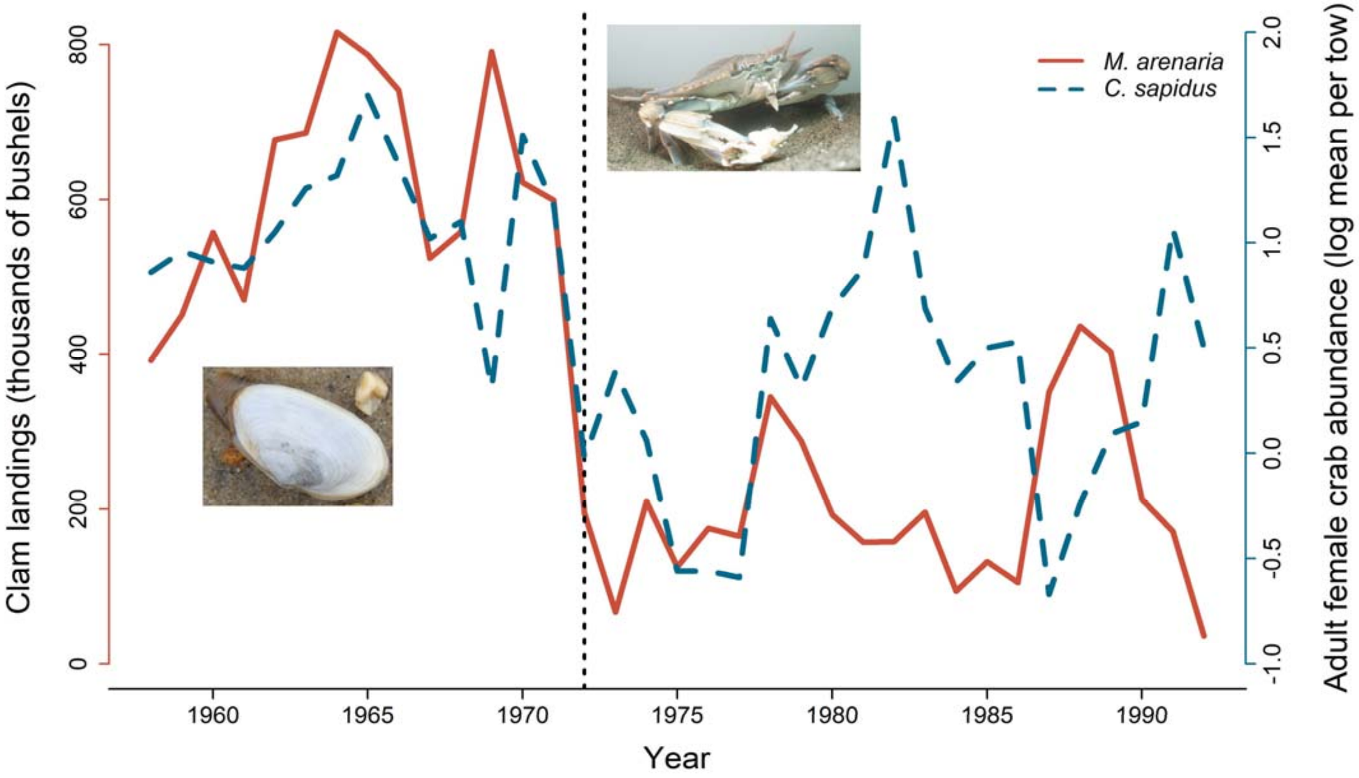

Figure 2. Time series for *Mya arenaria* landings (red) and adult female blue crab (*Callinectes sapidus*) abundance (blue). Blue crab data are log-transformed mean female abundance per tow (VIMS trawl survey). *Mya arenaria* data are fisheries landings (1000 bushels)[19]. Vertical dashed line represents Tropical Storm Agnes (1972), and the location of the changepoint from time series analysis. Photo credits: C.N. Glaspie (clam), R.N. Lipcius (crab).

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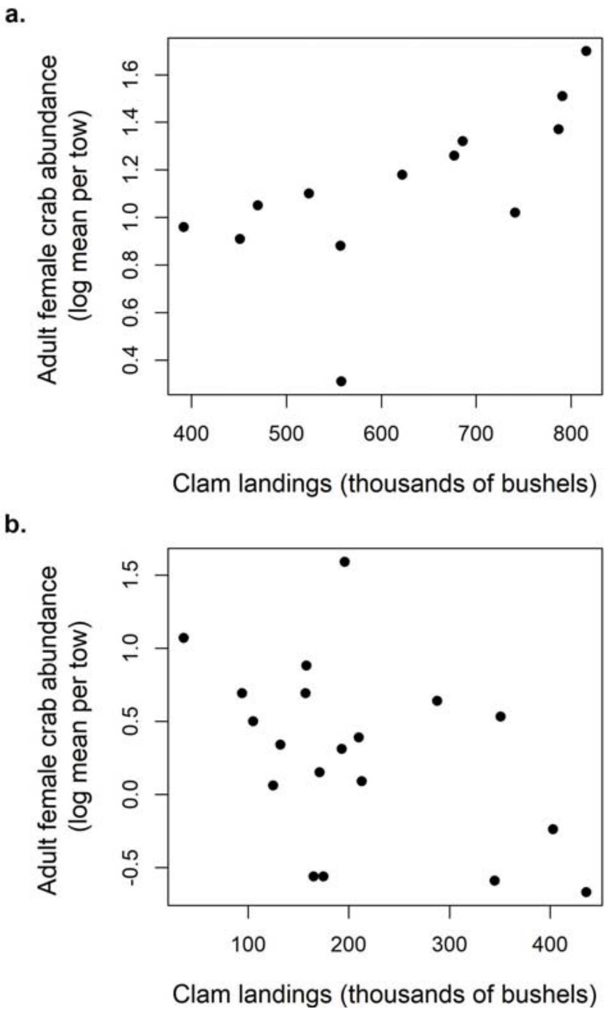

Figure 3. Scatter plots showing the relationship between crab abundance and clam landings before Tropical Storm Agnes in 1972 (a) and after the storm (b).

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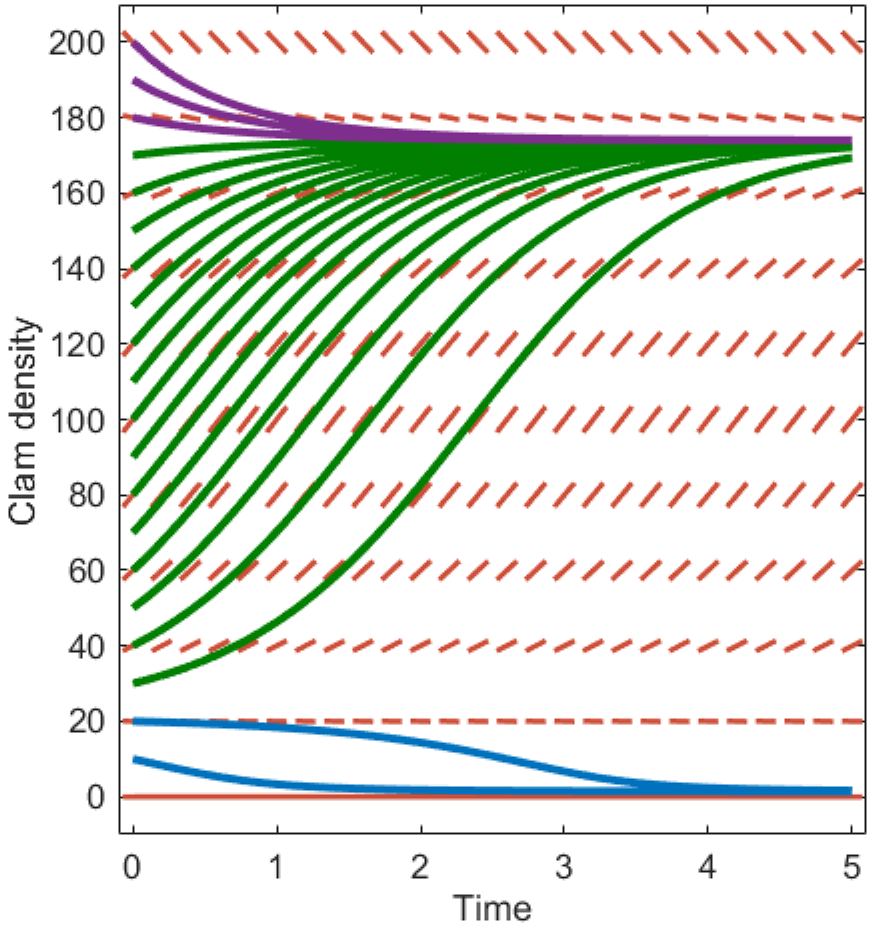

Figure 4. Slope field diagrams for predator-prey models. Trajectories of *Mya arenaria* density either approach a high-density stable steady state at carrying capacity (green and purple lines) or a low-density stable steady state at 1.41 clams m^{-2}. Trajectories diverge from an unstable steady state at 20.93 clams m^{-2}.