Empirical test of crab-clam predator-prey model predictions: storm-driven phase shift to a low-density steady state

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ABSTRACT

A dynamic systems approach can predict steady states in predator-prey interactions, but there are very few empirical tests of predictions from predator-prey models. Here, we examine the empirical evidence for the low-density steady state predicted by a Lotka-Volterra model of a crab-clam predator-prey system using data from long-term monitoring, a field survey, and a field experiment. We show that Tropical Storm Agnes in 1972 likely 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. This storm 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. Predator-prey models with these two species alone were capable of reproducing observations of clam densities and mortality rates, consistent with the idea that *C. sapidus* are a major driver of *M. arenaria* population dynamics. Over 40 y post-storm, *M. arenaria* densities hover near a low-density steady state predicted from the predator-prey model. Relatively simple models can predict phase shifts and identify alternative stable states, as shown by agreement between model predictions and field data in this system. The preponderance of multispecies interactions exhibiting nonlinear dynamics indicates that this may be a general phenomenon.

1. INTRODUCTION

Predators play a key role in ecosystem stability and function by consuming dominant competitors (Lubchenco & Gaines 1981, Boudreau & Worm 2012). Predators can also destabilize ecosystems or collapse food webs if they become too abundant, or if their prey do not have natural defenses against predation. Generally, predators and their prey have evolved over time to coexist.

Prey have anti-predator behaviors or morphological adaptations to avoid being eaten (Bibby et al. 2007, Whitlow 2010). Similarly, predators have adaptations or behaviors that help them to forage optimally and take advantage of prey when they are available (Meire & Ervynck 1986, Rindone & Eggleston 2011).

One of the ways the balance between predator and prey adaptations manifests in nature is through density-dependent predation. Predators can exhibit a numerical response to prey densities by increasing reproduction rates due to an overabundance of prey (demographic response) or by gathering in areas with relatively high densities of prey (aggregative response) (Holling 1959). An individual predator may also adjust its predation rate to prey density through a 'functional response' (changes in a predator's consumption rate in response to prey density). Density-dependent mechanisms tend to stabilize prey population dynamics (Royama 1992, Turchin 2003) and can maintain population viability when a population is reduced to low levels (Cushing 1975).

Certain characteristics of a predator-prey system can help predict which functional response will be observed. A linear relationship between consumption rate and prey density (type I functional response) is expected for organisms that do not actively search for prey, such as filter feeders. Most vertebrate and invertebrate predators exhibit a hyperbolic functional response that increases to an asymptote due to limits associated with prey handling, ingestion, and metabolism (type II functional response) (Hassell et al. 1977). Predators that feed upon cryptic or otherwise hard-to-find prey exhibit a sigmoidal functional response, where consumption rates increase slowly at low prey densities (type III functional response) (Holling 1959). Prey that avoid predators can achieve a low-density refuge; thus, the functional response can explain the distribution of prey items, and it can be used to predict the persistence of prey species at low densities (Eggleston et al. 1992).

There are many mathematical models that can be used to predict predator-prey dynamics (Briggs & Hoopes 2004). These models contain nonlinear functions describing the density-dependent interactions between predator and prey. Due to these nonlinearities, model behavior often includes shifts to alternative stable states (Drake & Griffen 2010). These states may include extinction of one or both species, or coexistence steady states where both predator and prey are able to coexist at densities predicted by the model. Multiple stable coexistence states are possible in fairly simple predator-prey functions (Mumby et al. 2007, Kramer & Drake 2010).

A dynamic systems approach can predict coexistence states in natural and managed systems. Steady states analysis been used to develop optimum harvesting and conservation strategies for forest and rangeland systems (Hritonenko et al. 2013, Bauch et al. 2016). The theory surrounding steady states and bifurcations is well developed, but there are very few empirical tests. To date, empirical tests of coexistence steady states in predator-prey systems have involved populations of small organisms such as unicellular organisms, yeast, small crustaceans, or bacteria (Luckinbill 1973, van den Ende 1973, Drake & Griffen 2010). Identifying or establishing coexisting predator-prey systems for use in testing model predictions has proven difficult, especially for macro-organisms. Of the few empirical tests of steady states that focus on macro-organisms, none examines interactions between natural populations of predators and prey (Kramer & Drake 2010, Jiang et al. 2018, McNickle & Evans 2018). Here, we show that a severe storm 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, in the face of predation by the blue crab *Callinectes sapidus*. We examine the empirical evidence for the low-density steady state predicted by a Lotka-Volterra model of this predator-prey system using data from long-term monitoring, a field survey, and a field experiment.

1.1. History of predator-prey system

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 (Orth & Moore 1983). Tropical Storm Agnes was a "100-year storm" that caused sustained, extremely low salinities (Figure 1) and increased sedimentation throughout Chesapeake Bay (Schubel 1976, Schubel et al. 1976). This storm has been blamed for the loss of seagrass in certain areas of Chesapeake Bay (Orth & Moore 1983), high mortality rates and recruitment failure in oysters *Crassostrea virginica* (Haven et al. 1976), and declines in abundance of the soft-shell clam *Mya arenaria*, which suffered a mass mortality after the storm (Cory & Redding 1976).

Mya arenaria was abundant enough to support a major commercial fishery throughout Chesapeake Bay prior to 1972 (Haven 1970). When the population declined abruptly after Tropical Storm Agnes, the fishery never recovered in lower Chesapeake Bay (Virginia) (Glaspie et al. 2018). 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 (Dungan et al. 2002); the fishery declined by 89% after the storm and has been near collapse since (NMFS).

The failure of *M. arenaria* to recover from storm-related declines has been attributed to predation, habitat loss, disease, rising temperatures, and overfishing (Glaspie et al. 2018). 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 (Dungan et al. 2002, Glaspie et al. 2018). More recently, disease has been blamed for an added minor decline in *M. arenaria* (Dungan et al.

2002); however, there is no evidence that disease prevalence or intensity are correlated with *M. arenaria* density (Glaspie et al. 2018).

Experimental evidence suggests that on a local scale, interactions between *M. arenaria* and their major predator, the blue crab *C. sapidus* (Meise & Stehlik 2003), are capable of keeping clams at low densities (Lipcius & Hines 1986, Seitz et al. 2001). *Mya arenaria* burrow deeply in sediments, and when clams are at low densities, crabs are unable to detect their presence (Lipcius & Hines 1986). The result is a low-density refuge for *M. arenaria*, driven by disproportionately low predation, which is characteristic of a sigmoidal functional response (Lipcius & Hines 1986, Seitz et al. 2001). 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 empirical evidence for a low-density steady state in this predator-prey system, and the impact of Tropical Storm Agnes on basin-scale population dynamics of *M. arenaria*.

2. MATERIALS & METHODS

Changepoint analysis of time series was conducted using R statistical software on *M. arenaria* landings (NMFS 2017) and log-transformed average adult female *C. sapidus* abundance (VIMS trawl survey) in the Chesapeake Bay from 1958-1992, with an AIC penalty and using the segment neighbor algorithm (Auger & Lawrence 1989). 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 in the early 1990s 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 sigmoidal functional response:

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

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 sigmoidal functional response (Hassell et al. 1977).

Models were parameterized using data from the literature as follows: P = 0.06 m^{-2} (MD DNR), r = 1.75 y^{-1} (Brousseau 1978), K = 200 m^{-2} (Abraham & Dillon 1986), T = 1 y, T_h = 0.0015 y (Lipcius & Hines 1986), b = 26.30 y^{-1} (Lipcius & Hines 1986), and c = 0.14 (Lipcius & Hines 1986). Analytical solutions of steady states were calculated using Matlab statistical software. Stability of each coexistence steady state was determined by examining the sign of eigenvalues.

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 (0.022 y) at an initial density of N = 48 m^{-2} to match the field predation experiments (Glaspie & Seitz 2018). 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% (Glaspie & Seitz 2018), and the resultant predator density that achieved observed mortality rates of juvenile *M. arenaria* was compared to published *C. sapidus* densities for Chesapeake Bay. Data and R code files are available in the Knowledge Network for Biocomplexity (KNB) repository (Glaspie 2019).

3. RESULTS

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 (near carrying capacity at 173.99 clams m^{-2}) 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 densities until perturbed past the unstable steady state in 1972 by Tropical Storm Agnes.

Thereafter, it was able to persist at low density due to the low-density refuge from blue crab predation (Lipcius & Hines 1986, Seitz et al. 2001), 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.

Predator-prey models with these two species alone were 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 (Lipcius & Hines 1986, Seitz et al. 2001, Meise & Stehlik 2003). 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 (Glaspie et al. 2018). In the field, juvenile *M. arenaria* exposed to predators suffered 76.3% higher mortality as compared to caged individuals (Glaspie & Seitz 2018). Predator exclusion treatments confirmed that blue crabs were responsible for most of the mortality of juvenile *M. arenaria* (Glaspie & Seitz 2018), 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 (Ralph & Lipcius 2014).

4. DISCUSSION

The observations, theory, and mechanistic basis indicate that *M. arenaria* was subjected to a storm-driven phase shift to low density, which has been maintained by blue crab predation in

Chesapeake Bay. Extreme weather events are costly, and they are likely to become even more common with predicted increases in the intensity and frequency of extreme events due to anthropogenic climate change (Settele et al. 2014). 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 (Thomson et al. 2012). Evidence for storm-driven phase shifts in coral reefs (Mumby et al. 2007), kelp ecosystems (Byrnes et al. 2011), and now soft-sediment communities (current study) suggests that management of ecosystems should include an examination of nonlinear interactions and the potential for phase shifts.

To our knowledge, this is one of a handful of empirical tests of predator-prey theory as a predictive tool in natural systems. More evidence is needed to fully evaluate the predictive potential of steady-state analysis involving predator-prey models, and the value of a dynamics systems approach to ecosystem modeling efforts. However, the approach described here can be adapted to a variety of predator-prey systems with available estimates of life history parameters, population density, and distribution. The approach may also be expanded to include more than two species, or encompass additional complexity, such as metabolic functions.

The concepts encapsulated in the crab-clam predator-prey system, including population self-limitation, consumer-resource oscillations, and the functional response are widespread in nature. These concepts may be considered “laws” of population ecology (Turchin 2001). Each concept listed above introduces nonlinear dynamics into population models, especially those with multiple interacting species. Given the preponderance of multispecies interactions exhibiting nonlinear dynamics, multiple steady states may be a general ecological phenomenon.

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Figures:

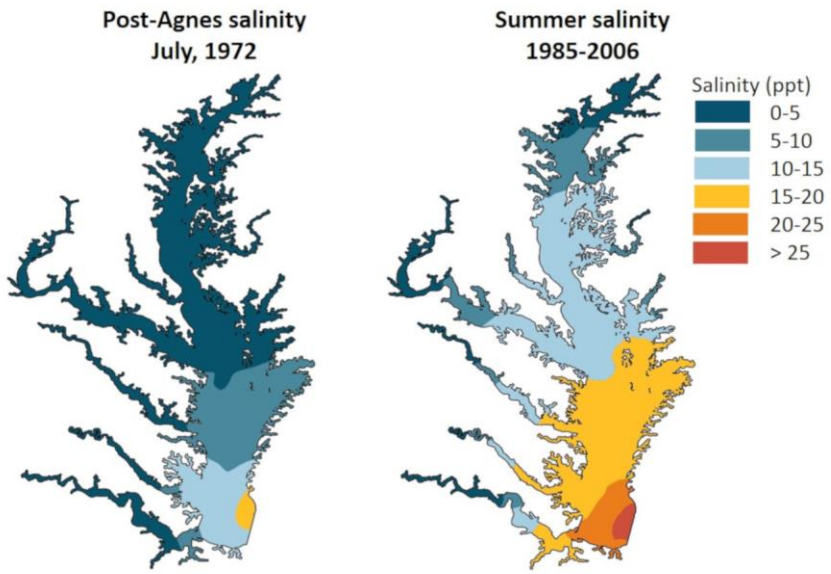

Figure 1. Pre- and post- storm salinity profiles. Salinity profiles for post-Agnes (left) and average summer (right) conditions. Post-Agnes salinity was measured over the period June 29 – July 3, 1972 (Schubel et al. 1976). The summer salinity profile (right) is average surface salinity for 1985-2006 (Weinberg 2008).

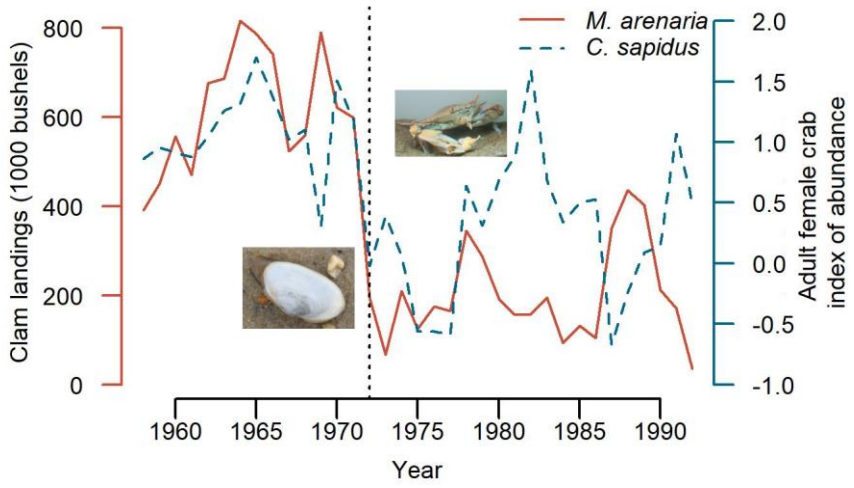

Figure 2. Predator-prey time series. Time series for soft-shell clam *Mya arenaria* landings (red) and adult female blue crab *Callinectes sapidus* index of abundance (blue). Blue crab data are log-transformed average female abundance per tow (VIMS trawl survey). *Mya arenaria* data are fisheries landings (1000 bushels) (NMFS Annual Commercial Landing Statistics). 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).

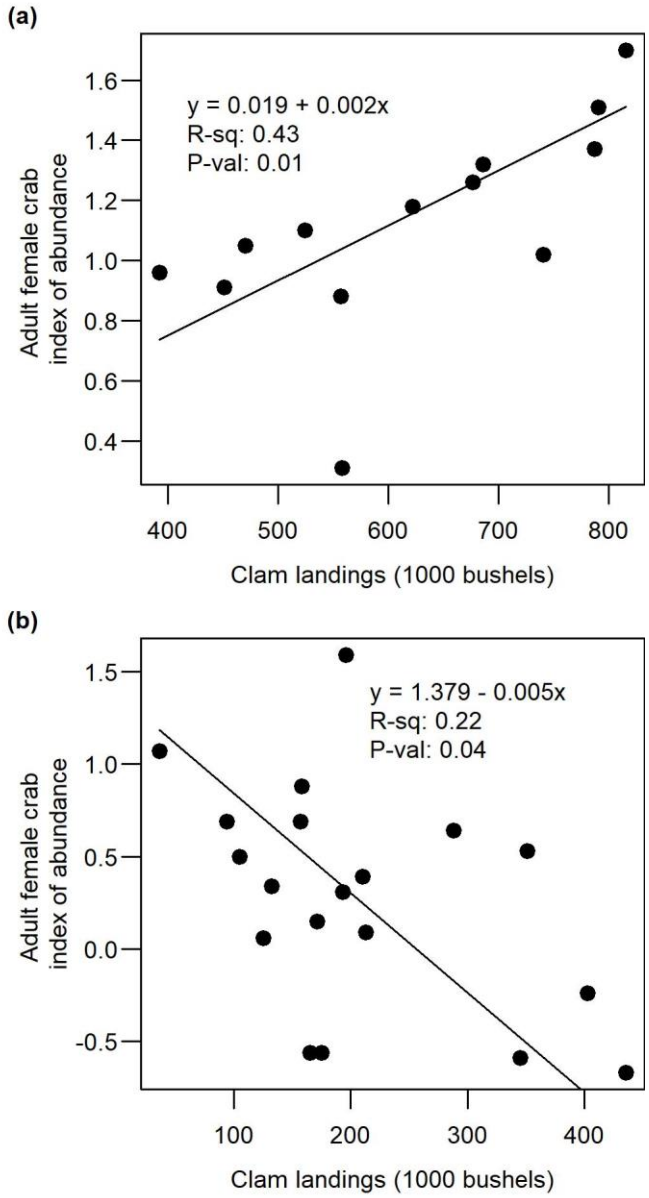

Figure 3. Pre- and post- storm relationship between crab index of abundance (log-transformed average female abundance per tow, VIMS trawl survey) and clam landings (fisheries-dependent data). (a) Before the storm, crab abundance was positively correlated with clam abundance (1 y lag). (b) After the storm, clam abundance was negatively correlated with crab abundance with (1 y lag).

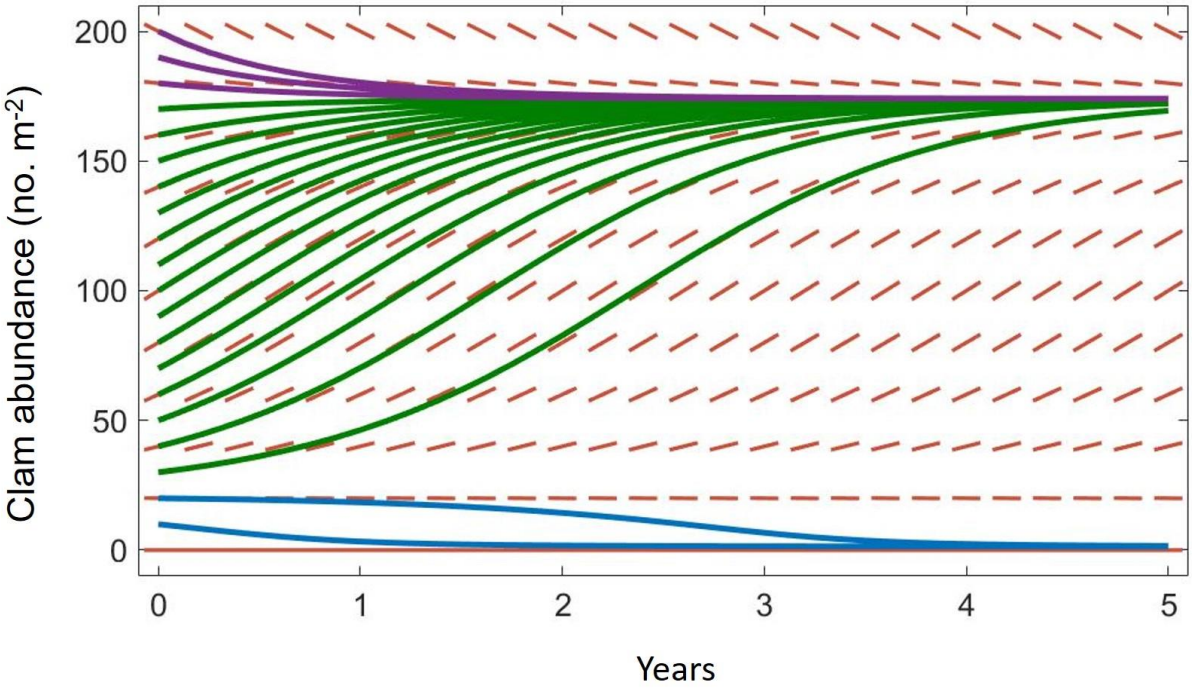

Figure 4. Slope field diagrams for predator-prey models. Trajectories of *Mya arenaria* density either approach a high-density stable steady state at carrying capacity (green and purple lines) or a low-density stable steady state at 1.41 clams m^{-2}. Trajectories diverge from an unstable steady state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