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. Predation rates observed in the field were similar to modeled mortality rates. Predator-prey models can be used to predict dynamics of natural populations, including phase shifts and densities at steady states. The preponderance of multispecies interactions exhibiting nonlinear dynamics indicates that this may be a general phenomenon.

Significance statement:

Biotic interactions often contain nonlinearities that result in complex and unpredictable ecosystem responses, including phase shifts to alternative stable states. Predator-prey theory may be used to predict population phase shifts and prevent unwanted ecological surprises if these models are validated against empirical data, especially from field-based studies. We use a Lotka-Volterra predator-prey model to predict prey densities and predation rates in a natural environment. Agreement between model predictions and field data in this crab-clam predator-prey system indicates that relatively simple models can be used to predict phase shifts and identify alternative stable states. The approach described here can be adapted to a variety of predator-prey systems to predict the impact of phase shifts on ecological communities.

Introduction:

Predators play a key role in ecosystem stability and function by consuming dominant competitors (*1*, *2*). 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 (*3*, *4*). Similarly, predators have adaptations or behaviors that help them to forage optimally and take advantage of prey when they are available (*5*, *6*).

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) (*7*). 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 (*8*, *9*) and can maintain population viability when a population is reduced to low levels (*10*).

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) (*11*). 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) (*7*). 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 (*12*).

There are many mathematical models that can be used to predict predator-prey dynamics (*13*). 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 (*14*). 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 (*15*, *16*).

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 (*17*, *18*). 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 (*19–21*). 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 (*16*, *22*, *23*). 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.

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 (*24*). Tropical Storm Agnes was a “100-year storm” that caused sustained, extremely low salinities (Figure 1) and increased sedimentation throughout Chesapeake Bay (*25*, *26*). This storm has been blamed for the loss of seagrass in certain areas of Chesapeake Bay (*24*), high mortality rates and recruitment failure in oysters *Crassostrea virginica* (*27*), and declines in abundance of the soft-shell clam *Mya arenaria*, which suffered a mass mortality after the storm (*28*).

Fig. 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 (*25*). The summer salinity profile (right) is average surface salinity for 1985-2006 (*29*).

Mya arenaria was abundant enough to support a major commercial fishery throughout Chesapeake Bay prior to 1972 (*30*). When the population declined abruptly after Tropical Storm Agnes, the

fishery never recovered in lower Chesapeake Bay (Virginia) (*31*). 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 (*32*); the fishery declined by 89% after the storm and has been near collapse since (*33*).

The failure of *M. arenaria* to recover from storm-related declines has been attributed to predation, habitat loss, disease, rising temperatures, and overfishing (*31*). 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 (*31*, *32*). More recently, disease has been blamed for an added minor decline in *M. arenaria* (*32*); however, there is no evidence that disease prevalence or intensity are correlated with *M. arenaria* density (*31*).

Experimental evidence suggests that on a local scale, interactions between *M. arenaria* and their major predator, the blue crab *C. sapidus* (*34*), are capable of keeping clams at low densities (*35*, *36*). *Mya arenaria* burrow deeply in sediments, and when clams are at low densities, crabs are unable to detect their presence (*35*). The result is a low-density refuge for *M. arenaria*, driven by disproportionately low predation, which is characteristic of a sigmoidal functional response (*35*, *36*). 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*.

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

Fig. 2. Predator-prey time series. Time series for soft-shell clam *Mya arenaria* landings (red) and adult female blue crab *Callinectes sapidus* abundance (blue). Blue crab data are log-transformed average female abundance per tow (VIMS trawl survey). *Mya arenaria* data are fisheries landings (1000 bushels) (*33*). 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).

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.

Fig. 3. Pre- and post- storm relationship between crab abundance (log-transformed average female abundance per tow, VIMS trawl survey) and clam landings (1000 bushels, 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).

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 (*35, 36*), 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.

Fig. 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}.

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 (*34–36*). 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 (*31*). In the field, juvenile *M. arenaria* exposed to predators suffered 76.3% higher mortality as compared to caged individuals (*37*). Predator exclusion treatments confirmed that blue crabs were responsible for most of the mortality of juvenile *M. arenaria* (*37*), 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 (*38*).

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 (*39*). 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 (*40*). Evidence for storm-driven phase shifts in coral reefs (*15*), kelp ecosystems (*41*), 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 (*42*). 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.

Methods:

Changepoint analysis of time series was conducted using R statistical software on *M. arenaria* landings (*43*) 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 (*44*). 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 (*11*).

Models were parameterized using data from the literature as follows: P = 0.06 m^{-2} (*45*), r = 1.75 y^{-1} (*46*), K = 200 m^{-2} (*47*), T = 1 y, T_h = 0.0015 y (*35*), b = 26.30 y^{-1} (*35*), and c = 0.14 (*35*). 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 (*37*). 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% (*37*), 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 (*48*).

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Figures:

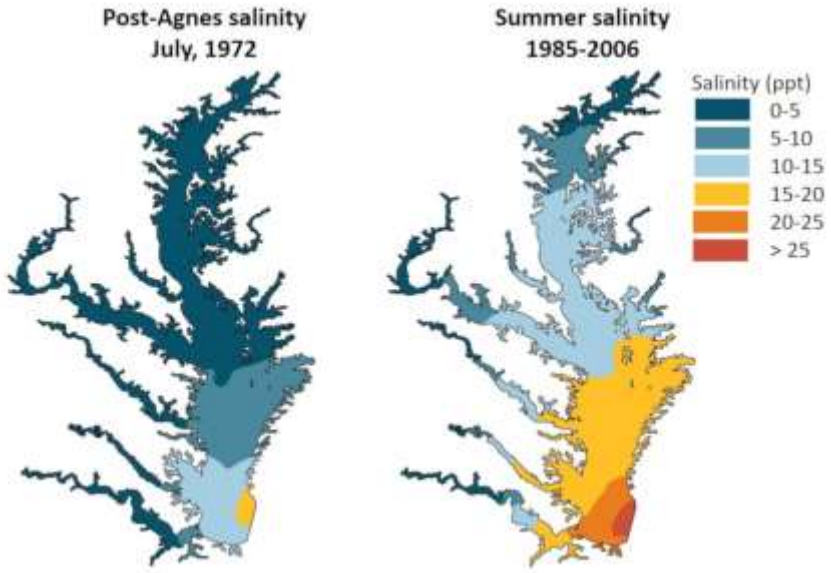

Figure 1.

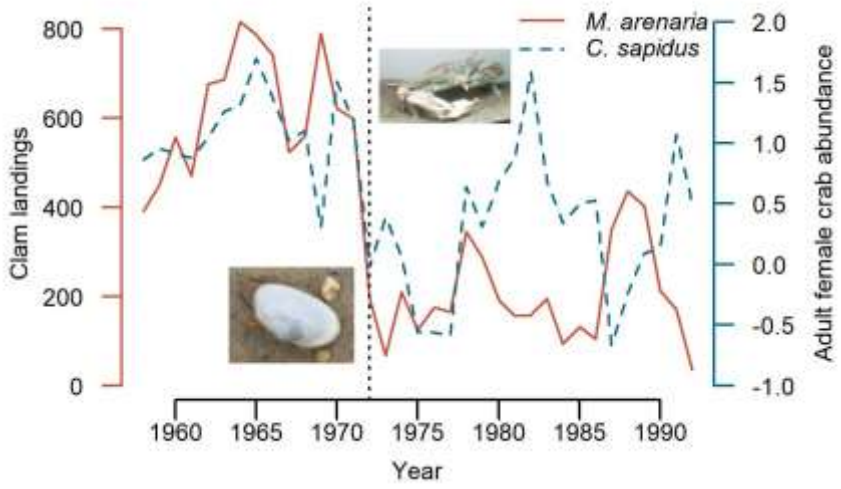
M. arenaria
C. sapidus
Clam landings
Adult female crab abundance
Year
800
600
400
200
0
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
1960
1965
1970
1975
1980
1985
1990

Figure 2.

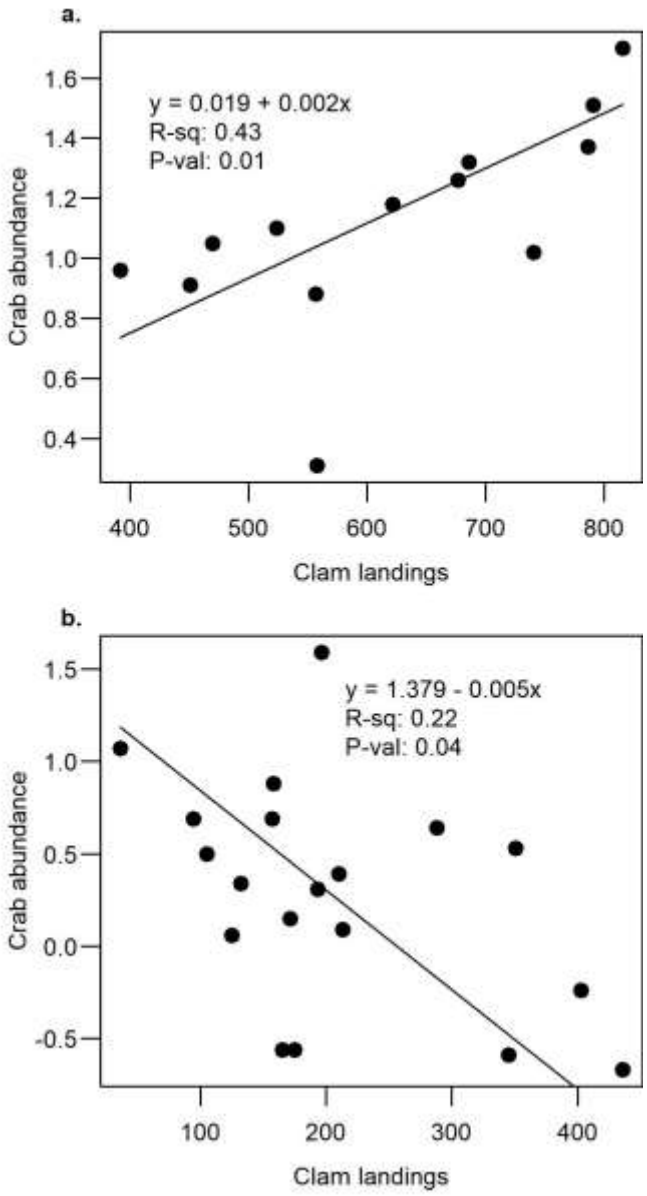
a.
y = 0.019 + 0.002x
R-sq: 0.43
P-val: 0.01
Crab abundance
1.6
1.4
1.2
1.0
0.8
0.6
0.4
400
500
600
700
800
Clam landings
b.
y = 1.379 - 0.005x
R-sq: 0.22
P-val: 0.04
Crab abundance
1.5
1.0
0.5
0.0
-0.5
100
200
300
400
Clam landings

Figure 3.

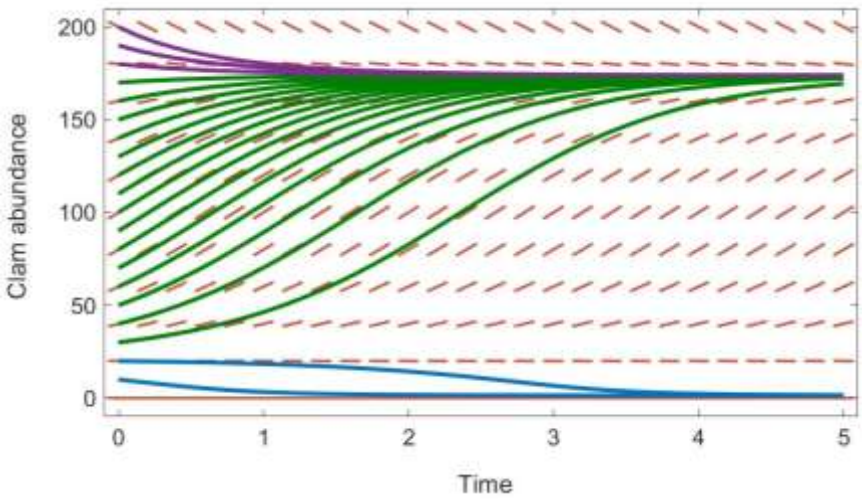

Figure 4.