A Competition Model Among Crayfish Species Subject to Predation

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Abstract

Native species of crayfish in a system of streams face competition from an invasive species of crayfish which is introduced as bait by fishermen. Both the native and invasive species of crayfish are subject to predation by fish. A system of difference equations was developed to model the interactions of the predators and prey in a localized region of a stream. The model includes three stages (or sizes) of the invasive species (*Orconectes rusticus*) since it can grow much larger than the native species. Two stages in the life of the native species (*Orconectes obscurus* and *Cambarus bartonii*) are modeled, while the predators lumped into one state variable. The model contains a large number of, as yet, un-estimated parameters. The task of estimating the model parameters suggests a number of experiments which may be carried out in the future. The relative competitive intensity of the crayfish species on each other is estimated from the respective sizes of the species at different life stages. An analysis of the qualitative dynamics of the system of difference equations was carried out to determine the asymptotic state of the system. Of interest is the persistence of the native species under competitive pressure from the invasive species coupled with the pressure of predation.

Introduction

A heierarchical approach to the development of the size-structured, three-species model will be outlined in this poster. Some of the initial stages of model development are classical, such as the competition and predator/prey models. Later stages of the model are specifically designed to attempt to capture the relevant interactions between the competing prey species, the predator, and their environment.

The next section of the poster will outline the discrete competition model involving an invasive crayfish species (*Orconectes rusticus*) and a single native crayfish species (lumped populations of *Orconectes obscurus* and *Cambarus bartonii*). Following that will be a discrete predator/prey model describing the relationship between the native crayfish species and a predator fish species. These two models will be combined into a third, more complex model capturing the competitive interaction of the two crayfish populations and the predatory fish species. This three-species model will be generalized in a later section by splitting the invasive crayfish species into three size classes and the native crayfish species into two size classes. The predator species will retain only a single size class.

Two-species Competition

In this section we develop and analyze a difference equation model describing the competitive interaction between two species of crayfish. The species denoted by u will be thought of as an invasive species and v will denote a native species. The model takes the form

$$u^{t+1} = u^t e^{r_u(1-(u^t+c_v v^t)/K_u)} \quad (1)$$
$$v^{t+1} = v^t e^{r_v(1-(c_u u^t+v^t)/K_v)}. \quad (2)$$

All parameters are assumed to be non-negative and may be interpreted as follows.

r_u: reproductive rate of the invasive species

r_v: reproductive rate of the native species

c_u: competitive effect of the native species on the invasive species

c_v: competitive effect of the invasive species on the native species

K_u: environmental carrying capacity for the invasive species

K_v: environmental carrying capacity for the native species

If $c_u c_v \neq 1$ then there may exist a fixed point in the interior of the positive quadrant:

$$(e_u, e_v) = \left(\frac{K_u - c_v K_v}{1 - c_u c_v}, \frac{K_v - c_u K_u}{1 - c_u c_v}\right).$$

We will assume $K_u > c_v K_v$ and that $K_v > c_u K_u$, which in turn implies that $1 > c_u c_v$.

The stability of the fixed point may be determined by substituting $u^t = e_u + \delta_u^t$ and $v^t = e_v + \delta_v^t$ into equations (1) and (2) and retaining only the terms which are linear in δ_u and δ_v. Rewriting this linear approximation as a matrix equation produces:

$$\begin{bmatrix} \delta_u^{t+1} \\ \delta_v^{t+1} \end{bmatrix} = A \begin{bmatrix} \delta_u^t \\ \delta_v^t \end{bmatrix} \quad \text{where}$$
$$A = I_2 - \hat{A} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} - \begin{bmatrix} \frac{e_u r_u}{K_u} & 0 \\ 0 & \frac{e_v r_v}{K_v} \end{bmatrix} \begin{bmatrix} 1 & c_v \\ c_u & 1 \end{bmatrix}.$$

The fixed point of the two-species competition model is asymptotically stable if both eigenvalues of the matrix lie inside the the unit circle in the complex plane. The value λ is an eigenvalue of A if and only if $\hat{\lambda} = 1 - \lambda$ is an eigenvalue of $\hat{A}$. The eigenvalues of $\hat{A}$ are

$$\widehat{\lambda_1} = \frac{1}{2}\left(\frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v} + \sqrt{\left(\frac{e_u r_u}{K_u} - \frac{e_v r_v}{K_v}\right)^2 + 4c_u c_v \frac{e_u r_u}{K_u}\frac{e_v r_v}{K_v}}\right)$$
$$\widehat{\lambda_2} = \frac{1}{2}\left(\frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v} - \sqrt{\left(\frac{e_u r_u}{K_u} - \frac{e_v r_v}{K_v}\right)^2 + 4c_u c_v \frac{e_u r_u}{K_u}\frac{e_v r_v}{K_v}}\right)$$

which are real by our non-negativity assumptions on the parameters and fixed point. We can also see that $\widehat{\lambda_2} < \widehat{\lambda_1}$ which implies that $\lambda_1 < \lambda_2$. Since we are assuming $1 > c_u c_v$ then

$$\sqrt{\left(\frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v}\right)^2 - 4(1 - c_u c_v)\frac{e_u r_u}{K_u}\frac{e_v r_v}{K_v}} < \frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v}$$

which implies that

$$0 < 1 - \lambda_1 < \frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v} \iff 1 - \frac{e_u r_u}{K_u} - \frac{e_v r_v}{K_v} < \lambda_1 < 1, \text{ and}$$
$$0 < 1 - \lambda_2 < \frac{1}{2}\left(\frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v}\right) \iff 1 - \frac{1}{2}\left(\frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v}\right) < \lambda_2 < 1.$$

Thus if $0 < \frac{e_u r_u}{K_u} + \frac{e_v r_v}{K_v} < 2$ the fixed point is asymptotically stable.

Predator/Single Prey

Now we consider a two-species interaction of the predator/prey type. This may represent the state of the ecosystem prior to the introduction of the invasive species. Consequently we will let v represent the prey while w represents the predator. A difference equation model of this situation is

$$v^{t+1} = v^t e^{r_v(1-v^t/K_v)-\beta_v w^t} \quad (3)$$
$$w^{t+1} = v^t\left(1 - e^{-\beta_v w^t}\right) \quad (4)$$

The new parameter of this section β_v is assumed to be non-negative and represents the predation rate of the predator on the prey. For an appropriate choice of model parameters there may exist a fixed point in the interior of the vw-plane. Suppose the equilibrium values of the two species are (v^*, w^*), then

$$r_v\left(1 - \frac{v^*}{K_v}\right) - \beta_v w^* = 0 \quad (5)$$
$$w^* = v^*\left(1 - e^{-\beta_v w^*}\right). \quad (6)$$

Solving equation (5) for v^* and substituting into equation (6) yields

$$\frac{w^*}{K_v} = \left(1 - \frac{\beta_v}{r_v}w^*\right)\left(1 - e^{-\beta_v w^*}\right).$$

Defining the two functions:

$$f(x) = \frac{x}{K_v} \quad \text{and} \quad g(x) = \left(1 - \frac{\beta_v}{r_v}x\right)\left(1 - e^{-\beta_v x}\right),$$

we can readily see that $f(0) = g(0) = g(r_v/\beta_v) = 0$. When $\frac{1}{K_v} < \beta_v$ there exists $0 < w^* < r_v/\beta_v$ such that $f(w^*) = g(w^*)$.

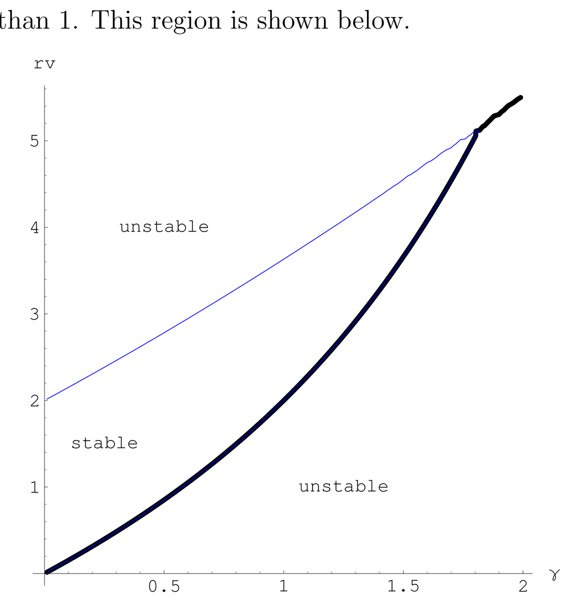
The stability of the fixed point may be determined by substituting $v^t = v^* + \delta_v^t$ and $w^t = w^* + \delta_w^t$ into equations (3) and (4) and retaining the terms up to linear order in δ_v and δ_w. In matrix form this becomes

$$\begin{bmatrix} \delta_v^{t+1} \\ \delta_w^{t+1} \end{bmatrix} = \begin{bmatrix} 1 - r_v + \beta_v w^* & -\beta_v v^* \\ \frac{w^*}{v^*} & \beta_v(v^* - w^*) \end{bmatrix} \begin{bmatrix} \delta_v^t \\ \delta_w^t \end{bmatrix}. \quad (7)$$

The fixed point of the predator-prey model is asymptotically stable if both eigenvalues of the matrix in equation (7) lie inside the the unit circle in the complex plane. The eigenvalues can be expressed as

$$\lambda_\pm = \frac{1}{2}\left[1 - r_v + \frac{\gamma}{1 - e^{-\gamma}} \pm \sqrt{(1 - r_v + \frac{\gamma}{1 - e^{-\gamma}})^2 - 4\gamma\frac{1 + (\gamma - r_v)e^{-\gamma}}{1 - e^{-\gamma}}}\right]$$

where we have replaced $\beta_v w^*$ by γ. This enables us to visualize the region in (r_v, γ)-space where the magnitudes of the eigenvalues are smaller than 1. This region is shown below.



Predator/Competing Prey

The model is generalized once again by considering the case of two competing prey species subject to predation by a third species. The difference equation model takes the form

$$u^{t+1} = u^t e^{r_u(1-(u^t+c_v v^t)/K_u)-\beta_u w^t} \quad (8)$$
$$v^{t+1} = v^t e^{r_v(1-(c_u u^t+v^t)/K_v)-\beta_v w^t} \quad (9)$$
$$w^t = u^t(1 - e^{-\beta_u w^t}) + v^t(1 - e^{-\beta_v w^t}) \quad (10)$$

where the variable u denoted the invasive prey species, v denotes the native prey species, and w denotes the predator species. All parameters are still assumed to be non-negative and have the same interpretations as in the previous models. In this section we are interested in the possibility of a nontrivial fixed point at which all three species are present. In order to keep the notation simple, this equilibrium will be denoted (u^*, v^*, w^*). At equilibrium the following set of equations must be satisfied:

$$r_u\left(1 - (u^* + c_v v^*)/K_u\right) = \beta_u w^* \quad (11)$$
$$r_v\left(1 - (c_u u^* + v^*)/K_v\right) = \beta_v w^* \quad (12)$$
$$u^*\left(1 - e^{-\beta_u w^*}\right) + v^*\left(1 - e^{-\beta_v w^*}\right) = w^* \quad (13)$$

Equations (11) and (12) can be solved for u^* and v^* as linear functions of w^*. Thus we have

$$u^* = e_u - \left(\frac{\beta_u K_u}{r_u} - \frac{\beta_v c_v K_v}{r_v}\right)\frac{w^*}{1 - c_u c_v},$$
$$v^* = e_v - \left(\frac{\beta_v K_v}{r_v} - \frac{\beta_u c_u K_u}{r_u}\right)\frac{w^*}{1 - c_u c_v}.$$

Substituting the expressions for u^* and v^* into equation (13) produces

$$(1 - c_u c_v)w^* = \left(1 - e^{-\beta_u w^*}\right)\left[K_u - c_v K_v - \left(\frac{\beta_u K_u}{r_u} - \frac{\beta_v c_v K_v}{r_v}\right)w^*\right] + \left(1 - e^{-\beta_v w^*}\right)\left[K_v - c_u K_u - \left(\frac{\beta_v K_v}{r_v} - \frac{\beta_u c_u K_u}{r_u}\right)w^*\right]$$

We will define the functions $f(x) = (1 - c_u c_v)x$ and

$$g(x) = \left(1 - e^{-\beta_u x}\right)\left[K_u - c_v K_v - \left(\frac{\beta_u K_u}{r_u} - \frac{\beta_v c_v K_v}{r_v}\right)x\right] + \left(1 - e^{-\beta_v x}\right)\left[K_v - c_u K_u - \left(\frac{\beta_v K_v}{r_v} - \frac{\beta_u c_u K_u}{r_u}\right)x\right].$$

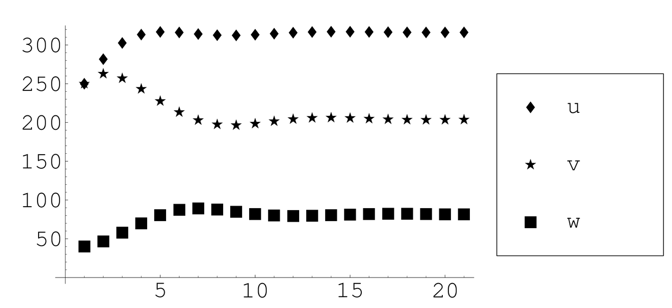
We can readily see that $f(0) = g(0)$ and there will be a nontrivial equilibrium with all three species present if $f(x) = g(x)$ for some $x > 0$. A sufficient condition for this intersection to take place is for $f'(0) < g'(0)$. Thus when $\beta_u e_u + \beta_v e_v > 1$ there exists $w^* > 0$ such that $f(w^*) = g(w^*)$.

The stability of the fixed point may be determined by substituting $u^t = u^* + \delta_u^t$, $v^t = v^* + \delta_v^t$, and $w^t = w^* + \delta_w^t$ into equations (8)–(10) and retaining only the terms which are linear in δ_u, δ_v, and δ_w. Rewriting this set of equations in matrix form produces:

$$\begin{bmatrix} \delta_u^{t+1} \\ \delta_v^{t+1} \\ \delta_v^{t+1} \end{bmatrix} = A \begin{bmatrix} \delta_u^t \\ \delta_v^t \\ \delta_v^t \end{bmatrix} \quad \text{where } A \text{ is}$$

$$I_3 - \begin{bmatrix} \frac{r_u u^*}{K_u} & 0 & 0 \\ 0 & \frac{r_v v^*}{K_v} & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1 & c_v & \frac{\beta_u K_u}{r_u} \\ c_u & 1 & \frac{\beta_v K_v}{r_v} \\ e^{-\beta_u w^*} - 1 & e^{-\beta_v w^*} - 1 & 1 - \frac{\beta_u u^*}{e^{\beta_u w^*}} - \frac{\beta_v v^*}{e^{\beta_v w^*}} \end{bmatrix}.$$

The eigenvalues of A must be found numerically. A number of different types of asymptotic behavior are possible for this model including the stable coexistence of all three species.



Size-Structured Model

The most detailed of the models studied assumes that the native species exists in two size classes designated “small” and “medium”. The invasive species can attain a third size, “large”. The additional size class allows us to explore the model behavior if the invasive species attains a size no longer subject to predation. The size-structured model has the form:

$$u_s^{t+1} = a_{u_s}u_s^t + (u_m^t + u_l^t)e^{r_u(1-(u_s^t+c_{um}u_m^t+c_{u_l}u_l^t+c_{vs}v_s^t+c_{vm}v_m^t)/K_u)-\beta_{us}w^t}$$
$$u_m^{t+1} = b_{u_s}u_s^t + f_{u_m}u_m^t e^{-\beta_{um}w^t}$$
$$u_l^{t+1} = g_{u_m}u_m^t + h_{u_l}u_l^t e^{-\beta_{u_l}w^t}$$
$$v_s^{t+1} = a_{v_s}v_s^t + v_m^t e^{r_v(1-(u_s^t+d_{um}u_m^t+d_{u_l}u_l^t+d_{vs}v_s^t+d_{vm}v_m^t)/K_v)-\beta_{vs}w^t}$$
$$v_m^{t+1} = b_{v_s}v_s^t + f_{v_m}v_m^t e^{-\beta_{vm}w^t}$$
$$w^{t+1} = u_s^t(1 - e^{-\beta_{us}w^t}) + u_m^t(1 - e^{-\beta_{um}w^t}) + u_l^t(1 - e^{-\beta_{u_l}w^t}) + v_s^t(1 - e^{-\beta_{vs}w^t}) + v_m^t(1 - e^{-\beta_{vm}w^t})$$

The competitive, reproductive, and predation rates may be interpreted as in the previous models. The novel parameters in the size-structured model are described below.

a_{u_s}: the proportion of small invasive species members who remain in the small size class during the next time period.

a_{v_s}: the proportion of small native species members who remain in the small size class during the next time period.

b_{u_s}: the proportion of small invasive species members who graduate to the medium size class during the next time period.

b_{v_s}: the proportion of small native species members who graduate to the medium size class during the next time period.

f_{u_m}: the proportion of medium invasive species members who remain in the medium size class during the next time period.

f_{v_m}: the proportion of medium native species members who remain in the medium size class during the next time period.

$g_{u.m}$: the proportion of medium invasive species members who graduate to the large size class during the next time period.

$h_{u,m}$: the proportion of large invasive species members who remain in the large size class during the next time period.

All parameters are assumed to be positive unless otherwise specified. We will assume throughout this section that $0 < a_{u_s} + b_{u_s} < 1$ which allows for a positive death rate associated with the small size class of the invasive species. Likewise we will assume that $0 < a_{v_s} + b_{v_s} < 1$. The death rates among members of the other size classes are implied by the following inequalities:

$$0 < f_{u_m} + g_{u_m} < 1 \quad \text{(medium invasives)}$$
$$0 < f_{v_m} < 1 \quad \text{(medium natives)}$$
$$0 < h_{u_l} < 1 \quad \text{(large invasives)}$$

Finding a nontrivial equilibrium in which all three species are present is tedious and best handled numerically. Assuming such as equilibrium exists, its coordinates for some $w^* > 0$ are given by

$$u_s^* = \frac{(1 - f_{u_m}e^{-\beta_{um}w^*})(1 - h_{u_l}e^{-\beta_{u_l}w^*})(BF - DE)}{b_{u_s}g_{u_m}(AD - BC)}$$
$$u_m^* = \frac{(1 - h_{u_l}e^{-\beta_{u_l}w^*})(BF - DE)}{g_{u_m}(AD - BC)}$$
$$u_l^* = \frac{BF - DE}{AD - BC}$$
$$v_s^* = \frac{(1 - f_{v_m}e^{-\beta_{vm}w^*})(CE - AF)}{b_{v_s}(AD - BC)}$$
$$v_m^* = \frac{CE - AF}{AD - BC}$$

where

$$A = c_{u_l} + \left(c_{u_m} + \frac{(1 - f_{u_m}e^{-\beta_{um}w^*})}{b_{u_s}}\right)\frac{1 - h_{u_l}e^{-\beta_{u_l}w^*}}{g_{u_m}}$$
$$B = c_{v_m} + c_{v_s}\frac{(1 - f_{v_m}e^{-\beta_{vm}w^*})}{b_{v_s}}$$
$$C = d_{u_l} + \left(d_{u_m} + \frac{(1 - f_{u_m}e^{-\beta_{um}w^*})}{b_{u_s}}\right)\frac{1 - h_{u_l}e^{-\beta_{u_l}w^*}}{g_{u_m}}$$
$$D = d_{v_m} + d_{v_s}\frac{(1 - f_{v_m}e^{-\beta_{vm}w^*})}{b_{v_s}}$$
$$E = K_u\left(1 - \frac{1}{r_u}\ln\left[\frac{(1 - a_{u_s})(1 - f_{u_m}e^{-\beta_{um}w^*})(1 - h_{u_l}e^{-\beta_{u_l}w^*})e^{\beta_{us}w^*}}{b_{u_s}(1 + g_{u_m} - h_{u_l}e^{-\beta_{u_l}w^*})}\right]\right)$$
$$F = K_v\left(1 - \frac{1}{r_v}\ln\left[\frac{(1 - a_{v_s})(1 - f_{v_m}e^{-\beta_{vm}w^*})e^{\beta_{vs}w^*}}{b_{v_s}}\right]\right)$$

It is assumed that $AD \neq BC$.

The stability of this equilibrium point can be found by substituting expressions of the form $u_s^* + \delta_{u_s}^t$, $u_m^* + \delta_{u_m}^t$, $u_l^* + \delta_{u_l}^t$, $v_s^* + \delta_{v_s}^t$, $v_m^* + \delta_{v_m}^t$, and $w^* + \delta_w^t$ into the model and retaining only the terms which are linear in δ_{u_s}, δ_{u_m}, δ_{u_l}, δ_{v_s}, δ_{v_m} and δ_w. The linearized system has the form

$$\begin{bmatrix} \delta_{u_s}^{t+1} \\ \delta_{u_m}^{t+1} \\ \delta_{u_l}^{t+1} \\ \delta_{v_s}^{t+1} \\ \delta_{v_m}^{t+1} \\ \delta_w^{t+1} \end{bmatrix} = (\mathcal{A} - \mathcal{BC}) \begin{bmatrix} \delta_{u_s}^t \\ \delta_{u_m}^t \\ \delta_{u_l}^t \\ \delta_{v_s}^t \\ \delta_{v_m}^t \\ \delta_w^t \end{bmatrix} \quad \text{where}$$

$$\mathcal{A} = \begin{bmatrix} a_{u_s} & \Gamma_u & \Gamma_u & 0 & 0 & 0 \\ b_{u_s} & 0 & 0 & 0 & 0 & 0 \\ 0 & g_{u_m} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & a_{v_s} & \Gamma_v & 0 \\ 0 & 0 & 0 & b_{v_s} & 0 & 0 \\ 1 & 1 & 1 & 1 & 1 & 0 \end{bmatrix}$$

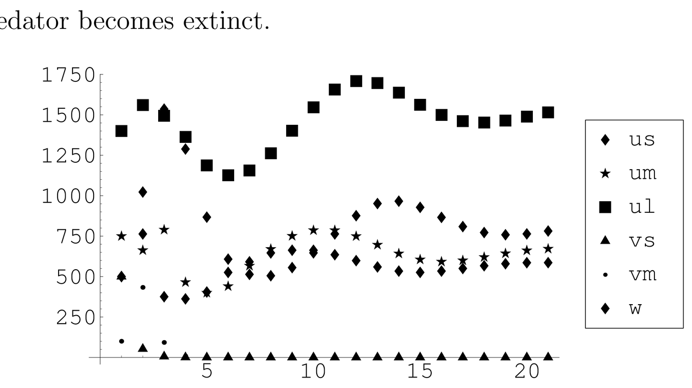
$$\mathcal{B} = \begin{bmatrix} \frac{(u_m^* + u_l^*)r_u\Gamma_u}{K_u} & 0 & 0 & 0 & 0 & 0 \\ 0 & f_{u_m}e^{-\beta_{um}w^*} & 0 & 0 & 0 & 0 \\ 0 & 0 & h_{u_l}e^{-\beta_{u_l}w^*} & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{v_m^* r_v \Gamma_v}{K_v} & 0 & 0 \\ 0 & 0 & 0 & 0 & f_{v_m}e^{-\beta_{vm}w^*} & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$\mathcal{C} = \begin{bmatrix} 1 & c_{u_m} & c_{u_l} & c_{v_s} & c_{v_m} & \frac{\beta_{u_s}K_u}{r_u} \\ 0 & -1 & 0 & 0 & 0 & u_m^*\beta_{u_m} \\ 0 & 0 & -1 & 0 & 0 & u_l^*\beta_{u_l} \\ 1 & d_{u_m} & d_{u_l} & d_{v_s} & d_{v_m} & \frac{\beta_{v_s}K_v}{r_v} \\ 0 & 0 & 0 & 0 & -1 & v_m^*\beta_{v_m} \\ e^{-\beta_{us}w^*} & e^{-\beta_{um}w^*} & e^{-\beta_{u_l}w^*} & e^{-\beta_{vs}w^*} & e^{-\beta_{vm}w^*} & -\Delta \end{bmatrix}$$

$$\Gamma_u = e^{r_u(1-(u_s^*+c_{um}u_m^*+c_{u_l}u_l^*+c_{vs}v_s^*+c_{vm}v_m^*)/K_u)-\beta_{us}w^*}$$
$$\Gamma_v = e^{r_v(1-(u_s^*+d_{um}u_m^*+d_{u_l}u_l^*+d_{vs}v_s^*+d_{vm}v_m^*)/K_v)-\beta_{vs}w^*}$$
$$\Delta = \beta_{u_s}u_s^* e^{-\beta_{us}w^*} + \beta_{u_m}u_m^* e^{-\beta_{um}w^*} + \beta_{u_l}u_l^* e^{-\beta_{u_l}w^*} + \beta_{v_s}v_s^* e^{-\beta_{vs}w^*} + \beta_{v_m}v_m^* e^{-\beta_{vm}w^*}$$

If all the eigenvalues of $\mathcal{A} - \mathcal{BC}$ lie inside the unit circle, then the fixed point is asymptotically stable. Due to the complexity of the linear system, the eigenvalues must be estimated numerically.

As in the single size model a variety of qualitative long-term dynamics are possible for the size-structured model. One example is given below in which the invasive species predominates while the predator becomes extinct.



Conclusion

Much work remains to be done on this model. Chiefly, ecologically realistic estimates of the parameters of the model must be determined either from the literature or from experiment. The susceptibility of the ecosystem to invasion must also be assessed. This could be done by simulating the introduction into the native species/predator ecosystem a small number of the invasive species. The model could also be extended in several ways. One extension would be to include in the model a predation rate of the crayfish species on the eggs used for reproduction by the fish (the nominal predator of the present model). Another extension would be to include a fourth species representing the result of hybridization of the native and invasive species.