Modeling predator-prey equations for *Ambystoma tigrinum* in the presence of phenotypic plasticity

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Abstract

1   Introduction

According to [4], "Phenotypic plasticity is the ability of an organism to change its phenotype in response to changes in the environment. Such plasticity in some cases expresses as several highly morphologically distinct results; in other cases, a continuous norm of reaction describes the functional interrelationship of a range of environments to a range of phenotypes. The term was originally conceived in the context of development, but is now more broadly applied to include changes that occur during the adult life of an organism, such as behaviour." *Ambystoma tigrinum*, the tiger salamander, is a classic example of this phenomenon. A species of salamander widespread in the U.S., the tiger salamander hatches from eggs into an aquatic larval form. In a "typical" growth trajectory, the larval form matures into an adult salamander capable of terrestrial life, then becomes sexually mature. Other trajectories include remaining in a legless aquatic form but maturing sexually to carry out the entire life cycle in the water (paedomorph), or, in a variant of this, developing huge jaws in the juvenile stage and becoming an aquatic, largely cannibalistic predator [5] [3].

In the "introduction" section of your paper you should give the reader a brief overview of the modeling problem and also the specific questions you will address in your particular paper. [1] How should your paper be structured? Please include all the sections that you see here in this assignment description.

2   Preliminaries

The model we will look at has four trophic levels. Fairy shrimp and other minute organisms (F) are at the bottom of the food chain and will be assumed to have logistic growth in the
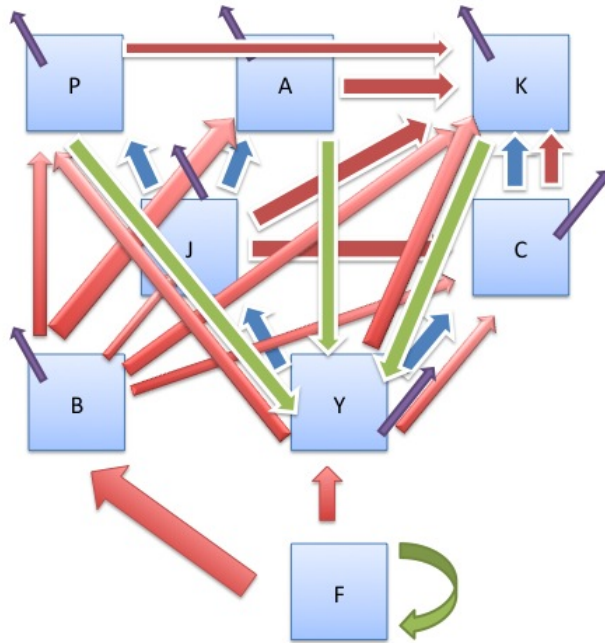
Figure 1: Box model for the full system. Green arrows represent growth, red predation, blue maturation and purple death.

absence of predators with a carrying capacity of 1 (in biomass). These are eaten by recently hatched salamander larvae, or "young of the year" (Y) and also by an assortment of other predators of similar size, such as bugs (B). The young of the year (Y) mature into one of two possible forms, either a larger larva that is a sexually immature juvenile (J) or a cannibalistic form of the juvenile (C). These in turn mature into adults capable of reproduction. Normal juveniles (J) can mature into paedomorphs (P) which are sexually mature but aquatic, never developing legs and lungs, or else they (J) can mature into terrestrial adults (A) which can live on land or in water. The cannibalistic juveniles (C) mature into cannibalistic adults (K) which are sexually mature and also remain completely aquatic.

The model described below makes some assumptions. It assumes that both maturation and reproduction are dependent on predation for all populations except F. The dependence is always modeled as a joint proportion as in the predator prey equations in chapter 9 of your book. Organisms other than F that are in mature form (B, P, A, K) have a natural death rate (like the predator does in the predator-prey equation). As written the model assumes that P and K prey on young of the year Y but A does not.

Note that due to the life stages, energy obtained by predation is returned to the system as maturation or birth, and thus does not necessarily add to the quantity of predator directly. Thus the energy flow does not represent strict mass action– for example the predation of A

on B removes mass from B but returns it to Y through a birth rate proportional to AB. All predation interactions are modeled as simple joint proportions. Thus the predation rate of K on C, for example, is given as $p_{KC}KC$. This term represents adult cannibals (K) eating juvenile cannibals (C). This mass is therefore removed from the C population. But it does not enter the K population directly as mass (for the same reason that you personally do not gain all the pounds you eat). Rather, the species gains biomass when K breeds and produces Y. So in the growth term for Y you will see this term reappear adjusted by some growth rate a_Y which has to take into account the loss of energy in eating but also the large clutch size of eggs. You can track every term this way– some energy goes into birth and some goes into maturation.

In the "preliminaries" section of your paper you should elaborate more fully on the assumptions made in the full model and also in your particular variation on it.

3   Model formulation

In this section of the paper you introduce the general model and also your variation on it.

Below are the equations for the general model. You should precede each equation by a sentence or two explaining what it means in English. For example, I'll do the first one:

Fairy Shrimp and other small organisms. The trophic system we are studying is based on the presence of small organisms, in this case fairy shrimp, denoted F. These are assumed to to have logistic growth in the absence of predation, with a normalized carrying capacity of 1. Predation is based loosely on mouth size, therefore the only predators of F are in the second trophic level (B and Y). Predation is assumed to be jointly proportional to both predator and prey.

$$F' = a_F F(1 - F) - p_{BF}BF - p_{YF}YF \tag{1}$$

$F' = $ logistic growth - pred by B - pred by Y

Larger insects such as beetles. Then you would put the next explanation here. And so forth.

$$B' = a_B p_{BF}BF - (p_{PB}P + p_{AB}A + p_{KB}K + gJ + p_{CB}C)B - d_B B \tag{2}$$

$B' = $ growth - predation by P, A, K, J and C - death

Young of the Year

$$Y' = a_Y((p_{PY}Y + p_{PB}B)P + p_{AB}AB$$
$$+(p_{KB}B + p_{KP}P + p_{KA}A + p_{KJ}J + p_{KY}Y + p_{KC}C)K) \tag{3}$$
$$-(p_{KY}K + p_{CY}C + p_{PY}P)Y - m_Y p_{YF}YF - d_Y Y$$

$Y' = $ growth from P & A eggs+ growth from K eggs - predation by K and C - maturation to J or C - death

Juveniles

$$J' = q_{YJ}m_Y p_{YF}YF - (p_{CJ}C + p_{KJ}K)J - m_J J(p_{JB}B + p_{JY}Y) - d_J J \tag{4}$$

J' = maturation from Y - predation by C and K - maturation to P or A - death

Cannibalistic Juveniles

$$C' = (1 - q_{YJ})m_Y p_{YF}YF - p_{KC}CK - m_C(p_{CY}CY + p_{CB}CB + p_{CJ}CJ) - d_C C \tag{5}$$

C' = maturation from Y - predation by K - maturation to K - death

Cannibalistic Adults

$$K' = m_C(p_{CY}CY + p_{CB}CB + p_{CJ}CJ) - d_K K \tag{6}$$

K' = maturation from C - death

Terrestrial Adults

$$A' = q_{JA}m_J J(p_{JB}B + p_{JY}Y) - p_{KA}KA - d_A A \tag{7}$$

A' = maturation from J - predation by K - death

Paedomorph Adults

$$P' = (1 - q_{JA})m_J J(p_{JB}B + p_{JY}Y) - p_{KP}KP - d_P P \tag{8}$$

P' = maturation from J - predation by K - death

Parameters in these eight equations

Table 1 lists the parameters with their roles and some default values. A biologically reasonable system loses energy as it passes from one trophic level to another. Thus growth rates for F, B, and Y are large compared to maturation rates. Predation rates represent losses from one trophic level, and because these are multiplied by either the growth or maturation rates as the energy enters the next level, there is an energy loss from the system. Other than this general observation, the constants in the table are arbitrary and no units are implied.

If you put these equations and parameters into Big Green syntax with some choice of initial conditions, you will have:

F=1, F' = 10*F*(1-F) - 2*B*F - 2*Y*F
B=.1, B' = (1*2*B*F - (.5*P+ .5*A + .1*K + .5*J +.1*C)*B -.001*B)
Y=0, Y' = (.3*(P*(.1*Y+.5*B) + .5*A*B) +
.3*(.1*K*B + K*(.1*P+.1*A+.2*J +.1*Y) + .2*K*C)
- (.1*K + .5*C + .1*P)*Y - .05*2*Y*F - .001*Y)
J=0, J' = .9*.05*2*Y*F - (.5*C + .2*K)*J - .02*.5*J*B -.001*J
C=0, C' = .1*.05*2*Y*F - .2*C*K - .02*C*(.5*Y + .1*B + .5*J) - .001*C
K=0, K' = .02*C*(.5*Y + .1*B + .5*J) - .001*K
A=.1, A' = .02*.9*.5*J*B -.1*K*A- .001*A
P=0, P' = .02*.1*.5*J*B - .1*K*P- .001*P
And the output (not all variables) of this system is shown in Figure 2.

| Parameter	Description	Default
a_F	growth of F	10
a_B	growth of B	1
$a_Y,$	growth of Y	.3
p_{BF}	predation rate of B on F	2
p_{YF}	predation rate of Y on F	2
p_{PB}	predation rate of P on B	.5
p_{AB}	predation rate of A on B	.5
p_{KB}	predation rate of K on B	.1
p_{JB}	predation rate of J on B	.5
p_{JY}	predation rate of J on Y	0
p_{CB}	predation rate of C on B	.1
p_{KY}	predation rate of K on Y	.1
p_{CY}	predation rate of C on Y	.5
p_{PY}	predation rate of P on Y	.1
p_{CJ}	predation rate of C on J	.5
p_{KJ}	predation rate of K on J	.2
p_{KJ}	predation rate of K on C	.2
p_{KP}	predation rate of K on P	.1
p_{KA}	predation rate of K on A	.1
$m_Y,$	maturation rate of Y	.05
m_J	maturation rate of J	.02
m_Y	maturation rate of C	.02
d_B	death rate of B	.001
d_Y	death rate of Y	.001
d_J	death rate of J	.001
d_C	death rate of C	.001
d_P	death rate of P	.001
d_A	death rate of A	.001
d_K	death rate of K	.001
q_{YJ}	probability of maturation of Y into form J	.9
q_{JA}	probability of maturation of J into form A	.9
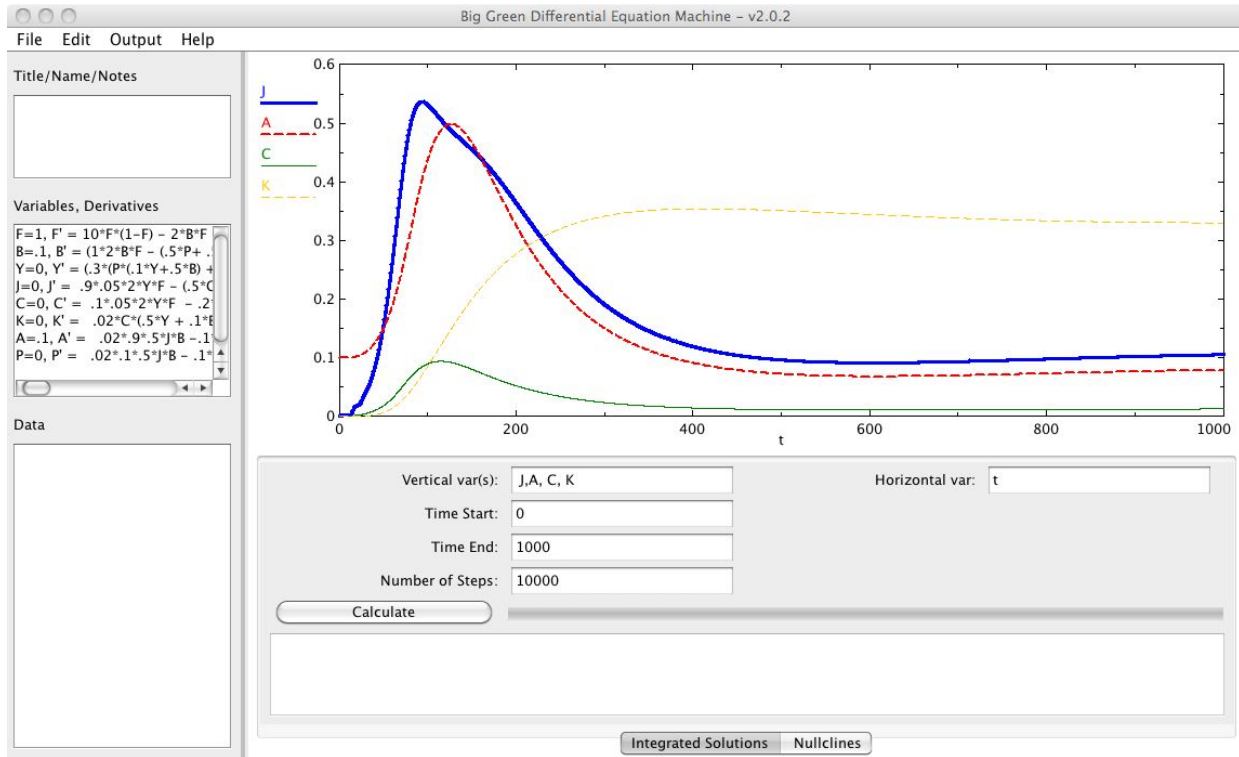
Figure 2: Big Green output with equations as indicated above

4 Mathematical Analysis

All papers will include the basic stability questions about two equilibrium states of the full model with default parameters. One state is the observed equilibrium in Figure 2. The other state is the one with no *Ambystoma* present. (There is a third with all populations set to zero and a fourth with just F.) Please compute equilibrium values, the Jacobian matrix, and eigenvalues for both of these states. You may use Big Green [2], matlab, online matrix calculators, whatever [1]. Extra credit if, by fiddling around with initial conditions, you find equilibrium states besides these three! When you report your Jacobian matrix (there will at least be three, at least one of which is expressed in variables) please put the variables in the order of the equations in this paper. Thanks!

In addition to the basic task of finding the equilibrium values, each team will have their own special research topic. There is overlap between these. For example, topics starting with the same number use the same submodel. Feel free to consult with others, but write your own paper (as a pair).

5 Numerical Methods

In this section you describe what sort of numerical tools you used and what software. This is analogous to the methods section of a lab report. How many runs? Which parameters where tested at what intervals? How did you determine when you found an equilibrium, limit cycle, etc.? All this is described here. You do not want your experiment to be "irreproducible". For numerical runs this means giving the reader enough information to duplicate your results. Include code you wrote as an appendix.

6 Results

Here you summarize your results. What did you find that was interesting? Graphs, tornado diagrams, etc. belong here. DO NOT include hundreds of images of time series runs, but do include one or two. Summarize the aspects of what you found graphically and in a table.

7 Conclusions

Here is where you translate your results into the biological setting. What does it mean if an equilibrium is stable in the full model but becomes unstable when one organism is removed? What are the biological implications of a limit cycle? Were you able to duplicate the results of an experiment? Each group has its own situation to address.

References

[1] DO NOT FORGET TO CITE REFERENCES PROPERLY AND THIS INCLUDES SOFTWARE

[2] BGDEM software, Brian Reed, 2002-2009

[3] Larson KL, W Duffy, E Johnson, MF Donovan, MJ Lannoo, "Paedocannibal" Morph Barred Tiger Salamanders (Ambystoma tigrinum mavortium) from Eastern South Dakota*American Midland Naturalist*, Vol. 141, No. 1 (Jan., 1999), pp. 124-139

[4] http://en.wikipedia.org/wiki/Phenotypic_plasticity

[5] Wissinger, SA, HH Whiteman, M Denoel, ML Mumford, and CB Aubee, Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations, *Ecology* 2010 **91 2** 549-559