Understanding basics of prey-predator interactions

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We consider a **prey-predator** system

$$\frac{dF_1}{dt} = r_1 F_1 \left(1 - \frac{F_1}{K_0}\right) - r_2 F_2 \frac{F_1^n}{h_1^n + F_1^n}$$

$$\frac{dF_2}{dt} = e_2 r_2 F_2 \frac{F_1^n}{h_1^n + F_1^n} - m_2 F_2 - d_2 F_2^2$$

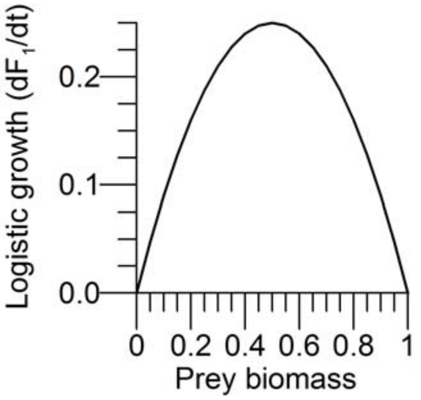
The prey *F1* (e.g. phytoplankton) grows logistically with the growth rate *r1* and the carrying capacity *K0*, consumed by the predator (e.g. zooplankton) according to a feeding response function of either Holling II (*n=1*; hyperbolic) or Holling III (*n=2*; sigmoidal) form with the maximum rate *r2* and half saturation constant *h1*.

The predator assimilates *e2* fraction of the food consumed, is subject to losses due to natural mortality at a rate *m2* and predation by top predators (e.g. fish) at a rate *d2* in linear and quadratic forms, respectively.

The system is characterized by 7 parameters;
r1, *K0 , r2* , *h1*, *e2* , *m2* , *d2*.

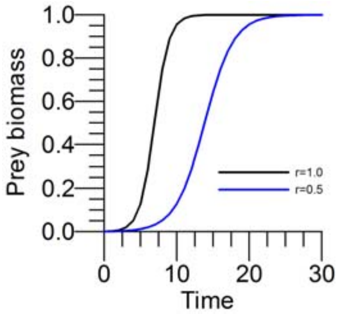
The logistic growth term combines the growth and loss processes;

$$r_1F_1\left(1-\frac{F_1}{K_0}\right)=r_1F_1-r_1\frac{F_1^2}{K_0}=r_1F_1-d_1F_1^2 \qquad (d_1=\frac{r_1}{K_0}) \quad and \quad r_1=r_1^*\cdot f(N,I,T)$$



The loss process is referred to as cannibalism or intraspecific competition (feeding among the population itself).

The growth process includes controlling factors such as nutrient uptake, light and temperature limitations shown by *f(N,I,T)* in the case of phytoplankton.



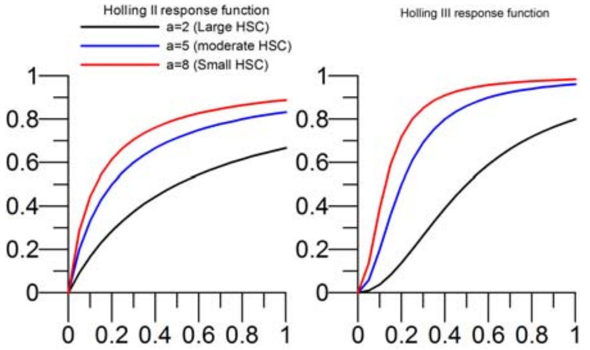
$$r_1F_1\left(1-\frac{F_1}{K_0}\right)=r_1F_1-r_1\frac{F_1^2}{K_0}=r_1F_1-d_1F_1^2$$

IMPLICATIONS:

1) According to the logistic equation, the productivity of prey (*dF1/dt*) is limited by the prey biomass when it is too low.
2) At the other extreme case (i.e. when the prey biomass approaches to the maximum at *K*), productivity tends to decrease due to intraspecific competition.
3) The optimal prey biomass growth is obtained by maintaining the biomass at *F1=K/2*.
4) When plotted versus time, prey biomass grows according to a sigmoidal (Holling type III) curve.
5) The steepest changes occur at half of the carrying capacity.

Holling feeding response functions

1) The value of *n* adjusts steepness of the curve and the value of h_1 adjusts the location of the midpoint of the curve with respect to biomass.
2) Smaller values of *h1* imply more efficient feeding (i.e. predator attains half of the growth by relatively low prey biomass consumption).



$$\frac{F_1^{\,n}}{h_1^n + F_1^{\,n}}$$

3) The Holling II and Holling III response functions are similar except a steeper rise of the curve at low prey biomass for the latter.
4) The latter attains its saturation value close to 1 at lower prey biomass. But this can be compensated by assigning a slightly higher value of the consumption rate in the case of the Holling II function.

How to examine stability properties of the prey-predator system ?

The prey-predator eq's may provide different dynamics like single or multiple stable equilibrium or unstable eq. (limit cycles; i.e. oscillations) depending on the choice of the parameter values.

Isocline analysis:

1) Set prey and predator equations to zero (i.e. dFi/dt = 0)
2) You have 2 eq's and 2 unknowns; express one state variable in terms the other
3) Plot these functions in F1-F2 space.

Setting the right hand side of prey eq. to zero and solving for *F2* as a function of *F1* gives the **prey isocline**

$$H(F_1) = F_2(F_1) = \frac{r_1}{r_2}(1-\frac{F_1}{K_0})\frac{h_1^n + F_1^n}{F_1^{n-1}}$$

Setting the right hand side of predator eq. to zero and solving for *F2* as a function of *F1* yields **predator isocline**

$$P(F_1) = F_2(F_1) = \frac{1}{d_2}\left[e_2 r_2 \frac{F_1^n}{h_1^n + F_1^n} + m_2\right]$$

4) Intersections of these two isoclines gives the points at which biomass growth of both species are zero. These lines divide the state space into the regions with positive and negative biomass growths of the prey and the predator.

5) Stable equilibrium of the prey and predator isoclines requires that the determinant of the Jacobian matrix is positive and transpose of the *Jacobian matrix* is negative.

5a) The first condition implies that the ratio of the slopes of isoclines must be less than one. This condition holds, for example, if *dP/dF1 > dH/dF1* . If this condition does not hold, then the equilibrium point is an unstable point.

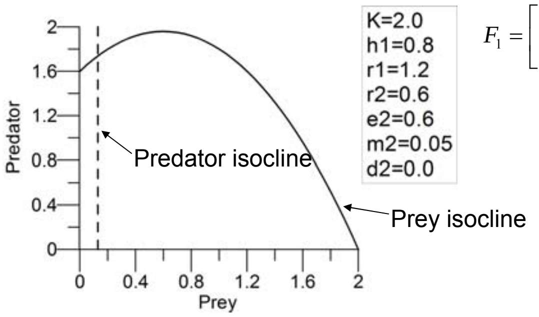
$$CONDITION\,1 \quad : \left(1 - \frac{dH/dF_1}{dP/dF_1}\right) > 0$$

5b) Even the 1st condition is satisfied, we need to check the second condition;

$$CONDITION\,2: \quad r_2\frac{F_1^n}{h_1^n+F_1^n}\left(\frac{dH}{dF_1}\right) - \frac{d}{dF_1}\left(r_2\frac{F_1^n}{h_1^n+F_1^n}\right)\cdot\frac{F_2}{\left(\dfrac{dP}{dF_1}\right)} < 0 \quad \text{must be}$$

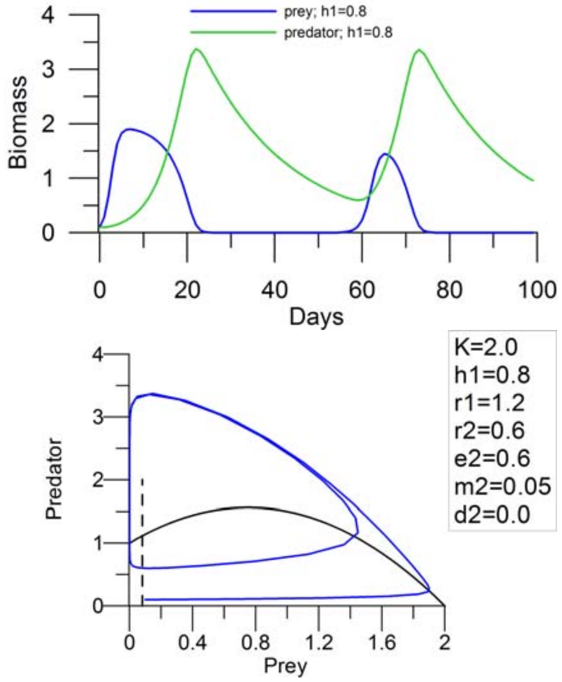
EXAMPLE: We choose n=1 (i.e. Holling II response function), and first examine the case with *d2=0.*

In the absence of the quadratic mortality term (*d2*=0), there will be no predator isocline as a function of F1, and it will be simply vertical lines (parallel to *F2* axis) at prey biomass values given by



$$F_1 = \left[\frac{\alpha h_1^2}{(1-\alpha)}\right]^{1/n} \quad where \quad \alpha = \frac{m_2}{e_2 r_2}$$

In our example, 1/(*dP/dF1*) ≡ 0 which makes the 2nd conditionpositive. The intersection point of the isoclines therefore represents an unstable equilibrium in which both prey and predator biomass oscillates in time. In other words, prey-predator system exhibits a limit cycle solution.



K=2.0
h1=0.8
r1=1.2
r2=0.6
e2=0.6
m2=0.05
d2=0.0

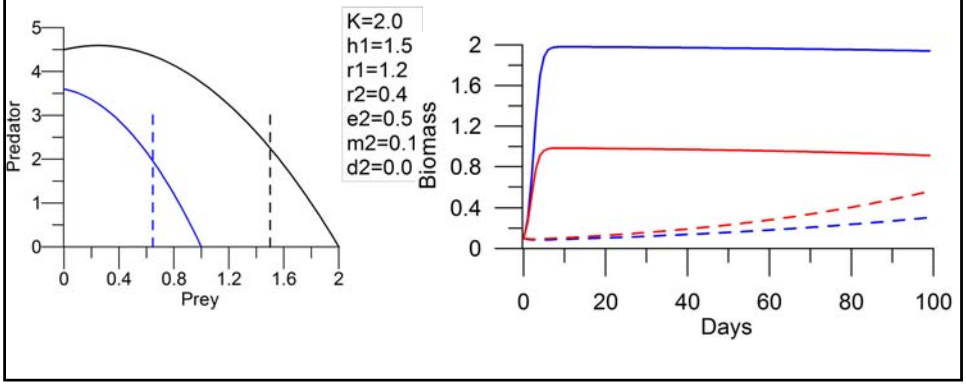
HOW TO STABILIZE THIS SYSTEM ?

According to this stability conditions, an unstable prey-predator system can be made stable if the intersection point is moved to the right hand side of the peak of the prey isocline where the slope of the prey isocline is negative.

HOW ?

1) by changing α and/or h1 in $F_1 = \left[\frac{\alpha h_1^2}{(1-\alpha)} \right]^{1/n}$ *where* $\alpha = \frac{m_2}{e_2 r_2}$ $(\alpha > 1)$

For example, (see the BLACK CURVE below)



K=2.0
h1=1.5
r1=1.2
r2=0.4
e2=0.5
m2=0.1
d2=0.0

Although the parameters setting given in the previous figure make the system stable, the values are quite unrealistic for zooplankton.

WHAT IS an alternative way of making the system stable ?

2) Change the prey isocline in such a way that its peak will shift to the left in such a way that the predator isocline should cross the prey isocline on the decreasing part of the curve.

Shifting the prey isocline to the left implies reducing carrying capacity (i.e. poorly productive system).
See BLUE CURVE IN THE PREVIOUS PLOT

WHAT IS IMPLICATION OF CHANGING THE CARRYING CAPACITY PARAMETER, K ?

We saw that increasing the carrying capacity (i.e. enrichment of the system) destabilizes the prey-predator system.
This was first pointed out by Rosenzweig in the 1960s, and called the "*paradox of enrichment*".

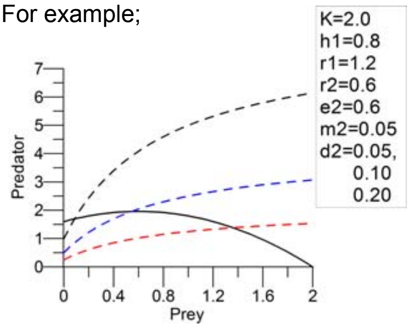
WHAT IS THE PARADOX?

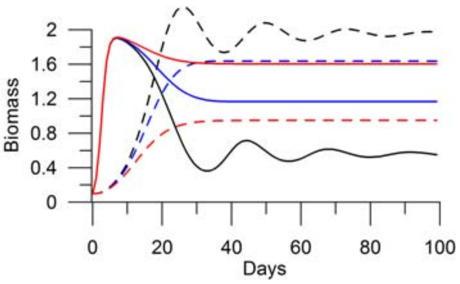
Such effects however hardly takes place in nature. Therefore, these oscillations generally reflect some missing processes in the model that make the system stable in nature.

3) Another mechanism for stability of the prey-predator system is to add the predation effect of higher predators (e.g. fish).
This is parameterized in our model by the quadratic mortality term.
If we repeat the previous example with the additional fish predation effect (i.e. d2 ≠ 0). Then, the predator isocline takes the form

$$P(F_1) = F_2(F_1) = \frac{1}{d_2}\left[e_2 r_2 \frac{F_1^n}{h_1^n + F_1^n} + m_2 \right]$$

For example;





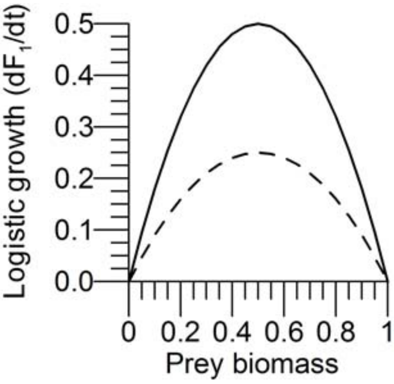
Thus, addition of the quadratic loss term to the predator equation stabilizes the solution and gives an single equilibrium of the system.

The next question:
whether such a prey-predator system can possess more than one equilibrium state for the same parameter set ?

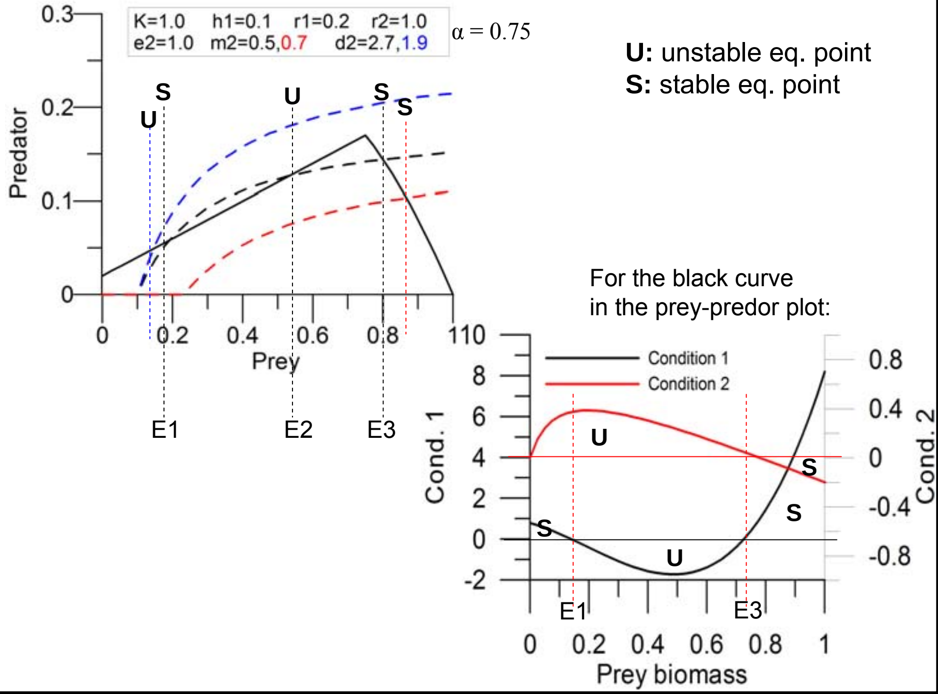
ANOTHER EXAMPLE: Consider a slightly modified system
in which the logistic growth is reduced by α.
(This parameter reduces the peak value of the logistic curve but keeps the envolope same).

$$\frac{dF_1}{dt} = r_1 F_1 \left(\frac{K_0 - F_1}{K_0 - \alpha} \right) - r_2 F_2 \frac{F_1}{h_1 + F_1}$$

$$\frac{dF_2}{dt} = e_2 r_2 F_2 \frac{F_1}{h_1 + F_1} - m_2 F_2 - d_2 F_2^2$$



where we further assume that the logistic growth function obeys
a(F1) = r1.F1 if F1<α
Otherwise ($F_1 \geq \alpha$) as given in eq. 1.



U: unstable eq. point
S: stable eq. point

For the black curve
in the prey-predor plot:

$$\frac{dF_1}{dt} = r_1F_1\left(\frac{K_0 - F_1}{K_0 - \alpha}\right) - r_2F_2\frac{F_1}{h_1 + F_1}$$

$$\frac{dF_2}{dt} = e_2r_2F_2\frac{F_1}{h_1 + F_1} - m_2F_2 - d_2F_2^2$$

STAB1 $CONDITION\,1 \quad : \left(1 - \frac{dH/dF_1}{dP/dF_1}\right) > 0$

$CONDITION\,2:$
STAB2

$$r_2\frac{F_1^n}{h_1^n + F_1^n}\left(\frac{dH}{dF_1}\right) - \frac{d}{dF_1}\left(r_2\frac{F_1^n}{h_1^n + F_1^n}\right)\cdot\frac{F_2}{\left(\frac{dP}{dF_1}\right)}$$

X1a=F1,
x2a=F2 $H(F_1) = F_2(F_1) = \frac{r_1}{r_2}(1 - \frac{F_1}{K_0})\frac{h_1^n + F_1^n}{F_1^{n-1}}$

X1b=F1
X2b=F2 $P(F_1) = F_2(F_1) = \frac{1}{d_2}\left[e_2r_2\frac{F_1^n}{h_1^n + F_1^n} + m_2\right]$

Summary:

$$\frac{dF_1}{dt} = r_1F_1\left(1-\frac{F_1}{K_0}\right) - r_2F_2\frac{F_1^n}{h_1^n+F_1^n}$$

J. H. Steele and E. W. Henderson (1981), The American Naturalist, 117(5), 676-691.

$$\frac{dF_2}{dt} = e_2r_2F_2\frac{F_1^n}{h_1^n+F_1^n} - m_2F_2 - d_2F_2^2$$

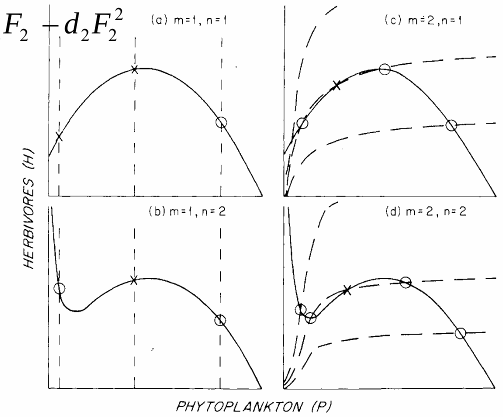


FIG. 4.—Phase plots of the equilibrium conditions for P and H from eqq. (4) and (5) with $m = 1, 2$; $n = 1, 2$. Solid line gives solutions with $dP/dt = 0$; dashed line gives solutions of $dH/dt = 0$ with a range of values of d. Intercepts marked by circles are stable equilibria; crosses indicate unstable equilibria.

J. H. Steele and E. W. Henderson (1981), The American Naturalist, 117(5), 676-691.

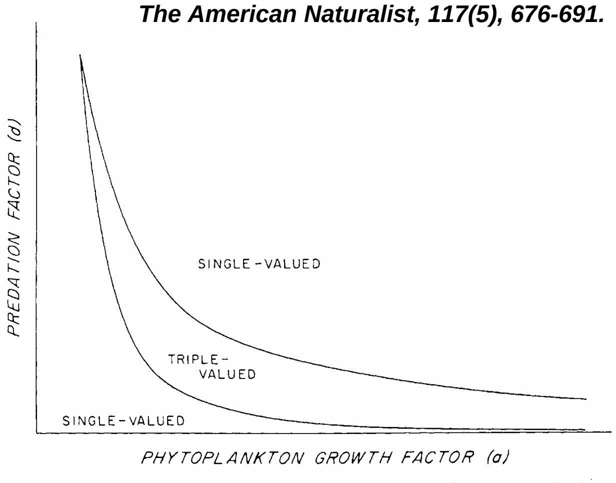
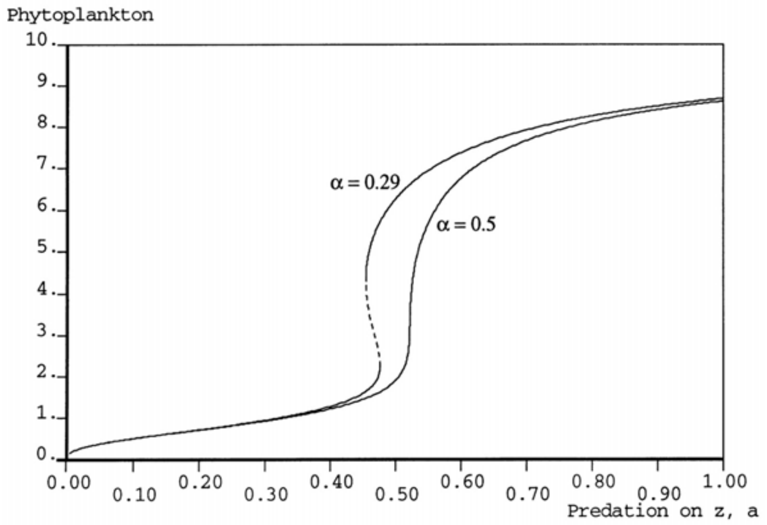


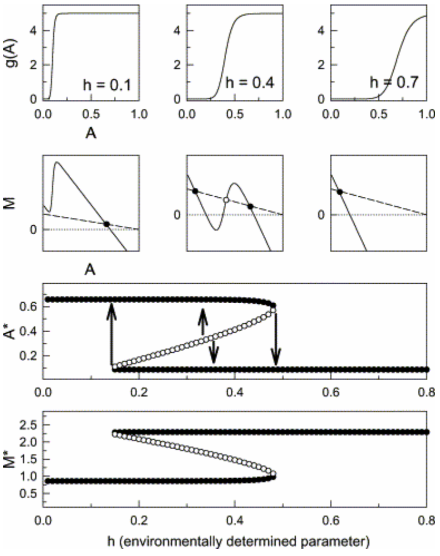
FIG. 7.—The relations between a and d which define the regions where single- and triple-valued solutions of eqq. (4) and (5) exist. Changes in a and d which transfer the system across the triple-valued region cause very large changes in P and H.

Edwards, A. M. et al. (2000) J. Plankton Res. 22, 1085-1112

The phytoplankton steady-state value changes as the predation on zooplankton, a, is increased. A solid line indicates where a steady state is stable, and a dashed line where it is unstable. Hysteresis occurs for = 0.29.



P. S. Petraitisa, S. R. Dudgeon (2004) Detection of alternative stable states in marine communities Journal of Experimental Marine Biology and Ecology, 300, 343– 371.



Mussels and seaweeds as alternative states in a model with a bifurcation fold.

Top row gives plots of g(A) vs. A at three values of h.

Middle row shows phase diagrams and zero isoclines for mussels (dashed lines) and seaweeds (solid lines) for three values of h.

Bottom two rows give plots of equilibrium values for seaweeds (A) and mussels (M*) vs. h.*

Solid dots are stable equilibrium points; open dots are unstable equilibrium points.