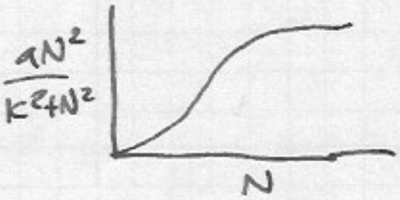
7.1

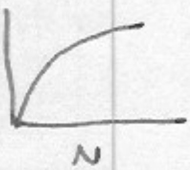
Generalized Modeling of Biological Systems

Density dependent growth of a single species

$$\frac{d}{dt}N = \underbrace{\frac{aN^2}{K^2+N^2}} - bN \qquad \text{OR} \qquad \frac{dN}{dt} = \underbrace{\frac{aN}{1+N}}_{\text{Type II}} - bN$$



- Type III
- growth is very low when N is very low
- Maximized (saturated) as N increases.
- Reproductive success requires 'aggregates'



Generalize the problem

$$\frac{d}{dt}N = S(N) - D(N)$$

★ This may be more accurate in terms of our knowledge of the system...

But the problem is in the analysis!

1) Solve for F.P.

$$\emptyset = S(N) - D(N)$$

$$S(N) = D(N)$$ — can't solve for N^*!

Define a new variable N^*

1) It is assumed to be positive
2) Not a placeholder for a value to be filled in later, but a formula surrogate for
   (*) EVERY POSITIVE STEADY state in the class of systems represented by $\dot{N} = S(N) - D(N)$

What determines the stability of N^*?

The derivative... which we will now start calling an eigenvalue:

$$\lambda = \frac{\partial}{\partial N}\dot{N} = \underbrace{\left.\frac{\partial S(N)}{\partial N}\right|_*}_{} - \underbrace{\left.\frac{\partial D(N)}{\partial N}\right|_*}_{}$$

These are unknown parameters in the system.

BUT hard to interpret biologically (slope of function @ fixed point)

we will use the identity:

$$\left.\frac{\partial S(N)}{\partial N}\right|_* = \frac{S(N^*)}{N^*} \left.\frac{\partial \log S(N)}{\partial \log N}\right|_* \Bigg\} \text{ holds for all } \begin{cases} S(N^*) > \varnothing \\ N^* > \varnothing \end{cases}$$

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$$\frac{\partial S(N)}{\partial N}\bigg|_* = \frac{S(N^*)}{N^*}\frac{\partial \log S(N)}{\partial \log N}\bigg|_* \quad \text{multiply by } \frac{\partial S(N)}{\partial S(N)}$$

$$= \frac{S(N^*)}{N^*}\frac{\partial \log S(N)}{\partial S(N)}\frac{\partial S(N)}{\partial \log N}$$

$$* \text{ where } \frac{\partial \log S(N)}{\partial S(N)}\bigg|_* = \frac{1}{S(N^*)}$$

(Proof of the relationship)

$$= \frac{1}{N^*}\frac{\partial S(N)}{\partial \log N}\bigg|_* \quad \text{multiply by } \frac{\partial N}{\partial N}$$

$$= \frac{1}{N^*}\underbrace{\frac{\partial N}{\partial \log N}}\frac{\partial S(N)}{\partial N}\bigg|_*$$

Define $N = e^u$ or $\log N = u$

$$\frac{\partial N}{\partial (\log N)}\bigg|_* = \frac{\partial e^u}{\partial \log e^u}\bigg|_* = \frac{\partial e^u}{\partial u}\bigg|_* = e^u\big|_* = N^*$$

$$= \frac{1}{N^*}N^*\frac{\partial S(N)}{\partial N}\bigg|_* = \frac{\partial S(N)}{\partial N}\bigg|_* \quad \text{QED}$$

Back to the problem

$$\frac{\partial S(N)}{\partial N}\bigg|_* = \frac{S(N^*)}{N^*}\frac{\partial \log S(N)}{\partial \log N}\bigg|_* \quad \underline{\underline{\text{and}}} \quad \frac{\partial D(N)}{\partial N}\bigg|_* = \frac{D(N^*)}{N^*}\cdot\frac{\partial \log D(N)}{\partial \log N}$$

Substitute to get! [also, notation is! $S(N^*) = S^*$]

$$\lambda = \frac{S^*}{N^*}\frac{\partial \log S}{\partial \log N} - \frac{D^*}{N^*}\frac{\partial \log D}{\partial \log N}$$

These are constants b/c functions evaluated @ steady state N^*

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we have taken

$$\frac{dN}{dt} = S(N) - D(N) \quad \text{and given} \begin{cases} n = \frac{N}{N^*} \\ s(n) = \frac{S(N)}{S(N^*)} \\ d(n) = \frac{D(N)}{D(N^*)} \end{cases}$$

so:

$$S(N) = S(N^*)\,s(n)$$

$$D(N) = D(N^*)\,d(n)$$

$$\frac{dn}{dt} = \frac{S(N^*)}{N^*}s(n) - \frac{D(N^*)}{N^*}d(n)$$

At ~~eq~~ steady state....

$$n = s(n) = d(n) = 1$$

unnormalized all steady states to 1

so we have

$$\emptyset = \frac{S(N^*)}{N^*} - \frac{D(N^*)}{N^*}$$

$$\alpha = \frac{S^*}{N^*} = \frac{D^*}{N^*}$$

Scale parameter

elasticities

$$\frac{dn}{dt} = \alpha\left[s(n) - d(n)\right]$$

$$\lambda = \alpha\left[\frac{\partial s(n)}{\partial n} - \frac{\partial d(n)}{\partial n}\right]$$

Characteristic

α is the timescale of the system

$$\frac{d}{dn}s(n) = \left.\frac{\partial \log S}{\partial \log N}\right|_* = \frac{N^*}{S(N^*)}\frac{\partial S(N)}{\partial N}$$

and given $\alpha = \frac{S^*}{N^*}$

we arrive back @

$$\lambda = \frac{\partial S(N)}{\partial N} - \frac{\partial D(N)}{\partial N}$$

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$$\frac{dn}{dt} = \alpha\left[S(n) - d(n)\right]$$

if $\alpha \uparrow$ bigger chge (faster)

if $\alpha \downarrow$ ~~slower~~ smaller chge (slower)

Now lets focus on the stability
- a function of elasticities

$$\lambda = \alpha\left(\frac{\partial}{\partial n}S(n) - \frac{\partial}{\partial n}d(n)\right) = \alpha\left(s_n - d_n\right)$$

Consider the Logistic

$$\frac{dN}{dt} = \underbrace{rN}_{S(N)} - \underbrace{\frac{rN^2}{K}}_{D(N)}$$

$$\frac{\partial}{\partial n}S(n) = \frac{N^*}{S(N^*)}\frac{\partial S(N)}{\partial N}\bigg|_* = \frac{N^*}{rN^*}r = 1$$

$$\frac{\partial}{\partial n}d(n) = \frac{N^*}{D(N^*)}\frac{\partial D(N)}{\partial N}\bigg|_* = \frac{N^*}{(rN^{*2}/K)}\frac{2rN}{K}\bigg|_* = \frac{1}{rN^*/K}\frac{2rN^*}{K} = 2$$

NOTE: This is independant of steady state!

Generally, the elasticity is related to the power of the function...

And stability is determined by the combined influence of elasticities

Consider Function $F(x) = aX^P$

$$f(x) = \frac{F(X)}{F(X^*)} = \frac{aX^P}{aX^{*P}} = x^P$$

$$\left.\frac{\partial f(x)}{\partial x}\right|_{x=1} = p x^{1-p} = p$$

If we know the elasticities of functions....

or the general range of elasticities...

We can say a lot about stability w/o knowing much about the system

Ex) $$\frac{d}{dt}N = \underbrace{\frac{aN^2}{k^2+N^2}}_{S(N)} - \underbrace{bN}_{D(N)}$$ $\left[\lambda = \alpha\left[s_N - d_N\right]\right]$

$D(N) \rightarrow$ know elasticity is $= 1$

$$s_N = \frac{N^*}{S(N^*)}\frac{\partial S(N)}{\partial N}$$

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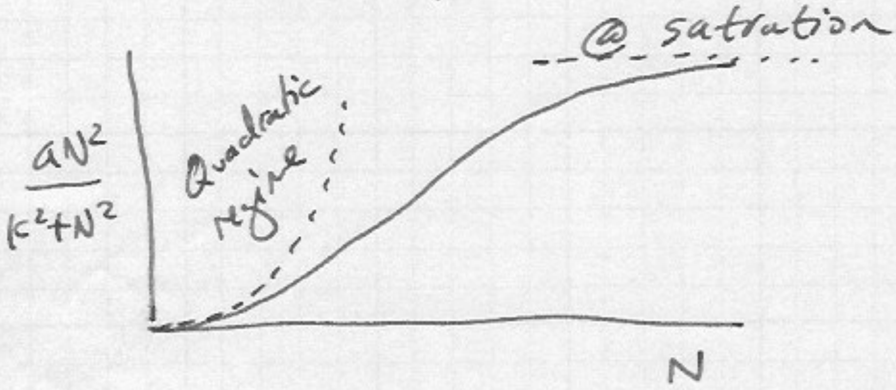
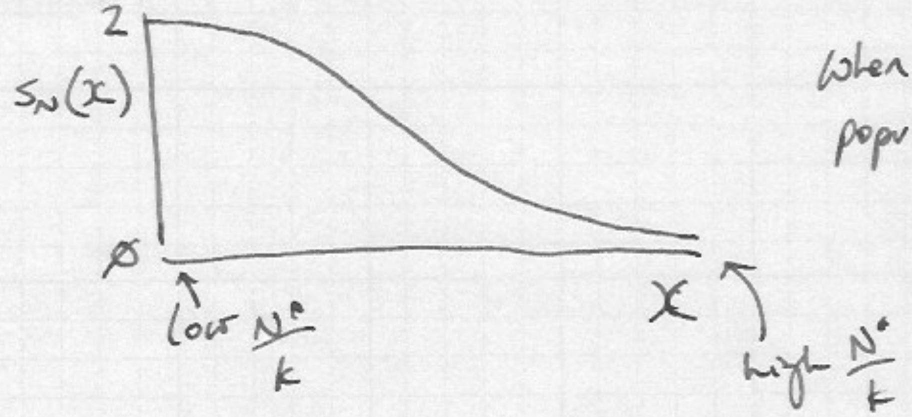
$$S_n = \frac{N^*}{S(N^*)} \frac{\partial S(N)}{\partial N}\Big|_*$$

$$= \cancel{\frac{1}{N^*}} \frac{k^2+N^2}{\alpha N^{*2}} \left(\frac{2\alpha k^2 \cancel{N^*}}{(k^2+N^2)^2}\right)$$

$$= \frac{2k^2}{k^2+N^2} \qquad x = \frac{N^*}{k}$$

$$S_n = \frac{2}{\left(1+\frac{N^2}{k^2}\right)} = \frac{2}{(1+x^2)}$$





When the steady state population is small

$S_n \to 2$

When the steady state population is large

$S_n \to Ø$

7-8.

Compare bifurcations when $a=b=1$

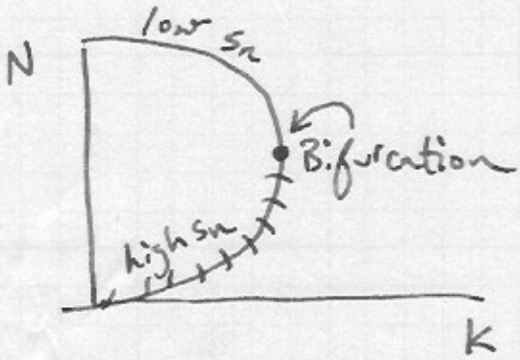
$$\frac{dN}{dt} = \frac{N^2}{K^2+N^2} - N \quad \text{vs.} \quad \frac{dN}{dt} = S(N) - D(N)$$

F.P. @ $\cancel{\Rightarrow}$ $\dfrac{N}{K^2+N^2} = 1$

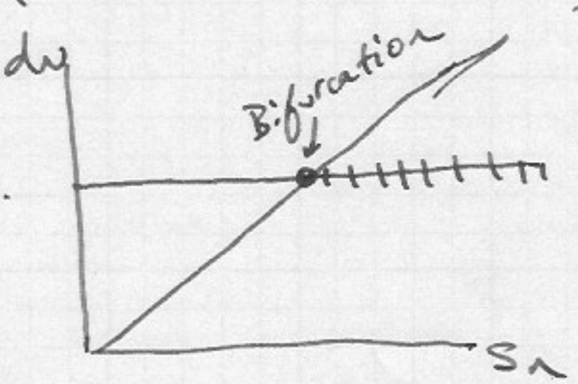
$$N - N^2 = K^2$$

$$N(1-N) = K^2$$

$$N^* = \frac{1}{2}\left(1 \pm \sqrt{1-4K^2}\right)$$



vs.



B/c dn is set, and sn varies.

- In conventional model, different numbers of steady states are found depending on specific functional form chosen.
- for a given set of parameter values multiple steady states can coexist that differ in stability.

Gen model: Gives insight into stability boundary present for All models

- Conventional model: more insight into dynamics (Allee effect) but only applies to specific model