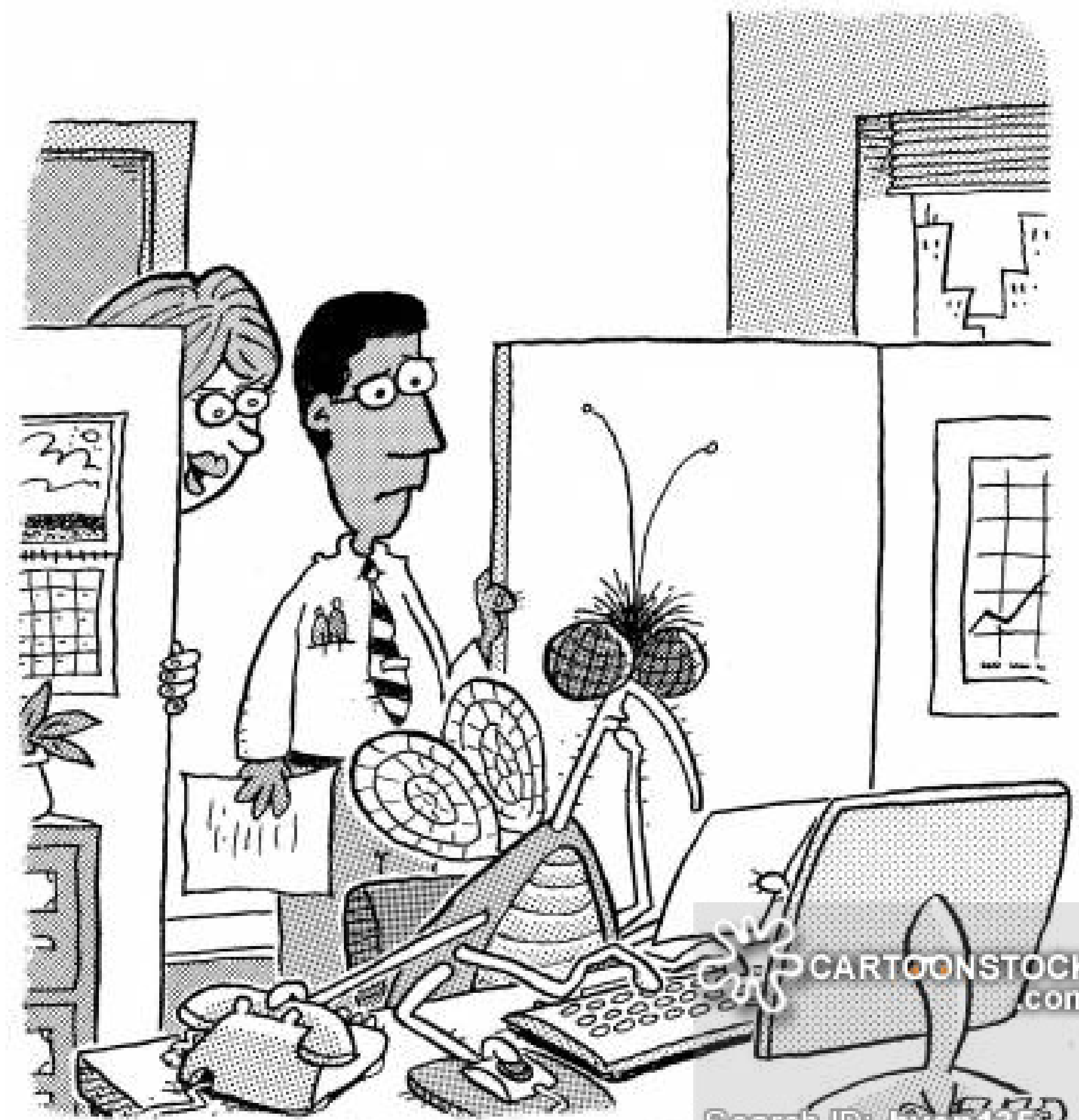
Stock-recruitment Part II

Reading:

Jennings et al. 2001. Marine Fisheries Ecology, Chapter 4 (section 4.2)

Advanced: Quinn and Deriso 1999, Chapter 3

"Stock recruitment funny"



"They're the ideal temp workers! Easy to train, industrious, punctual... And with a 13-day life-span, they conveniently die before collecting a paycheck!"

Recap: Stock-recruitment models

Models

- 1. Density Independent
- 2. Beverton-Holt
- 3. Ricker
- 4. Shepherd
- 5. Hockey stick
- Others…

- What did BH model look like?
- What is compensation?
- How does density dependence play into BH model?

William E. Ricker

Extra

3. Ricker Model

- Based on idea of density-dependence acting on the **adults**
  - Change in juv. abundance (N) affected by total mortality, Z
  - Assume Z described by linear function of *spawner abundance (S)*, affected by density independent (a) and density dependent (b) parameters
  - Leads to nonlinear differential equation (see Quinn and Deriso for solution)

$$\frac{dN}{dt} = -ZN$$

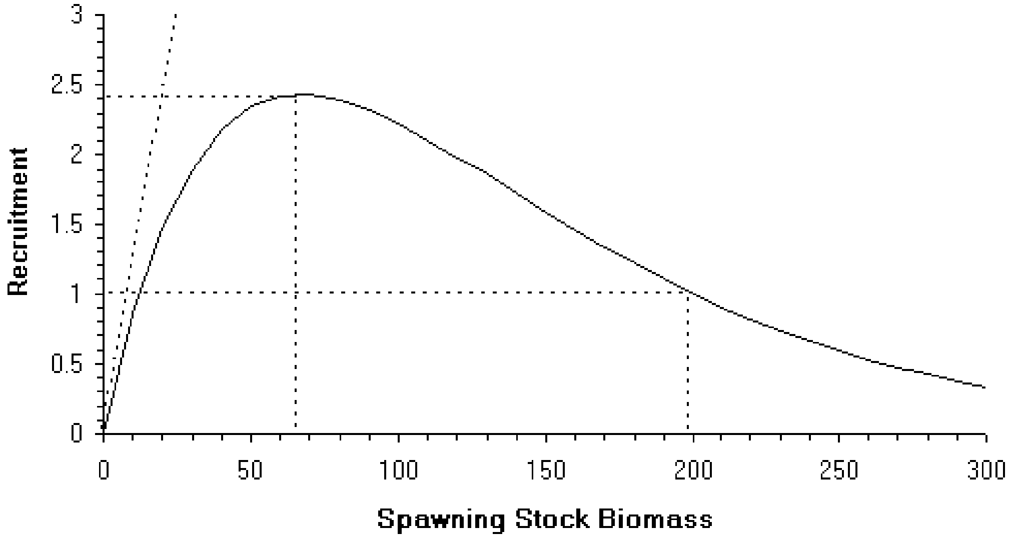
$$Z = a + bS$$

$$\frac{dN}{dt} = -(a + bS)N$$

3. Ricker Model

$$\boxed{R = aSe^{-bS}}$$

R



S

- R = number (or biomass) of recruiting individuals
- S = number (or biomass) of spawners
- a = productivity parameter (number of R per S at low S)
- b = parameter for degree of density dependence

- Basic property: “hump” shaped with declining R at higher S

3. Ricker Model

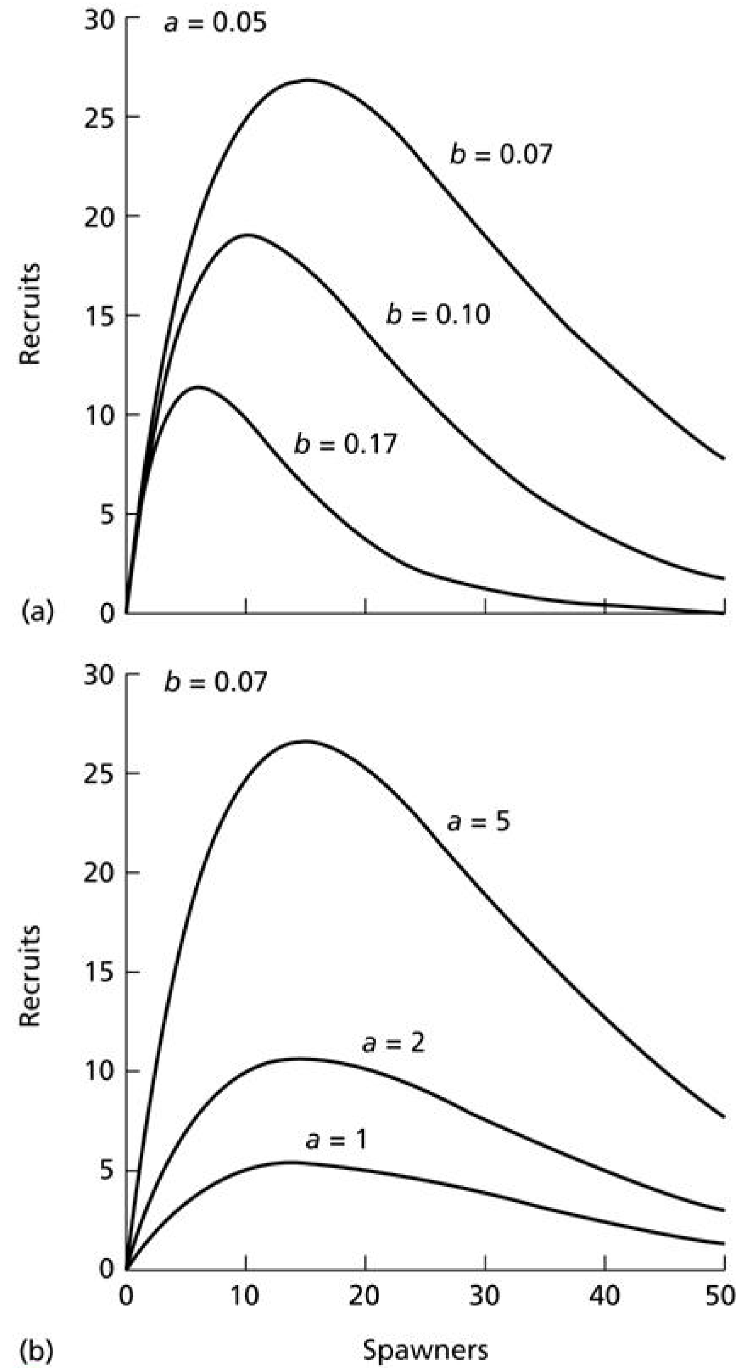
- Effects of changing parameters

$$\boxed{\mathrm{R} = aSe^{-bS}}$$

  - Maximum mean R occurs at S=1/b

- Alternative parameterization you might see:

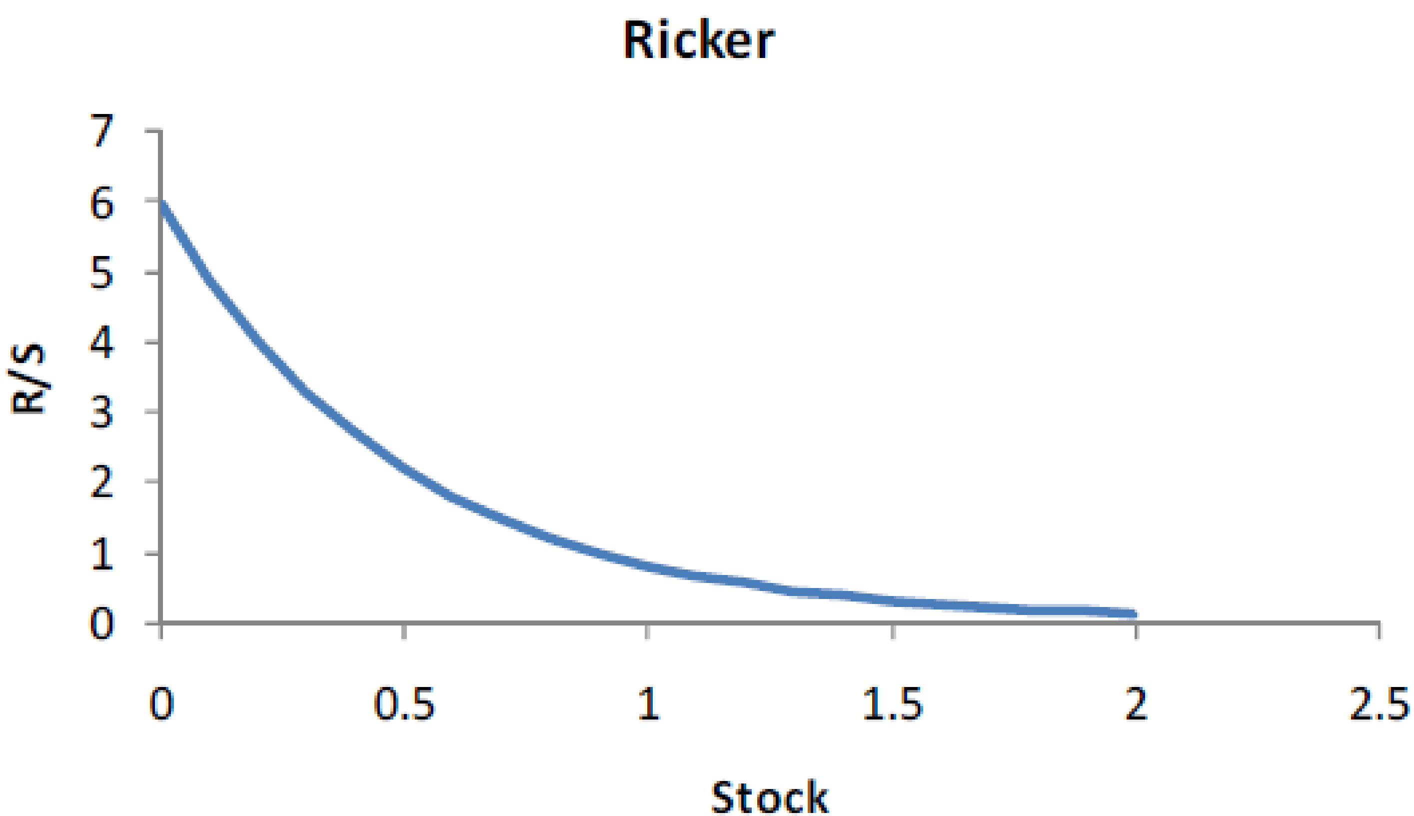
$$\mathrm{R} = Se^{a'-bS}$$



Jennings, Kaiser, Reynolds

3. Ricker Model

- What does survival proxy (R/S) look like?
  - Like, BH, has stabilizing effect on population at low S

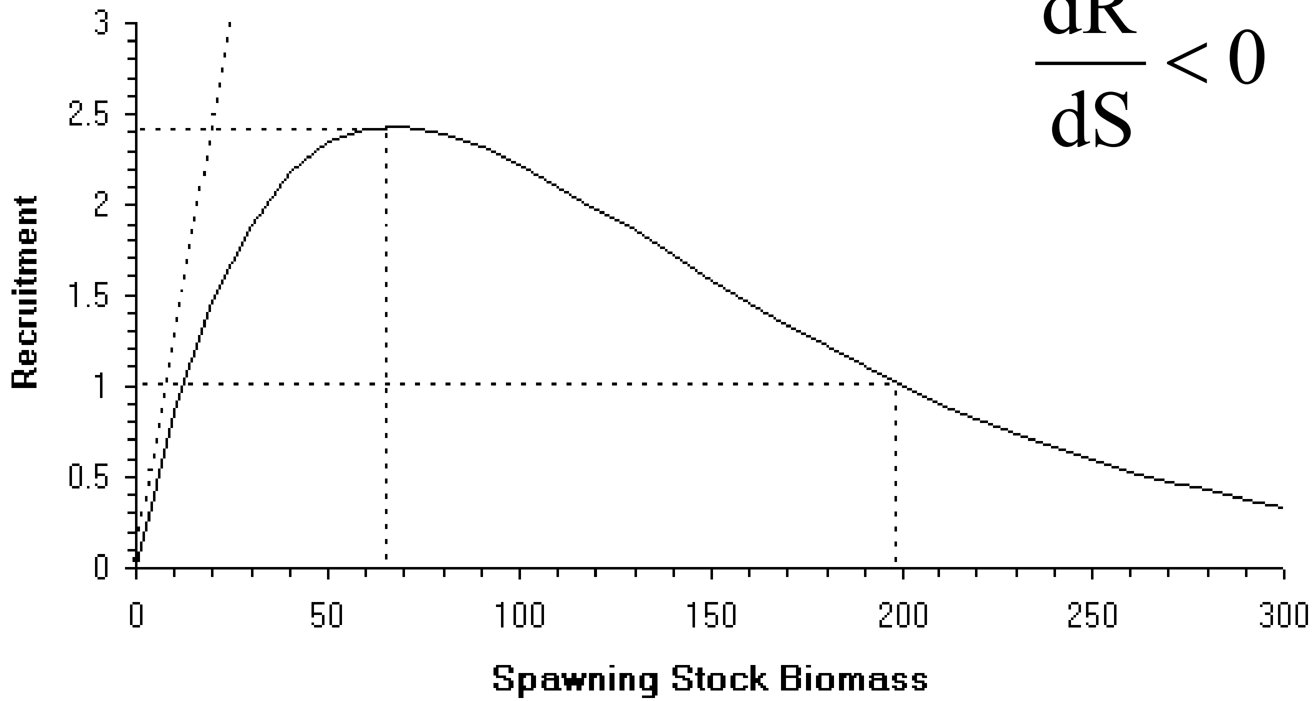


Ricker – overcompensation

- **Overcompensation** – decrease in recruitment with increasing spawning stock

$$\frac{dR}{dS} < 0$$

R



S

Ricker Overcompensation

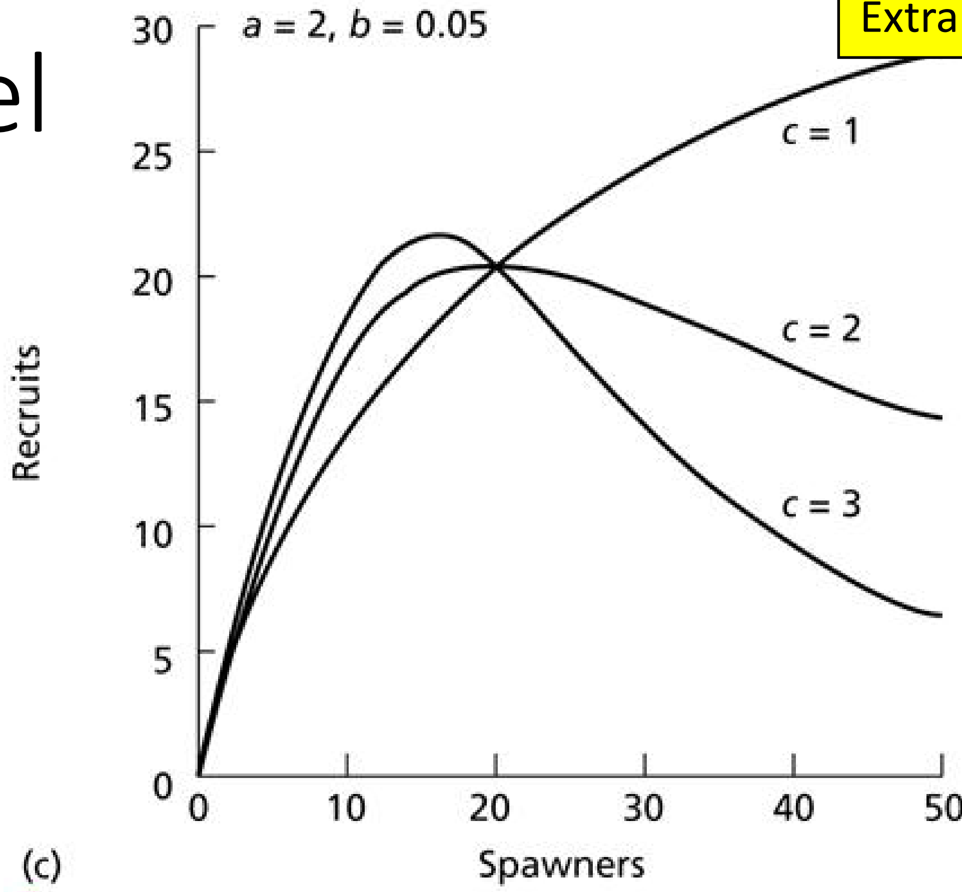
- Recruitment decreases at large stock sizes
- **Some possible causes:**
  - 1. Cannibalism of juveniles by adults
  - 2. Disease transmission from adults to juveniles
  - 3. Oxygen limitations due to heavy egg deposit that affects all eggs
  - 4. Spawning site damage by adults
  - 5. Density dependent growth with size-dependent predation

4. Shepherd Model

Extra

- Generalizing equation

$$R = \frac{aS}{1 + (bS)^c}$$



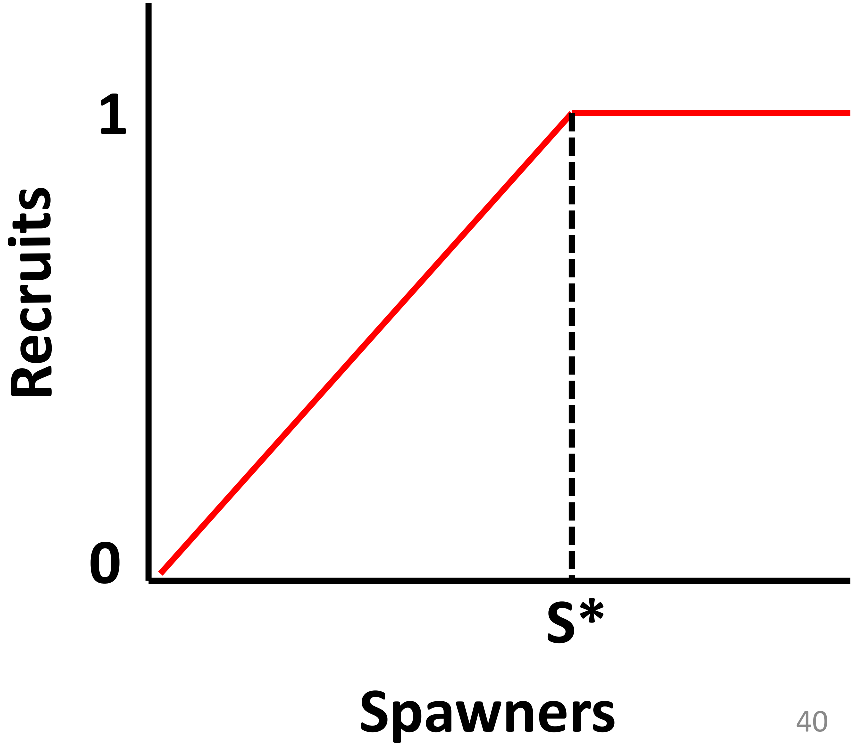
- a = productivity parameter (number of R per S at low S)
- b = parameter for degree of density dependence
- c = shape parameter
  - c<1: density-independent; c=1: Beverton-holt; c>1: Ricker shape
- Basic property: generalizing equation for other model shapes

Extra

5. Hockey stick model

- Segmented (change-point) regression
  - Slope a > 0 at the origin;
  - Slope a = 0 beyond pivotal spawner level, S*

$$R_t = \begin{cases} aS_t & \text{if } S_t < S^* \\ aS^* & \text{if } S_t \geq S^* \end{cases}$$



Stock-recruitment models

- Most common
  - Ricker
  - Beverton-Holt
- Others
  - Shepherd
  - Deriso-Schnute
  - Cushing
  - “Hockey-stick”
  - Unnormalized gamma density
  - Many others

Fitting Stock-recruitment models

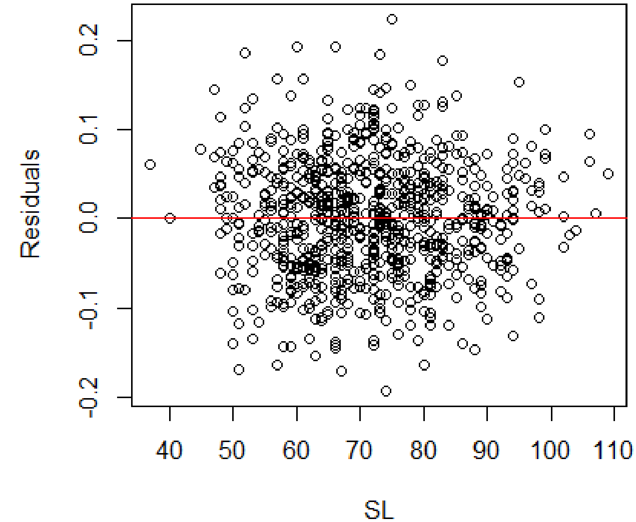
- Recommend using nonlinear regression
- Making the following assumptions:
  - No error in our estimate of S
  - Independent errors*
- But, model equation will depend on whether error is assumed to be additive or multiplicative

*see Quinn and Deriso 1999 (section 3.2) for “measurement error approach” and “autocorrelated errors” if these assumptions are grossly inappropriate

Additive vs. multiplicative error

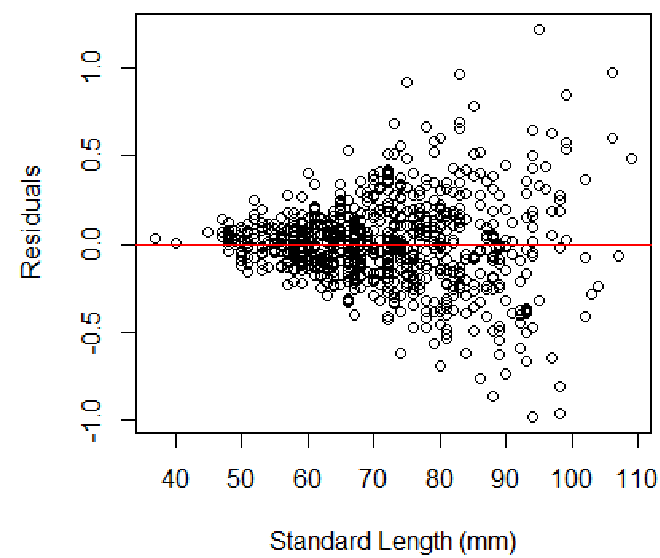
- Additive error
  - for a given model, the residuals will tend to have constant variance
  - Doesn't violate regression assumption of Homogeneity of Variance (HOV)

$$Y = f(X) + \varepsilon$$



- Multiplicative error
  - for a given model, the residuals will increase with higher values of X
  - This violates the HOV assumption for regression→ so log-transform equation to use regression

$$Y = f(X) \cdot e^{\varepsilon}$$



Log transforming to deal with multiplicative error

- Recall our example using W-L allometric model:

$$W = aL^b e^{\varepsilon}$$

Log-transform both sides of equation

$$\log(W) = \log(aL^b e^{\varepsilon})$$

Algebra

$$\log(W) = \log(a) + b \cdot \log(L) + \varepsilon$$

Now, the error is "additive" in our model, so we can use regression and OLS

Fitting Stock-recruitment models

- Our approach
  - use nonlinear regression (and OLS)
  - The equation we fit with nls() will depend on whether we assume additive or multiplicative error
  - *Multiplicative error is typically more appropriate for SR data*
- If using multiplicative error (& log transformation) → must use bias correction
  - Back transforming (i.e. exponentiating) estimates from log space introduces bias
  - *Bias correction*: multiply the back-transformed predicted values by a correction factor (CF), which depends on the standard error of the estimate (SEE; aka Residual SE)

Quinn and Deriso 1999, section 3.2

Fitting Stock-recruitment models

- Our approach

<u>Equations to fit using nonlinear regression</u>

More common!

	Additive error	**Multiplicative error** (log of R=f(S)e$^{\varepsilon}$ → log(R)=log(f(S))+ ε)
Density Independ.	$R = aS + \varepsilon$	$\ln(R) = \ln(aS) + \varepsilon$
Beverton Holt	$R = \dfrac{aS}{1 + bS} + \varepsilon$	$\ln(R) = \ln(aS/(1 + bS)) + \varepsilon$
Ricker	$R = aSe^{-bS} + \varepsilon$	$\ln(R) = \ln(aSe^{-bS}) + \varepsilon$

Note: “ln” is “natural log”, which in R, is written just as “log()”

Quinn and Deriso 1999, section 3.2

Fitting Stock-recruitment models

Example: Ricker Model with Multiplicative Error

$$\mathrm{R} = aSe^{-bS}e^{\varepsilon}$$

Log-transform

$$\ln(\mathrm{R}) = \ln(aSe^{-bS}) + \varepsilon$$

Fit using nonlinear regression, and estimate parameters:

$$\hat{a}, \hat{b}, \hat{\sigma}_{\varepsilon}^{2}$$

Back-transform & bias-correct

$$\hat{\mathrm{R}} = \hat{a}Se^{-\hat{b}S} \cdot e^{(\hat{\sigma}_{\varepsilon}^{2}/2)}$$

$$\mathrm{SEE} = \hat{\sigma}_{\varepsilon}^{2} = \sqrt{\frac{\Sigma(\mathrm{obs.} - \mathrm{pred.})^2}{\mathrm{n - (nos.\ parameters)}}}$$

Note: In R, SEE is the "residual standard error". Value stored in: summary(MyModel)$sigma

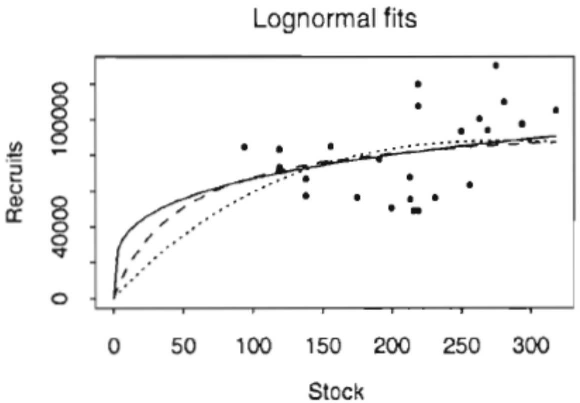
$$CF = e^{(\hat{\sigma}_{\varepsilon}^{2}/2)} = e^{(SEE/2)}$$

Sprugel 1983, Quinn and Deriso 1999

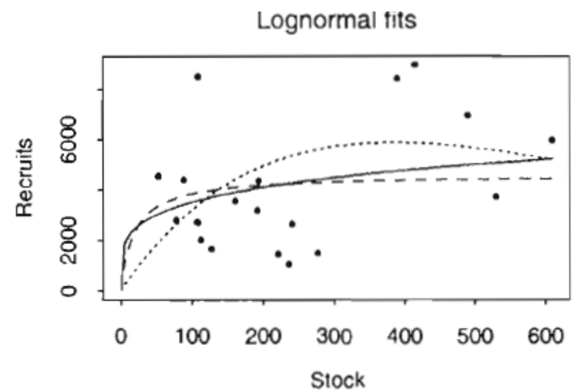
Examples of SR model fits

Thoughts? Why are fits so poor?

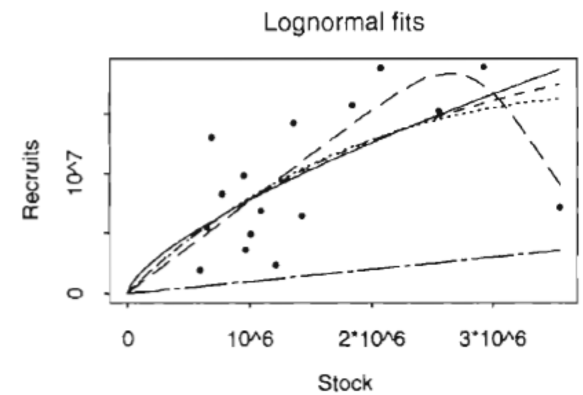
Yellowfin tuna
(Thunnus albacares)

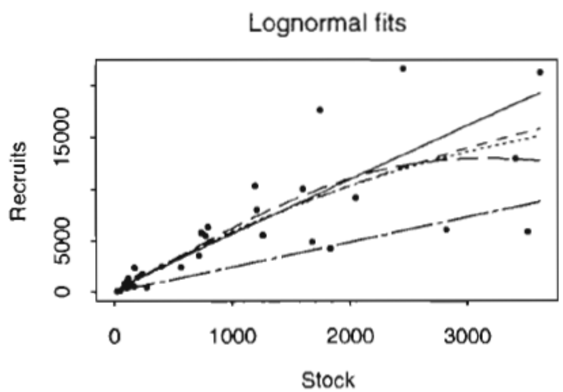


Petrale sole
(Eopsetta jordani)

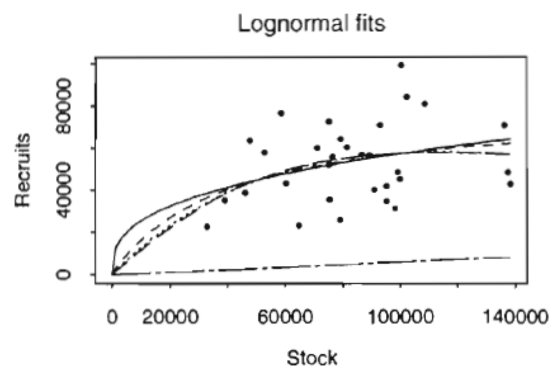


Pink salmon (Fraser river)
(Oncorhynchus gorbuscha)

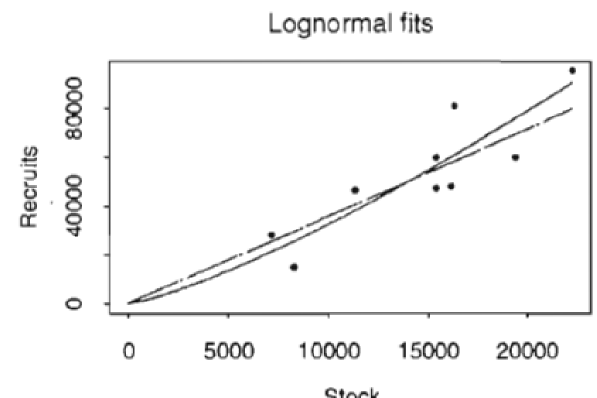




CA Sardine
(Sardinops sagax)



Atlantic cod (NAFO 3Ps)
(Gadus morhua)

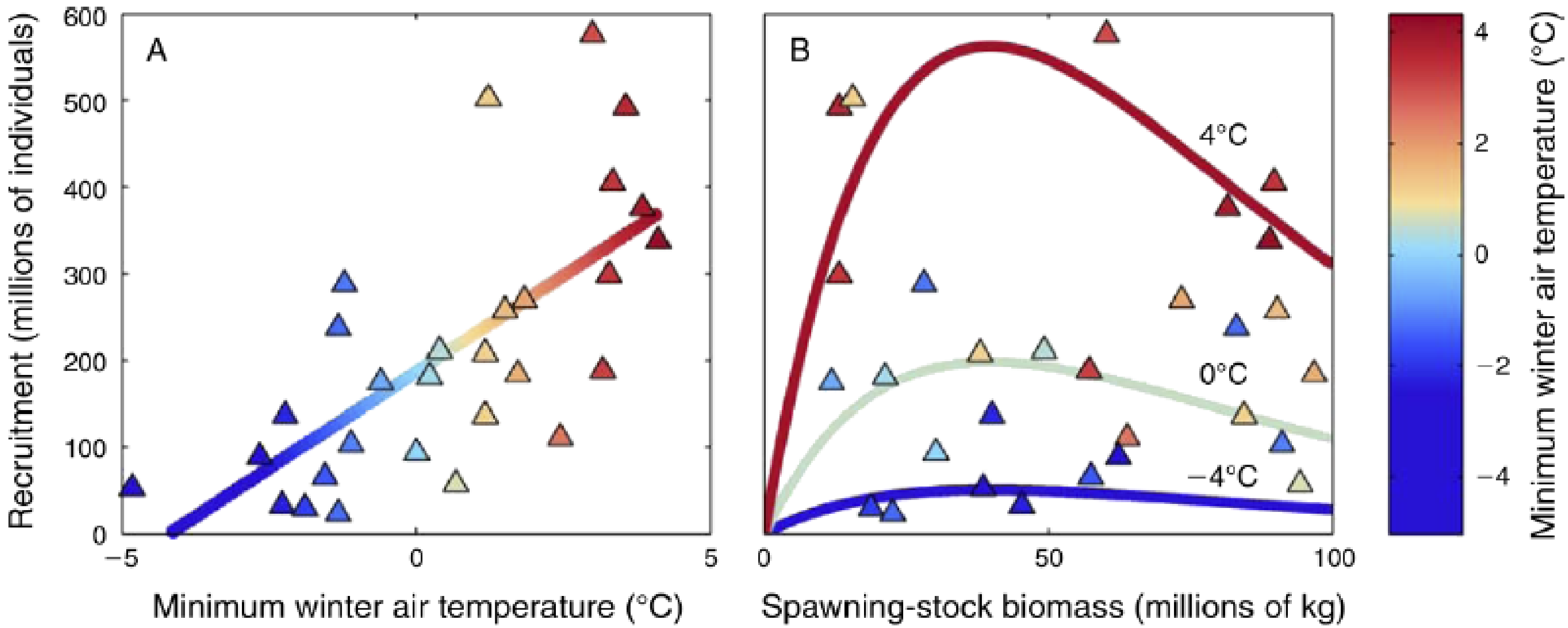


Summer flounder
(Paralichthys dentatus)

Myers et al. 1995

Some modifications to S-R Models

- Possible to build in environmental effects (e.g., temp for Atlantic Croaker)
- Account for error in S estimates
  - see Quinn & Deriso, Section 3.2.3



Hare et al. 2010

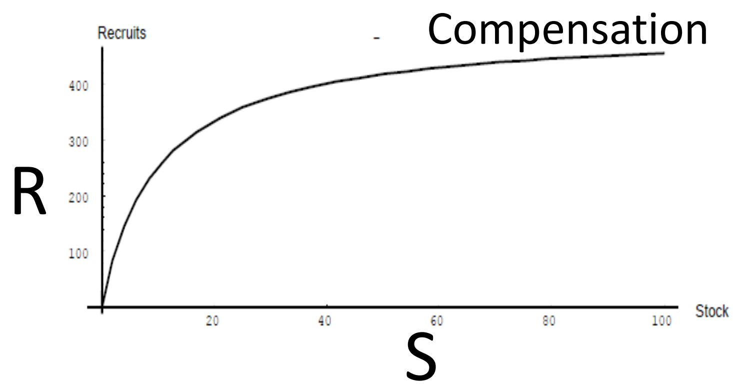
Summary

- Stock recruitment models
  - Relate the production of recruits to adult spawning stock
  - Critical for forecasting, assessing, and managing populations
  - Typically account for some type of density-dependence (DD)
  - Fits can be rather poor → lots of uncertainty
- Know definitions:
  - **Stock, Recruitment, Density dependence, Compensation**
- Stock recruitment models
  - **Beverton-Holt**
  - **Ricker**
  - Shepherd – Generalization of other models
  - “Hockey-stick”
  - Many others (Deriso-Schnute, Cushing, …)
- Fitting models
  - For us: assume multiplicative error (if have HOV problem) → log-transform model → use nonlinear regr. → back-transform & bias correct

Summary of BH and Ricker models

Beverton Holt

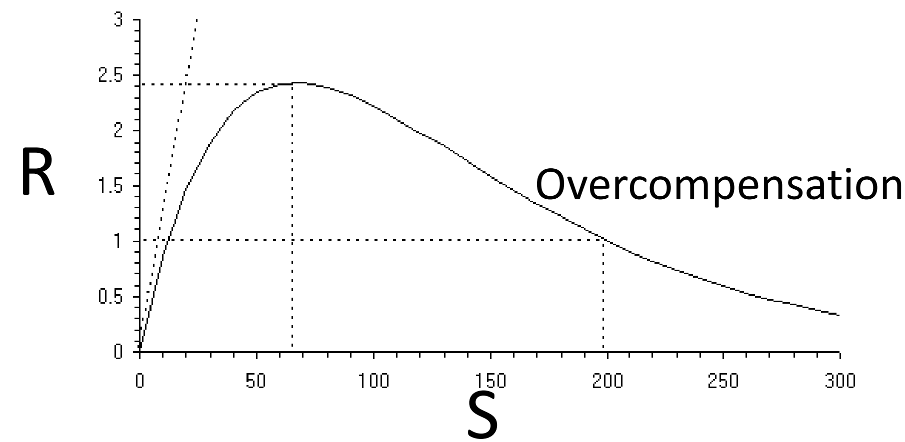
$$R = \frac{aS}{1+bS}$$



- Density dependence
  - Acts via juvenile stage (*know examples*)
- Parameters
  - a = productivity parameter
  - b = density dependence
- Shape: asymptotic

Ricker

$$R = aSe^{-bS}$$



- Density dependence
  - Acts via adult stage (*know examples*)
- Parameters
  - a = productivity parameter
  - b = density dependence
- Shape: dome