Stock-recruitment and reference points

Equilibrium reference point math

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Objectives

1. Understand how density dependence shapes population growth and identify the biological meaning of MSY, Bmsy, and Umsy for logistic population models (pen and paper)
2. Introduce common age-structured fish population model equations
3. Practice per-recruit and and equilibrium calculations for age-structured fish populations (R)
4. Practice equilibrium reference point calculation for age-structured fish populations (R)

The Knight and *Death* in The Seventh Seal by Ingmar Bergman

Logistic population growth

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right)$$

- r is the intrinsic population growth rate, K is carrying capacity, B is biomass
- Who here is good at math

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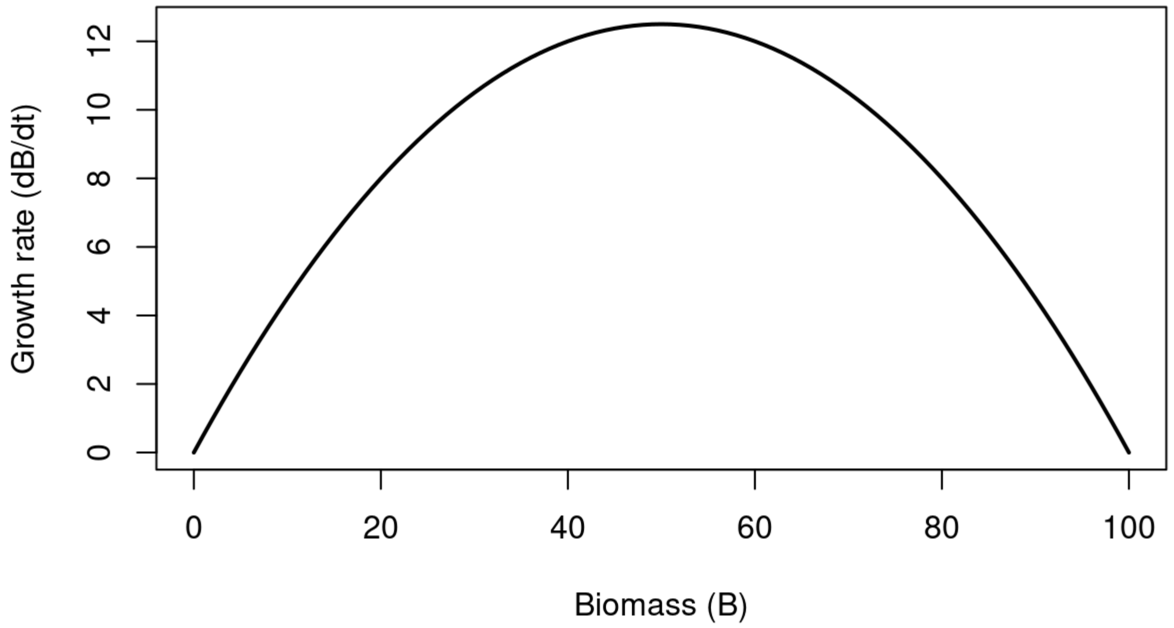
- Groups of three
- Do the math to calculate biomass at maximum sustainable yield (Bmsy), maximum sustainable yield (MSY), and exploitation rate at maximum sustainable yield (Umsy)

Logistic population growth: hints

```r
r <- 0.5
K <- 100
B <- 0:K # pick a range of B
dBdt <- r * B * (1 - B / K) # simulate dymamics
plot(B, dBdt,
  type = "l", lwd = 2,
  xlab = "Biomass (B)",
  ylab = "Growth rate (dB/dt)"
)
```



Logistic population growth: hints

- You need to add in a yield term (call it Y) to the equation and rearrange it
- Differentiate Y with respect to B
- Set the solution equal to zero and solve it (find the root)
- Use your solution to calculate MSY and Umsy

- **Bonus**. What happens if you repeat this exercise for the model:

$$\frac{dB}{dt} = rB$$

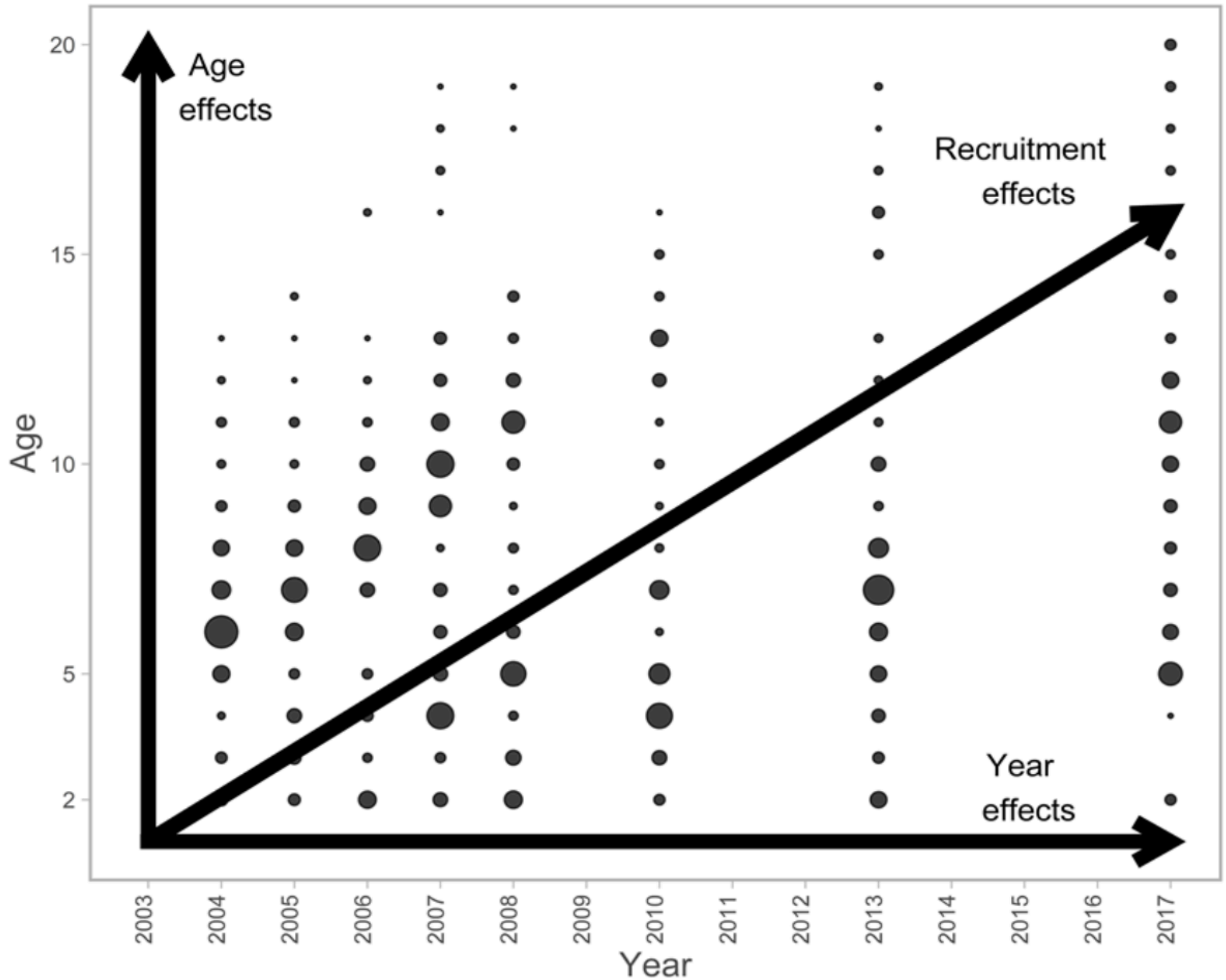
Death from The Seventh Seal by Ingmar Bergman

Why on earth are we doing this?

1. Analytic solution is the best solution if it exists
2. Biological reference points are not arbitrary, but rather emerge from biology of the system in question (or at least the models representing those systems)
3. More complicated models have yield vs. biomass curves that skew left or right (develop intuition)
    - Whales (often) skew right, fish (often) skew left
4. Density dependence (i.e., compensation) as ***the*** ecological basis for sustainable harvesting
5. Dependence of reference points on difference aspects of ecology
    - Bmsy vs. Umsy
6. Many critiques of MSY use this caricature of MSY
    - What are the problems of this approach, and does it have any value in modern fisheries management?

see also Larkin et al. 1977; Hilborn et al. 1995; 2015

Adding complexity: age-structure



Paloheimo's 'design effects' in catch at age data; Alberta Walleye

Age-structure

- Many of the ecological processes affecting fish are size dependent
- Maturity and variable reproductive output
- Somatic growth
- Mortality
- Vulnerability

- Where does density dependence enter a typical age-structured fish population dynamics model?

see methods in e.g., Hilborn and Walters 1992; Quinn and Deriso 1999

Age-structure

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- Where does density dependence enter a typical age-structured fish population dynamics model?
- Why?

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Equilibrium calculations in age-structured models

- Botsford and Wickham (1979) and Botsford (1981a, 1981b) developed a clever way to do many of the important equilibrium calculations needed for an age-structured analysis of fish population responses to harvesting
- Approach integrates ‘per-recruit’ methods with stock-recruitment
- Involves using survivorship-to-age-calculations in conjunction with age schedules of size, vulnerability, and fecundity to calculate equilibrium “incidence functions”
- Each incidence function represents a sum over ages of some quantity like fecundity, weighted by survivorship
  - Recognize survivorship is the net probability of surviving to some age

Walters and Martell 2004 box 3.1

Survivorship in the fished condition

- The following recursion captures the cumulative effect of fishing and natural mortality on animals as they age:

$$\mathrm{lx}_a = \begin{cases} 1 & \text{if } a = 1 \\ \mathrm{lx}_{a-1} \cdot e^{-Z_{a-1}} & \text{if } 2 \le a < a_{\max} \\ \dfrac{\mathrm{lx}_{a_{\max}-1} \cdot e^{-Z_{a_{\max}-1}}}{1 - e^{-Z_{a_{\max}}}} & \text{if } a = a_{\max} \end{cases}$$

where:

$$Z_a = F \cdot \mathrm{vul}_a + M$$

- F and M are instantaneous fishing and natural mortality
- Z is total instantaneous mortality
- vul_a is the vulnerability of an individual of age a to fishing

Walters and Martell 2004 box 3.1

Plus group misery 😭

For the plus group, we sum all untracked survivors:

$$\mathrm{lx}_{a_{\max}} = \sum_{j=1}^{\infty} \mathrm{lx}_{a_{\max}-1} \cdot e^{-Z_{a_{\max}-1}} \cdot \left(e^{-Z_{a_{\max}}}\right)^{j-1}$$

This is a geometric series with:

$$\sum_{j=0}^{\infty} r^j = \frac{1}{1-r}, \quad \text{where } r = e^{-Z_{a_{\max}}}$$

So:

$$\mathrm{lx}_{a_{\max}} = \mathrm{lx}_{a_{\max}-1} \cdot e^{-Z_{a_{\max}-1}} \cdot \frac{1}{1-e^{-Z_{a_{\max}}}} = \frac{\mathrm{lx}_{a_{\max}-1} \cdot e^{-Z_{a_{\max}-1}}}{1-e^{-Z_{a_{\max}}}}$$

Myers 2002

Survivorship in the fished condition cont'd

- A population at equilibrium with R recruits at age-1 should have $R \cdot lx_{a=2}$ age two year olds, and $R \cdot lx_{a=3}$ three year olds, etc.
- The annual egg production of the population at that fished equilibrium is then

$$\mathrm{ef} = \mathrm{R} \cdot \sum_{a=1}^{a_{max}} \mathrm{lx}_a \cdot \mathrm{f}_a$$

- where f_a is average fecundity at age
- Incidence function approach allows us to write important quantities, e.g., spawner biomass per recruit in the fished condition (sbrf):

$$\mathrm{sbrf} = \sum_{a=1}^{a_{max}} \mathrm{lx}_a \cdot \mathrm{w}_a \cdot \mathrm{mat}_a$$

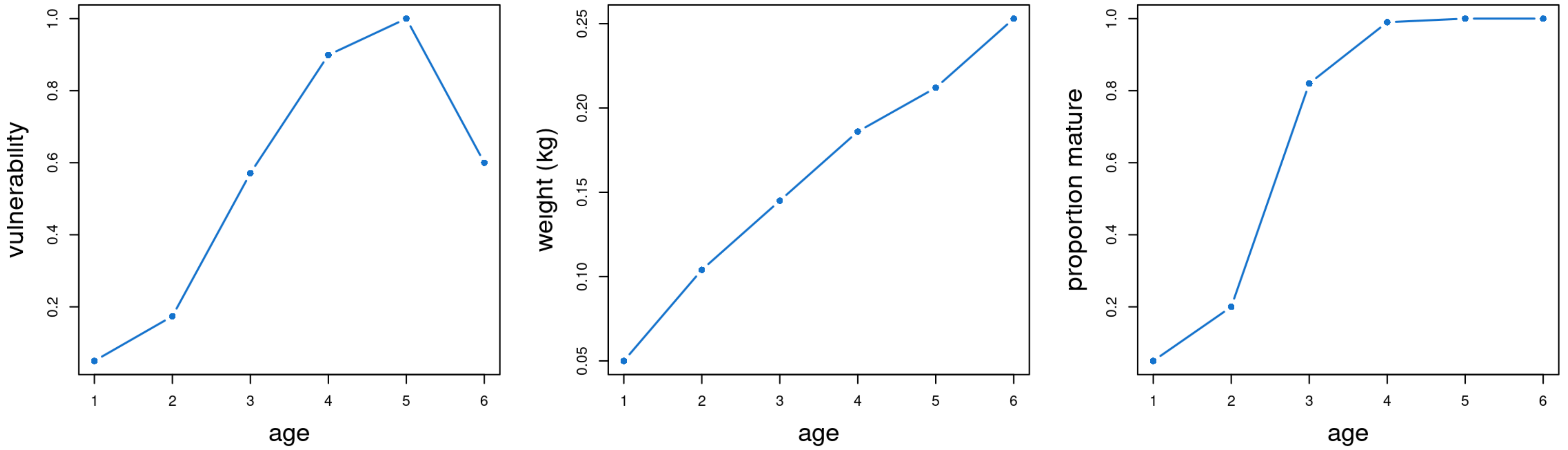
- Which is the average amount of spawner biomass that one recruit produces over its lifetime given this survivorship schedule, where w_a and mat_a are weight and proportion mature at age

Walters and Martell 2004 box 3.1

sbrf exercise

- Calculate spawner biomass per recruit in the fished condition (sbrf)
- Assume a plus group

```r
# life history vectors
vul <- c(0.05, 0.174, 0.571, 0.899, 1.000, 0.6) # vulnerability at age
wa <- c(0.05, 0.104, 0.145, 0.186, 0.212, 0.253) # weight at age
mat <- c(0.05, 0.20, 0.82, 0.99, 1.00, 1.00) # maturity at age
M <- 0.4 # instantaneous natural mortality
F <- 0.1 # instantaneous fishing mortality
```




```
My sbrf solution = 0.2729171
```

The power of Botsford incidence functions

- If we distinguish between survivorship in the fished lx_a and unfished lo_a condition, a blank canvas awaits

$$\mathrm{sbrf} = \sum_{a=1}^{a_{max}} \mathrm{lx}_a \cdot \mathrm{w}_a \cdot \mathrm{mat}_a$$

vs.

$$\mathrm{sbro} = \sum_{a=1}^{a_{max}} \mathrm{lo}_a \cdot \mathrm{w}_a \cdot \mathrm{mat}_a$$

- Can you use this logic to calculate vulnerable biomass per recruit in the fished and unfished condition (i.e., vbrf, vbro)?
- What about vulnerable biomass in the fished and unfished condition (i.e., vbf, vbo)?
- Recognize that in the literature these get different symbols i.e., ef vs. ϕ_e

Walters and Martell 2004 box 3.1

Botsford's most useful trick

- At any fished equilibrium, we can write the amount of spawner biomass generated on average as a function of the life history vectors weighted by the probability of surviving to each of those ages (i.e., as a function of F)

$$\mathrm{S} = \mathrm{R} \cdot \mathrm{sbrf}$$

- Allows us to re-write the Beverton-Holt and Ricker stock recruitment curves in terms of equilibrium recruitment given some fully vulnerable F

$$\mathrm{R} = \frac{\alpha \mathrm{S}}{1 + \beta \mathrm{S}} \quad \text{where} \quad \mathrm{S} = \mathrm{R} \cdot \mathrm{sbrf} \Rightarrow \quad \mathrm{R} = \frac{\alpha \cdot \mathrm{R} \cdot \ \mathrm{sbrf}}{1 + \beta \cdot \mathrm{R} \cdot \ \mathrm{sbrf}}$$

- And solving for equilibrium R:

$$\mathrm{R} = \frac{\alpha \cdot \mathrm{sbrf} - 1}{\beta \cdot \mathrm{sbrf}}.$$

Botsford's trickery with Beverton-Holt 😈🤓🤢

- Parameterizing stock-recruitment in terms of Ro and recK
- Consider a population at unfished equilibrium

$$\mathrm{So} = \mathrm{Ro} \cdot \mathrm{sbro}$$

- So and Ro are spawner biomass and recruitment at unfished equilibrium, so recruits per spawner in the unfished state is

$$\mathrm{recK} = \frac{\text{recruits per spawner biomass at low density}}{\text{recruits per spawner biomass at unfished density}}$$

$$\alpha \quad \text{is defined as recruits per spawner biomass at low density}$$

$$\frac{R_0}{S_0} = \frac{1}{\mathrm{sbro}} \quad (\text{recruits per spawner biomass at unfished density})$$

$$\Rightarrow \quad \alpha = \frac{\mathrm{recK}}{\mathrm{sbro}}$$

Myers and Barrowman 1999; 2002

Botsford's trickery with Beverton-Holt 😈🤓🤢

- Calculating β from Ro, sbro, and recK:

$$\mathrm{R} = \frac{\alpha \mathrm{S}}{1 + \beta \mathrm{S}} \quad \text{where} \quad \mathrm{So} = \mathrm{Ro} \cdot \mathrm{sbro} \Rightarrow \quad \mathrm{Ro} = \frac{\alpha \cdot \mathrm{Ro} \cdot \ \mathrm{sbro}}{1 + \beta \cdot \mathrm{Ro} \cdot \ \mathrm{sbro}}$$

- And solving for β:

$$\beta = \frac{\alpha \cdot \mathrm{sbro} - 1}{\mathrm{Ro} \cdot \mathrm{sbro}}.$$

Exercise: equilibrium recruitment

- Calculate equilibrium recruitment across a range of F values from low to high, plot R vs. F and R vs. S

```r
# life history vectors
vul <- c(0.05, 0.174, 0.571, 0.899, 1.000, 0.6) # vulnerability at age
wa <- c(0.05, 0.104, 0.145, 0.186, 0.212, 0.253) # weight at age
mat <- c(0.05, 0.20, 0.82, 0.99, 1.00, 1.00) # maturity at age
M <- 0.4 # instantaneous natural mortality
recK <- 5 # goodyear compensation ratio
Ro <- 10 # equilibrium unfished recruitment

n_ages <- length(mat) # number of age classes
ages <- 1:n_ages
# set up total instantaneous mortality at age Za vector
Za <- F * vul + M # F set to some arbitrary value (e.g., 0.1)
# calculate survivorship in the fished state
lx <- numeric(n_ages)
lx[1] <- 1 # initialize
for (i in 2:n_ages) lx[i] <- lx[i - 1] * exp(-Za[i - 1]) # calculate lx recursively
lx[n_ages] <- lx[n_ages - 1] / (1 - exp(-Za[n_ages])) # plus group correction
sbrf <- sum(lx * mat * wa)

# calculate survivorship in unfished state (i.e., F = 0)
lo <- numeric(n_ages)
lo[1] <- 1
for (i in 2:n_ages) lo[i] <- lo[i - 1] * exp(-M)
lo[n_ages] <- lo[n_ages - 1] / (1 - exp(-M)) # plus group
sbro <- sum(lo * mat * wa)
```

Suffering Knight from The Seventh Seal by Ingmar Bergman

One more equation: yield per recruit

- Recall that at equilibrium

$$\mathrm{S} = \mathrm{R} \cdot \mathrm{sbrf}$$

- Equilibrium yield (Y) can be defined as a function of fully vulnerable instantaneous fishing mortality (F):

$$Y(F) = R(F) \cdot \mathrm{YPR}(F)$$

- Where R(F) is recruitment as a function of fishing mortality and yield per recruit (YPR) is specified as

$$\mathrm{YPR}(F) = \sum_{\mathrm{a}=1}^{\mathrm{a_{max}}} \frac{\mathrm{w_a} \cdot \mathrm{vul_a} \cdot \mathrm{F}}{\mathrm{Z_a}} \cdot \mathrm{lx_a} \cdot \left(1 - \mathrm{e}^{-\mathrm{Z_a}}\right)$$

- Do people want to try and calculate equilibrium yield as a function of F? 🤔

Beverton and Holt 1957; Walters 1986

Equilibrium F_{MSY} and MSY calculations in age-structured fisheries models

- May help to think of it as a multi-step procedure:

$$\begin{array}{c}\text{Estimate}\\\text{stock-recruitment \&}\\\text{life history}\\\text{parameters}\end{array} \Rightarrow \begin{array}{c}\text{Compute}\\\text{equilibrium}\\\text{recruitment}\\R^*(F)\end{array} \Rightarrow \begin{array}{c}\text{Calculate}\\\text{equilibrium}\\\text{yield}\\Y^*(F)\end{array} \Rightarrow \begin{array}{c}\text{Solve for } F \text{ that}\\\text{maximizes } Y^*(F)\end{array}$$

- Find the F that maximizes Y:

$$F_{\text{MSY}} = F = \arg\max_F Y(F)$$

- How might we solve this?

see methods Walters and Martell box 3.1

Proxy reference points

- In the absence of stock recruitment, sometimes a fraction of So (i.e., 0.3-0.4So) is used as a proxy for MSY
- Depends on risk tolerance and biology
- What do you think?

Key caveats and known failure points

- Dome shaped vulnerability
- Interaction of vulnerability and maturity schedule
- High values of Fmsy
- The can arise, but you want to know why this is happening
- Ricker vs. Beverton-Holt
- Bias correcting parameters: if you bias correct something and then plug it into another equation…
- Still an equilibrium answer!

Danse macabre from The Seventh Seal by Ingmar Bergman

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