

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 , B_{msy} , and U_{msy} for logistic population models (pen and paper)
2. Introduce common age-structured fish population model equations
3. Practice per-recruit 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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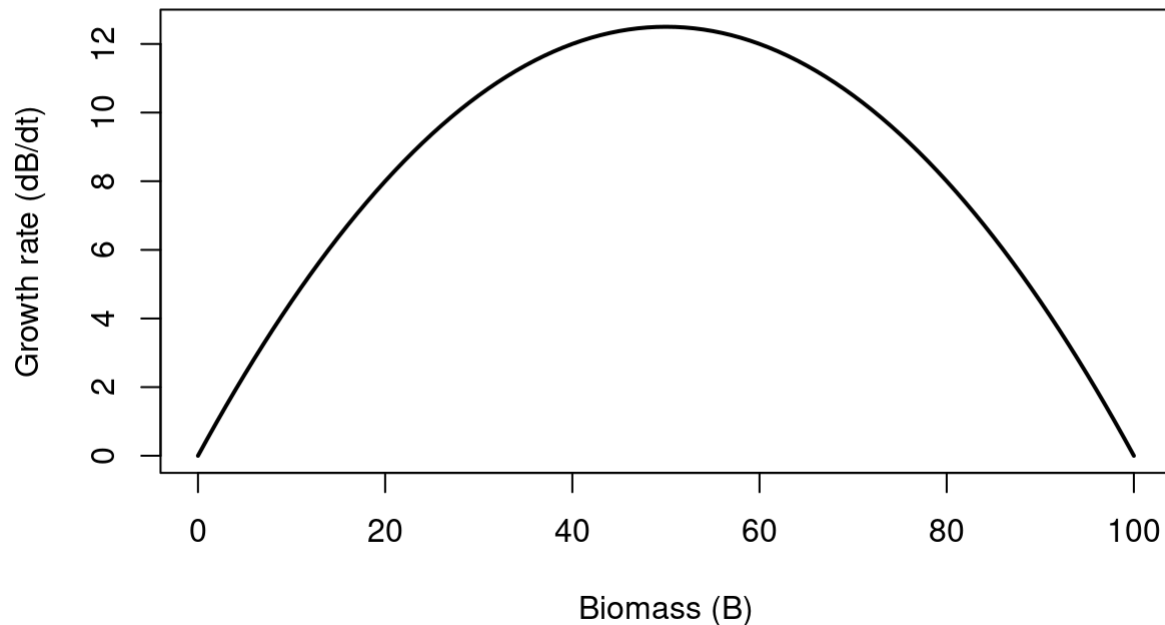
Logistic population growth

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- r is the intrinsic population growth rate, K is carrying capacity, B is biomass
- Who here is good at math
- Groups of three
- Do the math to calculate biomass at maximum sustainable yield (B_{msy}), maximum sustainable yield (MSY), and exploitation rate at maximum sustainable yield (U_{msy})

Logistic population growth: hints

```
1 r <- 0.5
2 K <- 100
3 B <- 0:K # pick a range of B
4 dBdt <- r * B * (1 - B / K) # simulate dynamics
5 plot(B, dBdt,
6      type = "l", lwd = 2,
7      xlab = "Biomass (B)",
8      ylab = "Growth rate (dB/dt)"
9 )
```



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 U_{msy}
- **Bonus.** What happens if you repeat this exercise for the model:

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

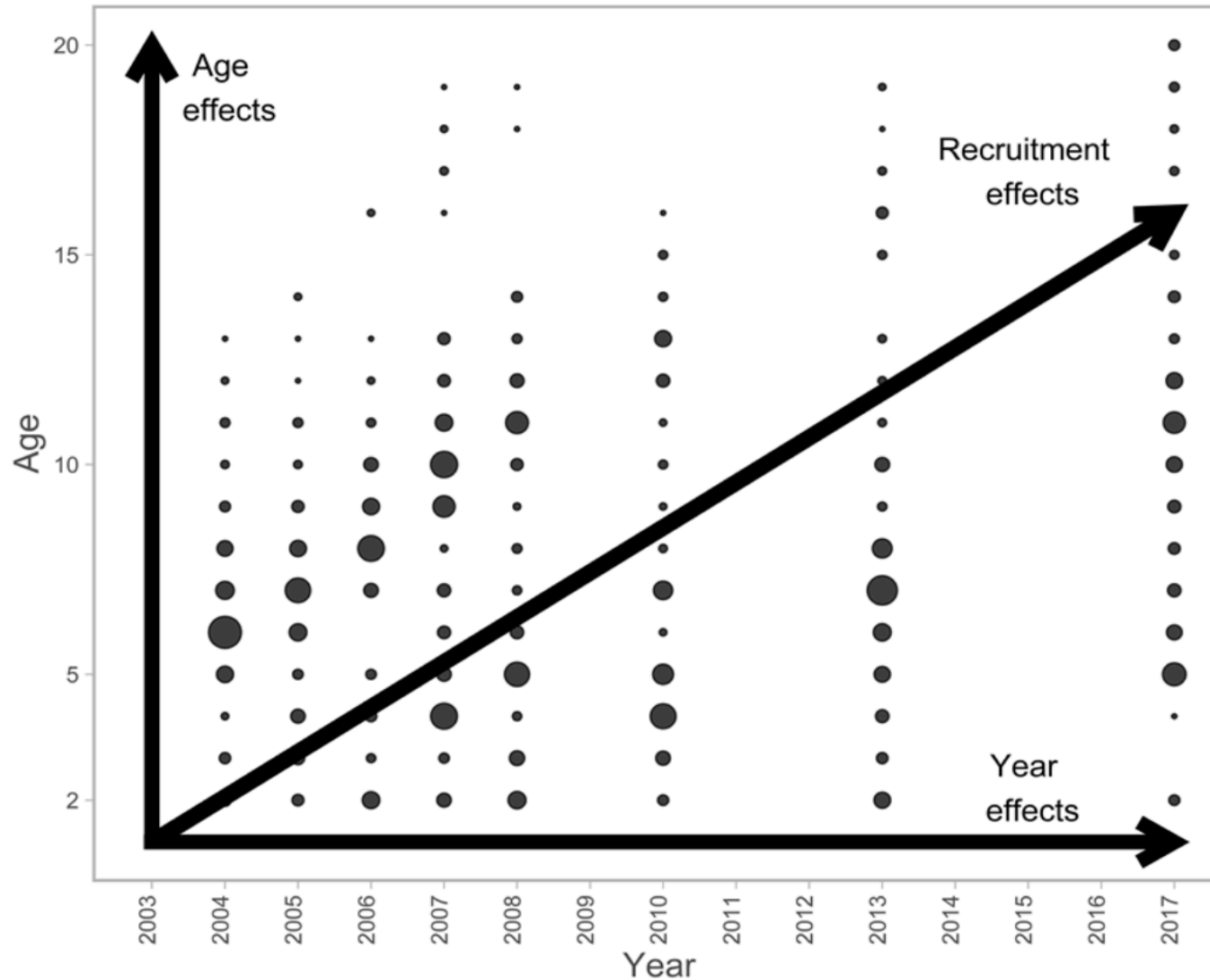


Death from *The Seventh Seal* by Ingmar Bergman

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?

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?

Age-structure

- Many of the ecological processes affecting fish are size dependent
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- Where does density dependence enter a typical age-structured fish population dynamics model?
 - Why?

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

Survivorship in the fished condition

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

$$l x_a = \begin{cases} 1 & \text{if } a = 1 \\ l x_{a-1} \cdot e^{-Z_{a-1}} & \text{if } 2 \leq a < a_{\max} \\ \frac{l x_{a_{\max}-1} \cdot e^{-Z_{a_{\max}-1}}}{1 - e^{-Z_{a_{\max}}}} & \text{if } a = a_{\max} \end{cases}$$

where:

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

- 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

Plus group misery 🥲

For the plus group, we sum all untracked survivors:

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

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:

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

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

$$ef = R \cdot \sum_{a=1}^{a_{max}} lx_a \cdot f_a$$

- 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):

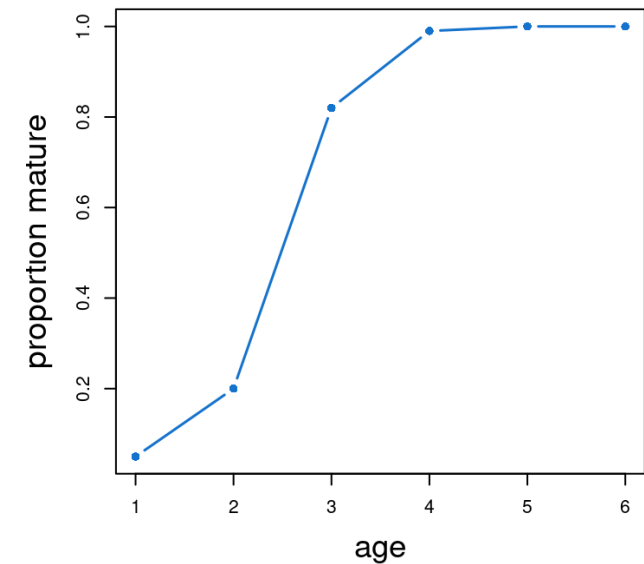
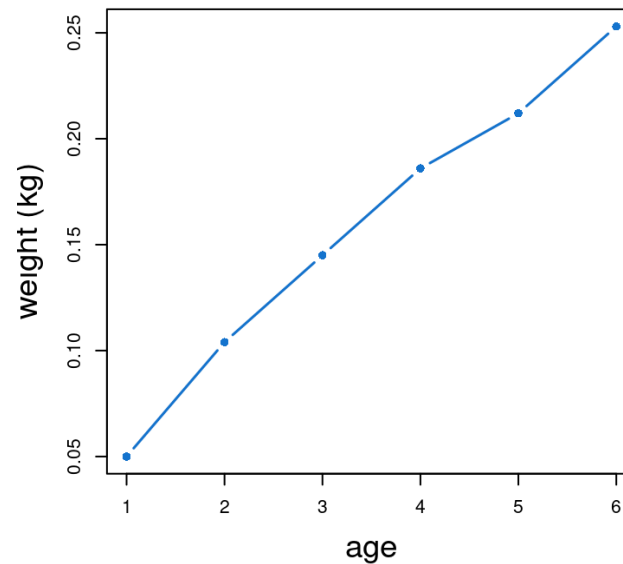
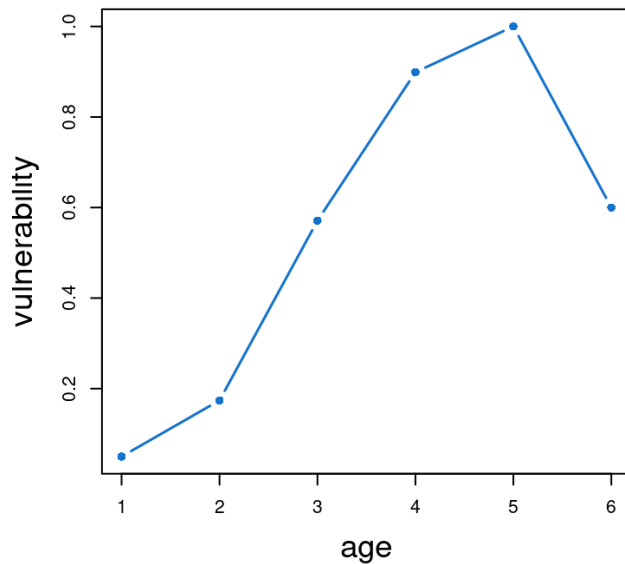
$$sbrf = \sum_{a=1}^{a_{max}} lx_a \cdot w_a \cdot mat_a$$

- 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

sbrf exercise

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

```
1 # life history vectors
2 vul <- c(0.05, 0.174, 0.571, 0.899, 1.000, 0.6) # vulnerability at age
3 wa <- c(0.05, 0.104, 0.145, 0.186, 0.212, 0.253) # weight at age
4 mat <- c(0.05, 0.20, 0.82, 0.99, 1.00, 1.00) # maturity at age
5 M <- 0.4 # instantaneous natural mortality
6 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

$$sbrf = \sum_{a=1}^{a_{max}} lx_a \cdot w_a \cdot mat_a$$

vs.

$$sbro = \sum_{a=1}^{a_{max}} lo_a \cdot w_a \cdot mat_a$$

- 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

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)

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

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

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

- And solving for equilibrium R :

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

Botsford's trickery with Beverton-Holt



- Parameterizing stock-recruitment in terms of R_0 and $recK$
- Consider a population at unfished equilibrium

$$S_0 = R_0 \cdot s_{bro}$$

- S_0 and R_0 are spawner biomass and recruitment at unfished equilibrium, so recruits per spawner in the unfished state is

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

α is defined as recruits per spawner biomass at low density

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

$$\Rightarrow \alpha = \frac{recK}{s_{bro}}$$

Botsford's trickery with Beverton-Holt 🐈🧐😬

- Calculating β from R_0 , s_{bro} , and $reck$:

$$R = \frac{\alpha S}{1 + \beta S} \quad \text{where} \quad S_0 = R_0 \cdot s_{bro} \Rightarrow R_0 = \frac{\alpha \cdot R_0 \cdot s_{bro}}{1 + \beta \cdot R_0 \cdot s_{bro}}$$

- And solving for β :

$$\beta = \frac{\alpha \cdot s_{bro} - 1}{R_0 \cdot s_{bro}}.$$

Exercise: equilibrium recruitment

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

```
1 # life history vectors
2 vul <- c(0.05, 0.174, 0.571, 0.899, 1.000, 0.6) # vulnerability at age
3 wa <- c(0.05, 0.104, 0.145, 0.186, 0.212, 0.253) # weight at age
4 mat <- c(0.05, 0.20, 0.82, 0.99, 1.00, 1.00) # maturity at age
5 M <- 0.4 # instantaneous natural mortality
6 reck <- 5 # goodyear compensation ratio
7 Ro <- 10 # equilibrium unfished recruitment
8
9 n_ages <- length(mat) # number of age classes
10 ages <- 1:n_ages
11 # set up total instantaneous mortality at age Za vector
12 Za <- F * vul + M # F set to some arbitrary value (e.g., 0.1)
13 # calculate survivorship in the fished state
14 lx <- numeric(n_ages)
15 lx[1] <- 1 # initialize
16 for (i in 2:n_ages) lx[i] <- lx[i - 1] * exp(-Za[i - 1]) # calculate lx recursively
17 lx[n_ages] <- lx[n_ages - 1] / (1 - exp(-Za[n_ages])) # plus group correction
18 sbrf <- sum(lx * mat * wa)
19
20 # calculate survivorship in unfished state (i.e., F = 0)
21 lo <- numeric(n_ages)
22 lo[1] <- 1
23 for (i in 2:n_ages) lo[i] <- lo[i - 1] * exp(-M)
24 lo[n_ages] <- lo[n_ages - 1] / (1 - exp(-M)) # plus group
25 sbro <- sum(lo * mat * wa)
```



Suffering Knight from The Seventh Seal by Ingmar Bergman

One more equation: yield per recruit

- Recall that at equilibrium

$$S = R \cdot sbrf$$

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

$$Y(F) = R(F) \cdot YPR(F)$$

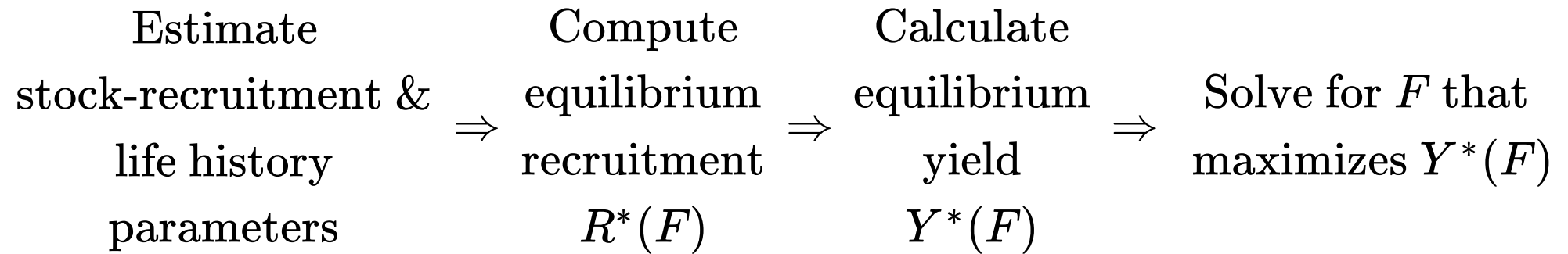
- Where $R(F)$ is recruitment as a function of fishing mortality and yield per recruit (YPR) is specified as

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

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

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

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



- Find the F that maximizes Y :

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

- How might we solve this?

Proxy reference points

- In the absence of stock recruitment, sometimes a fraction of S_0 (i.e., $0.3-0.4S_0$) 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 F_{msy}
 - This 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!

Homework

- Derive Ricker α and β in terms of R_0 , s_{bro} , and $recK$ following the methods in this presentation



Danse macabre from *The Seventh Seal* by Ingmar Bergman

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