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A Perspective On Steepness and Its Implications for Fishery Management

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PERSPECTIVE

A perspective on steepness, reference points, and stock assessment

Marc Mangel, Alec D. MacCall, Jon Brodziak, E.J. Dick, Robyn E. Forrest, Roxanna Pourzand, and Stephen Ralston

JACK BASKIN SCHOOL OF ENGINEERING
BIOTECHNOLOGY, INFORMATION TECHNOLOGY, NANOTECHNOLOGY



Outline

- Density Dependence and Population Biology
- What is Steepness?
- Strategic Fishery Management: The Stock Assessment Process
- Connections Between Steepness and Reference Points: Previous Observations
- The Reproductive Biology of Steepness
- Implications for Reference Points
- Fixing Steepness at 1
- Moving Forward
- Conclusions



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Density Dependence and Population Biology

Fundamental Law of Population Biology

Next year's population = This year's population
+ Reproduction
+ Immigration
- Death
- Emigration

Density Dependence and Population Biology

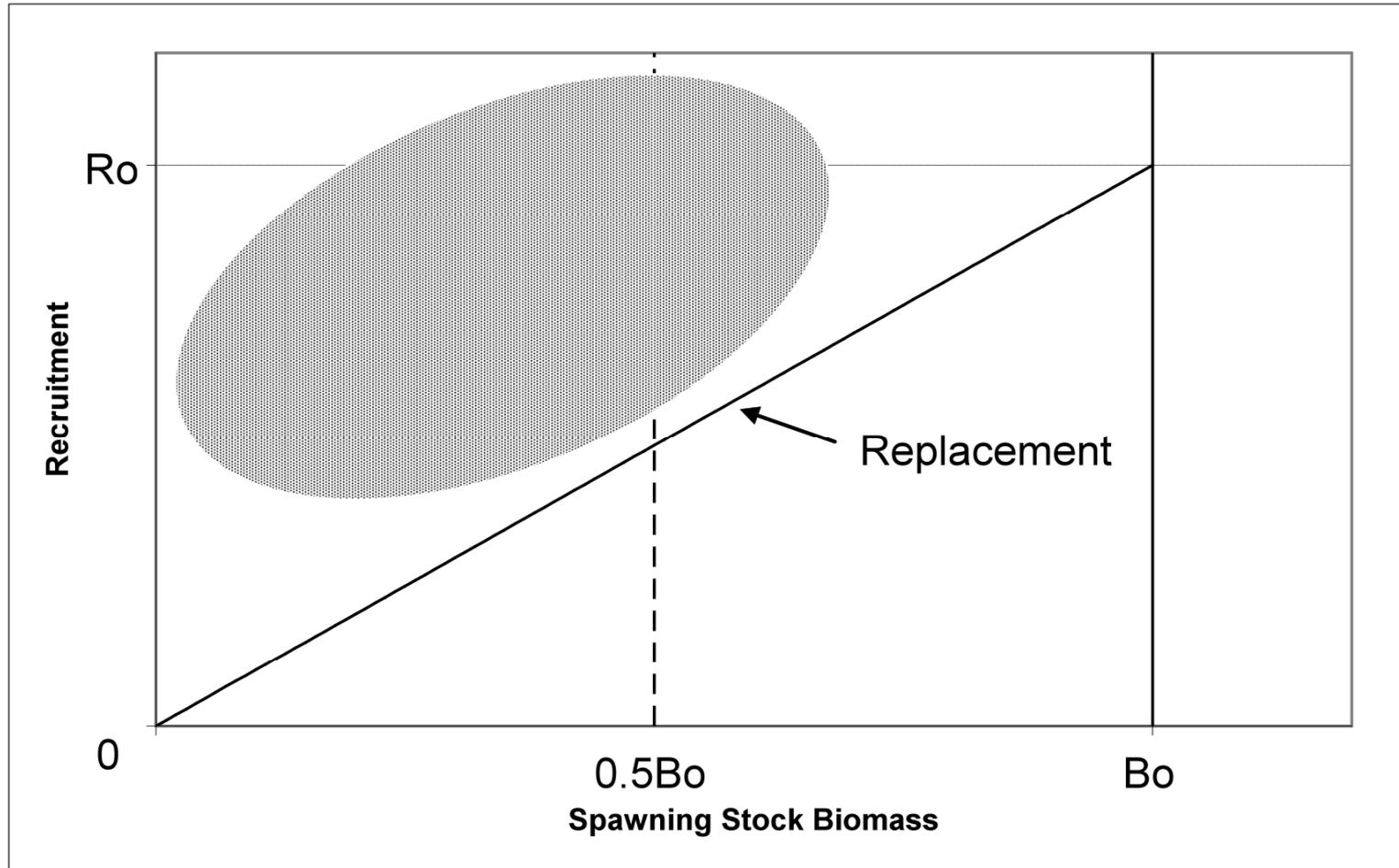
Fundamental Law of Population Biology

Next year's population = This year's population
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+ Immigration
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- Emigration

Reproduction (“Recruitment”)

= Function of this year's population size
and reproductively active
individuals (“Spawners”)

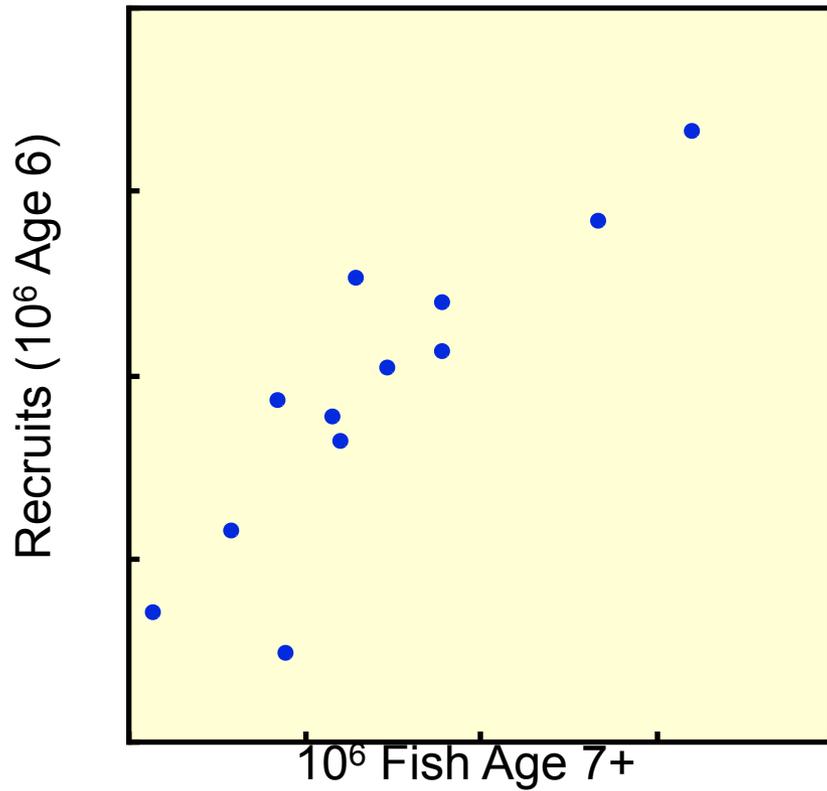
Because of Density Dependence There Are Points in Biomass-Recruitment Space That Lie Above the Replacement Line



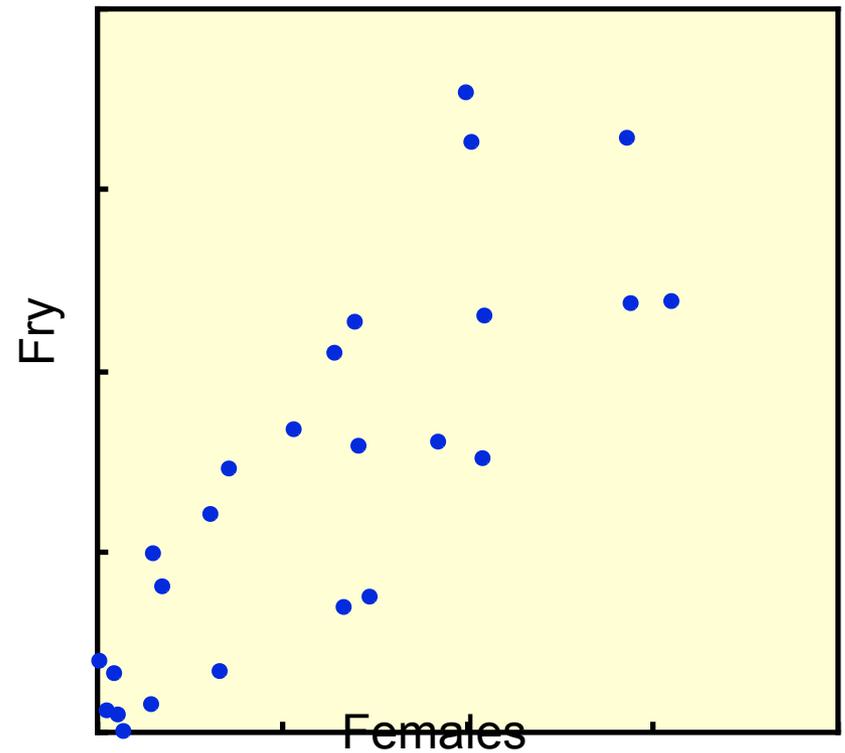
But The Data Are Noisy...



Walleye Pollock (Kamchatka)

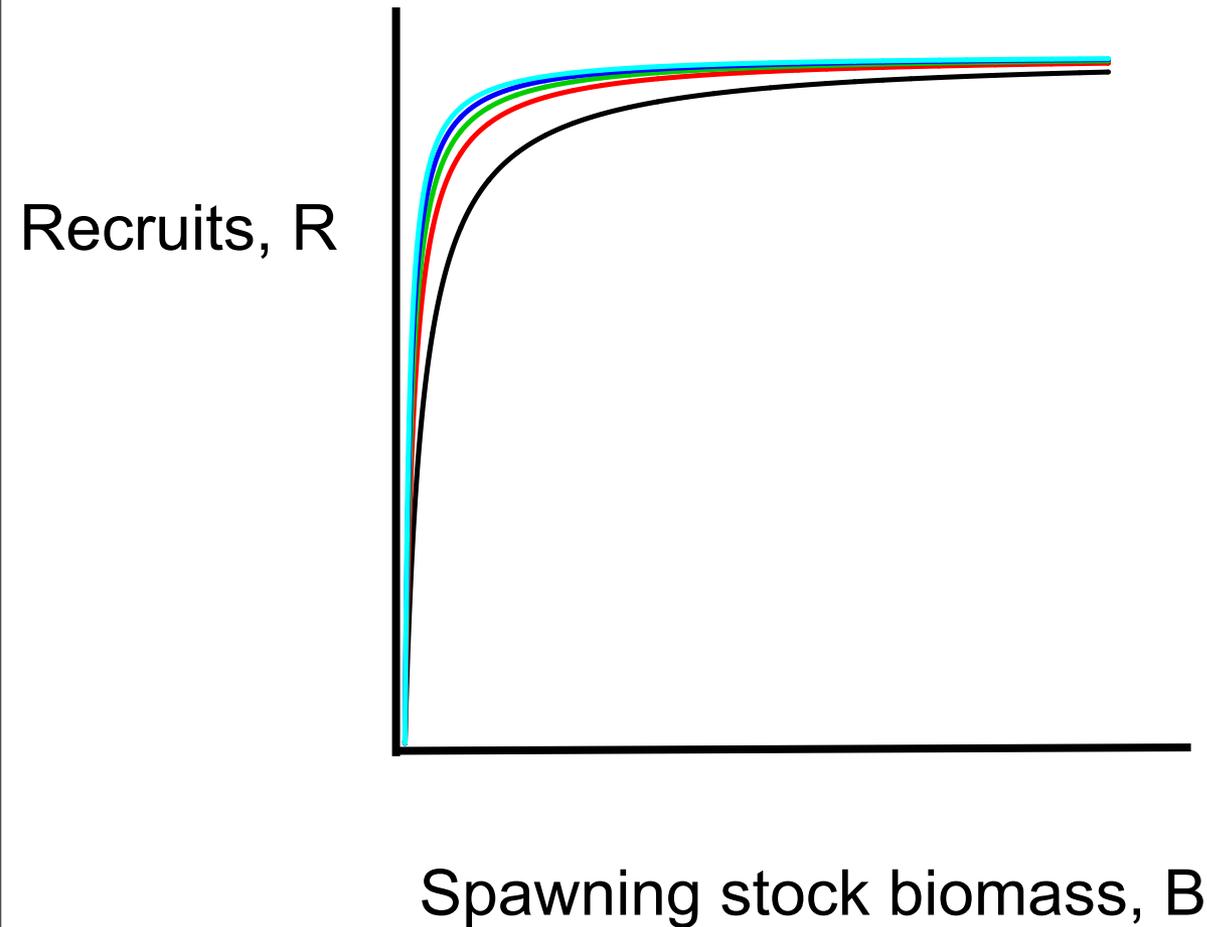


Alaskan Pink Salmon

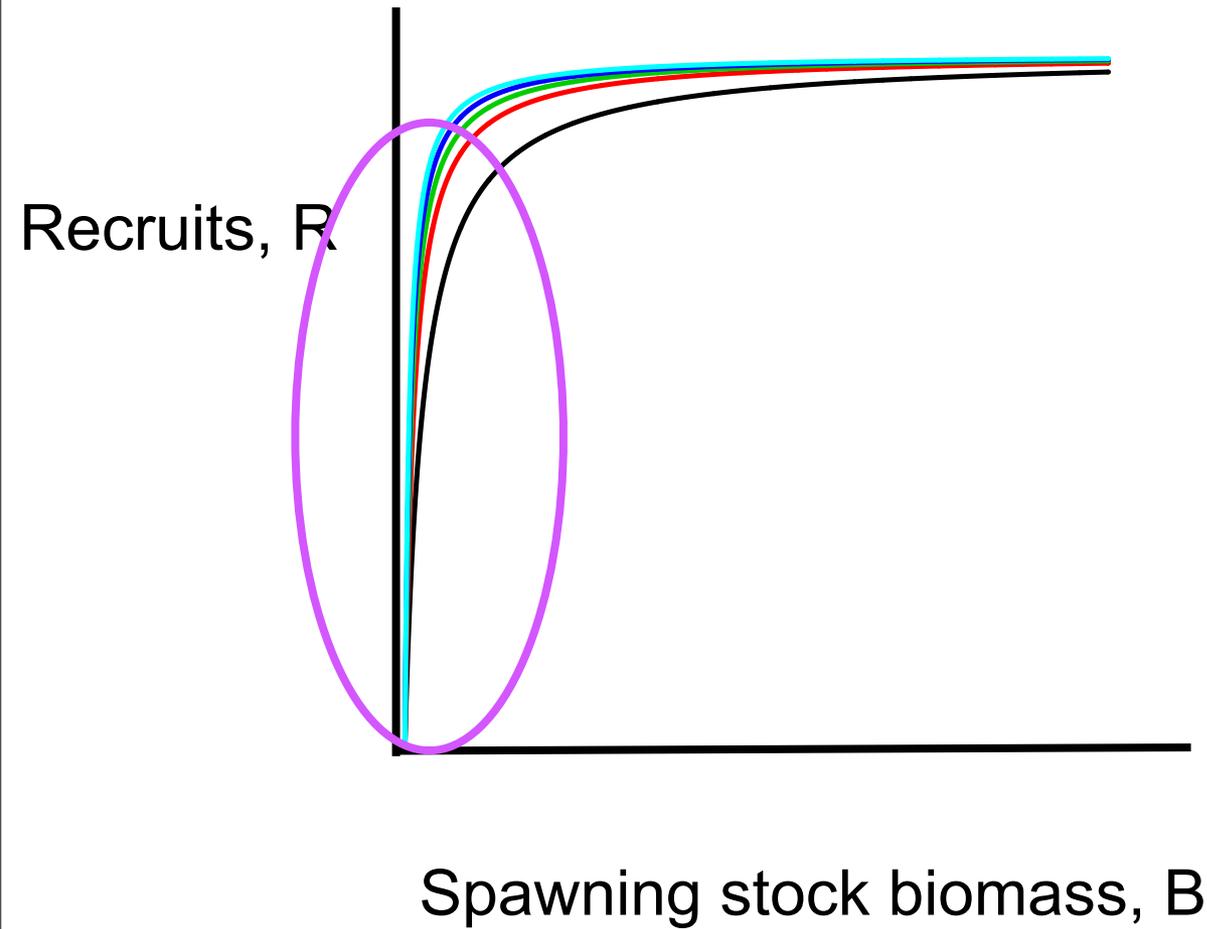


Data from R.A.Myers, J.Bridson, and N.J.Barrowman (1995) Summary of Worldwide Spawner and Recruitment Data. Can. Tech. Rep. Fish. Aquat. Sci. 2020

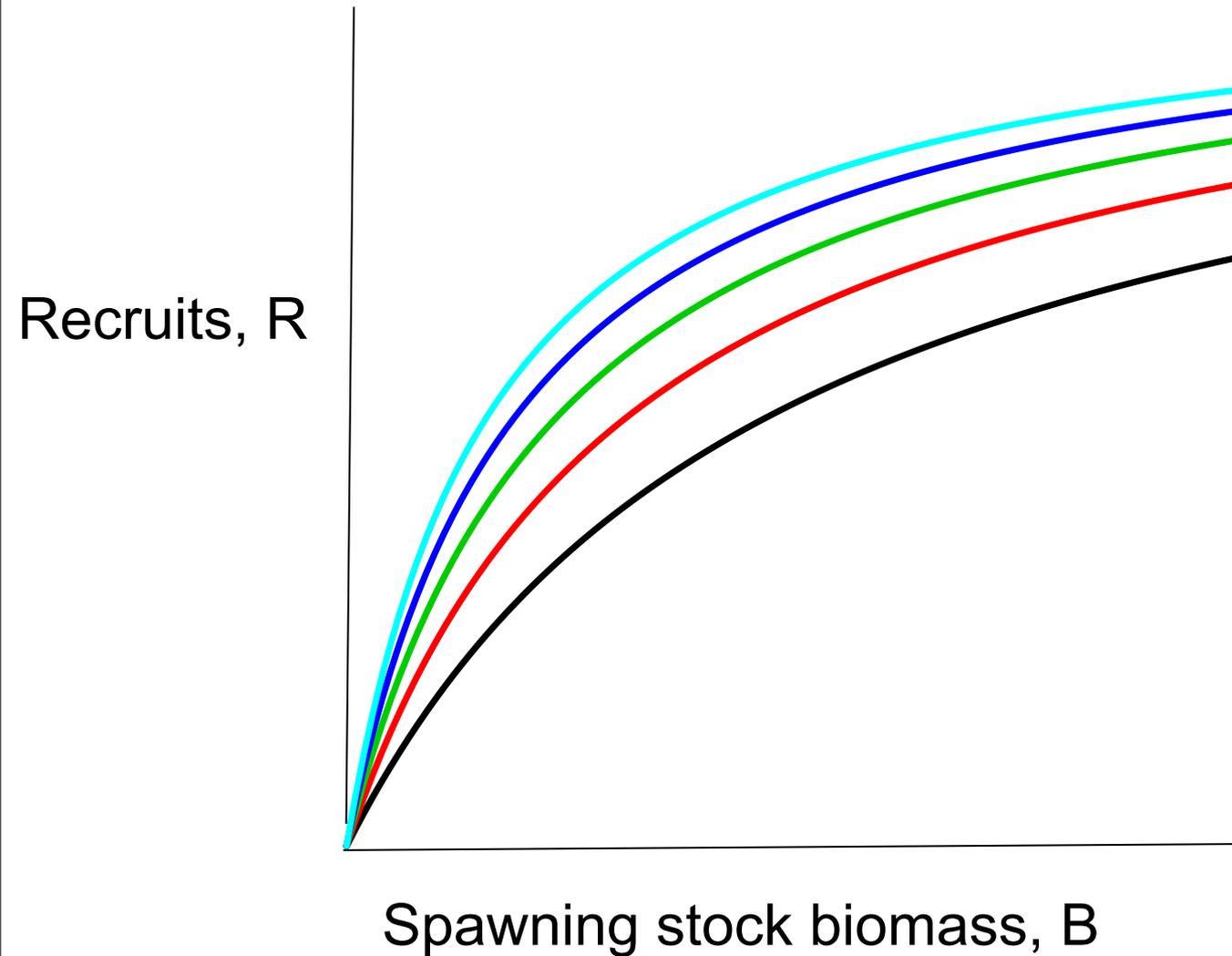
Classical Solution: Parametric Stock-Recrument Relationships -- The Beverton Holt SRR



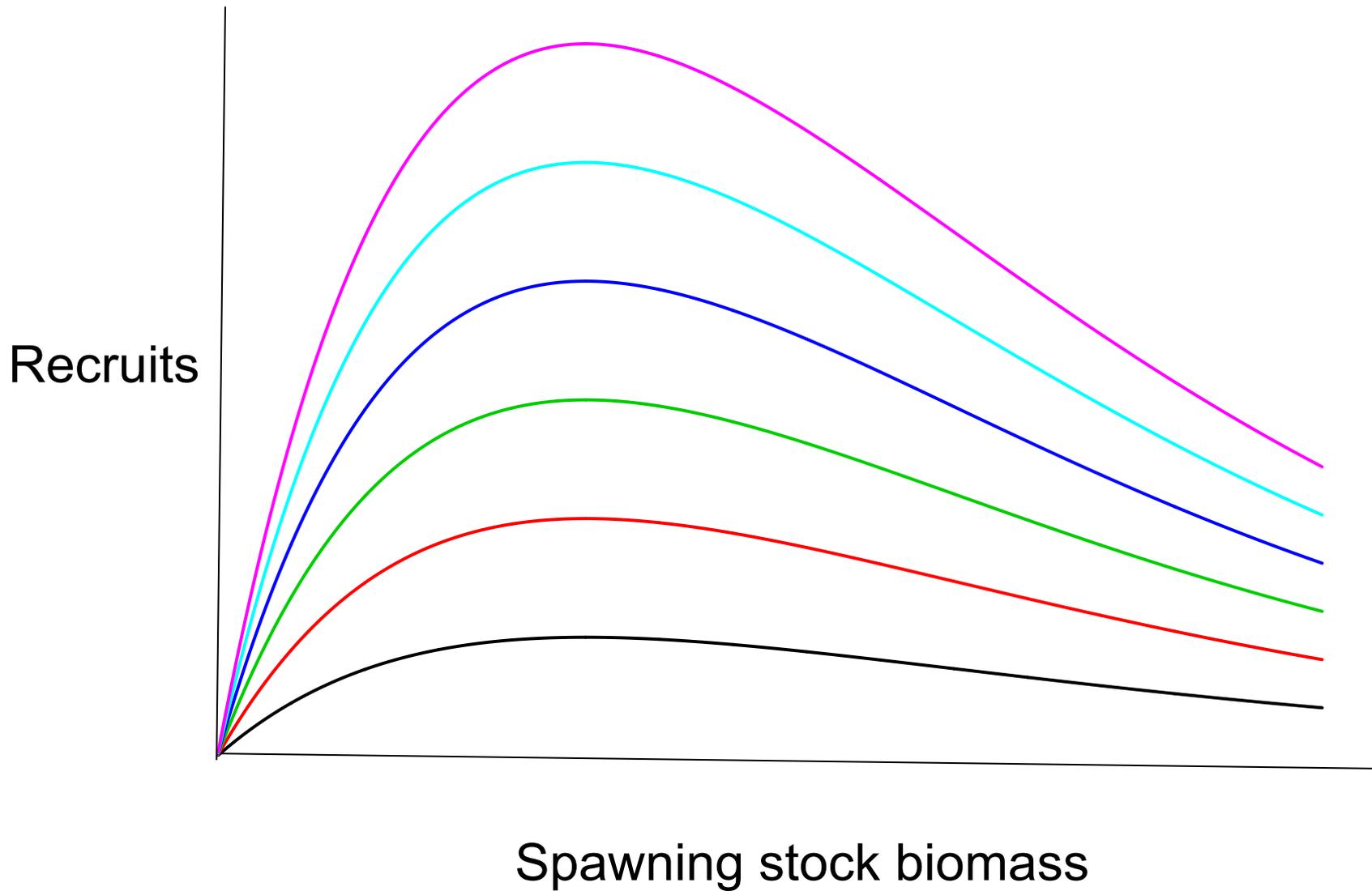
Classical Solution: Parametric Stock-Recruitment Relationships



Classical Solution: Parametric Stock-Recruitment Relationships



The Ricker SRR





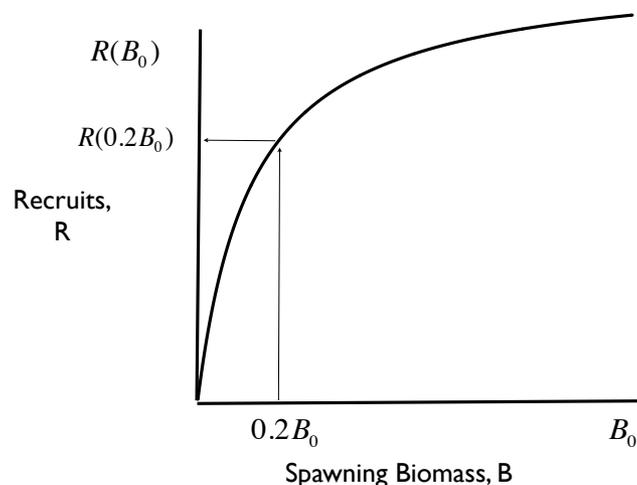
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What is Steepness: Mace and Doonan (1988)

Steepness: Fraction of the recruitment at the unfished the spawning biomass when the spawning biomass is 20% of the unfished size

$$h = \frac{R(0.2B_0)}{R(B_0)}$$

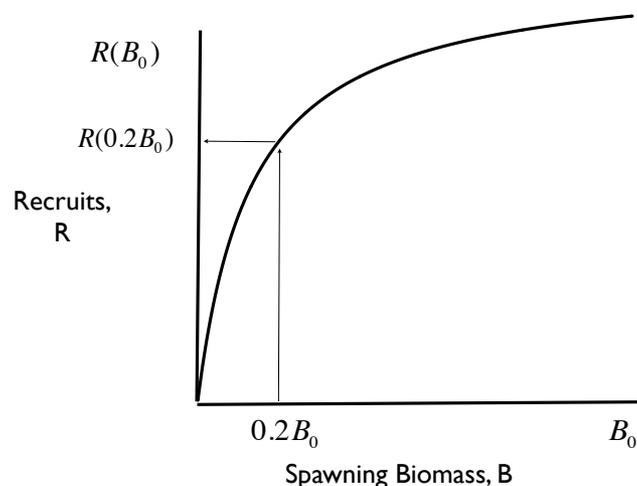


Mace, P. and I.J. Doonan. 1988. A Generalised Bioeconomic Simulation Model for Fish Population Dynamics. New Zealand Fishery Assessment Research Document 88/4, Fisheries Research Centre, MAFFish, POB 297, Wellington, NZ

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Parameters of the SRR can be related to steepness and unfished biomass and recruitment



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Strategic Fishery Management: The Stock Assessment Process

- Organize all of the data (catch, survey, fishery dependent, fishery independent)
- Fit the data to a model of population dynamics
- Use the fitted model to investigate state of the stock and management options

Reference Points of Strategic Fishery Management

Unfished Biomass

$$B_0$$

Biomass giving Maximum Sustainable Yield (MSY)

$$B_{MSY}$$

Biomass giving Maximum Net Productivity (MNP)

$$B_{MNP}$$

Rate of Fishing Mortality giving MSY

$$F_{MSY}$$

Spawning biomass per recruit when fished at rate giving MSY divided by that when unfished

$$SPR_{MSY}$$

Reference Points of Strategic Fishery Management

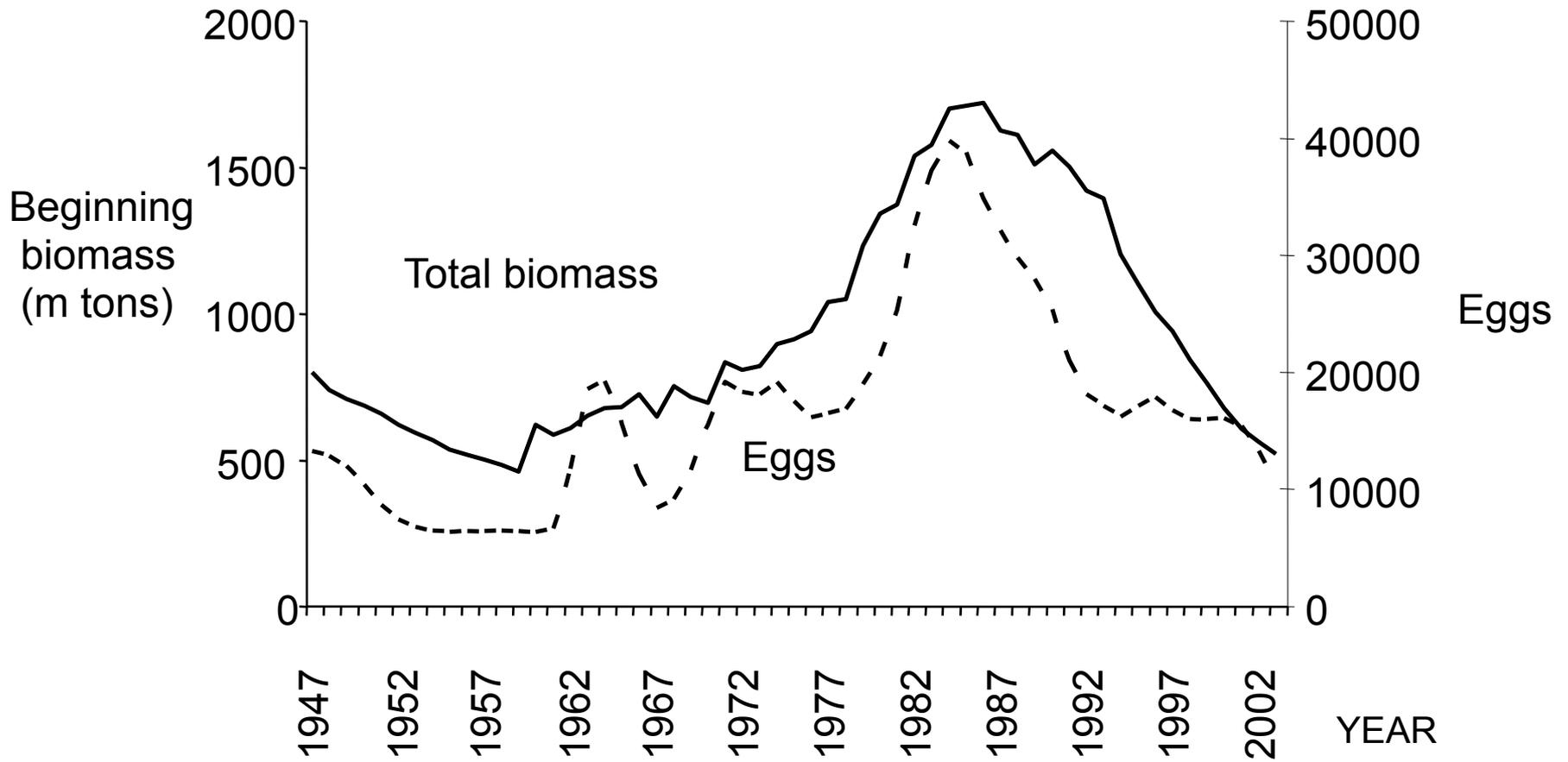
Maximum Excess Recruitment

MER

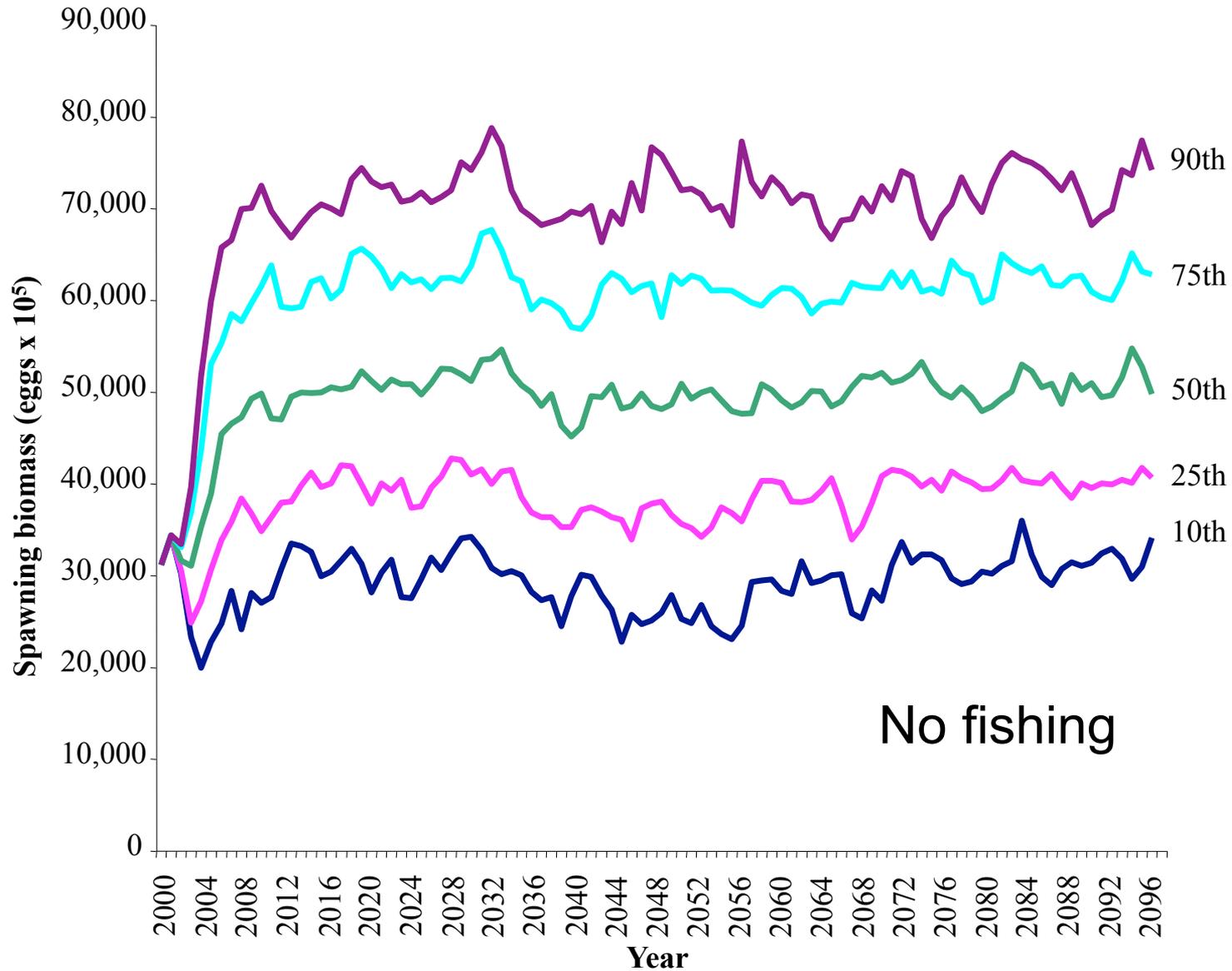
Ratio of MER to that in an unfished population

*SPR*_{*MER*}

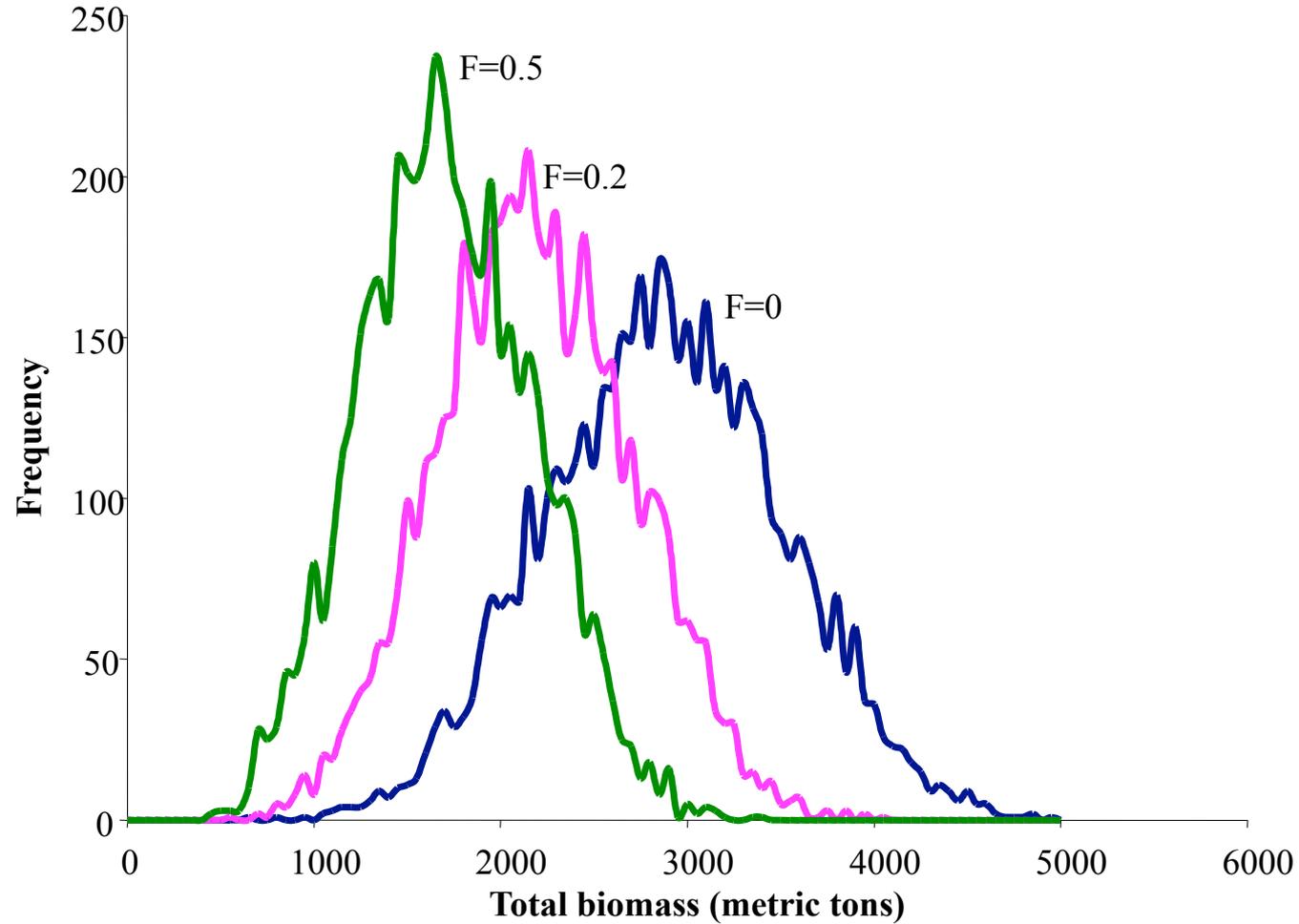
The Stock Assessment Process: Reconstruct the Trajectories of Biomass and Reproduction



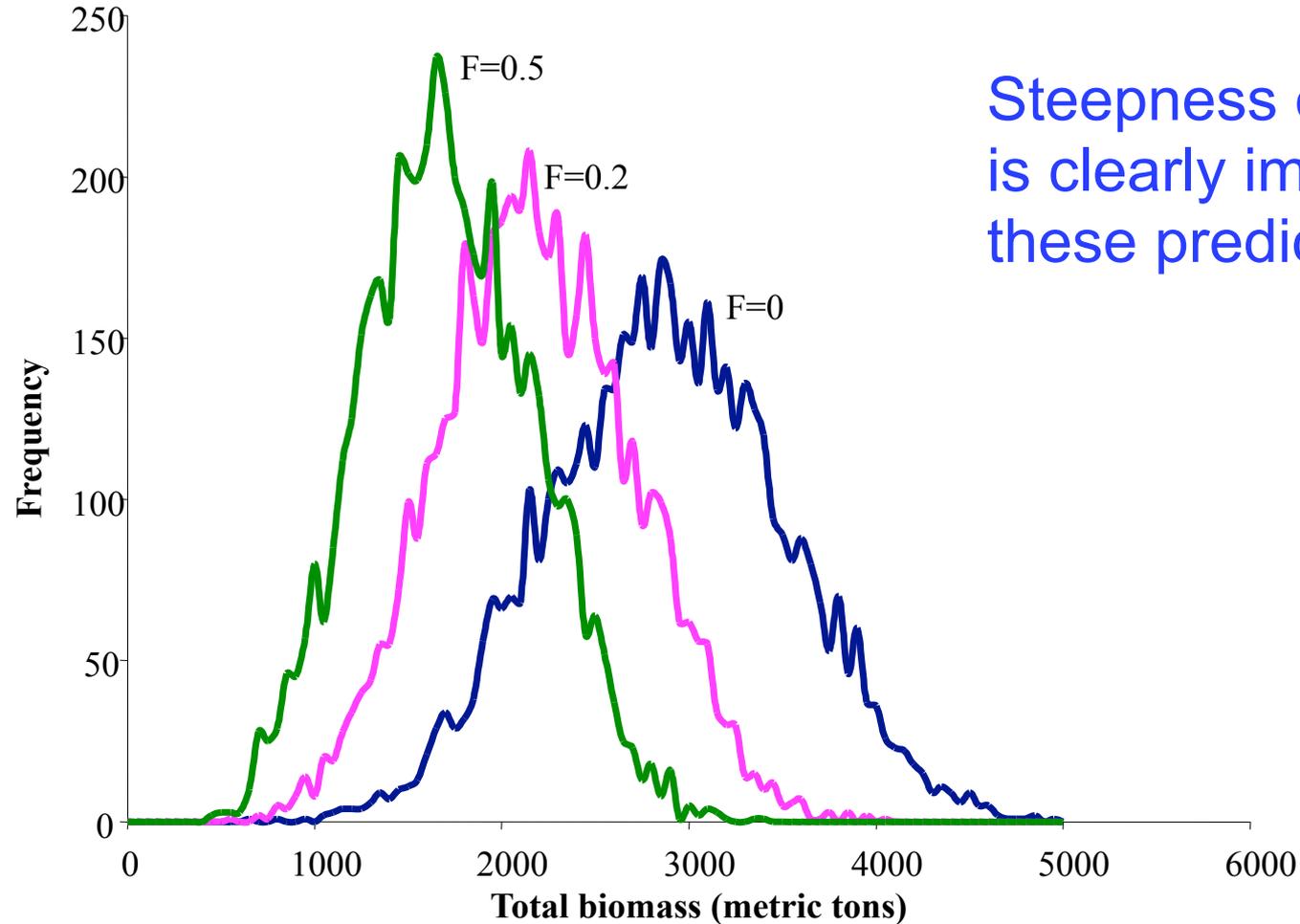
The Stock Assessment Process: Forward Project the Fate of the Stock



The Stock Assessment Process: Frequency Distribution of Biomass Projected Under Different Scenarios About Fishing

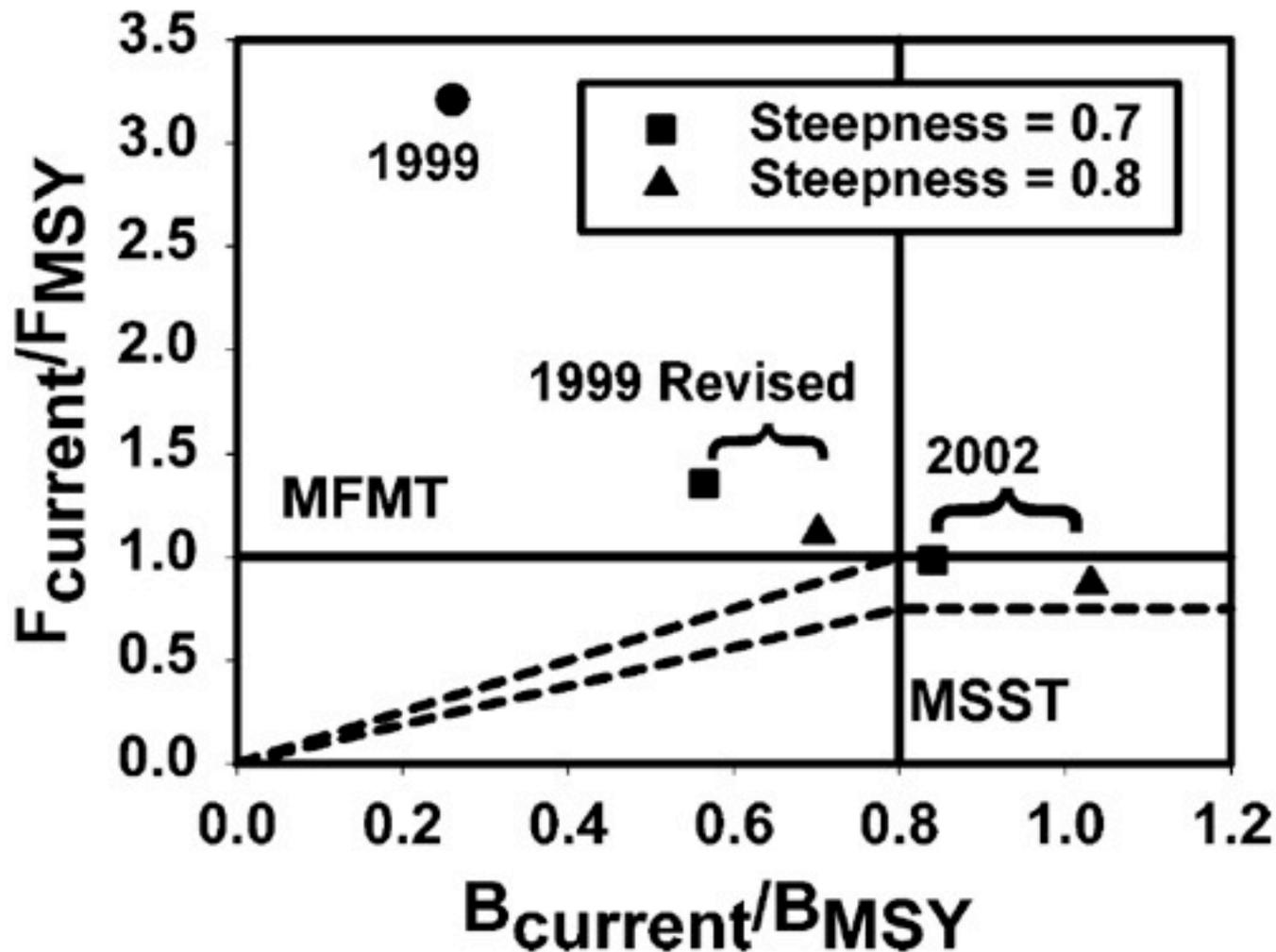


The Stock Assessment Process: Frequency Distribution of Biomass Projected Under Different Scenarios About Fishing



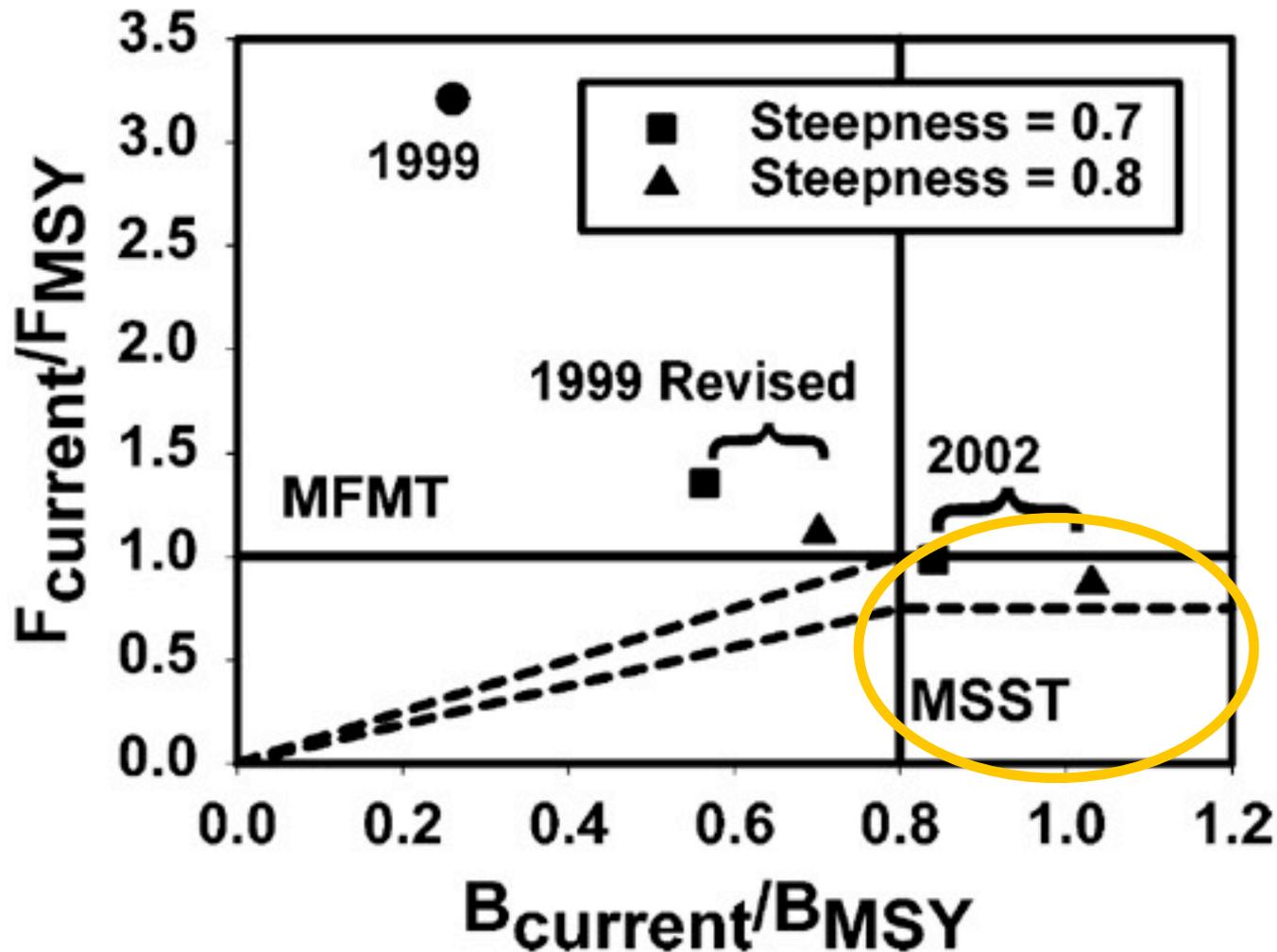
Steepness of the SRR is clearly important in these predictions.

Steepness is Often Fixed In Stock Assessments



KA Rose and JH Cowan, Jr. 2003. Annual Review of Ecology and Systematics 34:127

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Connections Between RPs and Steepness Have Been Noted

Williams (NA J Fish Mang. 2002)

MSY increases with steepness but depends on age at maturity and selectivity.

SPR_{MSY} determined by steepness but independent of age at maturity and selectivity

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Williams (NA J Fish Mang. 2002)

MSY increases with steepness but depends on age at maturity and selectivity.

SPR_{MSY} determined by steepness but independent of age at maturity and selectivity

Punt et al (Fish. Res. 2008)

F_{MSY} is an increasing function of steepness but depends on life history parameters and selectivity

B_{MSY} / B_0 and SPR_{MSY} nearly perfectly predicted by steepness

Connections Between RPs and Steepness Have Been Noted

Brooks et al (ICES J. Mar. Sci 2010)

$$SPR_{MER} = \frac{1}{2} \sqrt{\frac{1-h}{h}}$$

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1) Why is this so?

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Begs us to answer three questions

- 1) Why is this so?
- 2) What does it mean for the process of stock assessment?

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Begs us to answer three questions

- 1) Why is this so?
- 2) What does it mean for the process of stock assessment?
- 3) What should we do given the answer to 2)?

First: Some Other Examples

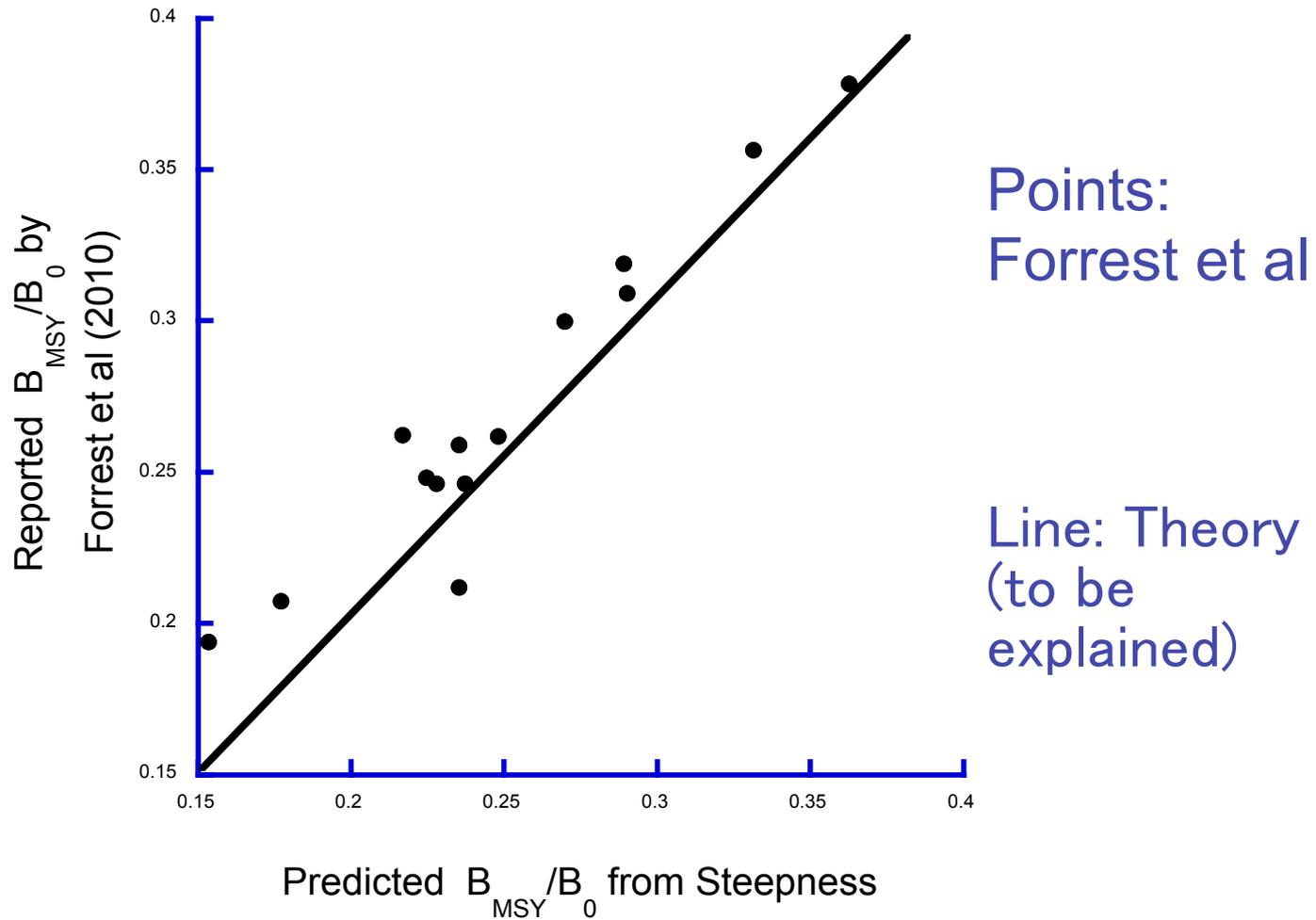
Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock–recruit function

Robyn E. Forrest, Murdoch K. McAllister, Martin W. Dorn, Steven J.D. Martell, and Richard D. Stanley

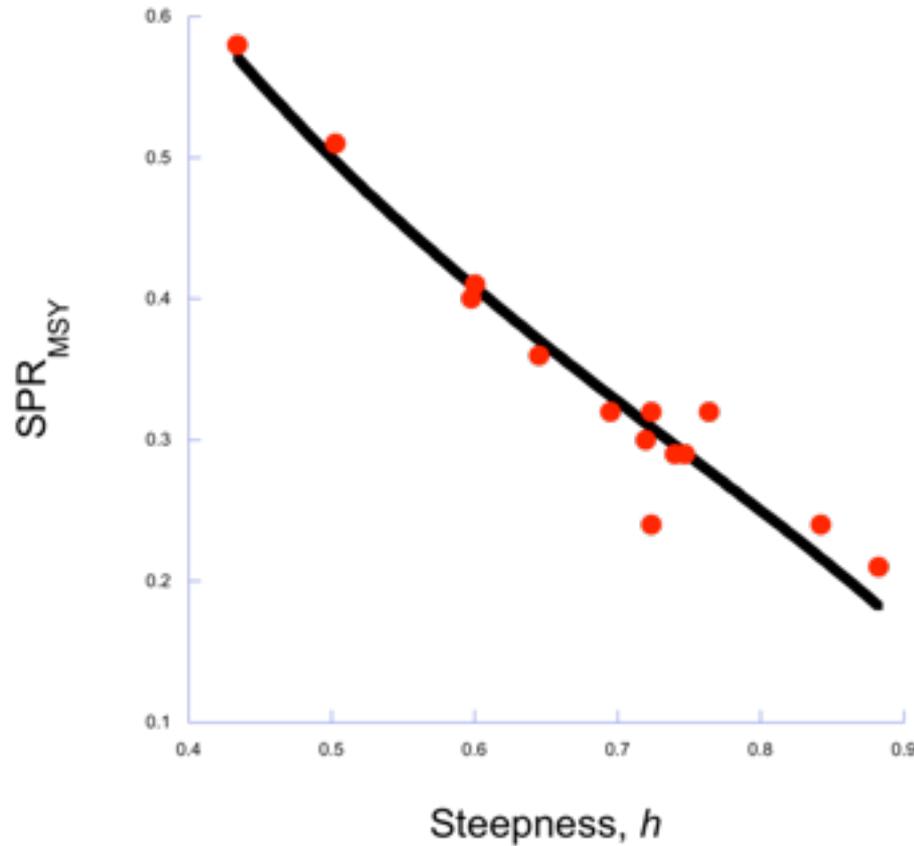
CJFAS 65:286 (2008)

"Some other observations are worth noting For the 14 populations, there was strong negative relationship between h and at [the MSY harvest fraction] under both Beverton-Holt ($r=-0.96$) and Ricker ($r=-0.94$) recruitment (Figs 8a, 8b). This might be expected, as populations with stronger recruitment compensation are expected to be able to be sustained at lower levels of spawning biomass."

The Results of Forrest et al Are Nearly Perfectly Predicted by Steepness



And Other Results of Forrest et al Are Nearly Perfectly Predicted by Steepness Alone



Points: Forrest et al

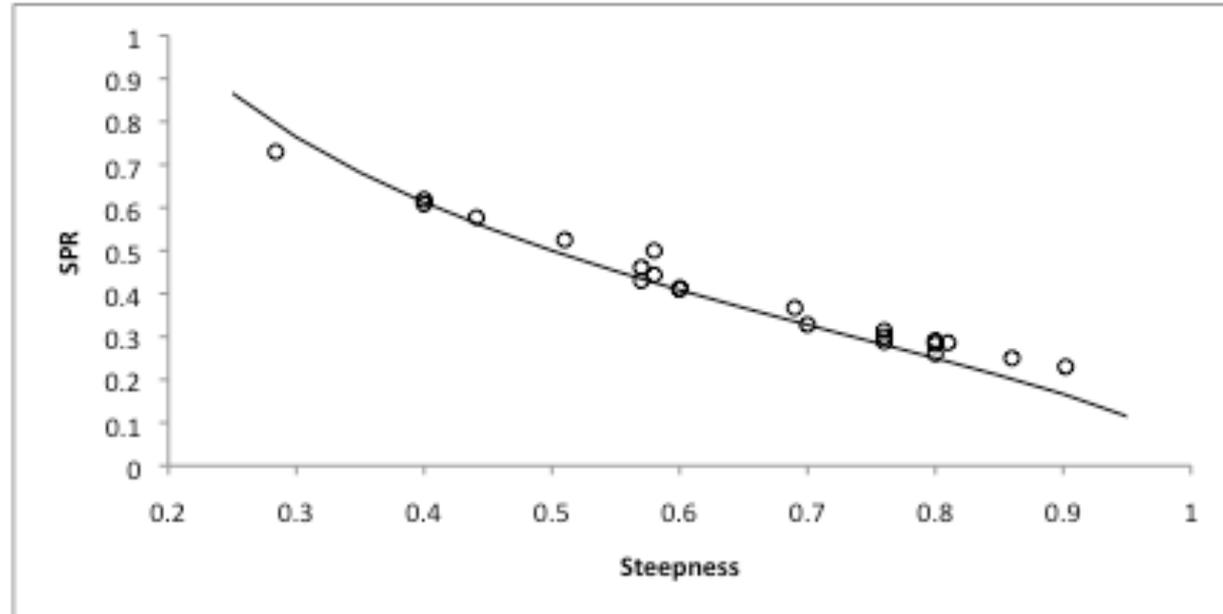
Line: Theory (to be explained)

Some Stock Assessments with BH-SRR and Fixed Steepness

Common Name	Scientific Name	Citation
	<i>Scorpaenichthys</i>	
Cabezon	<i>marmoratus</i>	Cope and Key 2009
Canary Rockfish	<i>Sebastes pinniger</i>	Stewart 2009
Cowcod	<i>Sebastes levis</i>	Dick et al. 2009
Darkblotched		Wallace and Hamel
Rockfish	<i>Sebastes crameri</i>	2009
Greenstriped		
Rockfish	<i>Sebastes elongatus</i>	Hicks et al. 2009
Lingcod	<i>Ophiodon elongatus</i>	Hamel et al. 2009
Splitnose		
Rockfish	<i>Sebastes diploproa</i>	Gertseva et al. 2009
Arrowtooth		Kaplan and Helser
Flounder	<i>Atheresthes stomias</i>	2007
Black Rockfish,		
North	<i>Sebastes melanops</i>	Wallace et al. 2007
Black Rockfish,		
South	<i>Sebastes melanops</i>	Sampson 2007
Blue Rockfish	<i>Sebastes mystinus</i>	Key et al. 2008
Chilipepper		
Rockfish	<i>Sebastes goodei</i>	Field 2008
		Gertseva and
Longnose Skate	<i>Raja rhina</i>	Schirripa 2008

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Points: SPR estimated from complicated stock assessments.

Line: The theory (to be explained)



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A Theory for The Reproductive Ecology of Steepness: The Production Model

Dynamics of Biomass

$$\frac{dB}{dt} = \frac{\alpha_p B}{1 + \beta B} - (M + F)B$$

Steady state in the absence of fishing

$$B_0 = \frac{1}{\beta} \left(\frac{\alpha_p}{M} - 1 \right)$$



So that

$$\frac{\alpha_p}{M}$$

is a **dimensionless (Beverton) number** of the life history

Steepness is

$$h = 0.2 \cdot \frac{1 + \beta B_0}{1 + 0.2\beta B_0}$$



$$h = 0.2 \cdot \frac{1 + \beta B_0}{1 + 0.2\beta B_0} \quad \text{and} \quad B_0 = \frac{1}{\beta} \left(\frac{\alpha_p}{M} - 1 \right)$$

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So that

$$\beta B_0 = \left[\frac{\alpha_p}{M} - 1 \right]$$

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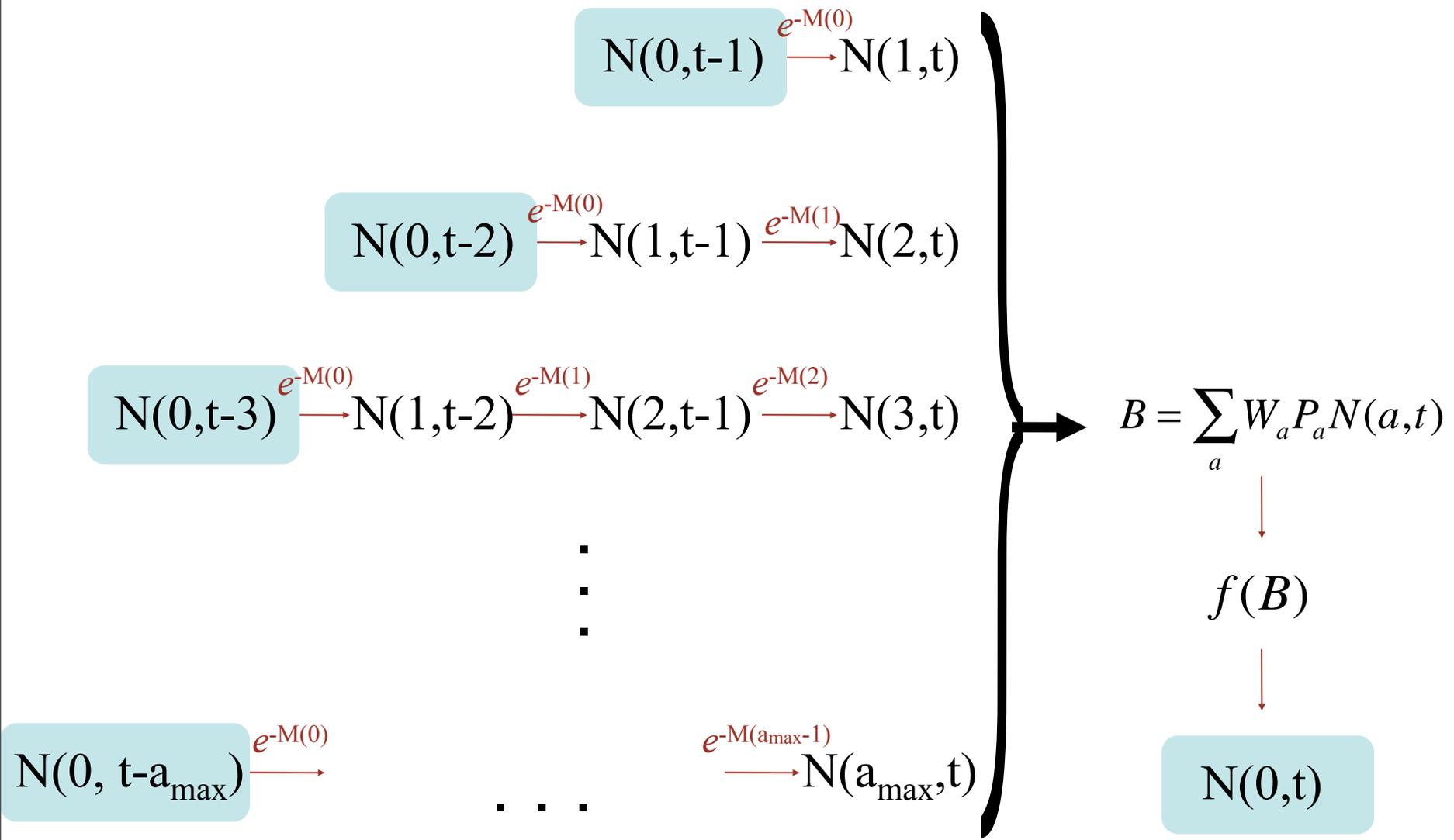
$$\beta B_0 = \left[\frac{\alpha_p}{M} - 1 \right]$$

And steepness is

$$h = \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}}$$

Constant for constant Beverton number

The Age Structured Model



The Age Structured Model

Population dynamics, beyond eggs/larvae

$$N(a, t) = N(a - 1, t - 1)e^{-Z(a-1)}$$

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$$N(a, t) = N(a - 1, t - 1)e^{-Z(a-1)}$$

Spawning biomass

$$B_s(t) = \sum_{a=1}^{a_{\max}} N(a, t)W_f(a)p_{f,m}(a)$$

The Age Structured Model

Population dynamics, beyond eggs/larvae

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Spawning biomass

$$B_s(t) = \sum_{a=1}^{a_{\max}} N(a, t)W_f(a)p_{f,m}(a)$$

Recruits

$$N(0, t) = \frac{\alpha_s B_s(t)}{1 + \beta B_s(t)}$$

In the steady state

$$\bar{N}(a) = S(a) \cdot R_0$$

$$R_0 = \frac{\alpha_s B_0}{1 + \beta B_0}$$

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$$B_0 = \sum_{a=1}^{a_{\max}} \bar{N}(a) W_f(a) p_{f,m}(a)$$

Define

$$\bar{W}_f = \sum_{a=1}^{a_{\max}} S(a) W_f(a) p_{f,m}(a)$$

Average mass of a spawning fish

$$R_0 = \frac{\alpha_s R_0 \bar{W}_f}{1 + \beta \cdot R_0 \bar{W}_f}$$

$$R_0 = \frac{\alpha_s R_0 \bar{W}_f}{1 + \beta \cdot R_0 \bar{W}_f}$$

Steepness is

$$h = \frac{\frac{\alpha_s \cdot 0.2 R_0 \bar{W}_f}{1 + \beta \cdot 0.2 R_0 \bar{W}_f}}{R_0}$$

$$R_0 = \frac{\alpha_s R_0 \bar{W}_f}{1 + \beta \cdot R_0 \bar{W}_f}$$

Steepness is

$$h = \frac{\frac{\alpha_s \cdot 0.2 R_0 \bar{W}_f}{1 + \beta \cdot 0.2 R_0 \bar{W}_f}}{R_0}$$

But

$$\beta R_0 \bar{W}_f = \alpha_s \bar{W}_f - 1$$

$$R_0 = \frac{\alpha_s R_0 \bar{W}_f}{1 + \beta \cdot R_0 \bar{W}_f}$$

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But

$$\beta R_0 \bar{W}_f = \alpha_s \bar{W}_f - 1$$

So that

$$h = \frac{0.2 \alpha_s \bar{W}_f}{1 + 0.2 [\alpha_s \bar{W}_f - 1]} = \frac{\alpha_s \bar{W}_f}{4 + \alpha_s \bar{W}_f}$$

Connecting Age-Structured and Production Models

Age-structured

Production

$$\frac{\alpha_s \bar{W}_f}{4 + \alpha_s \bar{W}_f} \approx \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}}$$

These are the
same if

Connecting Age-Structured and Production Models

Age-structured

Production

$$\frac{\alpha_s \bar{W}_f}{4 + \alpha_s \bar{W}_f} \approx \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}}$$

These are the same if

$$S(a) = e^{-Ma}$$

Constant mortality

Connecting Age-Structured and Production Models

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$$1 - e^{-Ma_{\max}} \approx 1$$

Long-lived

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Long-lived

$$\frac{1}{1 - e^{-M}} \approx \frac{1}{M}$$

M is small

Connecting Age-Structured and Production Models

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M is small

$$W_f(a) \sim \text{constant}$$

Mass at age constant



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Looking at Some Reference Points for the Production Model

$$\frac{dB}{dt} = \frac{\alpha_p B}{1 + \beta B} - (M + F)B$$

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What is F_{MSY} ?

Looking at Some Reference Points for the Production Model

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What is F_{MSY} ?

$$\frac{F_{MSY}}{M} = \sqrt{\frac{\alpha_p}{M}} - 1$$

Looking at Some Reference Points for the Production Model

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But

$$h = \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}}$$

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$$\frac{F_{MSY}}{M} = \sqrt{\frac{\alpha_p}{M}} - 1$$

But

$$h = \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}} \qquad \text{so that} \qquad \frac{\alpha_p}{M} = \frac{4h}{1-h}$$

Thus, elementary calculus, used wisely, shows that:

$$\frac{F_{MSY}}{M} = \sqrt{\frac{4h}{1-h}} - 1$$

- Only two of the three parameters natural mortality, steepness, and fishing mortality giving MSY can be treated as freely estimated parameters in an estimation procedure.

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$$\frac{F_{MSY}}{M} = \sqrt{\frac{4h}{1-h}} - 1$$

- Only two of the three parameters natural mortality, steepness, and fishing mortality giving MSY can be treated as freely estimated parameters in an estimation procedure.
- It is logically inconsistent to try to estimate all three of them in a stock assessment based on the BH-SRR. This inconsistency may show up as poor model fit and be modeled as 'noise'.

Thus, elementary calculus, used wisely, shows that:

$$\frac{F_{MSY}}{M} = \sqrt{\frac{4h}{1-h}} - 1$$

- Only two of the three parameters natural mortality, steepness, and fishing mortality giving MSY can be treated as freely estimated parameters in an estimation procedure.
- It is logically inconsistent to try to estimate all three of them in a stock assessment based on the BH-SRR. This inconsistency may show up as poor model fit and be modeled as 'noise'.
- Furthermore, note that setting steepness equal to 1, makes F_{MSY} infinite.

More On Reference Points:

Another common management strategy is to choose the fishing mortality rate that produces a steady state biomass that is x per-cent of the unfished biomass (F_x).

$$\frac{1}{\beta} \left(\frac{\alpha_p}{M + F_x} - 1 \right) = \frac{x}{\beta} \left(\frac{\alpha_p}{M} - 1 \right)$$

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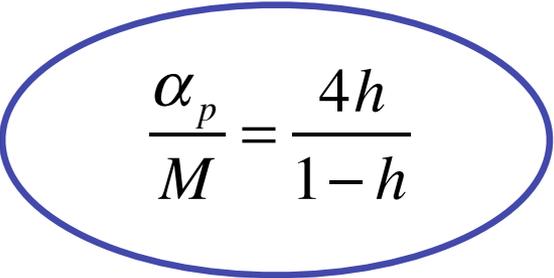
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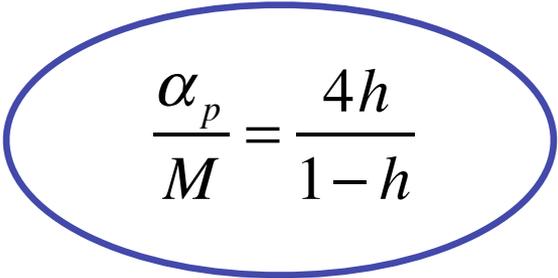
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$$\frac{F_x}{M}$$

is completely determined by x and steepness

More Results Another primary management reference point is the biomass that gives maximum net recruitment, B_{MNP} .

$$\frac{B_{MNP}}{B_0} = \frac{\sqrt{\frac{\alpha_p}{M} - 1}}{\frac{\alpha_p}{M} - 1} = \frac{\sqrt{\frac{4h}{1-h} - 1}}{\frac{4h}{1-h} - 1}$$

Thus, the single parameter steepness determines both of the major reference management points

An Example

Suppose in a data-poor stock assessment we assert that $h=0.8$, $M=0.15$.

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$$MSY = 0.09B_0$$

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$$MSY = 0.09B_0$$

The only free parameter that can be estimated in this stock assessment is unfished biomass (or alternatively the strength of density dependence of recruitment), and it is clear that its estimated value is strongly conditional on assumed values of M and/or h .

“Okay, that is true for the production model, but not for the age-structured model because of selectivity curves”

▪

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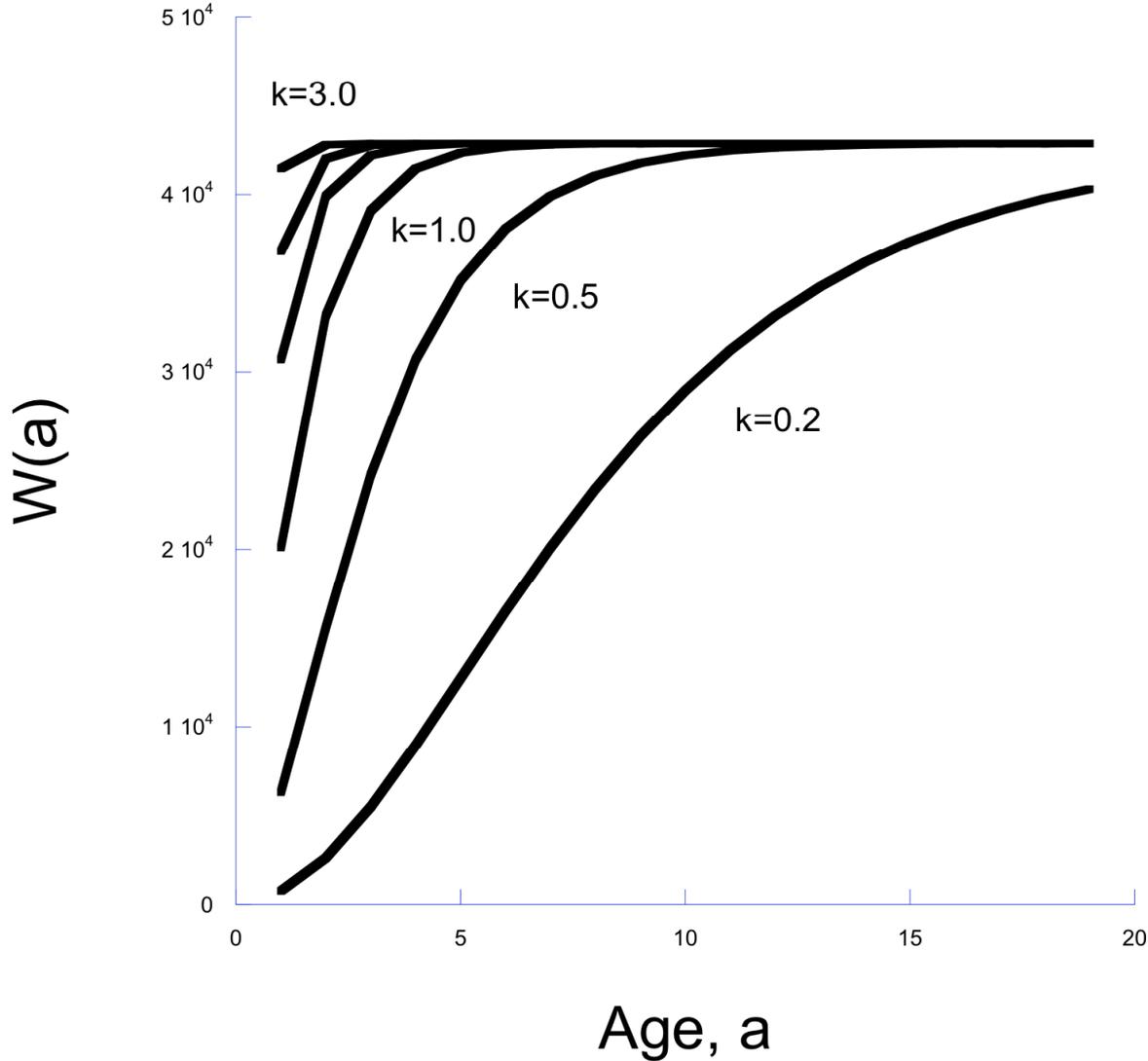
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Hypothesis:

$$F_{MSY} \bar{W}_f = g(h)$$

Faster Growth Makes the Age Structured Model More and More Like a Production Model



The Test of the Hypothesis: Scaled Results

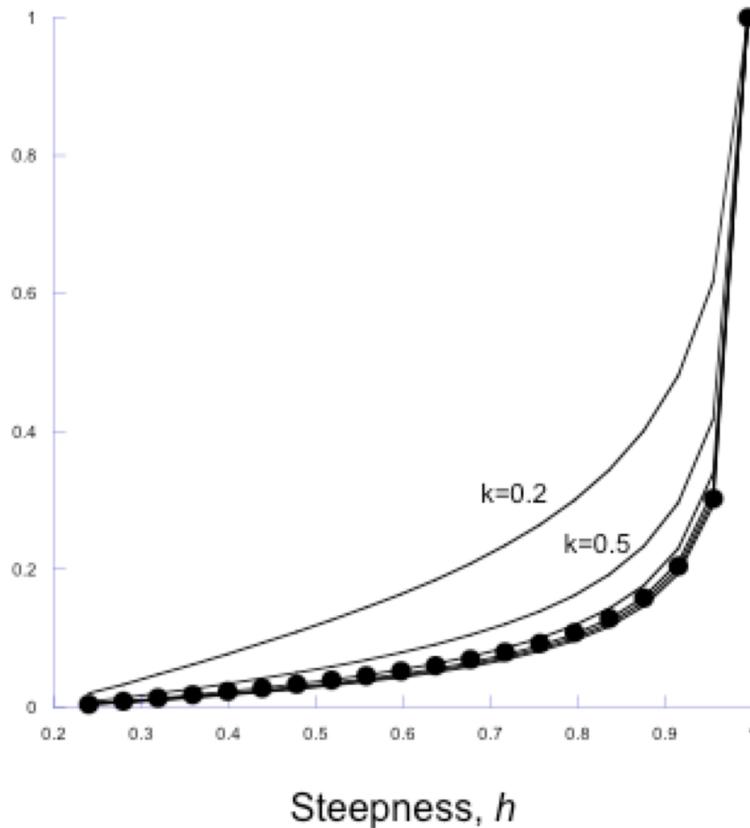
Points: Production Model
Lines: Age Structured Model

$$F_{MSY} \bar{W}_f$$

(lines)

$$\sqrt{\frac{4h}{1-h}} - 1$$

(points)



Constant mortality

Long-lived

M is small

Mass at age constant

“Your Results Depend on the Fishery Selectivity Curve and Fishing Mortality Giving MSY So Do Not Generalize”

Spawning Biomass Per Recruit (SBR) at Fishing Mortality F

$$SBR(F) = \sum_{a=1}^{20} \bar{N}(a)W(a)p_m(a) \prod_{a'=0}^{a-1} e^{-M(a)-s(a)F}$$

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Spawning Potential Ratio for the Production Model

$$SPR_{MSY} = \frac{SBR(F_{MSY})}{SBR(0)} = \sqrt{\frac{M}{\alpha}} = \sqrt{\frac{1-h}{4h}}$$

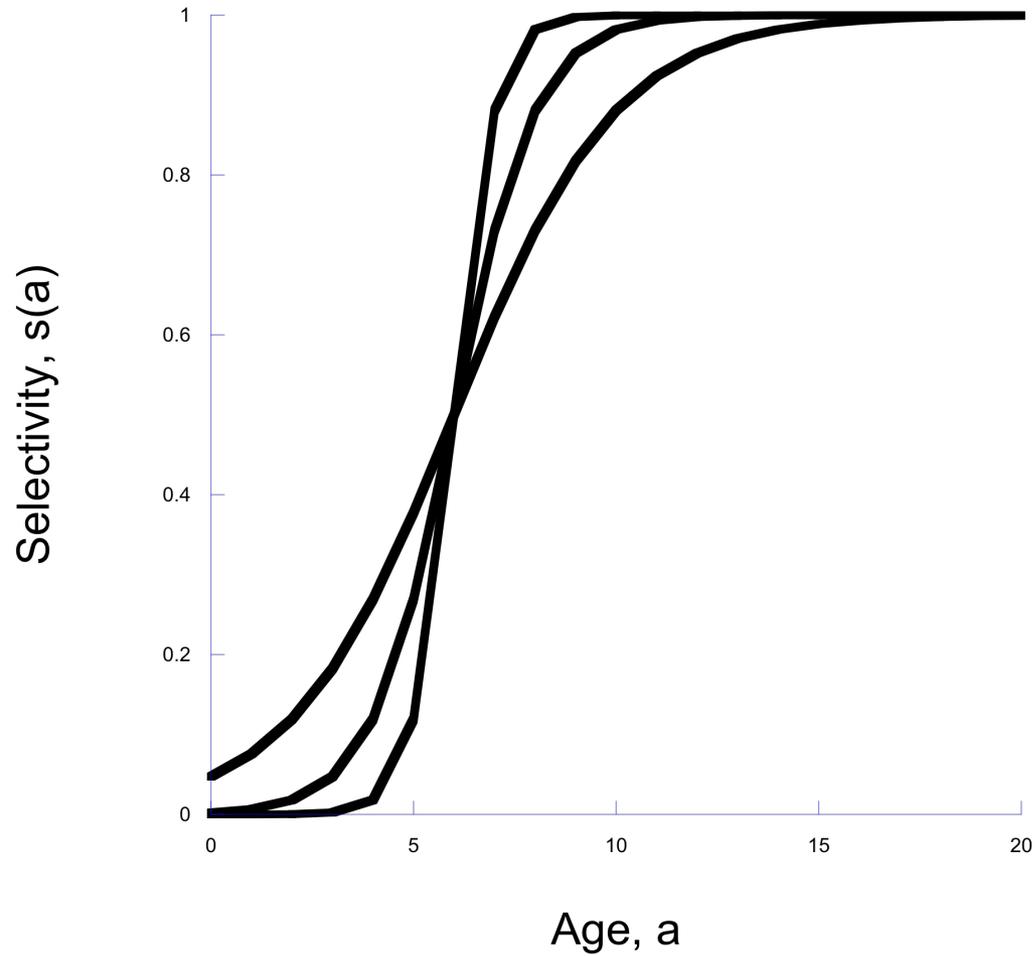
Note

$$SPR_{MSY} \rightarrow 0$$

as

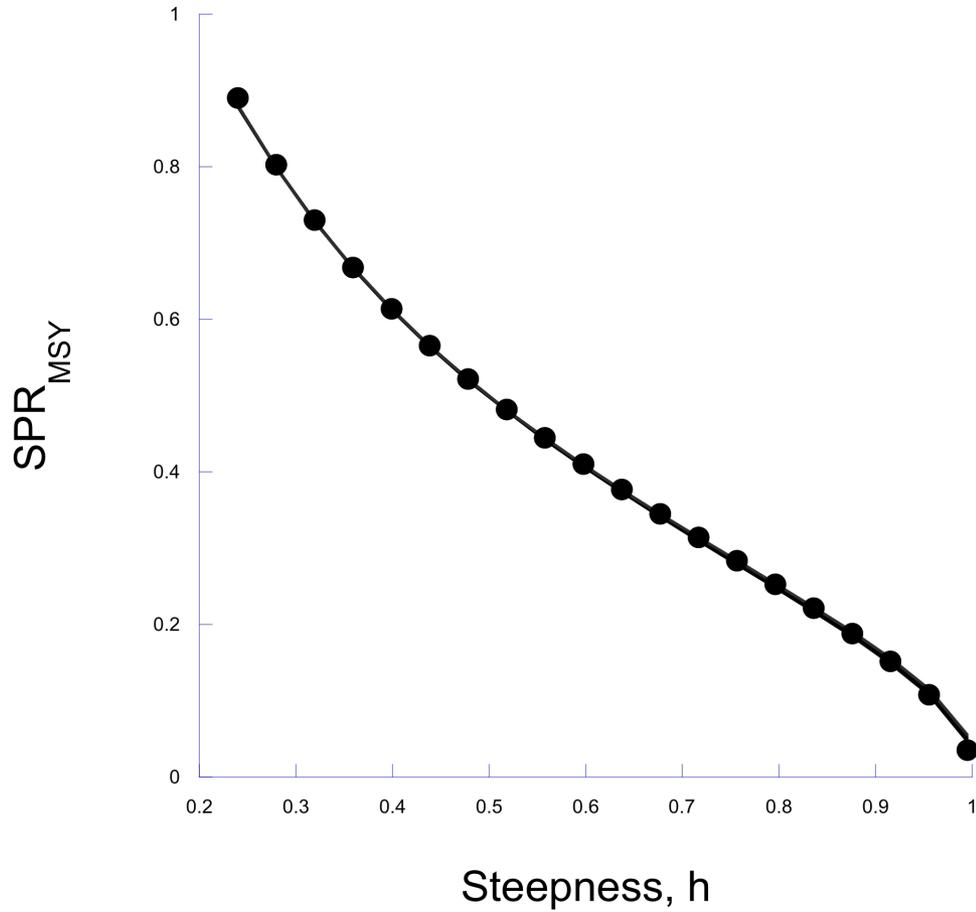
$$h \rightarrow 1$$

Another Example: Three Selectivities, Six Ages at Maturity



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Outline

- Density Dependence and Population Biology
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- Strategic Fishery Management: The Stock Assessment Process
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Fixing Steepness at 1: Biological Interpretation

$$h = \frac{\frac{\alpha_p}{M}}{4 + \frac{\alpha_p}{M}}$$

$$h \rightarrow 1 \quad \text{as} \quad \frac{\alpha_p}{M} \rightarrow \infty$$

The stock is either infinitely productive or infinitely long-lived (or both)

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There is no evidence yet of Darwinian demons in fish

Fixing Steepness at 1: Biological Interpretation (continued)

$$\frac{F_{MSY}}{M} = \sqrt{\frac{4h}{1-h}} - 1$$

As $h \rightarrow 1$

$$\frac{F_{MSY}}{M} \rightarrow \infty$$

Since the stock is infinitely productive, we can fish it infinitely hard!!!

Fixing Steepness at 1: Probabilistic Interpretation

$h = 1$ means

$$\Pr\{R(0.2B_0) = R_0\} = 1$$

With certainty, recruitment at 20% of unfished biomass is unfished recruitment. Is this what we mean?

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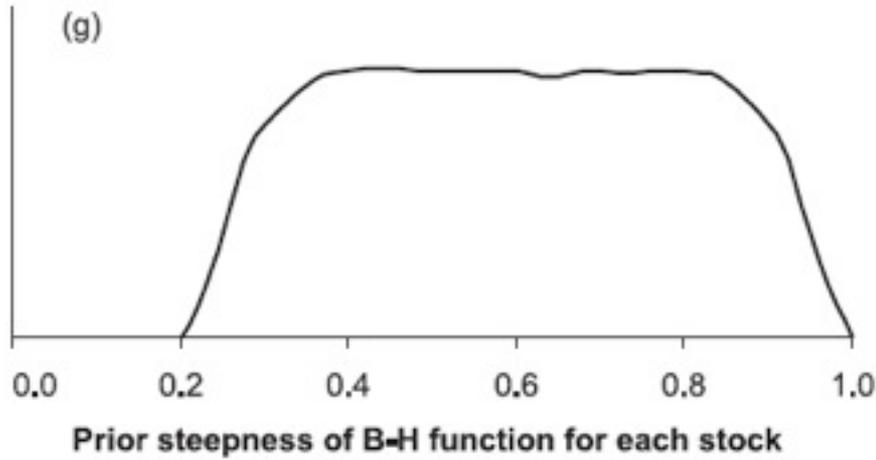
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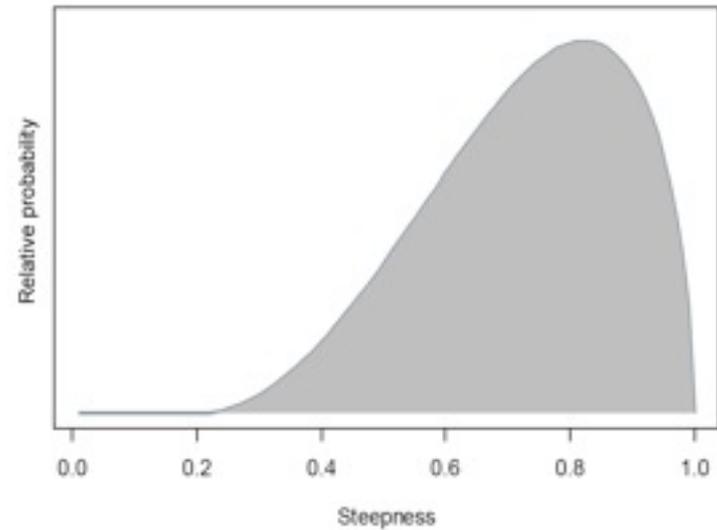
Steepness ranges between 0.2 and 1.0 (tied down at both ends by biology)

Thus, steepness should have a probability distribution



Michielsens and McAllister.
2004. CJFAS 61:1032-1047

Harley et al. 2009.
Bigeye Tuna Assessment





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Three Options for Moving Forward

Do Not Fix Steepness and Mortality Rate

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Replace the BH-SRR by a SRR that Avoids the Problem

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Replace the BH-SRR by a SRR that Avoids the Problem

Be fully honest about the limitations of the data and the stock assessment

Do Not Fix Steepness and Mortality Rate

When will data be informative?

Use Simulation Methods to determine what kinds of data are necessary so that steepness and natural mortality can be estimated in the stock assessment

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Already started:

Lee, H.-H. et al. 2011. Estimating natural mortality within a fisheries stock assessment model: An evaluation using simulation analysis based on twelve stock assessments. *Fisheries Research* 109: 89-94.

Lee, H.-H. et al. 2012. Can steepness of the stock–recruitment relationship be estimated in fishery stock assessment models? *Fisheries Research* 125-126: 254-261.

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Replace the *BH-SRR* by a *SRR* that Avoids the Problem

An example: Maynard Smith/Shepherd model

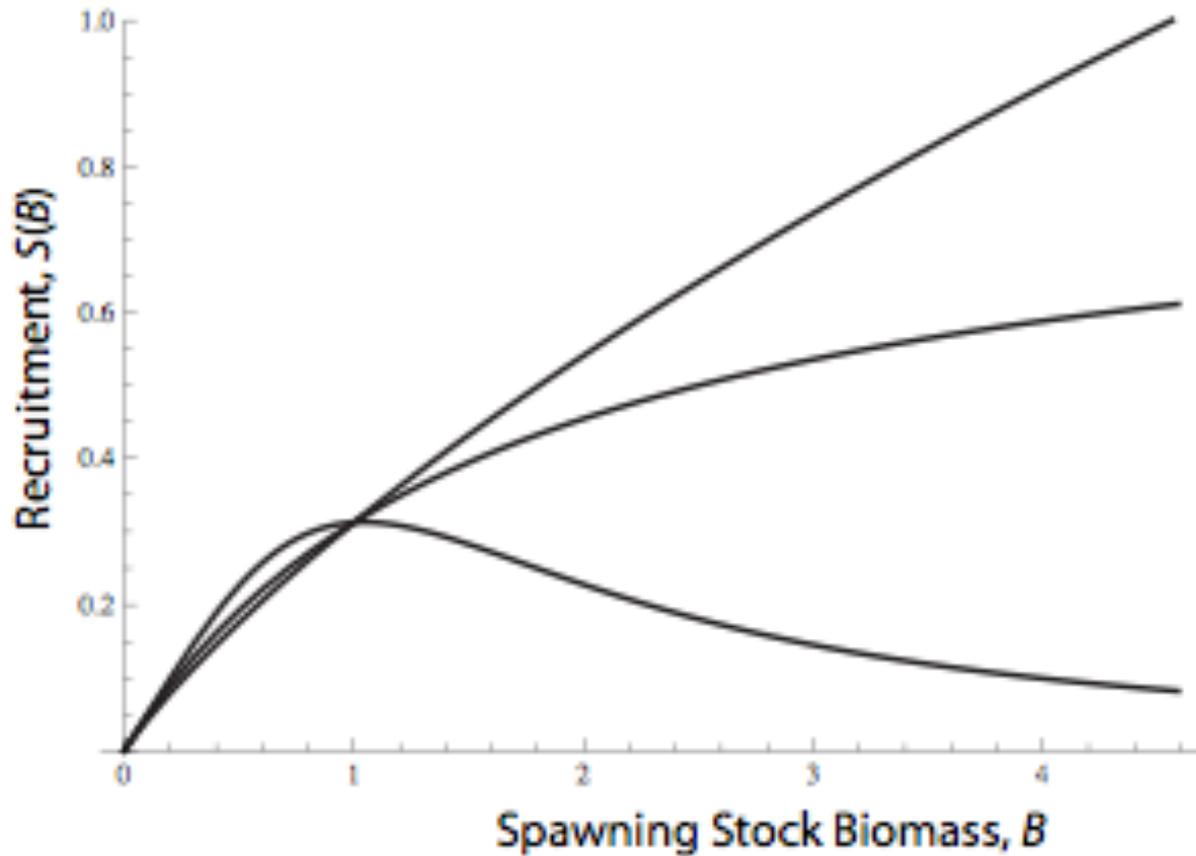
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$$\frac{dB}{dt} = \frac{\alpha_p B}{1 + \beta B^n} - (M + F)B$$



$n > 1$, Cushing-like

$n = 1$, Beverton-Holt

$n < 1$, Ricker-like

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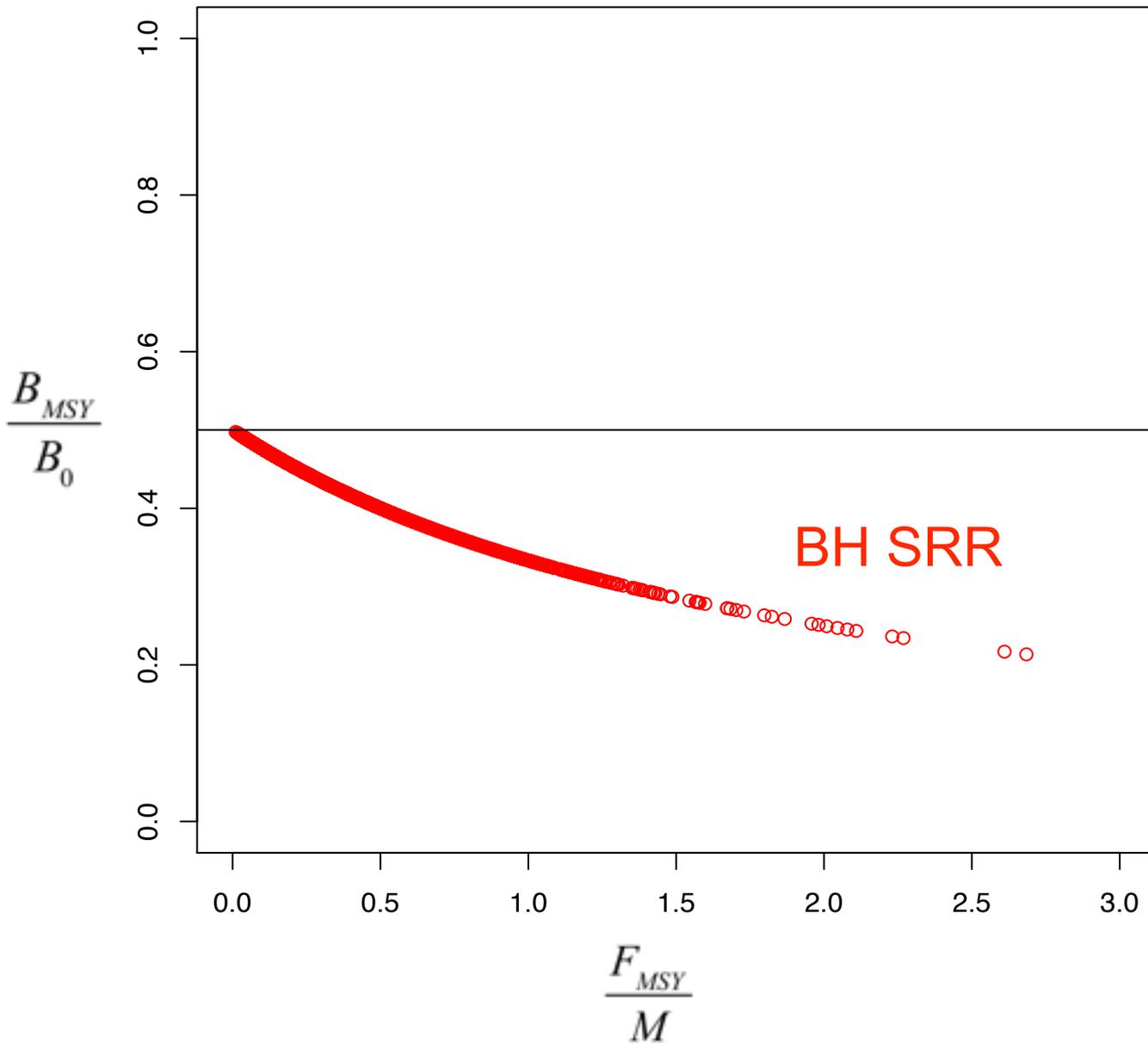
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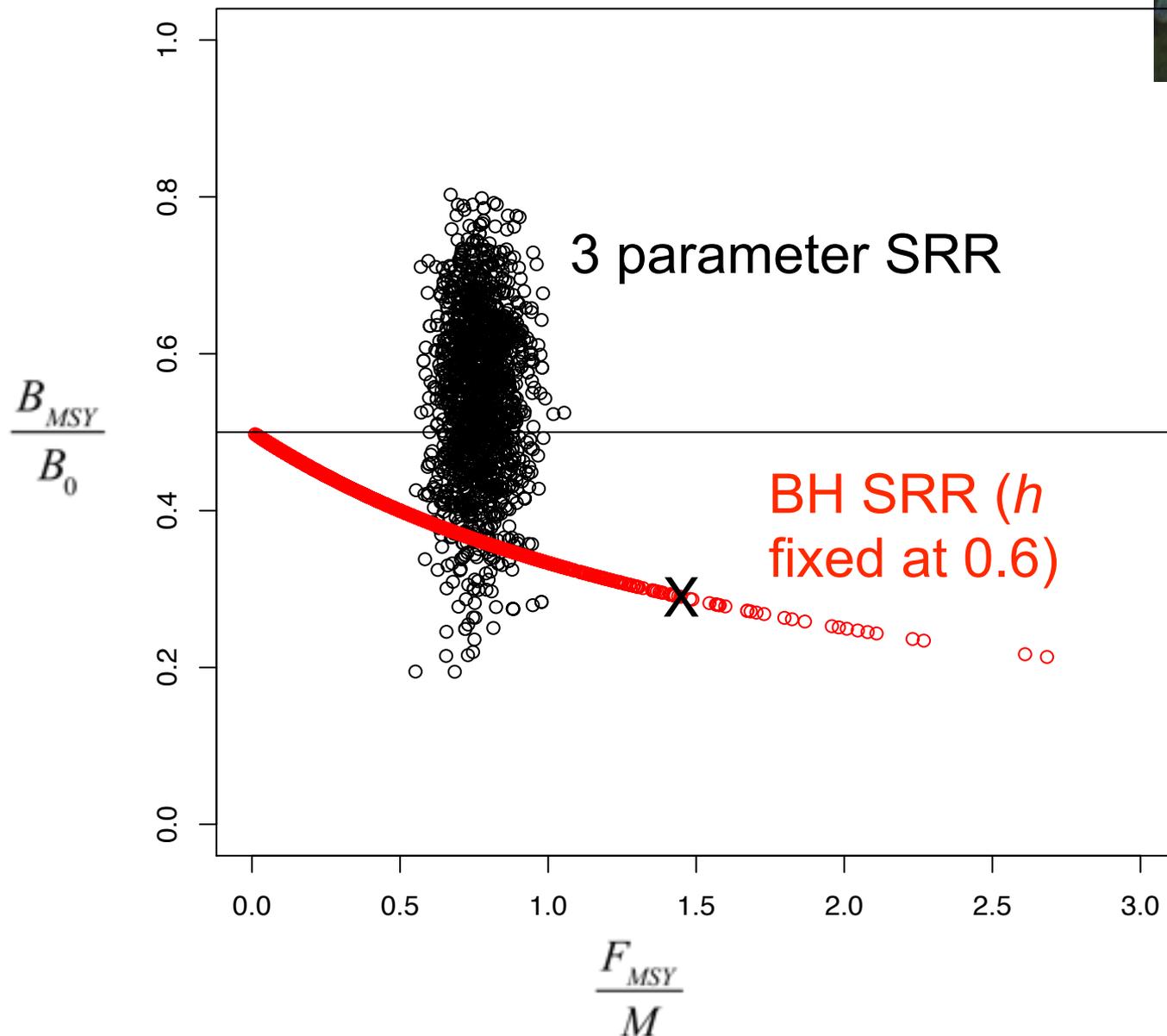
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There is still an undetermined parameter for the analysis -- the data can tell us something! - or we can integrate over the potential range of n

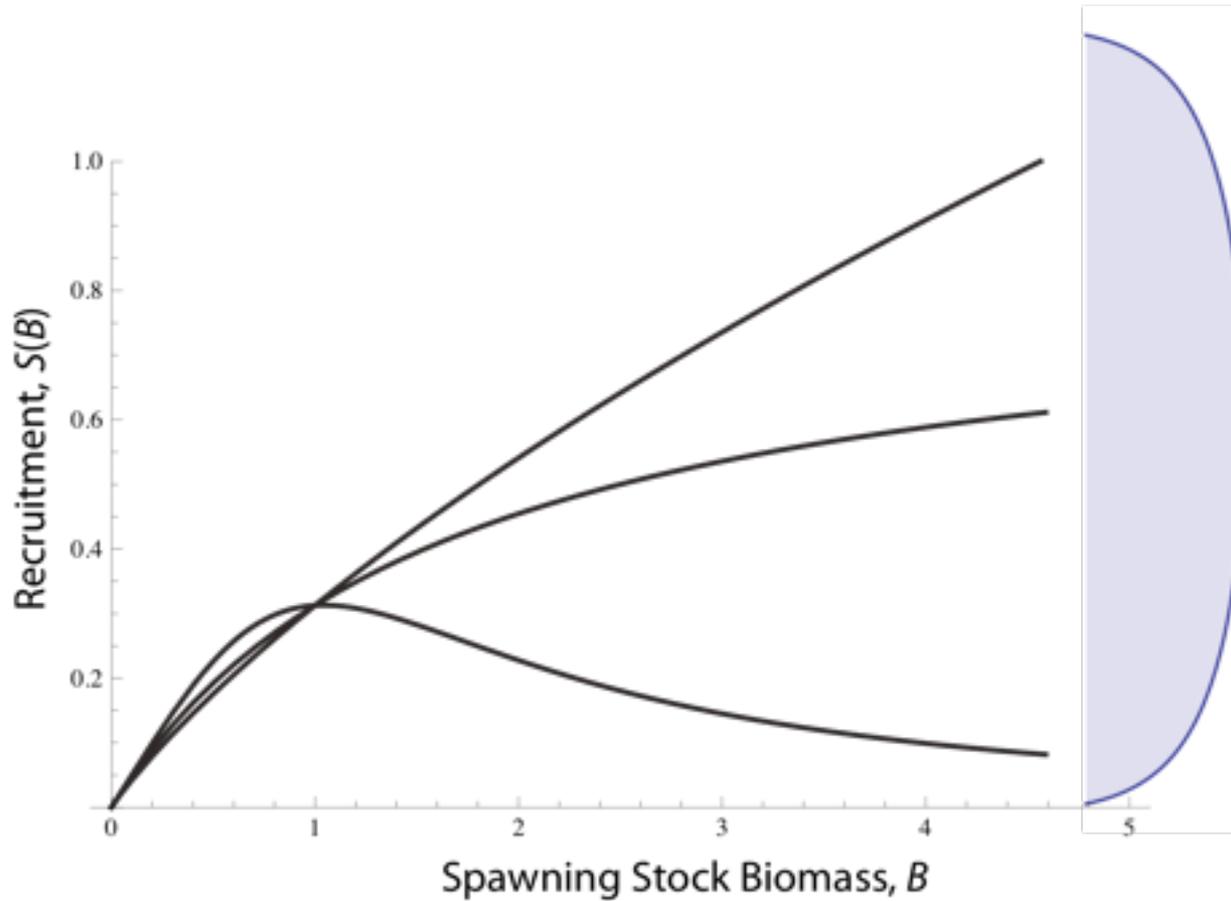
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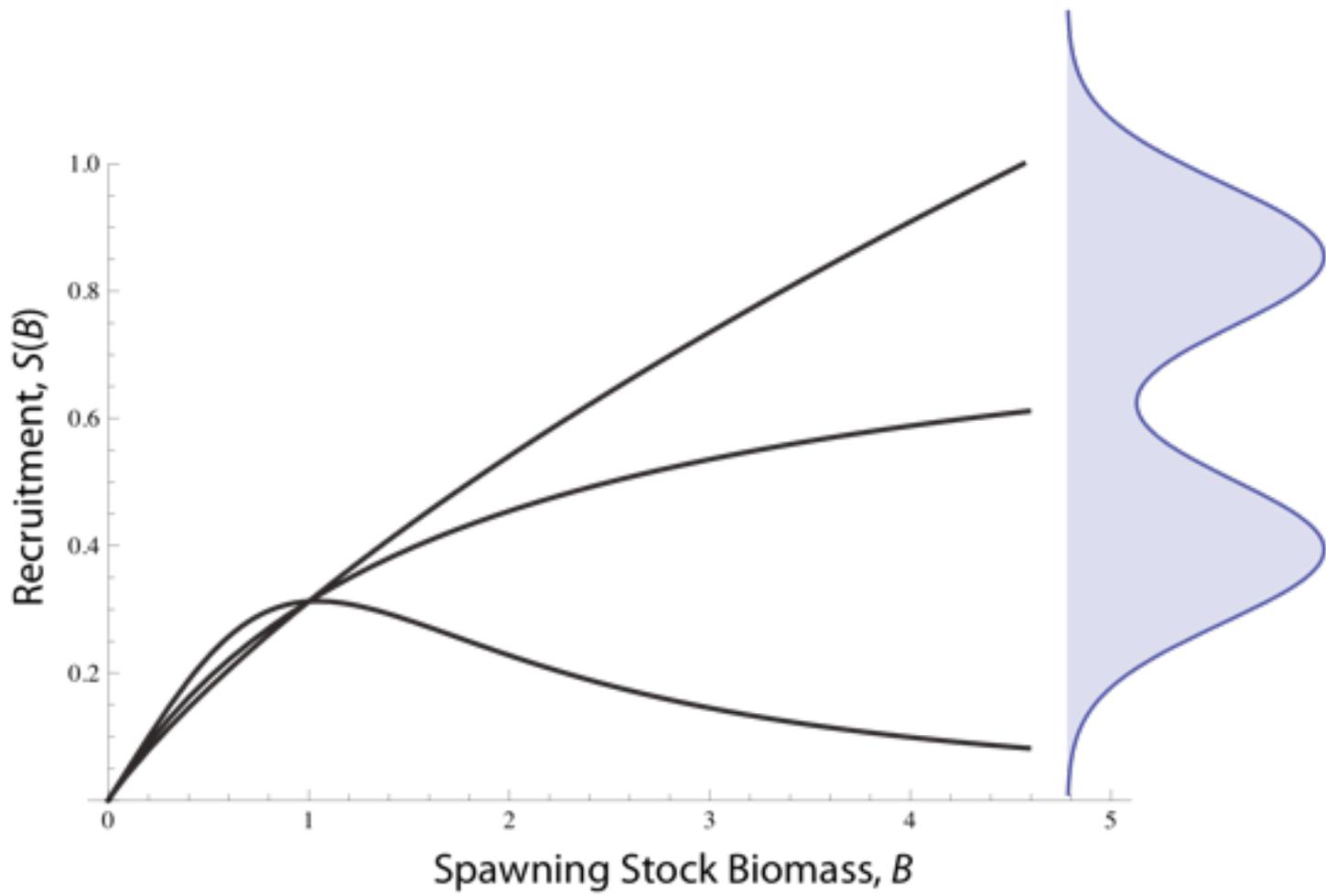


We Can Do a Meta-analysis on the Parameter, And It Might Look Like This

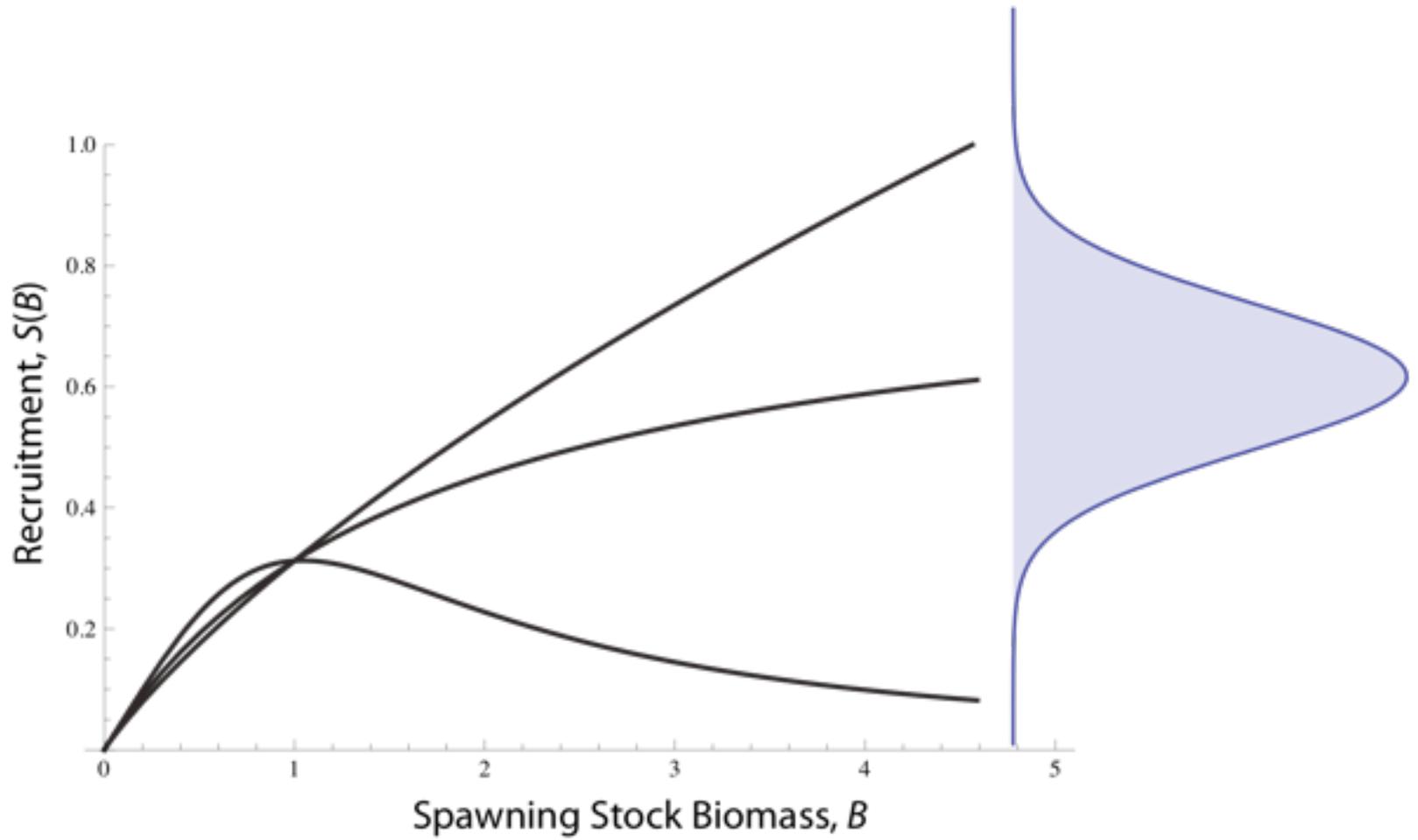


Distribution of n

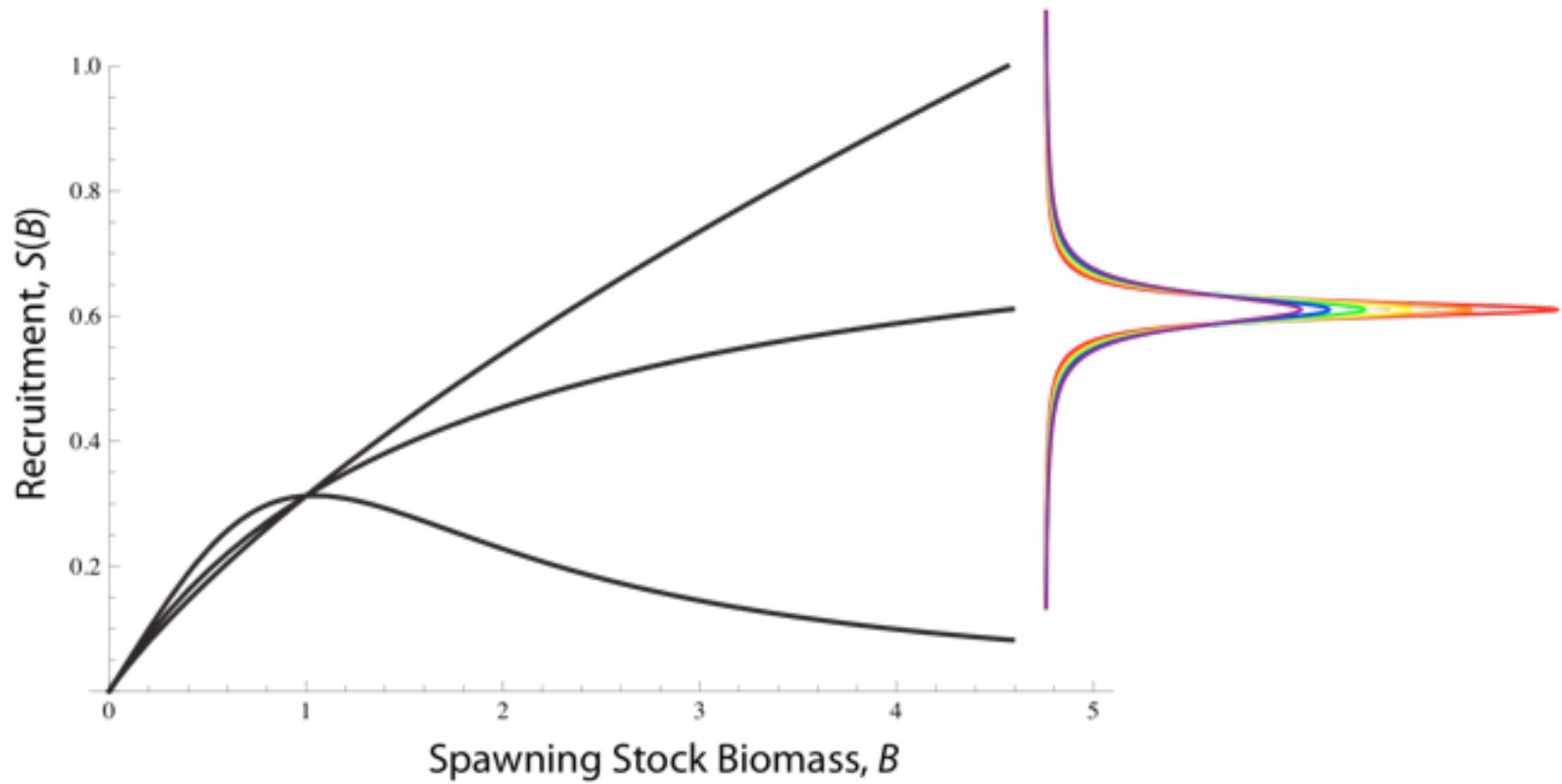
Or The Meta-analysis Could Yield This



Or This



But Not Likely This



Be fully honest about the limitations of the data and the stock assessment

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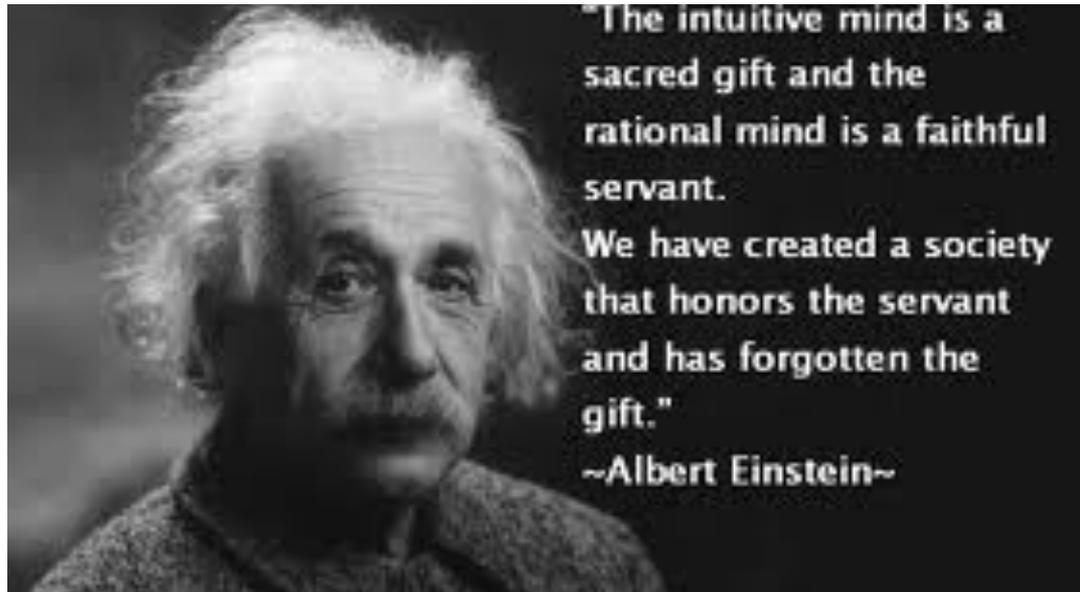
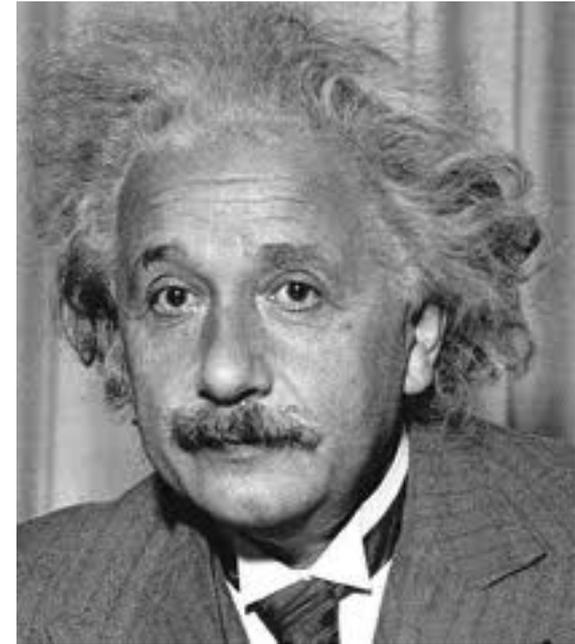
- Management policy with biomass targets or rebuilding plans on a fixed time table with specified probability may often overstep what can realistically be expected from a defensible assessment of an individual stock.
- The community of stock assessment scientists needs to agree on workable protocols for several classes of life history parameters, ecosystem types, fishery histories that are reasonably robust in achieving management objectives in the face of scientific uncertainty. Developing good proxies and protocols is a scientific matter. It should be based on meta analyses and management strategy evaluation.



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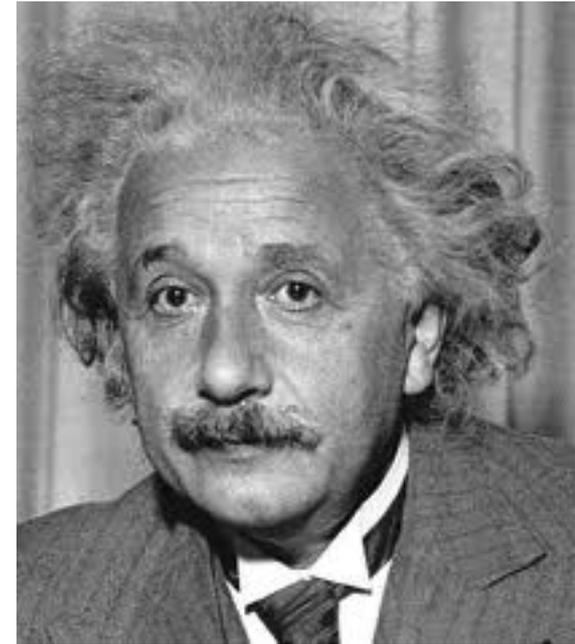
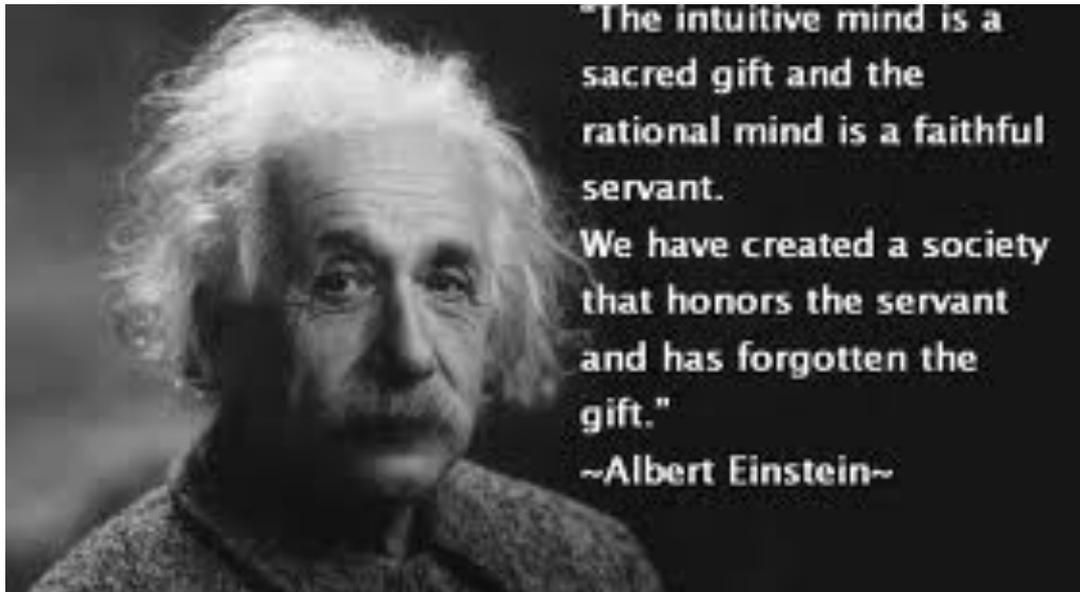
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Conclusions, Part 1: A scientific theory should be as simple as possible, but no simpler.



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This is a case of a too simple theory



Conclusions, Part 2

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- Environmental forcing can be built into the early life history through fluctuations in mortality rate and into productivity through fluctuations in egg production.

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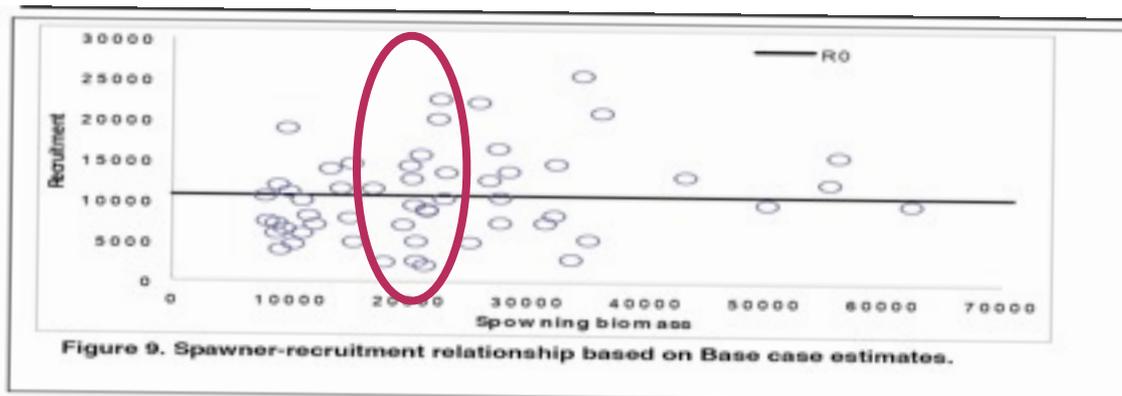
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Recruitment independent of stock size does not mean $h=1$ (with probability 1 the recruitment at 20% of spawning stock size is the same as R_0). Rather it means *any* percentage of recruitment is possible: h has a uniform distribution (tied down at small values and near 1).

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The first responsibility of scientists is to the integrity of science and it is critical to be explicit about what is known and not known. And there is not a moment to be lost.





A Few Citations



He, X., Mangel, M. and A. MacCall. 2006. A prior for steepness in stock-recruitment relationships, based on an evolutionary persistence principle. *Fishery Bulletin* 104: 428-433

Mangel, M., Brodziak, J.K.T., and G. DiNardo. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish and Fisheries* 11:89-104.

Enberg, K., Jorgensen, C. , and M. Mangel. 2010. Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1708-1719.

Mangel, M., MacCall, A.D., Brodziak, J., Dick, E.J., Forrest, R.E., Pourzand, R., and S. Ralston. 2013. A perspective on steepness, reference points, and stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences* 70:930-940