The effect of spawner age on stock productivity: influences of life-history pattern and recruitment variability

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Outline

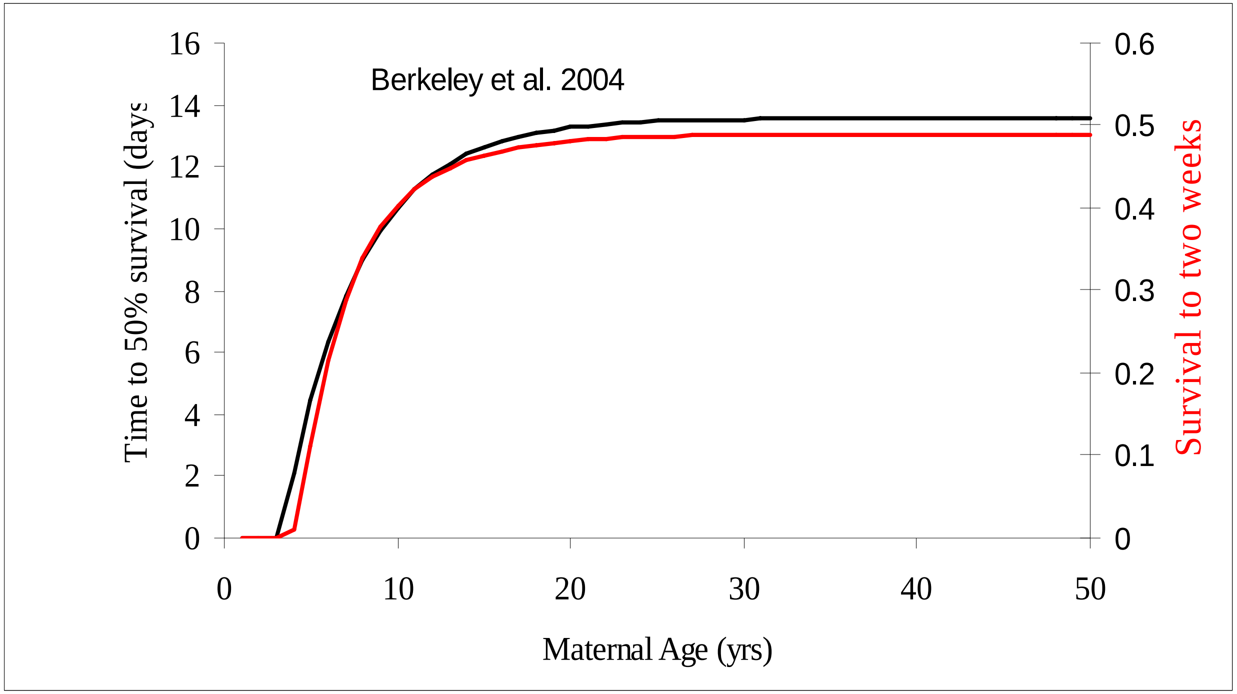
1) Define “maternal effects” and its relationship to traditional stock-recruit theory

2) Describe how maternal effects may affect estimates of stock productivity

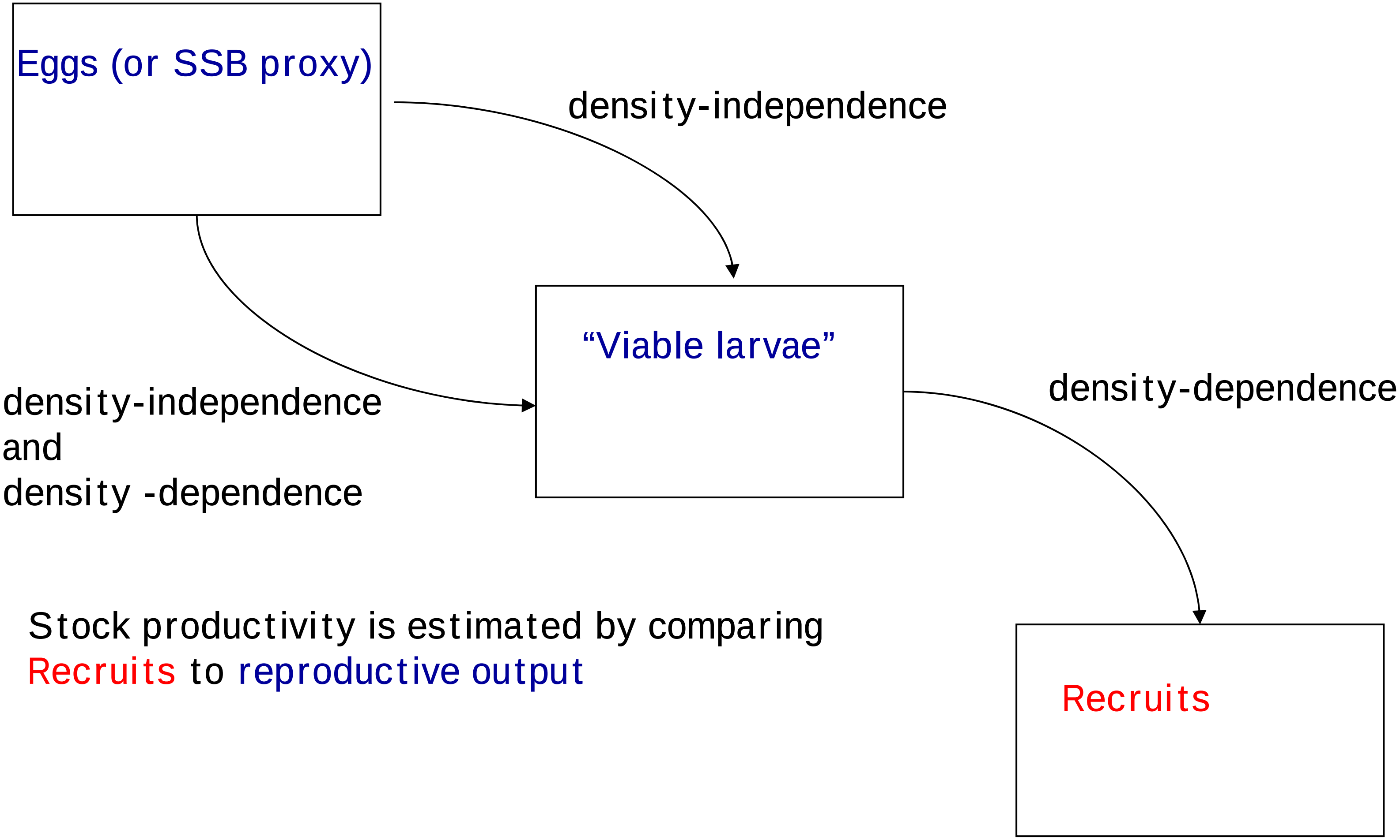
3) Present results of simulation modeling that evaluates how maternal effects may affect estimates of stock productivity under a range of stochastic recruitment patterns and life-history types

What are “maternal effects”?

An association of larval survival with spawner age. For marine species, this has been examined for cod and rockfish. Berkeley et al. (2004) observed maternal effects in laboratory studies of black rockfish, suggesting that conservation of age-structure may be an important management consideration.



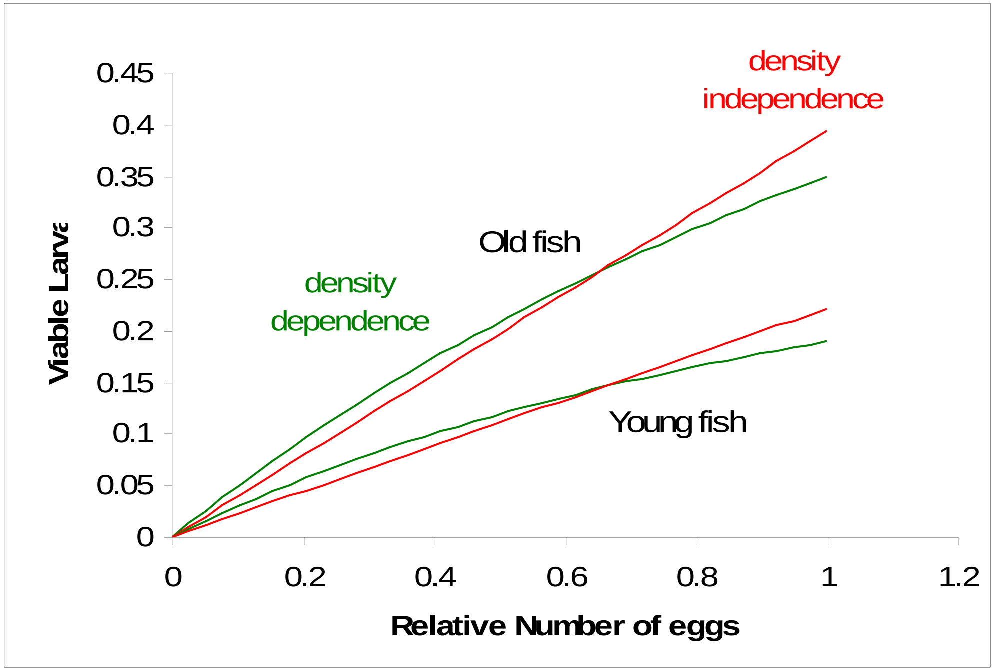
Conceptual model of maternal effects and recruitment



Stock productivity is estimated by comparing
Recruits to reproductive output

Relationship of viable larvae to eggs for a given age

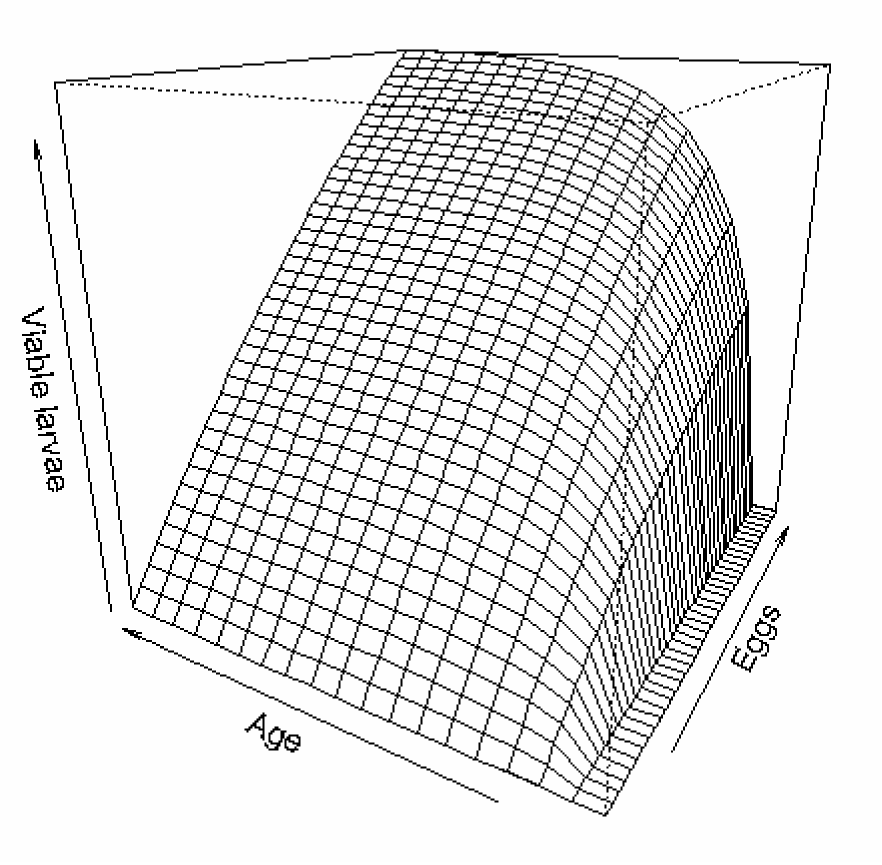
Berkeley's larval survival curves for black rockfish were modified to reflect life-history differences for POP and cod



Density –independent viable larvae (DIVL)

Density-dependent viable larvae (DDVL)

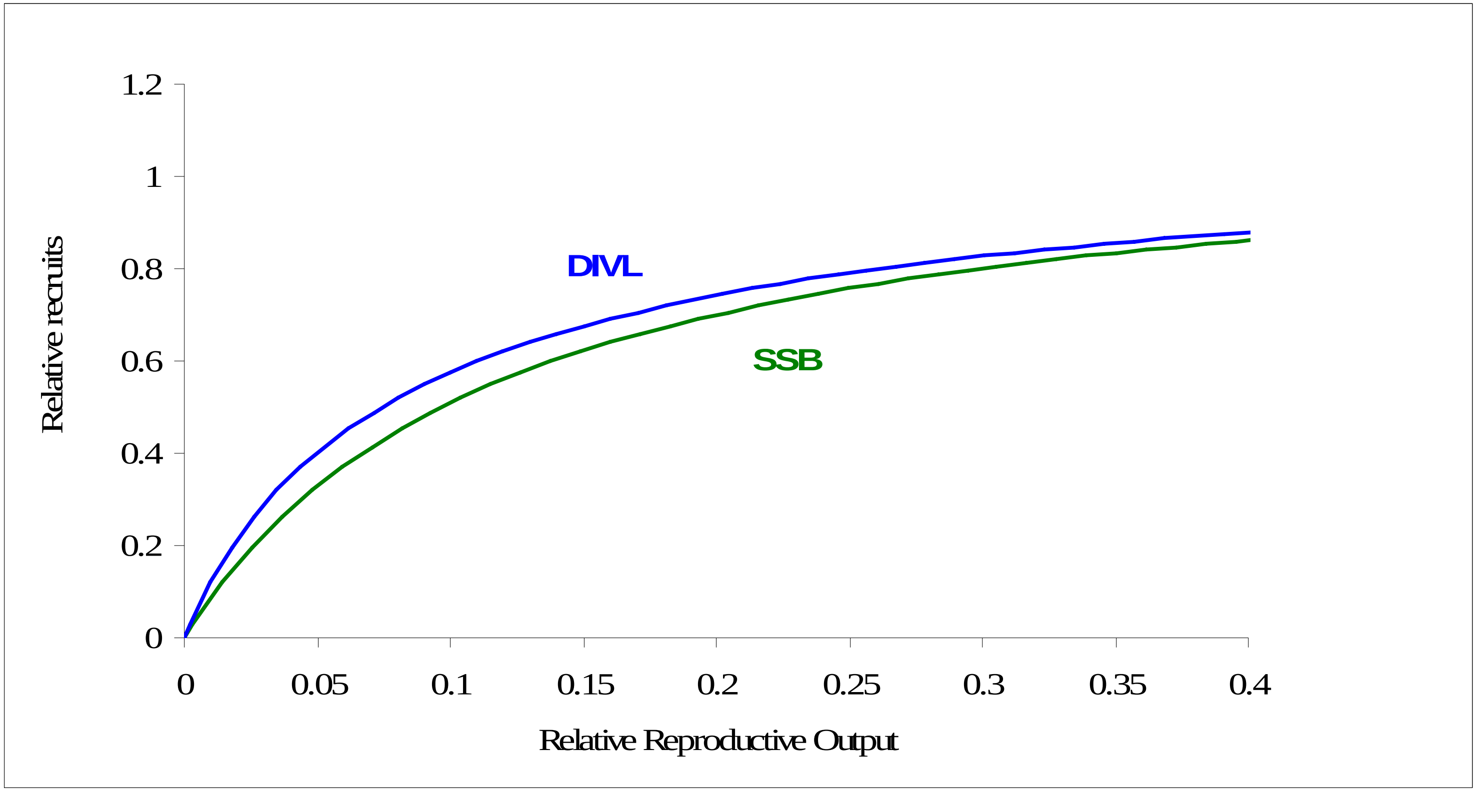
Density-dependent production of viable larvae (Beverton-Holt curve)



Effect upon stock-recruitment curves

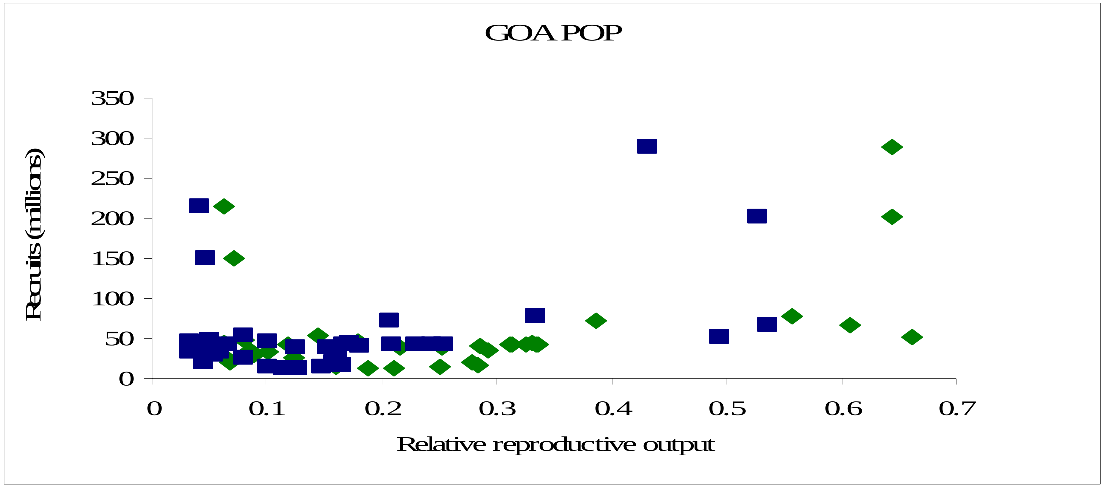
Steepness (*h*) – a function of the slope of the SR curve at low stock sizes

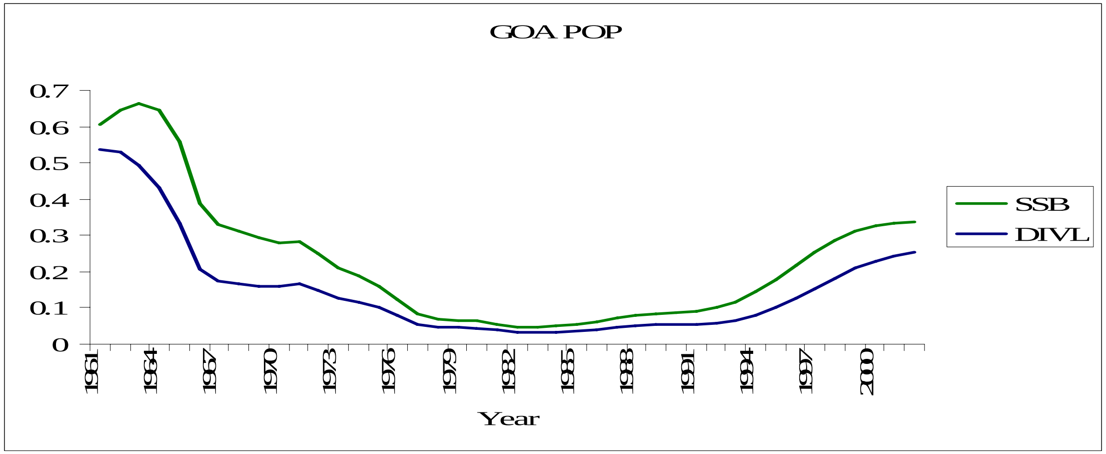
We might generally expect estimates of steepness to increase when we consider maternal effects, based on equilibrium theory



How would estimates of reproductive output and steepness respond with stochastic recruitment?

GOA POP – one example





Estimated steepness may be a function of how often the relative DIVL is less than relative DDVL

How is estimated productivity affected under a variety of life-history types, recruitment patterns, and harvest levels?

Stochastic Simulations

2 life-history types (Aleutian Islands POP and EBS cod)
5 levels of recruitment residual autocorrelation (ρ) (0.0,0.2,0.4,0.6,0.8)
5 levels of harvest rates ($F_{100\%}$, $F_{80\%}$,$F_{60\%}$,$F_{40\%}$,$F_{20\%}$)

For each combination of LH pattern, ρ, and harvest rate, we have:

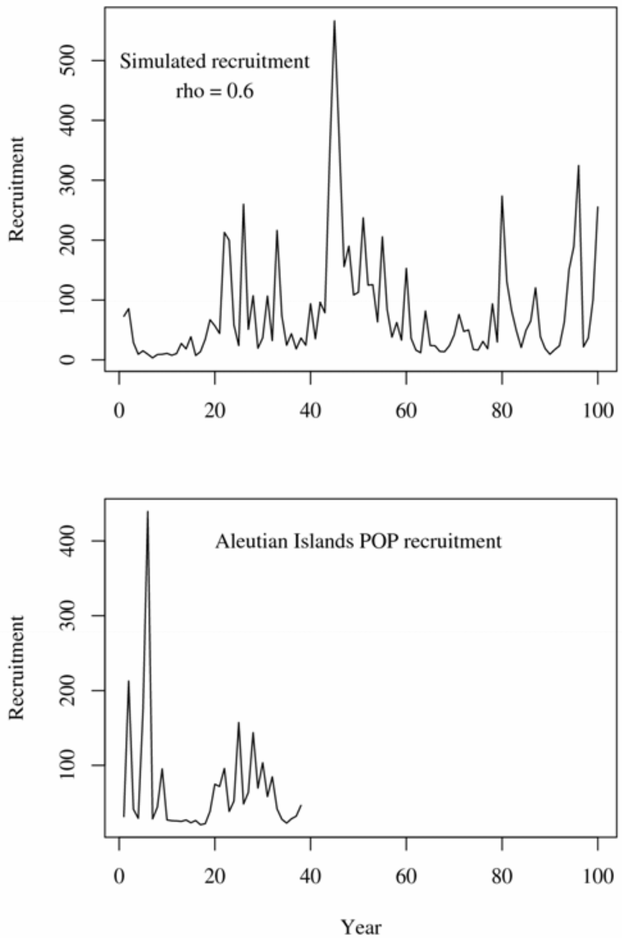
Operating model: Generate 200 datasets, each with recruits and three measures of reproductive potential SSB, DIVL, and DDVL.
Recruits estimated from Beverton- Holt SSB-recruitment curve with process error. Larval survival parameters for each species were modified from Berkeley's black rockfish data
Each case starts with a population in equilibrium with F=0, and the F_{spr} rate is applied for 100 years.

Estimation model: For each dataset, estimate the stock-recruitment parameter steepness (h) and R_0 for each of the three measure of reproductive potential.

Differences in life history between BSAI POP and EBS Pacific cod

	POP	Cod
Age at first maturity	6	3
Age at 50% maturity	10	5
Longevity	100 yrs	15 yrs
Mortality Rate	0.05	0.37
Fecundity	300,000	~7,000,000
Standard deviation of recruitment residuals	1.0	0.75
Steepness of SSB-R curve	0.5	0.75

Modeling of recruitment variability



$$R_{i+recage} = f(SSB_i)e^{(\rho\gamma_{i-1}+\sqrt{1-\rho^2}\sigma_r\varepsilon_i)}$$

Output from simulation modeling

Relative reproductive output:

$$SSB_t \,/\, SSB_{F=0} \qquad DIVL_t \,/\, DIVL_{F=0} \qquad DDVL_t \,/\, DDVL_{F=0}$$

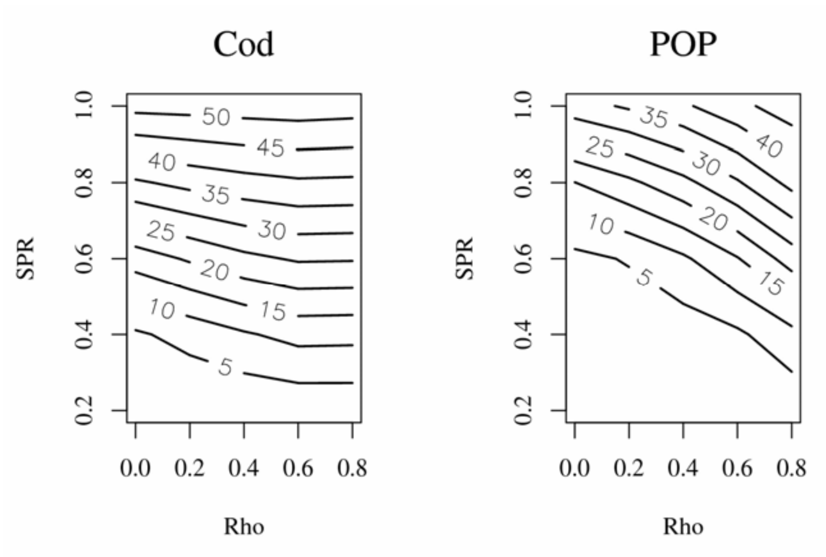
Relative steepness:

$$h_{DIVL} \,/\, h_{SSB} \qquad h_{DDVL} \,/\, h_{SSB}$$

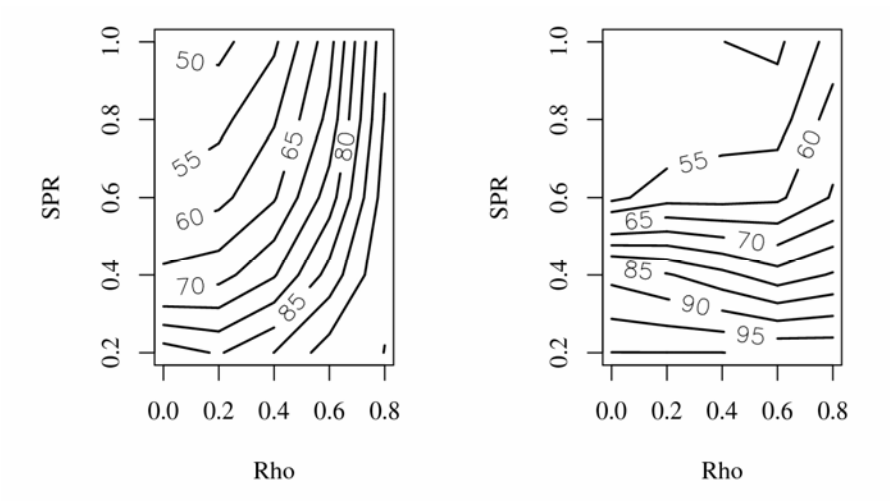
What is the average proportion of years where the relative DIVL of DDVL exceeds relative SSB?

What is the proportion of datasets where h_{divl} or h_{ddvl} exceeds h_{ssb}?

Comparison of DIVL to SSB

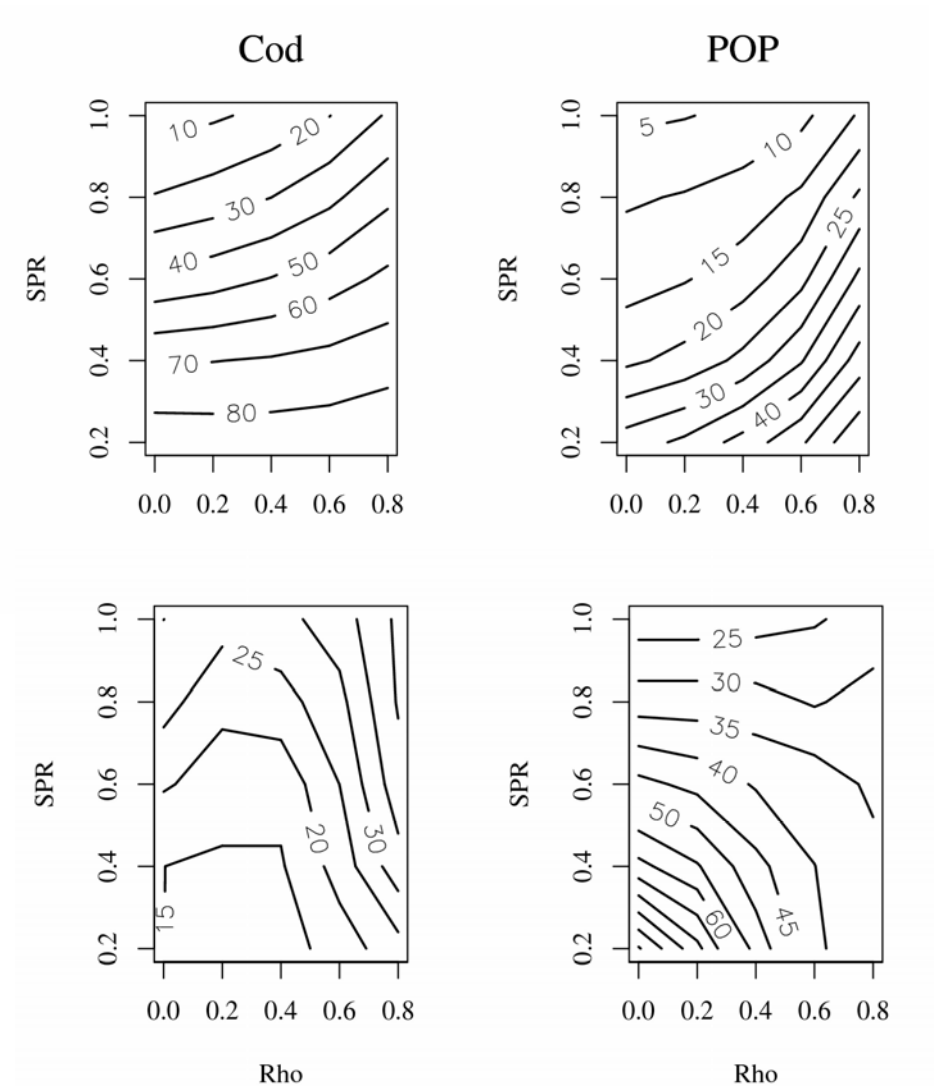


Average Percentage of years where DIVL > SSB



Percentage of datasets where $h_{divl} > h_{ssb}$

Comparison of DDVL to SSB



Average Percentage of years where DDVL > SSB

Percentage of datasets where $h_{ddvl} > h_{ssb}$

Conclusions

1) The Beverton-Holt curve can be easily modified to consider the production of viable larvae as a function of eggs and spawner age.

2) With stochastic recruitment patterns, strong recruitment pulses can differentially affect various measures of reproductive output. This can affect the estimation of productivity.

3) Estimation of stock productivity is a function of several factors, including longevity, autocorrelation of recruitment residuals, harvest rate, and extent of density dependence in producing viable larvae.

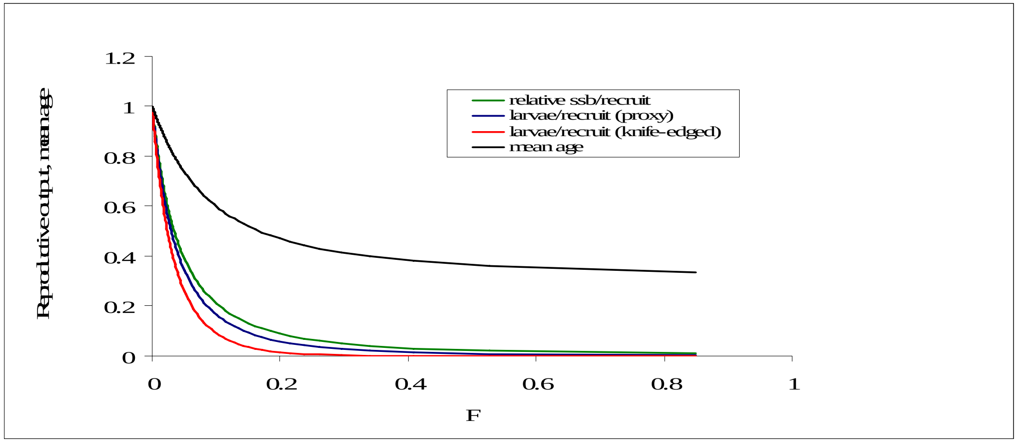
4) Estimates of stock productivity are sensitive to relative differences in reproductive potential at low stock sizes, and the range of stock sizes observed is a function of the longevity (due to the "buffering" of recruitment variability). This variation in range of stock sizes can affect estimates of productivity with different measures of reproductive output.

Future work

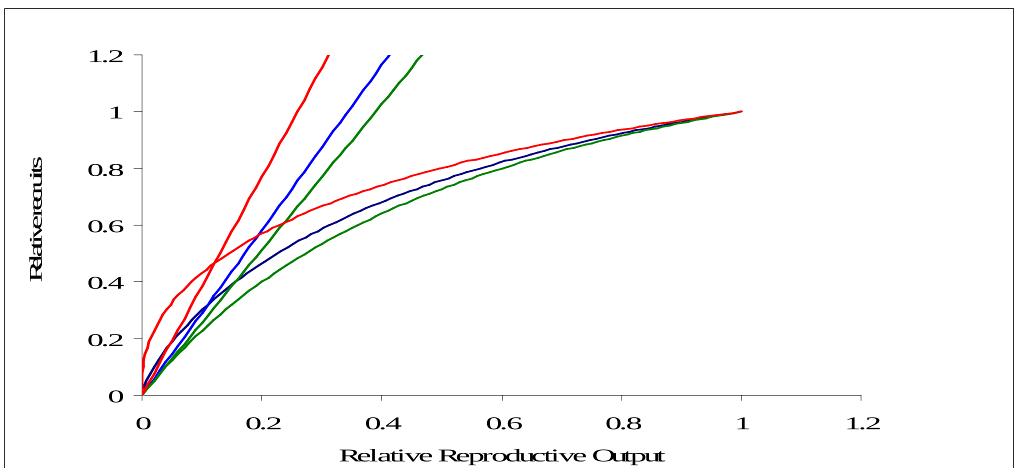
1) What are optimal harvest strategies for stocks with different life-history types?

2) Incorporate spatial patterns of reproductive biology

Stock productivity and life-history parameters are not independent



Implies more conservative exploitation rates



Implies increased exploitation rates

Objectives

1) How does stochastic changes in recruitment variability affect production of reproductive output, and how would this differ for stock of different life-histories?

2) How does intensity of fishing affect production of reproductive output?

How are “viable larvae” produced?

Viable larvae are those that survive an initial period in which the egg production of younger age classes is discounted.

Often modeled as density-independent survival during this period (i.e, setting b= 0 in Beverton-Holt formulation) . We could also have density-dependence in production of viable larvae

Beverton-Holt recruitment model

$$\alpha = e^{(a\Delta t)}$$

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

Discrete-time solution

$$\beta = \frac{b}{a}(e^{(a\Delta t)} - 1)$$

$$N_{t+\Delta} = \frac{1}{\frac{b}{a}(e^{a(\Delta t)} - 1) + \frac{e^{a(\Delta t)}}{N_t}}$$

Goals

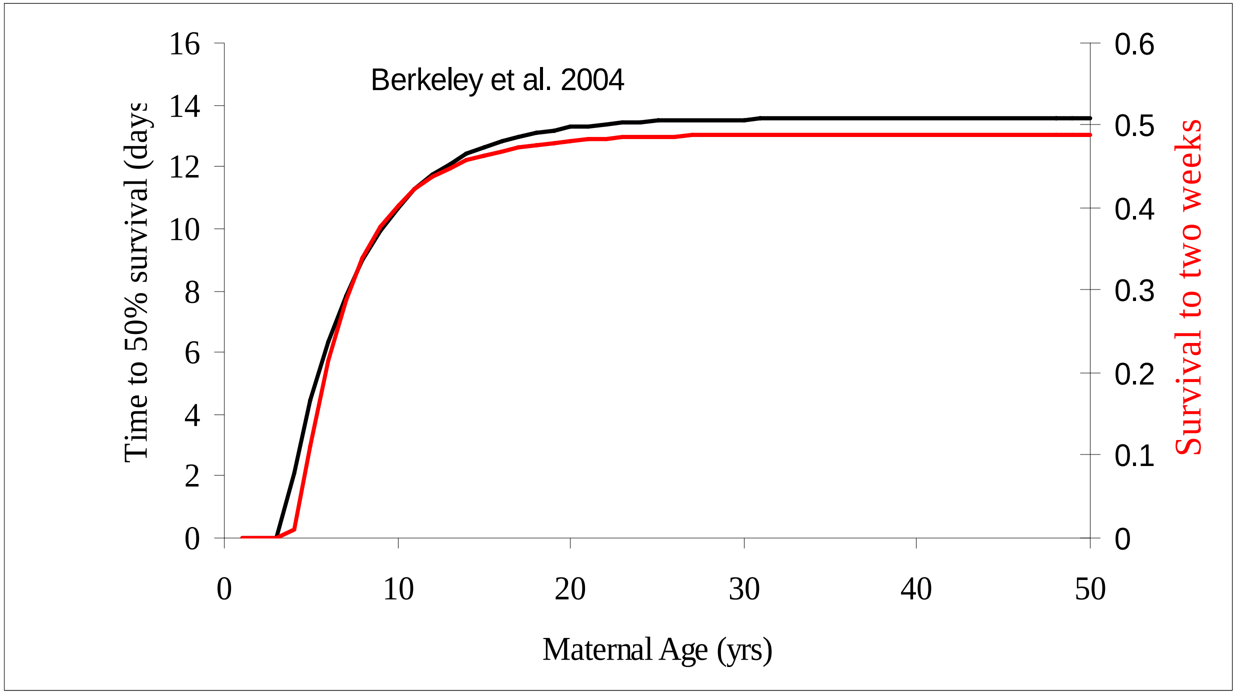
1) Estimate F_{MSY} for Alaska POP and compare to current estimates of of $F_{40\%}$.

2) Evaluate how age-specific changes in larval survival may affect optimal harvest policy by using larvae as a measure of stock reproductive capacity.

Theoretical Considerations

Age-specific effects on larval viability can be considered as a “penalty” that discounts reproductive output from younger spawners relative to older spawners.

The effect of this factor on harvest policy reference points can be obtained by rescaling population productivity from SSB “to viable larvae”



Theoretical Considerations

If the conversion of SSB to viable larvae operates in a linear (density-independent) manner, there will be no effect upon the SR analyses – this is essentially rescaling the data. This would occur if the proportion at age is independent of stock density.

$$Larvae = \sum_a s_a f_a m_a p_a N \qquad Biomass = \sum_a w_a m_a p_a N$$

$$Larvae / Biomass = \frac{\sum_a s_a f_a m_a p_a}{\sum_a w_a m_a p_a}$$

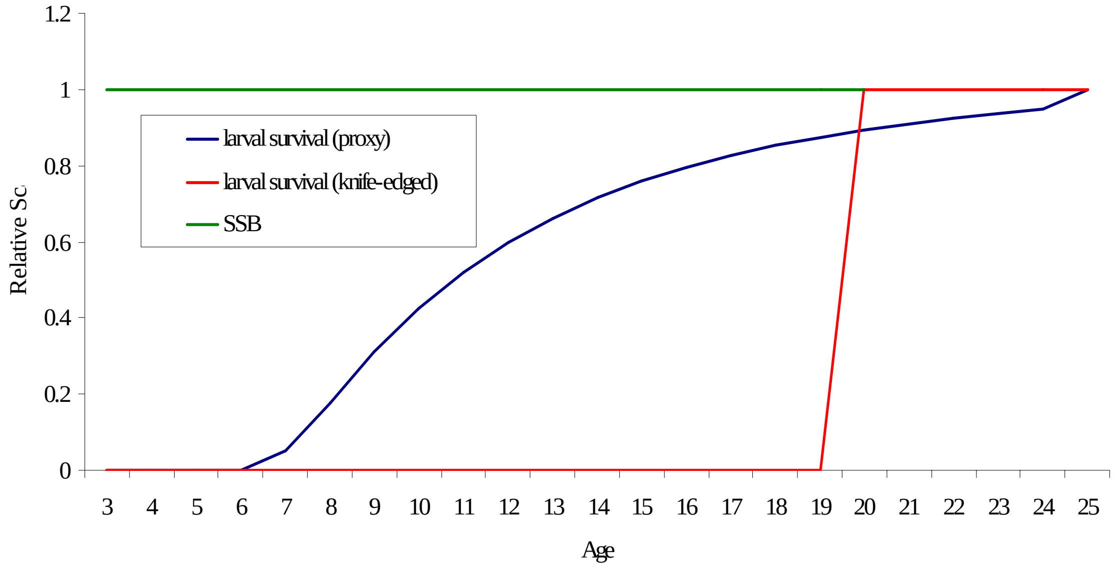
= Constant with density if fecundity (f), larval survival (s), maturity (m) and proportion at age (p) do not change with density

Methods

Consider an equilibrium population. What are the equilibrium numbers of "viable larvae", recruits, and spawning stock biomass as a function of fishing mortality?

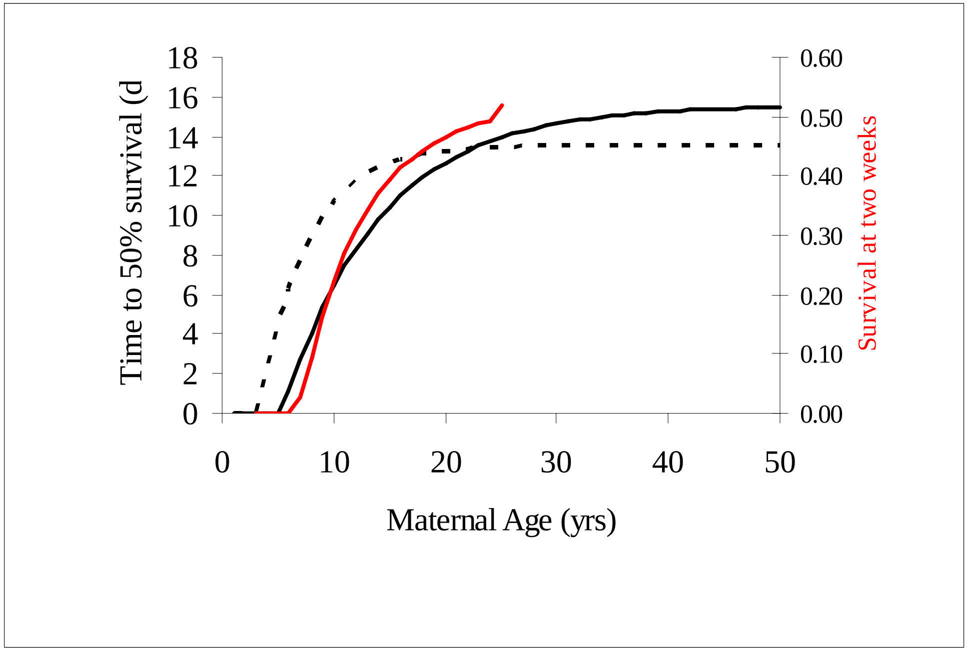
$$N_a = N_r e^{-\sum_{i=r}^{a-1} (sel_i F + M_i)}$$

N_r = initial number at recruitment age r
sel_i = fishery selectivity at age i



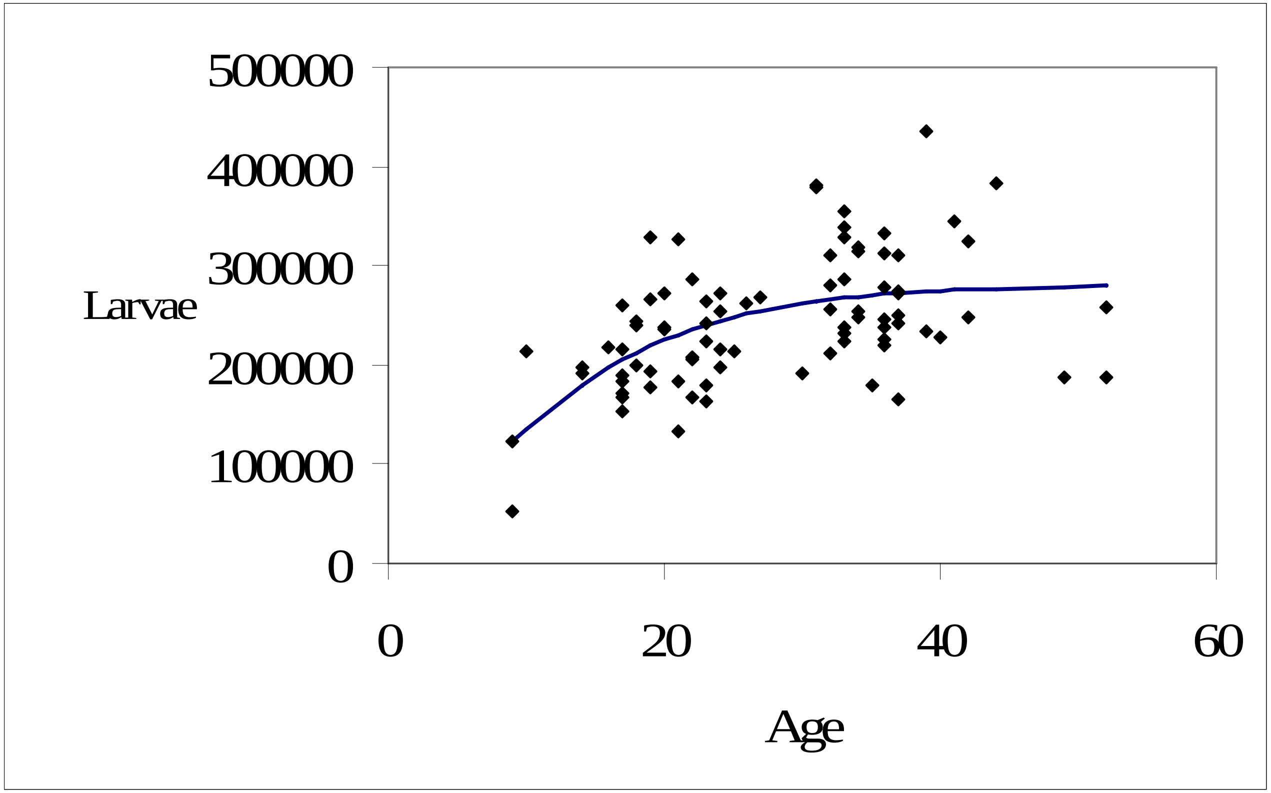
Larval survival

Time to 50% survival observed by Berkeley (2004a) for black rockfish (dashed line) and hypothesized relationship for POP (solid line).

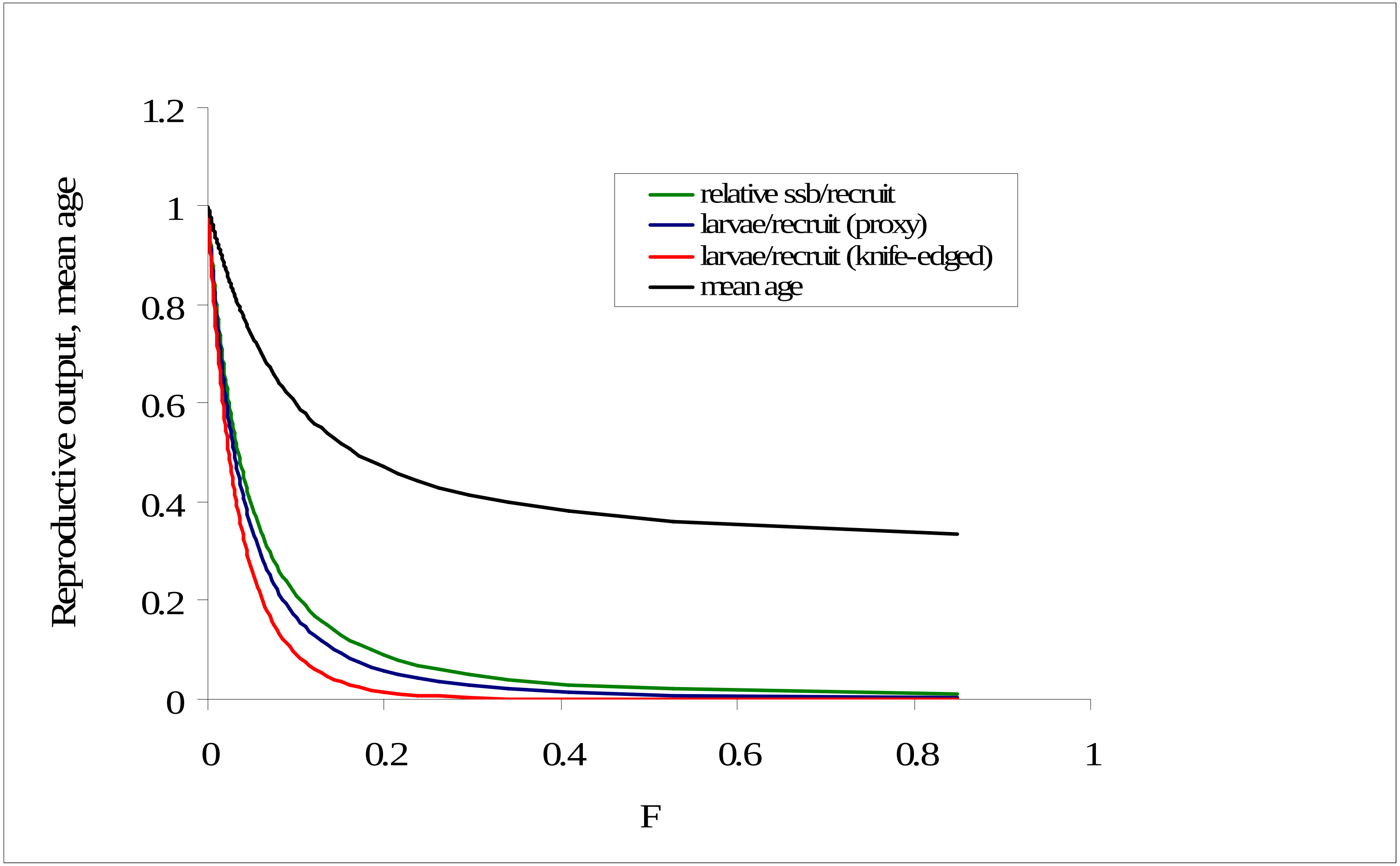


Fecundity

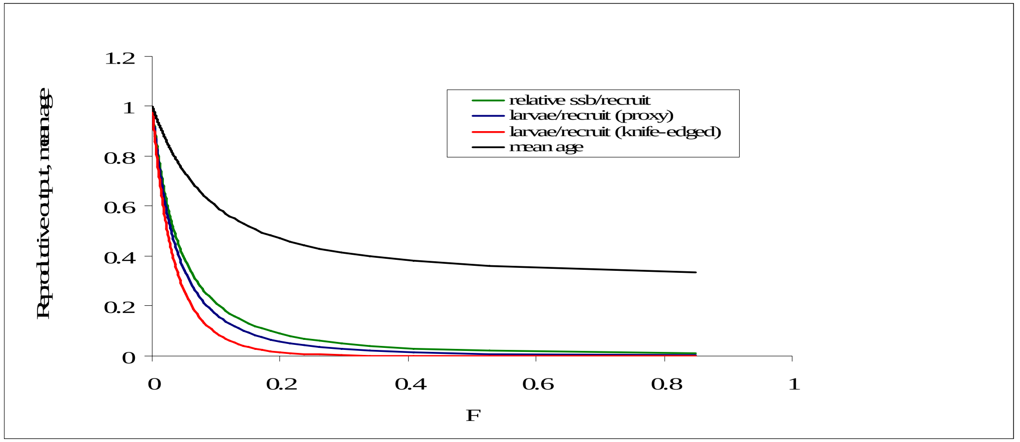
Relationship between larval production and age for Vancouver Island POP (courtesy of Bruce Leaman, IPHC).



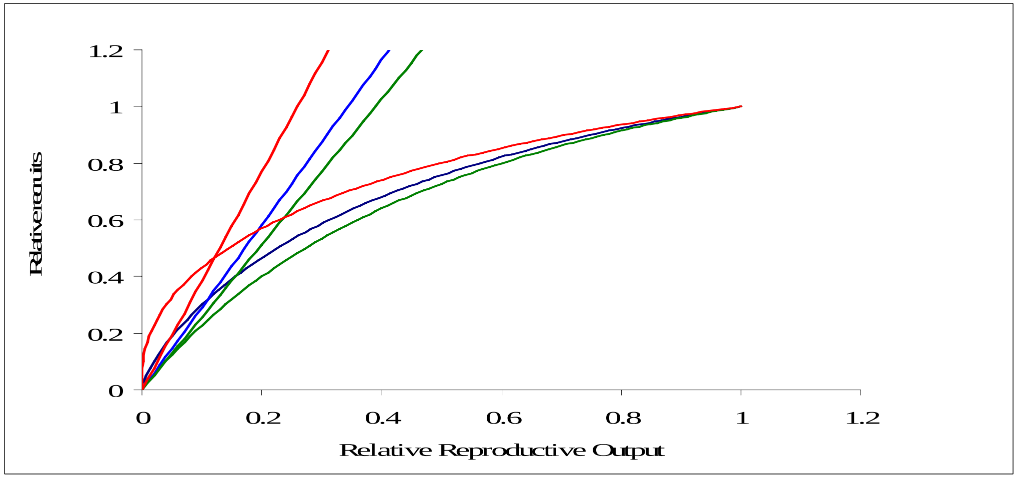
Effect of fishing on mean age, SSB, and viable larvae



Stock productivity and life-history parameters are not independent

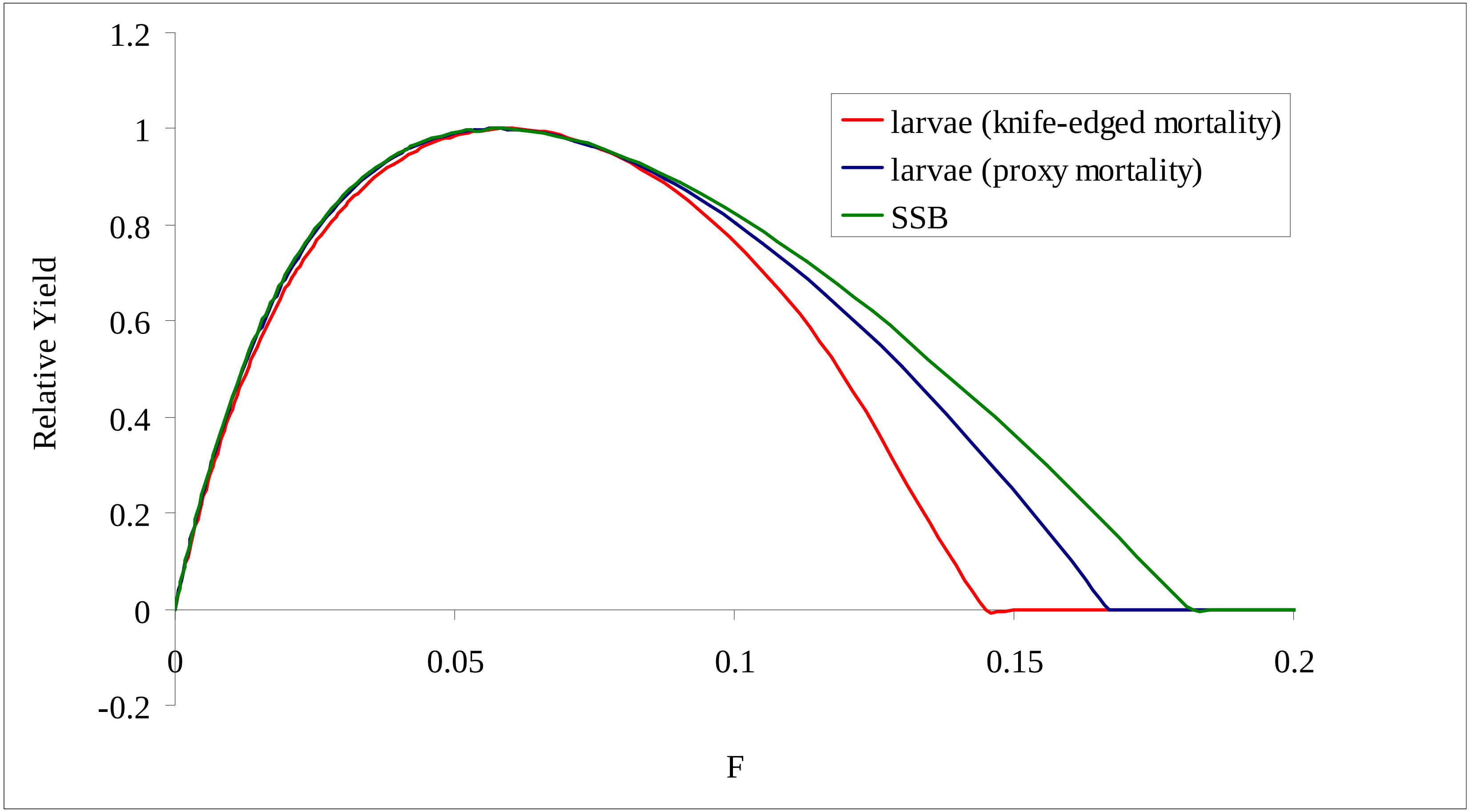


Implies more conservative exploitation rates

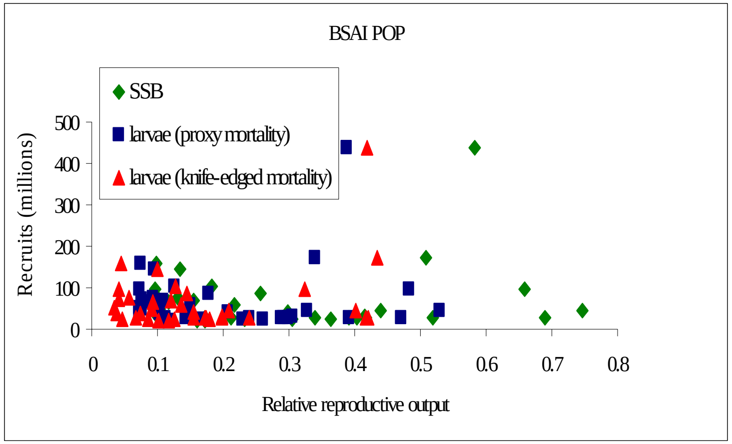


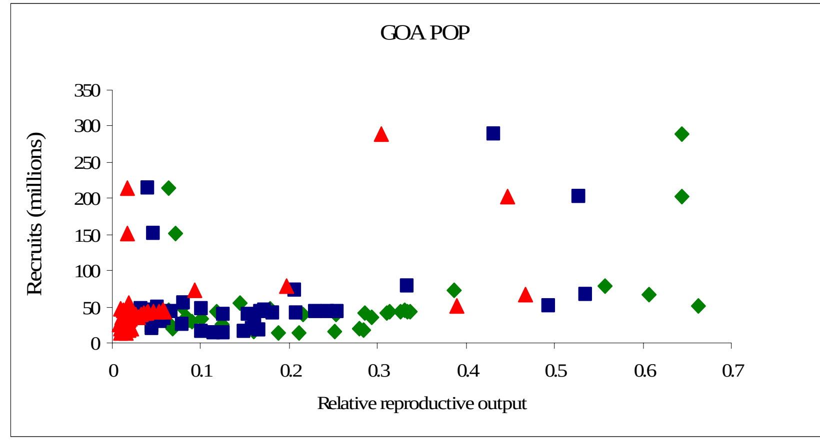
Implies increased exploitation rates

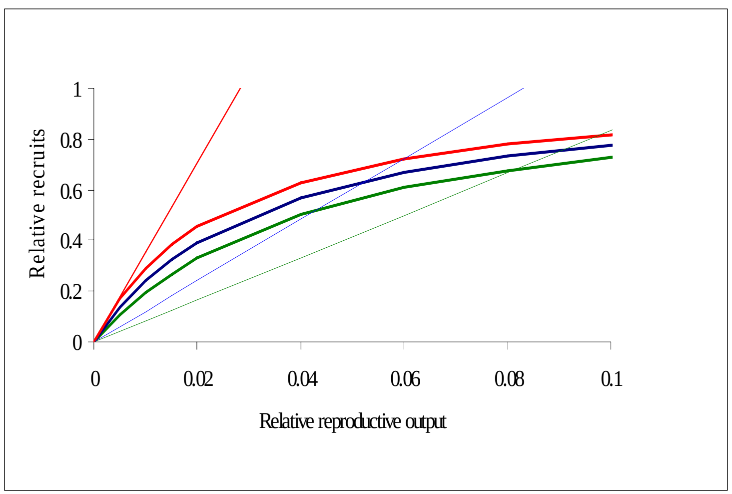
Relative yield plots

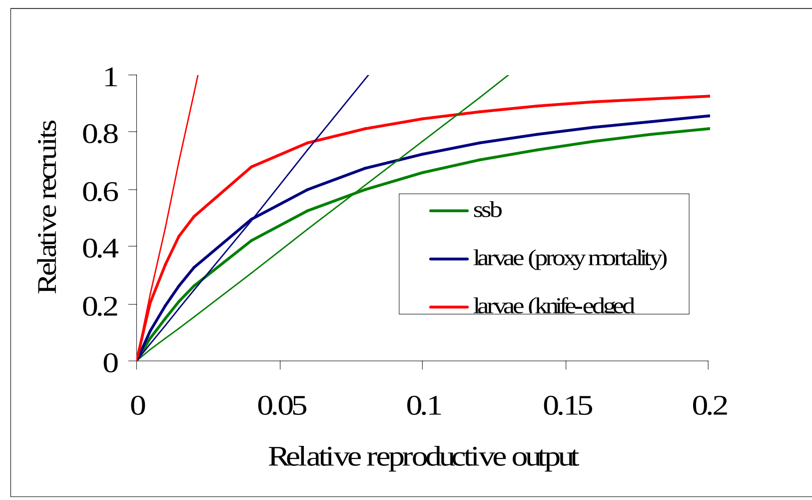


Application to Alaska POP

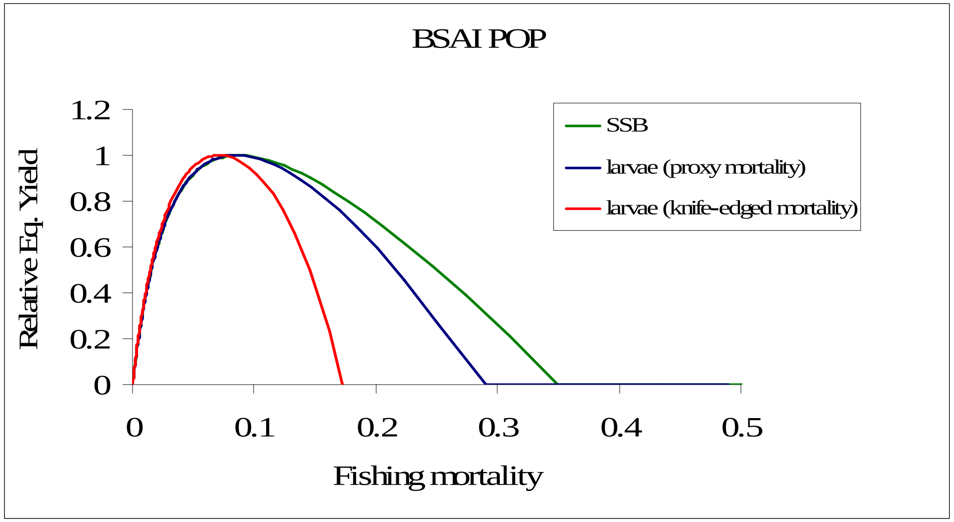


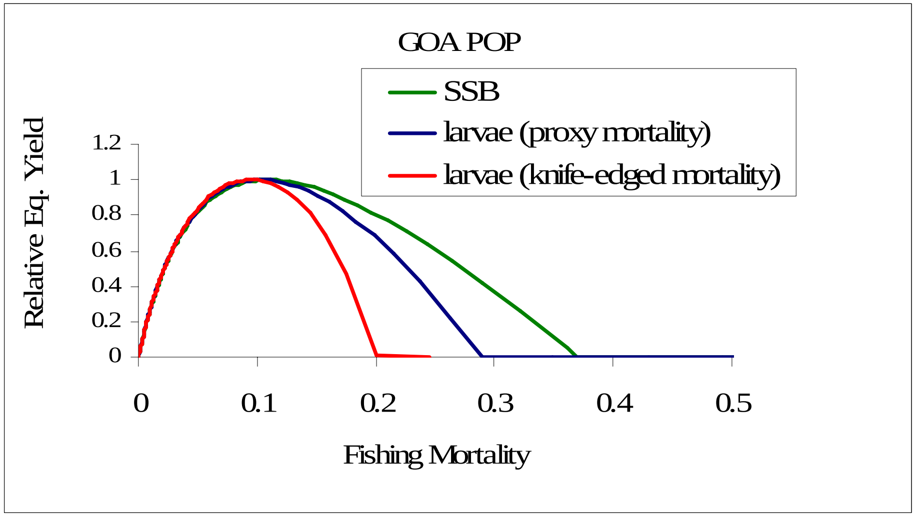






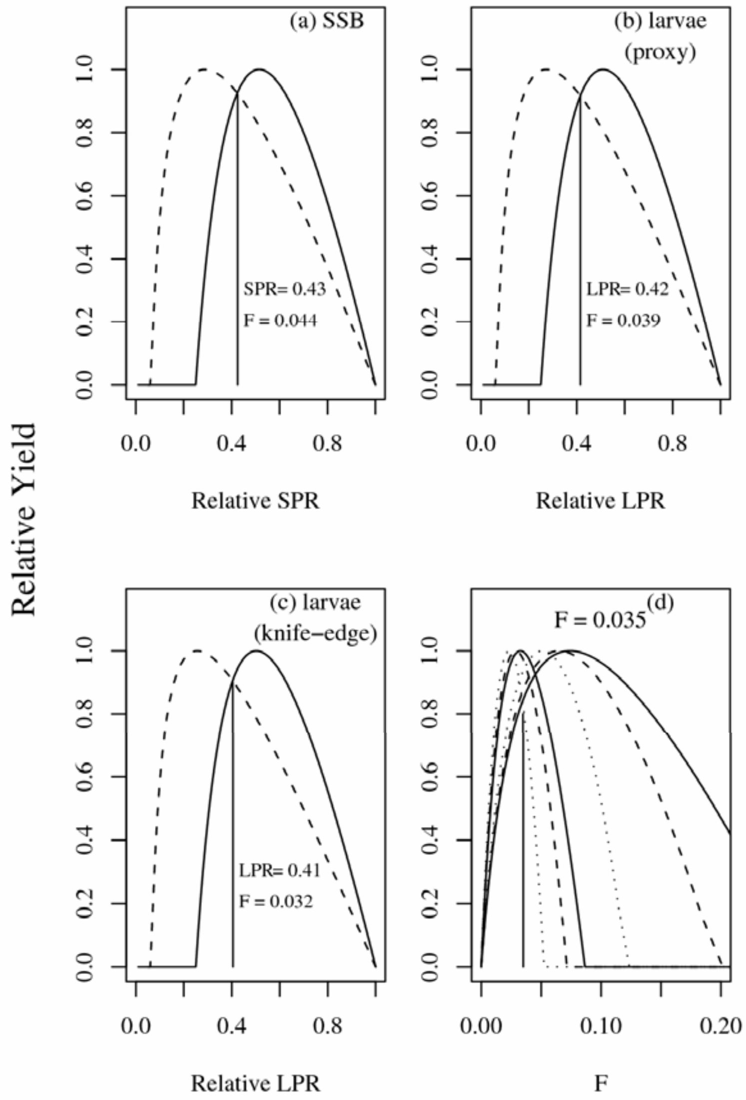
Yield curves





What is the effect upon $F_{spr\%}$ reference points?

More conservative reference points are obtained.



Conclusions

1) Converting reproductive capacity to units of “viable larvae” affects both the stock recruitment curve and proportion of reproductive capacity conserved (per recruit) for a given fishing mortality.

2) These two effects counteract each other, and the estimation of F_{msy} for a given stock will depend upon which effect is dominant.

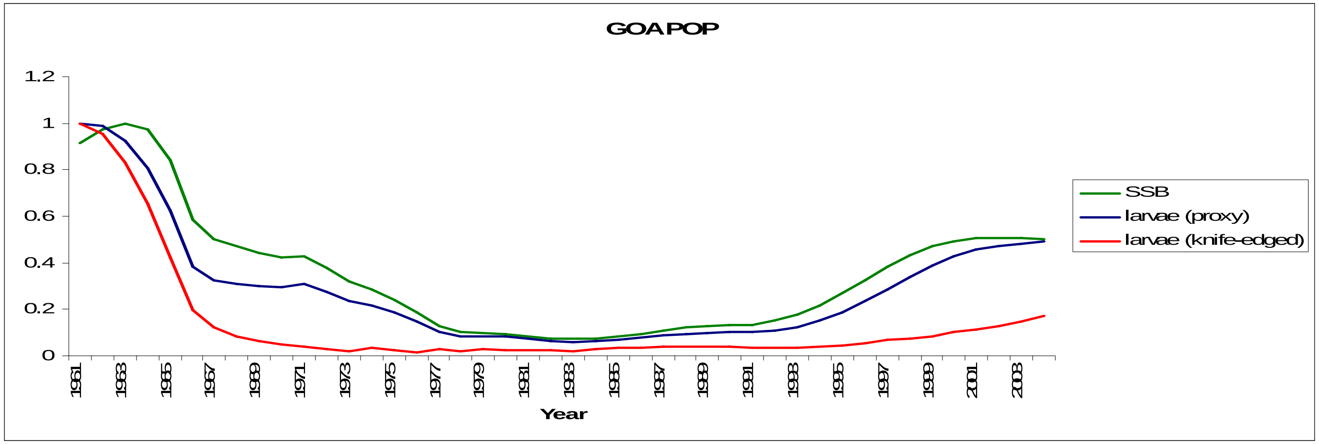
3) Uncertainty in maternal effects on larval survival may imply more conservative $F_{xx\%}$ rates than would be obtained by using SSB as the measure of reproductive output.

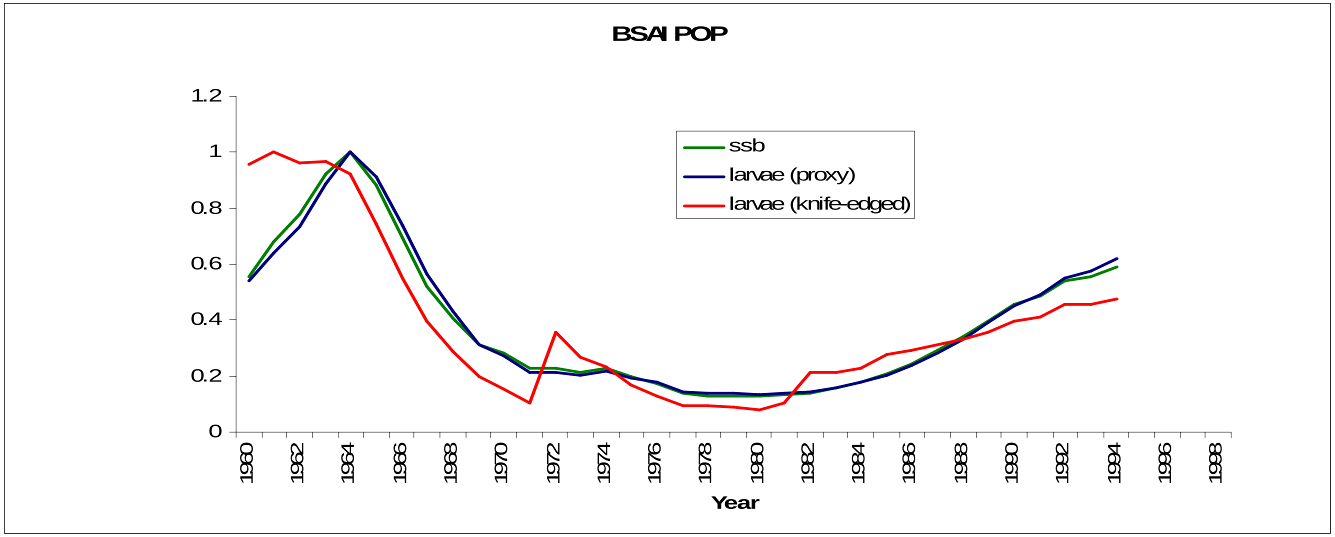
4) For Alaska POP, current estimates of $F_{40\%}$ are more conservative than estimated F_{msy}. Using different measures of reproductive capacity has little effect in estimated F_{msy} .

Estimates of F_{msy} for Alaska POP

Stock	Reproductive potential	Steepness	$F_{40\%}$	Percent unfished SSB or larvae at F_{msy}	F_{msy}
AI POP	SSB	0.86	0.049	0.25	0.087
	larvae (proxy mortality)	0.89	0.042	0.21	0.084
	larvae (knife-edged mortality)	0.91	0.033	0.17	0.070
GOA POP	SSB	0.81	0.060	0.24	0.111
	larvae (proxy mortality)	0.85	0.049	0.2	0.101
	larvae (knife-edged mortality)	0.93	0.036	0.12	0.095

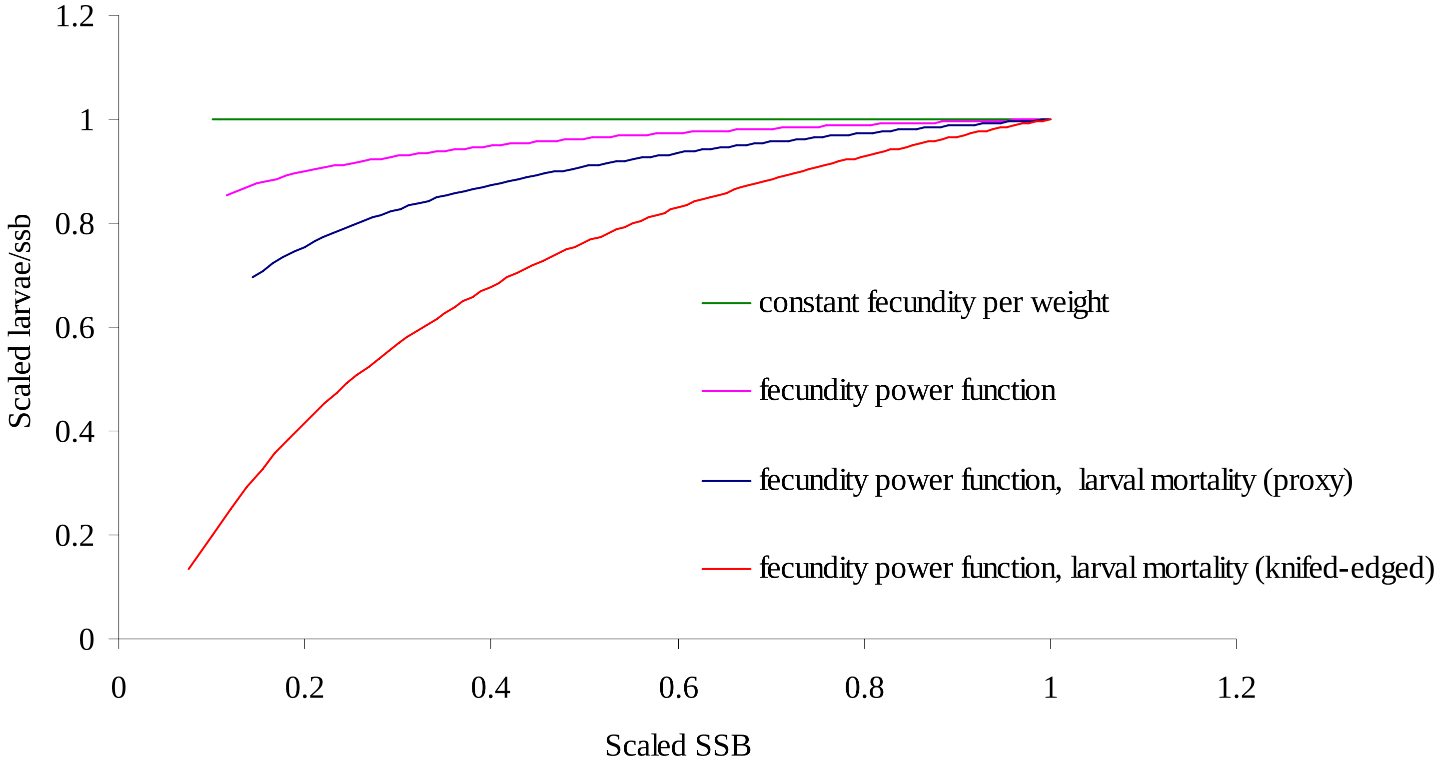
Time series of reproductive output



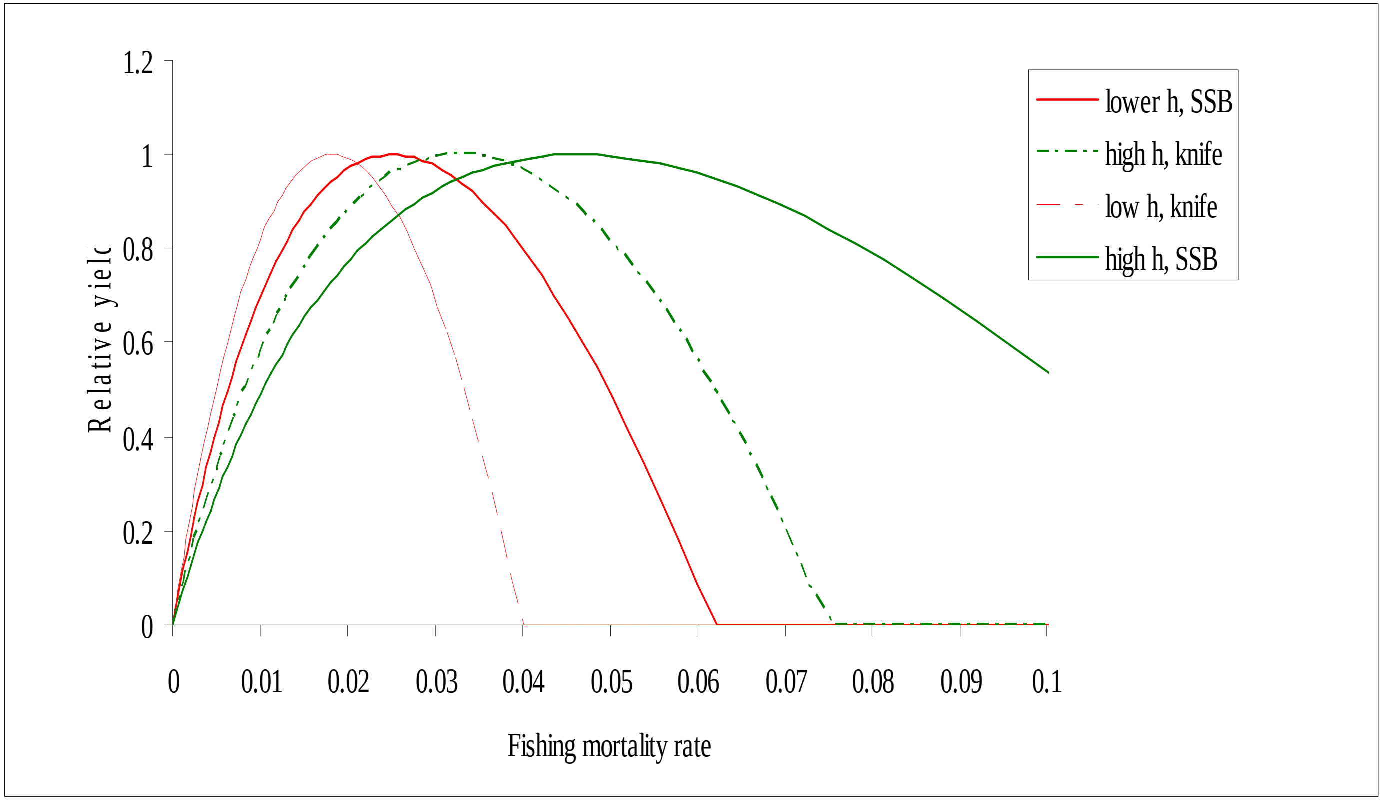


Sources of Density-Dependence

As fishing increases, the population becomes younger and relatively smaller. Density-dependence in larval production occurs if fecundity is a function of fish size, and more so if we also consider age-dependent larval survival.



Theoretical yield curves



Has the age composition of Alaska rockfish changed over time?