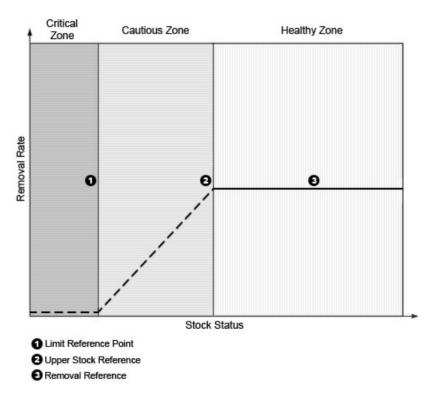
Marine Institute

Lecture 3: Population Models and Management Reference Points

Noel Cadigan



CFER

Centre for Fisheries Ecosystems Research





F6004 Lecture 3 Outline

Population Models Management Reference Points (Haddon Text Chapter 2)

- 1) Exponential and Logistic models
- 2) The surplus production model
- 3) Yield per recruit (age-based)
 - a) Fmax and derivatives (e.g., F0.1)
 - b) Age, weight and F how to get the most from a fishery
 - c) Uncertainties in yield per recruit.
- 4) Spawner per recruit
- 5) Age-based Maximum Sustainable Yield (MSY)
- 6) Discrete- and Continuous-time models

Other References

- 1) Mace, P.M., 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(1), pp.110-122.
- 2) <u>Introduction section</u> of Cadigan, N.G., 2012. Fitting a non-parametric stock—recruitment model in R that is useful for deriving MSY reference points and accounting for model uncertainty. *ICES Journal of Marine Science*, 70(1), pp.56-67.

Population models

- A biological population is a collection of individuals
- Properties: size, growth, immigration and emmigration rates, size (age/length) structure, geographical distribution
- The dynamic behaviour of a population refers to changes in its properties (size, age structure, etc) over time.

Population models

- Mathematical equations used to model population dynamics are only abstract representations
- But are useful to explore population processes and how populations may respond to external factors
- We use models to predict what populations will do in the future

Simple assumptions for pooled model

- All animals in the population have the same ecological properties (no age structure or other morphological/genetic effects, immigration=emmigration, if at all)
- There are no significant delays in population processes
- Model parameters are constants, with no seasonal/environmental/ecosystem variations

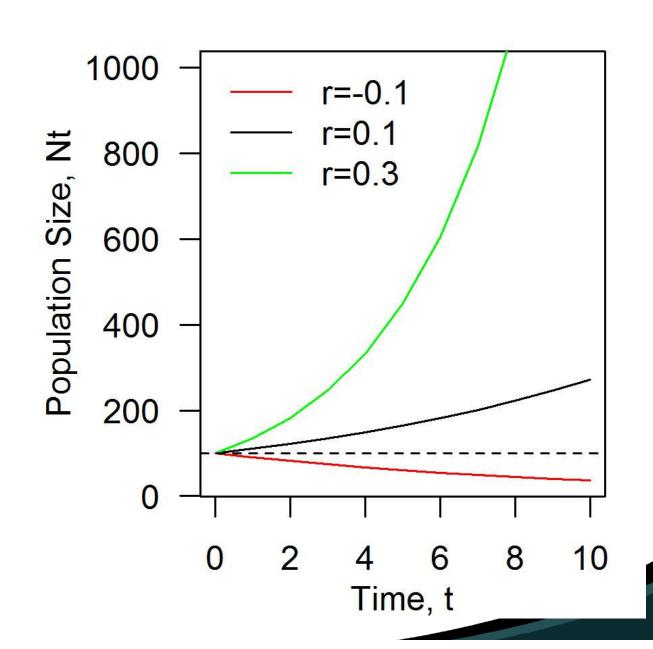
Density-Independent Growth

- A population growing in an unlimited environment (e.g. colonizing organisms – bacteria in a new environment, disturbed environments)
- Let R be the difference between the birth rate (B)
 and death rate (D)
- -dN/dt = (B-D)xN = RxN

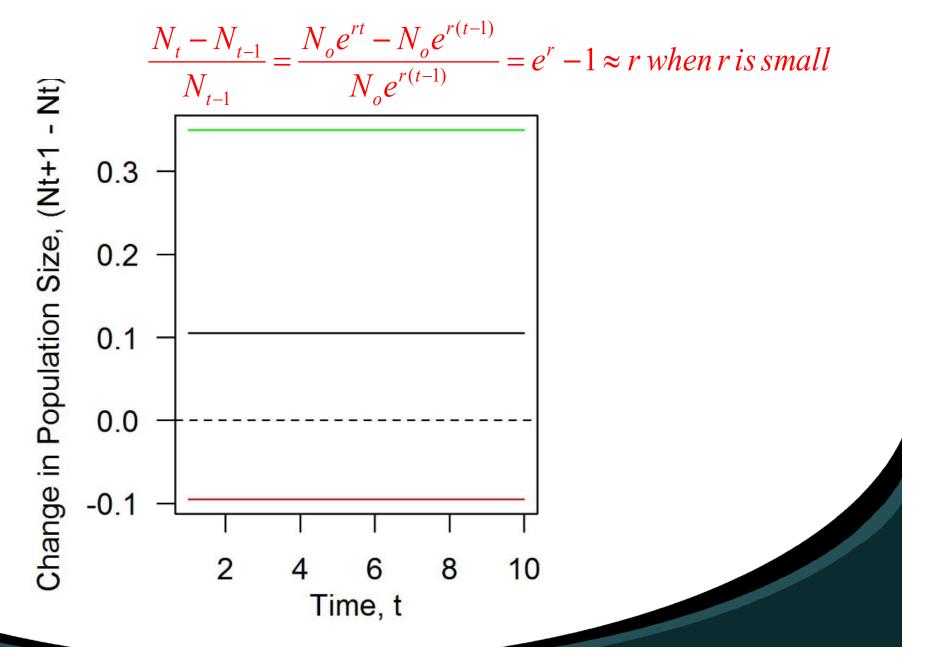
Exponential Growth Model

- A discrete time approximation is $N_t = RN_{t-1}$
- so $N_1 = RN_o$, $N_2 = RN_1 = R^2N_o$, ..., $N_t = R^tN_o$.
- Let r = log(R), $R = e^r$, and $N_t = e^{rt} N_o$.
- r is the intrinsic rate of increase
- This is the exponential growth model
- The solution to the differential equation dN(t)/dt = rN(t) is $N(t) = e^{rt} N_o$.
- If r<0 it is an exponential death (or decay) model

Exponential Growth Model



Exponential Growth Model



Density-dependent Growth

- No population can grow indefinitely
- all populations exist in limited environments
- exponential growth can only be a short-term phenomenon

- $-dN/dt = (b_N d_N)N$
- $-b_N = b_{max} b_1 N$ is density-dependent birth rate
- $-d_N = d_{min} + d_1 N$ is density-dependent death rate
- $-b_{max}$ and d_{min} are birth and death rates at low population size
- $-b_1$ and d_1 are parameters that control how birth and death rates change with population size

- A population is in equilibrium if its size is not changing;
- That is, dN/dt = 0.
- For the logistic model, dN/dt = 0 implies that the population size at equlibirium (denoted as N = K) is

$$-b_N = d_N = >> b_{max} - b_1 K = d_{min} + d_1 K$$

And solving for K gives

$$-K = (b_{max} - d_{min})/(b_1 + d_1) = r/(b_1 + d_1)$$

K is often called the carrying capacity

$$\frac{dN(t)}{dt} = (b_N - d_N)N$$

$$= \{b_{max} - b_1 N - (d_{min} + d_1 N)\}N$$

$$= \{b_{max} - d_{min} - (b_1 + d_1)N\}N$$

$$= \{r - (b_1 + d_1)N\}N$$

i.e. r = bmax - dmin

$$\begin{split} \frac{dN(t)}{dt} &= (b_N - d_N)N \\ &= \{b_{max} - b_1 N - (d_{min} + d_1 N)\}N \\ &= \{b_{max} - d_{min} - (b_1 + d_1)N\}N \\ &= \{r - (b_1 + d_1)N\}N \\ &= rN\left(1 - \frac{b_1 + d_1}{r}N\right) \end{split}$$
 i.e. $K = r/(b_1 + d_1)$

$$\frac{dN(t)}{dt} = (b_N - d_N)N$$

$$= \{b_{max} - b_1N - (d_{min} + d_1N)\}N$$

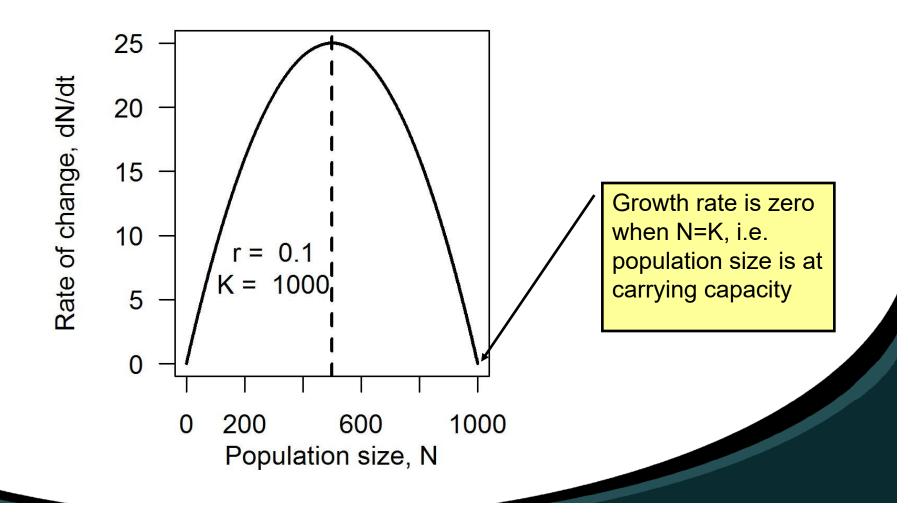
$$= \{b_{max} - d_{min} - (b_1 + d_1)N\}N$$

$$= \{r - (b_1 + d_1)N\}N$$

$$= rN\left(1 - \frac{b_1 + d_1}{r}N\right)$$
i.e. $K = r/(b_1 + d_1)$

$$= rN\left(1 - \frac{N}{K}\right)$$
The more usual form of the logisite growth equation

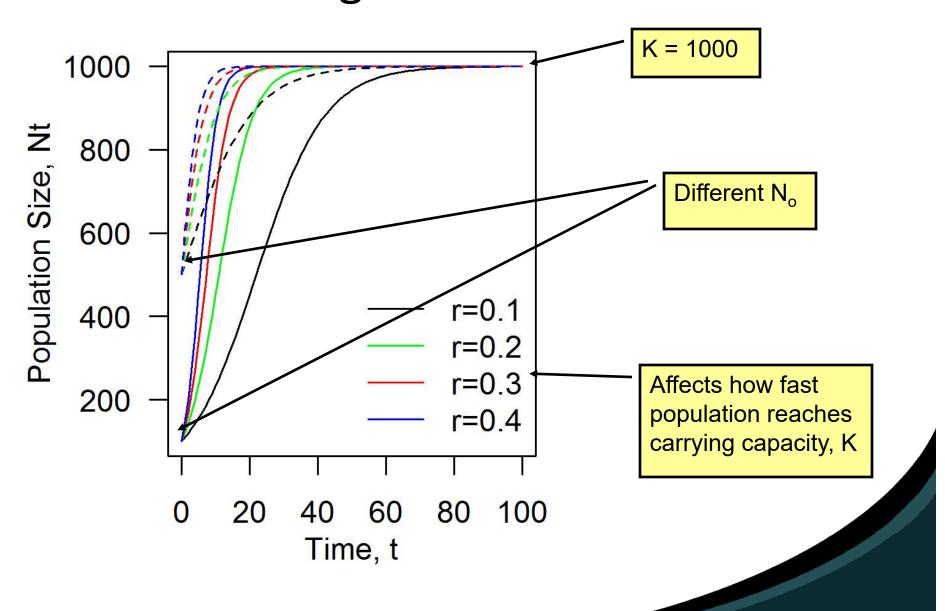
– The growth rate (dN/dt) of the population is maximized when N = K/2.

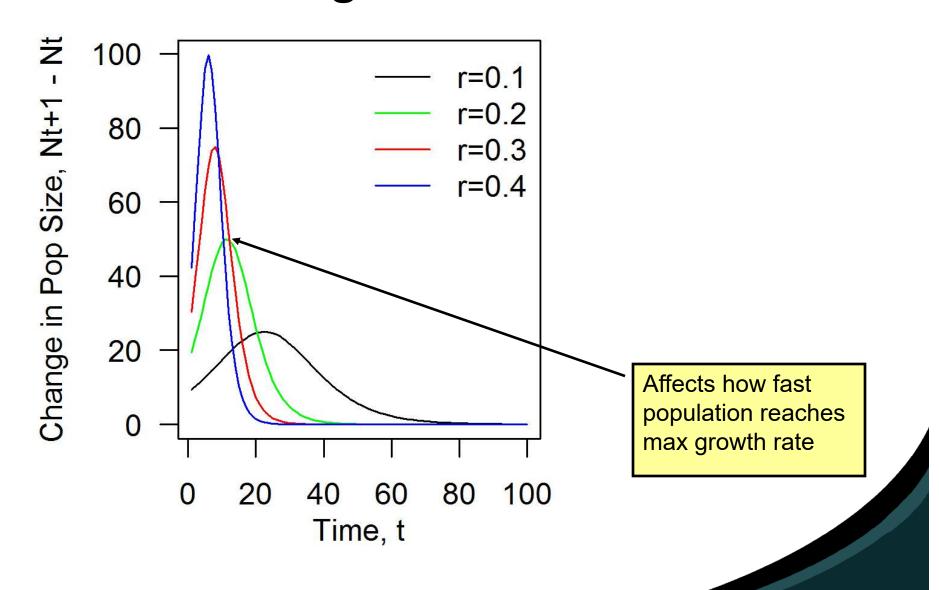


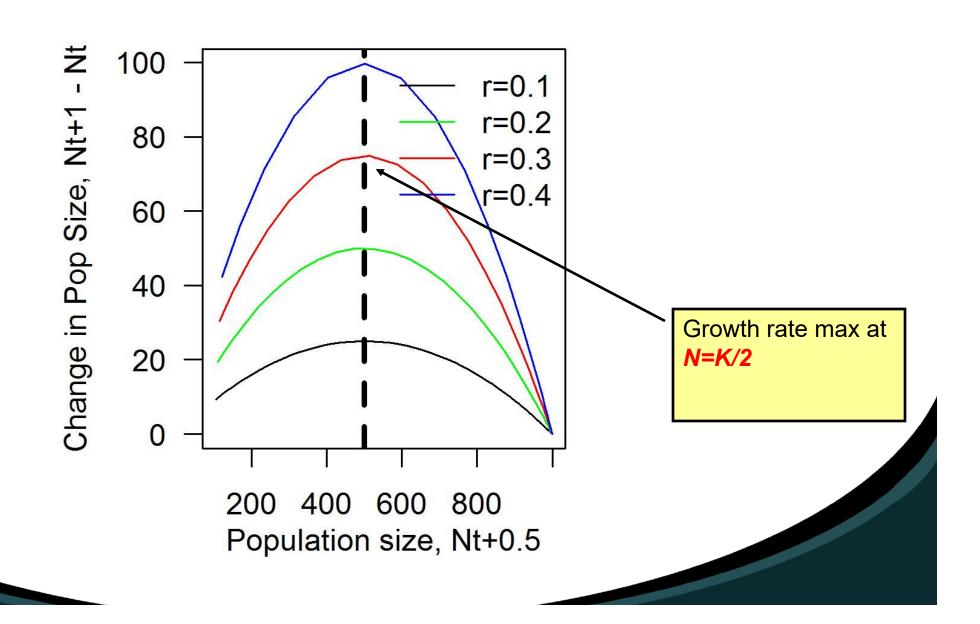
– The solution to the differential equation define by $dN/dt = (b_N - d_N)N$ is

$$N(t) = \frac{KN_o \exp(rt)}{K - N_o + N_o \exp(rt)}$$

$$= \frac{K}{1 + \gamma \exp(-rt)}, \text{where } \gamma = \frac{K - N_o}{N_o}$$







- Usually $r \le 1$ and the logistic growth model converges (either decreases or increases) to a stable equilibrium (K).
- If r > 1 then the model can oscillate, and if r > 2.6 then the result is chaos unpredictable behaviour that changes depending on starting conditions.
- In most applications $r \le 1$.

Discrete Logistic Growth

$$\frac{dN_t}{dt} \approx \frac{N_{t+1} - N_t}{\Delta t = t + 1 - t} = rN_t \left(1 - \frac{N_t}{K}\right)$$

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right)$$

- Better for populations in seasonal environments, or when there are non-overlapping generations or discrete cohorts
- This happens when there is a restricted spawning season,
 which is the case for many northern fish stocks

Discrete Logistic Growth

 If there is an extra source of known annual total mortality, such as fishing, then this can be added as an extra term

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right) - C_t$$

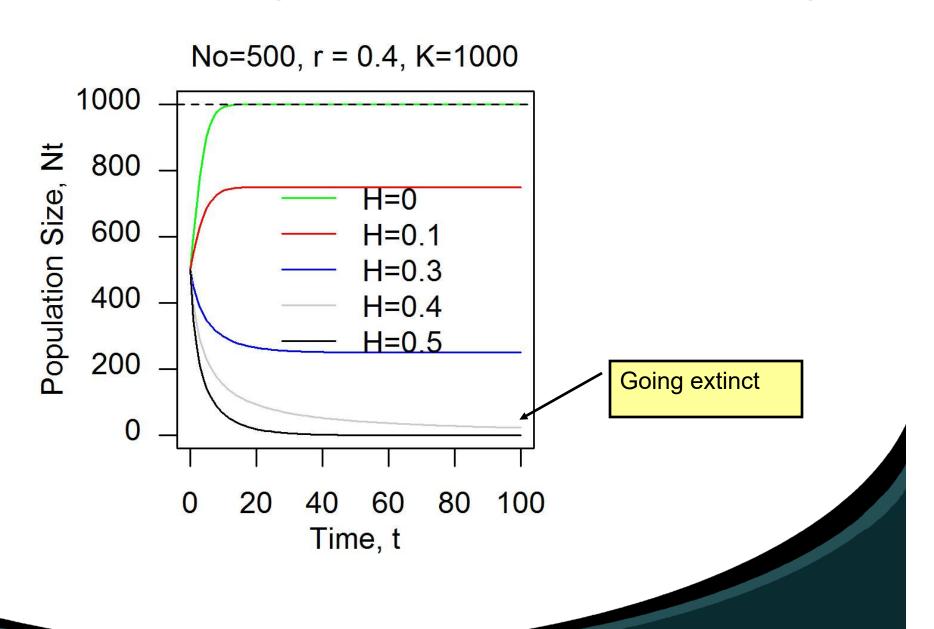
- If $C_t = H \times N_t$ then

$$N_{t+1} = N_t + r^* N_t \left\{ 1 - \frac{N_t}{K^*} \right\}$$

- Where $r^* = r - H < r$ and $K^* = K(r - H)/r < K$

H must be < r

Discrete Logistic Growth with Fishing



Discrete Logistic Model for Fisheries

 Usually work with stock biomass (B; weight) and not abundance (N; numbers)

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t$$

- If $C_t = H \times B_t$ then

$$B_{t+1} = B_t + r^* B_t \left\{ 1 - \frac{B_t}{K^*} \right\}$$

- Where $r^* = r - H < r$ and $K^* = K(r - H)/r < K$

Discrete Logistic Model for Fisheries

- It is not difficult to show that the exploitation rate that maximizes sustainable (i.e. equilibrium) yield is $H_{MSY} = r/2$.
- The resulting equilibrium biomass when exploitating at rate H = r/2 is $B_{MSY} = K/2$.
- Obviously the MSY catch is $C_{MSY} = B_{MSY} r/2$.
- A Surplus Production Model

Surplus Production models

- The simplest analytical method that provides for a full stock assessment
- The overall effects of recruitment, growth, and mortality are combined into a single production function
- Age, size, sex, and other differences are ignored
- Only need a time series of total catch data, and a relative abundance index time series (CPUE or survey)
- Estimation later!

Surplus Production models

- One objective of stock assessment is to describe how a stock has responded to different levels of fishing pressure
- Age-based models are better for this
- But when ages are not available then age-aggregated production models can still be useful
- Also know as biomass dynamic models
- They may be preferred for reference points (less so)

Surplus Production models

- It is a challenge to do a good stock assessment using production models because a fairly long time series with a fairly wide range of catch levels and abundance index levels is required to get reliable estimates
- They are not that precise for short term forecasts
- But they are commonly used to test the reliablity of more complex models
- And find use in multi-species and spatial models

Surplus Production models (SPMs)³¹

 The simplest SPM is derived from the discrete logistic population model, which for biomass is

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K} \right)$$

- Recall that the biomass growth rate is maximum when $B_t = K/2$.
- The stock is at equilibrium $(B_t = B_{t-1})$ when $B_t = K$.
- If $B_t > K$ then the stock will decrease in size.

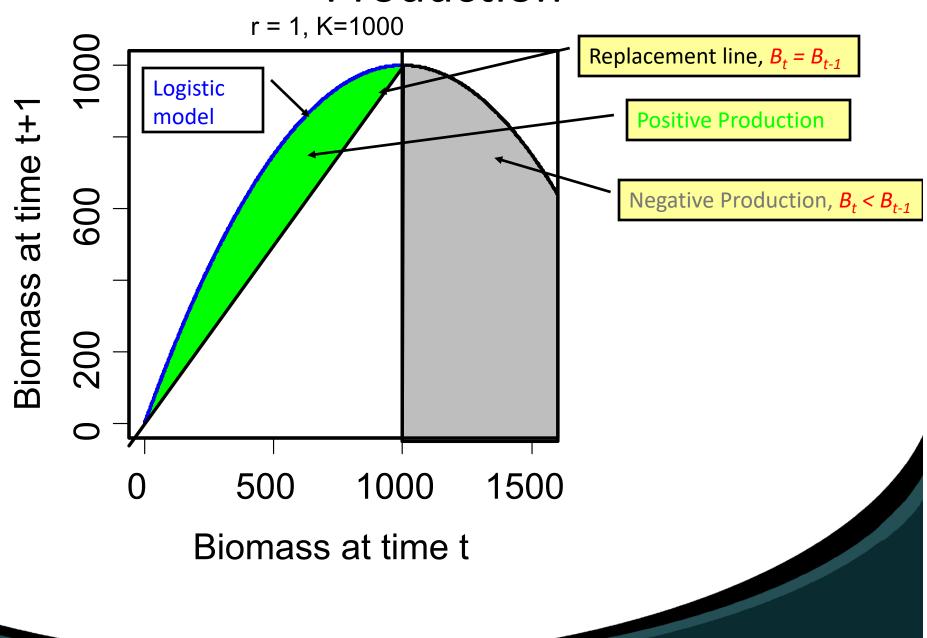
Surplus Production models (SPMs)

 The annual stock growth (i.e. production) is given by

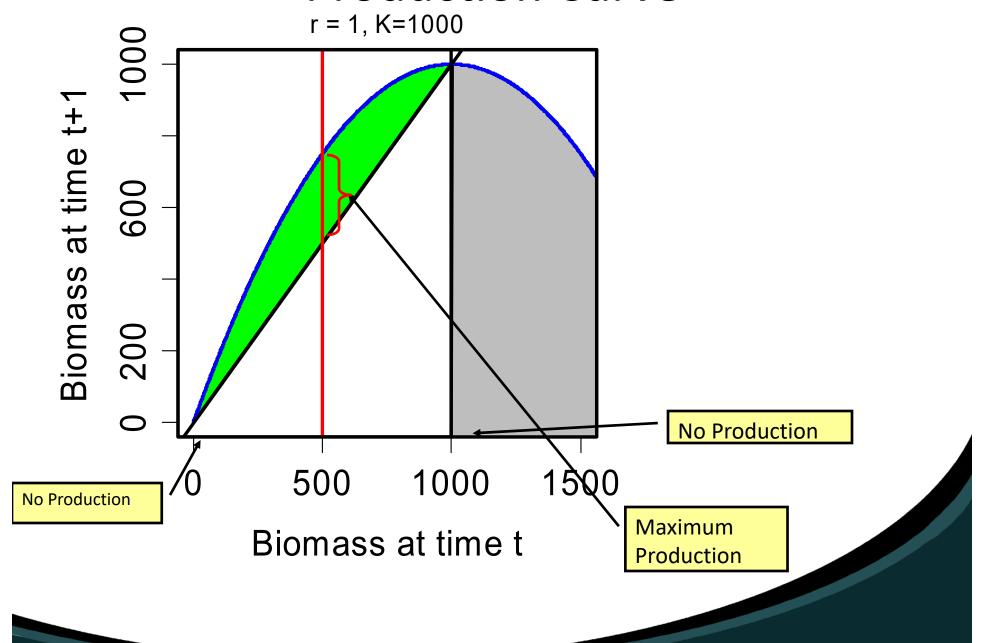
$$g(B_t) = rB_t \left(1 - \frac{B_t}{K}\right)$$

 This is the amount that could be harvested without decreasing biomass

Production



Production Curve



SPMs for exploited stocks

The Schaefer SPM is

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K} \right) - C_t$$

- Where C_t are the annual fishery catches
- If we divide both sides of this equation by K, and let $P_t = B_t/K$, then $P_{t+1} = P_t + rP_t(1-P_t) C_t/K$
- The parameters to estimate are B_o (or P_o), r, and K.

Equilibrium methods

- There are several pages in Haddon on equilibrium methods for fitting SPM's
- People do not use these methods anymore
- Haddon does not recommend them
- I don't understand them
- I won't say anything more about them

Other versions of SPMs

- basic form: $B_{t+1} = B_t + g(B_t) C_t$.
- classic Schaefer

symmetric production curve, as a function of B,

$$g(B_t) = rB_t \left(1 - \frac{B_t}{K} \right)$$

- Modified Fox $g(B_t) = \log(K)rB_t \left(1 - \frac{\log(B_t)}{\log(K)}\right)$

lim p -> 0

Modified Pella and Tomlinson

asymmetric production curve

$$g(B_t) = \frac{r}{p} B_t \left\{ 1 - \left(\frac{B_t}{K} \right)^p \right\}$$

Other versions of SPMs

 Prager (2002) studied a similar generalized SPM and concluded that it should be applied with skepticism and in conjunction with the more robust Schaefer form.

Prager, MH. 2002. Comparison of logistic and generalized surplus-production models applied to swordfish, *Xiphias gladius*, in the north Atlantic Ocean. Fish. Res. 58, 41-57.

- He advised that unless a good external estimate of the model shape (i.e. p) was available, the Schaefer model appeared more suitable for routine assessment use.
- He found that estimates of the generalized shape parameter were highly sensitive to outliers.

SPMs

- Irrespective of stock size, it is possible to take the surplus production in a fishery without changing stock size
- A good strategy would be to bring the stock to the level that produces maximum production (i.e. B = K/2) and harvest the production.
- This is a simplistic view, and a major assumption is that the stock's "environment" is stationary.
- This never happens for very long.

SPMs

- Size-selective fishing is common, and this changes the size- and age-structure of the population, and the production function
- In practise is often difficult to reliably estimate B_o , r, and K. These parameters are highly correlated.
- It is well understood that in a multi-species environments, you cannot harvest the single species MSY for all species simultaneously.
- The ecosystem MSY will be less than the sum of single species MSY's

- Age-structured models are usually superior to simple biomass dynamics models for modelling stock dyamics.
- Different age groups contribute different amounts of biomass to total catch – older ages usually contribute more.
- Older age fish tend to have higher egg production
- If the necessary information is available, then agestructured models can better reflect natural population processes and the impacts of fishing.
- Ages provide additional information on reproduction

- Age-structured models usually follow cohorts.
- A cohort is the portion of a population born in the same year.
- The stock consists of multiple cohorts.
- We speak of recruitment as the number of fish when first exploited by the fishery.
- Fisheries usually do not exploit age 0 fish, and we can think of recruitment starting at age a_r .

- Let $N_{t,c}$ denote the number of fish in the population in year t and for cohort c.
- If there is no immigration of emmigration, or if immigration = emmigration, then a cohorts abundance can only decline with time due to mortality processes.
- The fundamental equation of most cohort models is

$$N_{t+1,a+1} = N_{t,a}e^{-Z}$$
 N can only decline with time for a cohort

- where $Z \ge 0$ is the annual total mortality rate.
- The cohort is c = t a

– The number of deaths, as a fraction of $N_{t,c}$, is

$$\frac{N_{t,c} - N_{t+1,c}}{N_{t,c}} = 1 - e^{-Z} \approx Z \text{ when Z is small}$$

- The total mortality rate is composed of a component due to fishing (F) and a component due to natural causes (M);
- that is Z = M + F.
- Will see more on these models in a later lecture

- We can imagine fishing a cohort over a number of years, from the recruitment age until the cohort is essentially fished out.
- That is, we can first fish them at recruitment age a_r , then the following year we can fish the survivors at age $a_r + 1$, then the next year at age $a_r + 2$, and so on.
- If a constant fishing mortality rate F is applied each year, then we can compute the total yield over its lifespan that a cohort will produce.
- Let W_a denote the weight of an age a fish in the cohort.

- The fishery catch-at-age each year is a fraction of the total number of deaths, $D_{a,t}$
- The fraction F_{α}/Z_{α} of deaths is due to fishing.
- Hence, the catch weight at age is $CW_{a,t} = W_a D_{a,t} F_a / Z_a$

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- The fraction F_{α}/Z_{α} of deaths is due to fishing.
- Hence, the catch weight at age is $CW_{a,t} = W_a D_{a,t} F_a / Z_a$
- Note that we have made F and Z to be age specific.
 Most fisheries are size and age specific, and natural mortality (M) may also vary with age.
- M will certainly be higher for very young fish, but it is
 often reasonable to assume that M is constant over the
 ages that are recruited to a fishery.
- Hence, Z depends on age via $Z_a = M + F_a$.

cohort

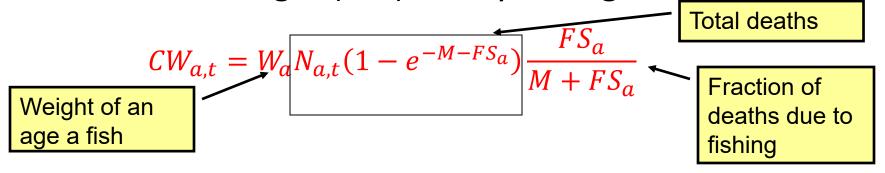
- For simplicity we assume that $F_a = FxS_a$, where S_a is known from external sources, and $max_aS_a = 1$
- So we can still do yield-per-recruit as a function of F.
- Each year, the total number of deaths $D_{a,t}$ is a function of total mortality rate, Z_a .
- that is,

$$\begin{split} D_{a,t} &= N_{a,t} - N_{a+1,t+1} \\ &= N_{a,t} - N_{a,t} e^{-Z_a} \\ &= N_{a,t} \left(1 - e^{-M - FS_a} \right) \end{split}$$

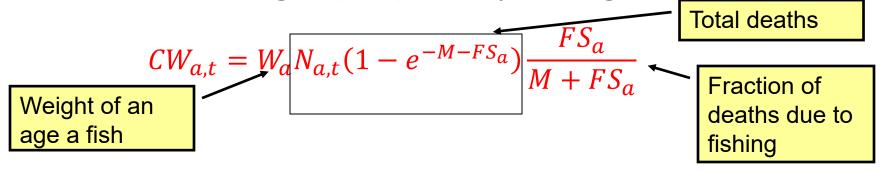
- The catch weight (CW) each year is given by

$$CW_{a,t} = W_a N_{a,t} (1 - e^{-M - FS_a}) \frac{FS_a}{M + FS_a}$$

The catch weight (CW) each year is given by



- The catch weight (CW) each year is given by



Assume a_r=0. The total yield from X recruits in year
 t is

$$Y(F) = \sum_{a=0}^{\infty} CW_{a,t+a}$$

• YPR is
$$\frac{Y(F)}{X} = \frac{\sum_{a=0}^{\infty} CW_{a,t+a}}{X}$$

- Recall that $N_{a,t} = N_{a-1,t-1}e^{-M-FS_{a-1}}$
- This equation can be used recursively to compute the catch at age in each year given some initial number of recruits, X.
- Let H_a denote the fraction of the stock at the beginning of each year that is caught by the fishery (i.e. the harvest rate)
- $H_a(F) = (1 e^{-M FS_a}) \frac{FS_a}{M + FS_a}$

$$CW_{0,t} = W_0 X H_0(F)$$

$$CW_{0,t} = W_0 X H_0(F)$$

$$CW_{1,t+1} = W_1 N_{1,t+1} H_1(F)$$

= $W_1 X e^{-M-FS_0} H_1(F)$

$$CW_{0,t} = W_0 X H_0(F)$$

$$CW_{1,t+1} = W_1 N_{1,t+1} H_1(F)$$

= $W_1 X e^{-M-FS_0} H_1(F)$

$$CW_{2,t+2} = W_2 N_{2,t+2} H_2(F)$$

= $W_2 X e^{-2M-F(S_0+S_1)} H_2(F)$

$$CW_{0,t} = W_0 X H_0(F)$$

$$CW_{1,t+1} = W_1 N_{1,t+1} H_1(F)$$

$$= W_1 X e^{-M-FS_0} H_1(F)$$

$$CW_{2,t+2} = W_2 N_{2,t+2} H_2(F)$$

$$= W_2 X e^{-2M-F(S_0+S_1)} H_2(F)$$

$$CW_{a,t+a} = W_a N_{a,t+a} H_a(F)$$

$$= W_a X e^{-aM-F\sum_{i=0}^{a-1} S_i} H_a(F)$$

$$\frac{Y(F)}{X} = \frac{\sum_{a=0}^{\infty} CW_{a,t+a}}{X} = W_0 H_0(F) + \sum_{a=1}^{\infty} W_a e^{-(aM+F\sum_{i=0}^{a-1} S_i)} H_a(F)$$

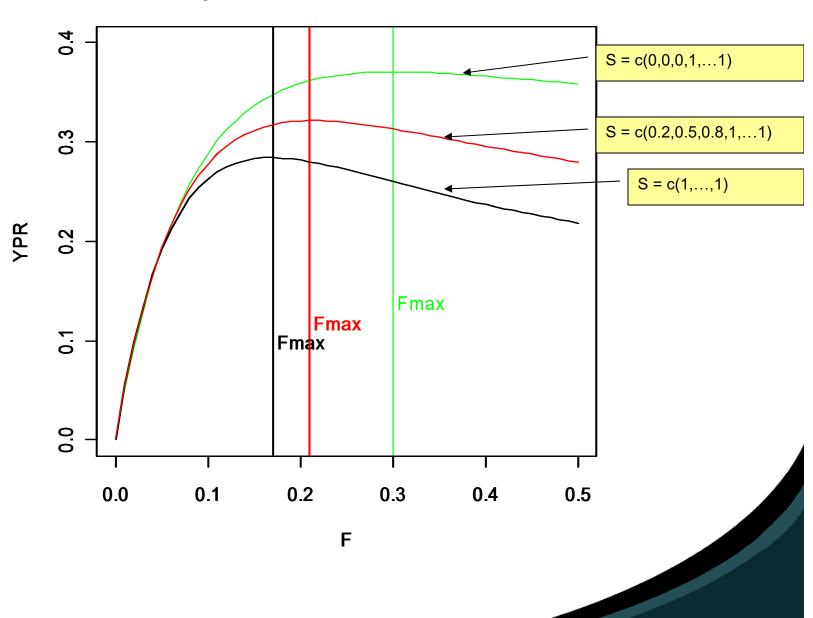
For age at recruitment a_r

$$\frac{Y(F)}{X} = W_{a_r} H_{a_r}(F) + \sum_{i=1}^{\infty} W_{a_r+i} e^{-(iM+F\sum_{j=0}^{i-1} S_{a_r+j})} H_{a_r+i}(F)$$

Age	N	Annual Survivorship	Catch numbers	weight	catch w	eight				
3	1000	1	164.839977	0.15	24.73					
4	670.3	0.670320046	110.495541	0.278	30.68					
5	449.3	0.670320046	74.0673761	0.394	29.21					
6	301.2			0.599	29.74					
7	201.9	0.670326946	33.28061738	0.862	28.69					
8	135.3	0.670320046								
9	90.72	0.670320046			23.51					
10	60.81	0.670320046	10.02392932	2.028	20.33					
11	40.76	0.670320046	6.719240766	2.653	17.83					
12	27.32	0.670320046	4.504041779	3.141	14.15	N_{t+1} = survivorship,				
13	18.32	0.670320046	3.019149493	3.844	11.01	eyn(-	exp(-Z), times N _t			
14	12.28	0.670320046	2.023796427	4.043	8.182	CXP(-	∠ <i>)</i> , ШП	C3 IV _t		
15			1.356591314	4.252	5.768					
16	5.517	0.670320046	0.909350352	4.471	4.066		(1 :	(DD (
17	3.698	0.670320046	0.60955577	4.702	2.866			PR for		
18	2.479	0.670320046	0.408597452	4.945	2.02		F=0.2 a	and		
19	1.662	0.670320046	0.273891063	5.2	1.424		M=0.2			
20	1.114	0.670320046	0.18359467	5.469	1.004					
					281.7	0.282				

Yield per Recruit

- We have expressed YPR as a function of fully recruited fishing mortality, F.
- We can plot YPR versus F.
- The value of F that maximizes YPR is sometimes used as a fishing mortality reference point.
- $-F_{max}$ maximizes yield
- But it may not be sustainable.



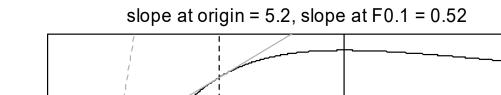
YPR R code

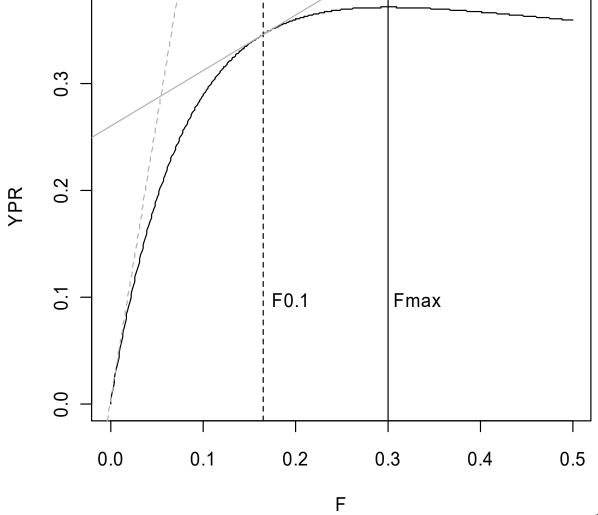
```
YPR <- function(f){
                                             YPR is an R function you
  n.age = length(sel)
                                             create, that gives the YPR for
  fa = f*sel
                                             a value of F you give the
  za = m + fa
                                            function
  cza = cumsum(c(0,za[1:(n.age-1)]))
  YPR = sum(exp(-cza)*weight*fa*(\cancel{1}-exp(-za))/za)
  return(YPR)
age=3:20
weight = c(0.15, 0.278, 0.4894, 0.599, 0.862, 1.163, 1.572, 2.028, 2.653,
3.141,3.844,4.043,4.252,4.471,4.702,4.945,5.200,5.469)
m=rep(0.2,length(a/ge))
ypr1 = YPR(0.2)
print(ypr1)
```

Yield per Recruit – F0.1

- -F0.1 is the fishing mortality rate at which the slope of the YPR curve (as a function of F) is 10% of the slope at the origin.
- Fishing at F0.1 is an ad hoc procedure; it is more conservative or risk adverse than fishing at F_{max} .
- For a small loss in yield, one can gain considerable stock resilience to poor recruitment years and other sources of uncertainty.

F0.1





Continuous Time Population dynamics model

- Let n(t) be the abundance of a cohort at age t.
- dn(t)/dt = -z(t)n(t) where $z(t) \ge 0$ is the total mortality rate: $n(t) = n(0)\exp\{-\int_0^t z(x)dx\}$
- z(t) = f(t) + m(t) where f(t) ≥ 0 is the fishing mortality rate and m(t) ≥ 0 is the natural mortality rate function of age t.
- $f(t) = f \times s(t)$, where s(t) is the fishery selection function of age t with $max_t s(t) = 1$
- Only consider constant f harvest strategies

In Continuous-Time

- no immigration or emigration
- cohort size still only declines with age because of mortality processes.

Yield

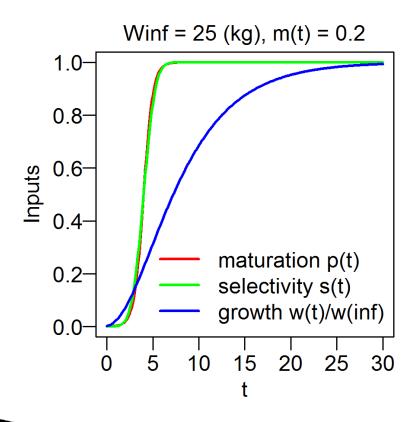
- Let $S(t) = \int_0^t s(x)dx$ and $M(t) = \int_0^t m(x)dx$.
- Let R = n(0)
- $n(t) = R \exp\{-fS(t) M(t)\} = R\Lambda(t, f)$
- where $\Lambda(t, f) = \exp\{-fS(t) M(t)\}$ is cumulative survival from size R at t=0 to size n(t)
- Fishery yield (in weight):

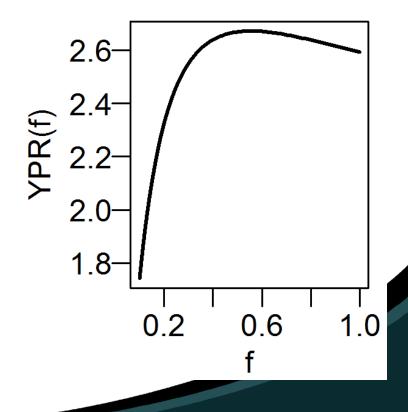
$$Y(f) = \int_0^\infty w(t)f(t)n(t)dt$$
$$= fR \int_0^\infty w(t)s(t)\Lambda(t,f)dt$$

Yield per recruit

$$YPR(f) = Y(f)/R = f \int_0^\infty w(t)s(t)\Lambda(t,f)dt$$

YPR(f) is usually a quasi-concave function of f





Yield per Recruit – assumptions/uncertainties

- stock is in equilibrium with respect to F
- natural mortality and growth rates are known and constant over time.
- maximizing yield may not lead to sustainable fisheries

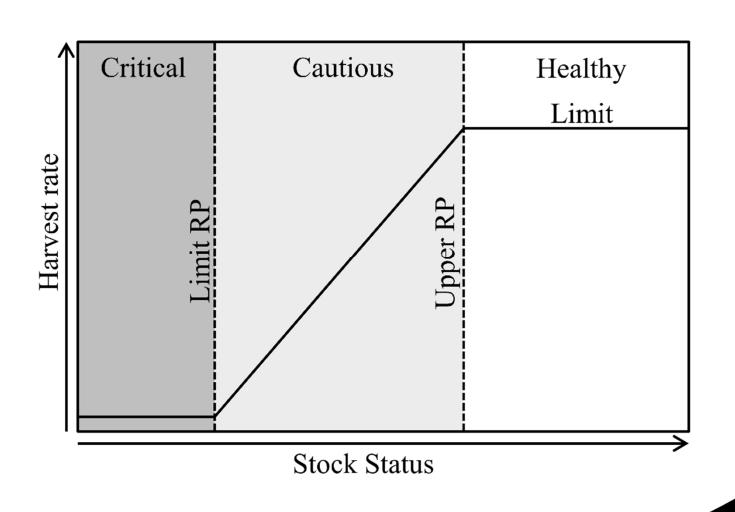
YPR Criticisms

- YPR F RPs essentially ignore the effects of fishing on the mature stock biomass (i.e. spawning stock biomass, SSB)
- Maintaining SSB at a good productive level is important for sustainable fisheries
- You need a level of SSB that can produce good recruitment to support fisheries in the future
- -YPR reference points do not consider this, and it is possible that fishing at F_{max} or F0.1 can seriously reduce SSB and lead to stock collapse.

Harvest strategy and RPs

- Reference points (RPs) are important for <u>sustainable</u> and <u>successful</u> fisheries management
- as part of a pre-defined fishery harvest control rule where
- prescribed actions should occur when the population size or harvest rates exceed the RPs.

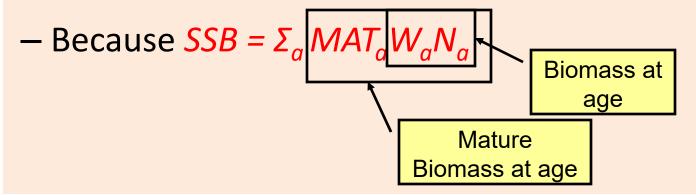
Harvest strategy and RPs



Harvest strategy and RPs

- RPs often derived from an <u>equilibrium</u> <u>analysis</u> of a population dynamics model that accounts for fishing effects
- RPs can have substantial economic and social implications
- especially via eco-labeling of the sustainability of fisheries.

- Similar to a YPR analysis, a SPR analysis examines how much spawner biomass a recruit can produce over it lifetime.
- Similar to YPR analysis, you need to know weights-at-age (W_a), fishery selectivity-at-age, and natural mortality to compute SPR, but in addition you need to know the proportion mature at age (MAT_a)



Spawner per-recruit RPs

- YPR RPs do not account for impacts on the adult fish population
- SPR F RPs have the objective of preserving a fraction of SSB compared to unfished SSB (f = 0)
- Spawner potential ratio (%) (%SPR)

$$%SPR(F_{x\%}) = \frac{100*SPR(F_{x\%})}{SPR(0)} = x\%$$

- Note that SPR(f) and SSB(f) are decreasing functions of f (see next few slides)
- Clark showed that $F_{35\%}$ usually close to F_{msy} ??
- SPR F RPs commonly used in US.

$$SPR(F) = W_{a_r} MAT_{a_r} + \sum_{i=1}^{\infty} W_{a_r+i} MAT_{a_r+i} e^{-iM-F\left(\sum_{j=0}^{i-1} S_{a_r+j}\right)}$$

- SPR F_X reference points are set so that SSB SPR is x% of the result with no fishing (F=0)
- IN US commercial fisheries, percentage used to define <u>overfishing</u> are in the 20-35% range.
- Keeping F's below these levels should avoid stock depletion (Goodyear, 1993).

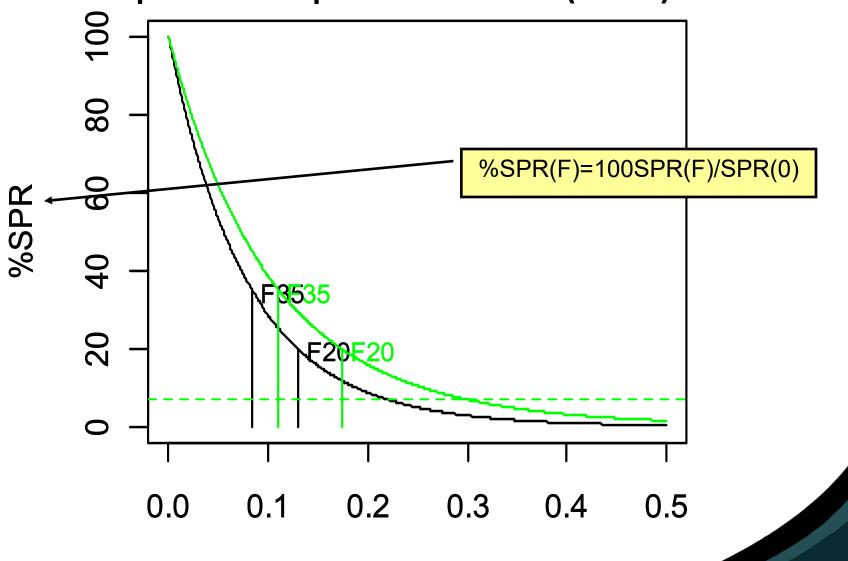
Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: Foundation and current use. In: S.J. Smith, J.J. Hunt, and D. Rivard (Eds.), Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

The Effect of Recruitment Variability on the Choice of a Target Level of Spawning Biomass Per Recruit

William G. Clark International Pacific Halibut Commission Seattle, Washington

Abstract

Deterministic computations with a range of spawner-recruit curves and groundfish life history parameters have shown that a high average yield virtually can be assured by applying the fishing mortality rate that reduces spawning biomass per recruit to 35% of the unfished level (denoted $F_{35\%}$). Stochastic trials reported here indicate that the presence of random variation in recruitment calls for a slightly higher target level of spawning biomass per recruit—around 40%—especially if the recruitment deviations have a high serial correlation. The year-to-year variability of yield is hardly affected by the target level of spawning biomass per recruit, but the frequency of episodes of low spawning biomass—if defined as less than 20% of the unfished level—may be reduced substantially by fishing at $F_{40\%}$ rather than $F_{35\%}$, even though there is only a small difference in average spawning biomass between $F_{35\%}$ and $F_{40\%}$.



F

```
SPR <- function(f){
                        SPR R code
  n.age = length(sel)
  fa = f*sel
  za = m + fa
  cza = cumsum(c(0,za[1:(n.age-1)]))
  SPR = sum(exp(-cza)*weight*mat)
  return(SPR)
age=3:20
weight = c(0.15, 0.278, 0.394, 0.599, 0.862, 1.163, 1.572, 2.028, 2.653,
3.141,3.844,4.043,4.252,4.471,4.702,4.945,5.200,5.469)
mat = c(0,0,0,0,0,0.002,0.006,0.022,0.077,0.242,0.529,0.651,0.756,
0.837,0.895,0.934,0.959,0.975)
m=rep(0.2,length(age))
spr1 = SPR(0.2)
print(spr1)
```

Continuous-Time

Mature biomass:

$$SSB(f) = R \int w(t) mat(t) \Lambda(t, f) dt$$

Spawner biomass per recruit

$$SPR(f) = SSB(f)/R = \int_0^\infty w(t)mat(t)\Lambda(t,f)dt$$

SPR(f) is a monotone decreasing function of f

Continuous-Time

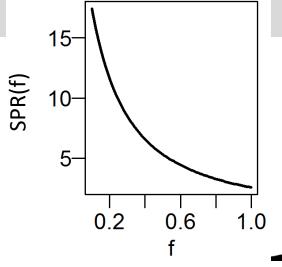
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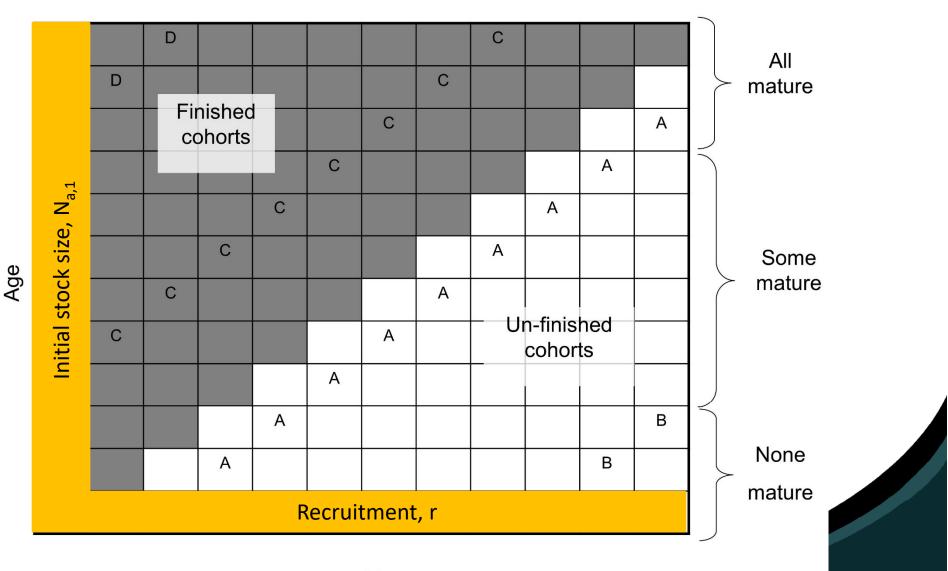


Population dynamics model

- We can apply the age-based model for successive cohorts
- To form a long age-structured time-series
- At equilibrium (as t -> ∞) the age-structure of the population does not change
- Total yield and SSB for all cohorts is the same as the total yield and SSB a cohort produces over its life time.

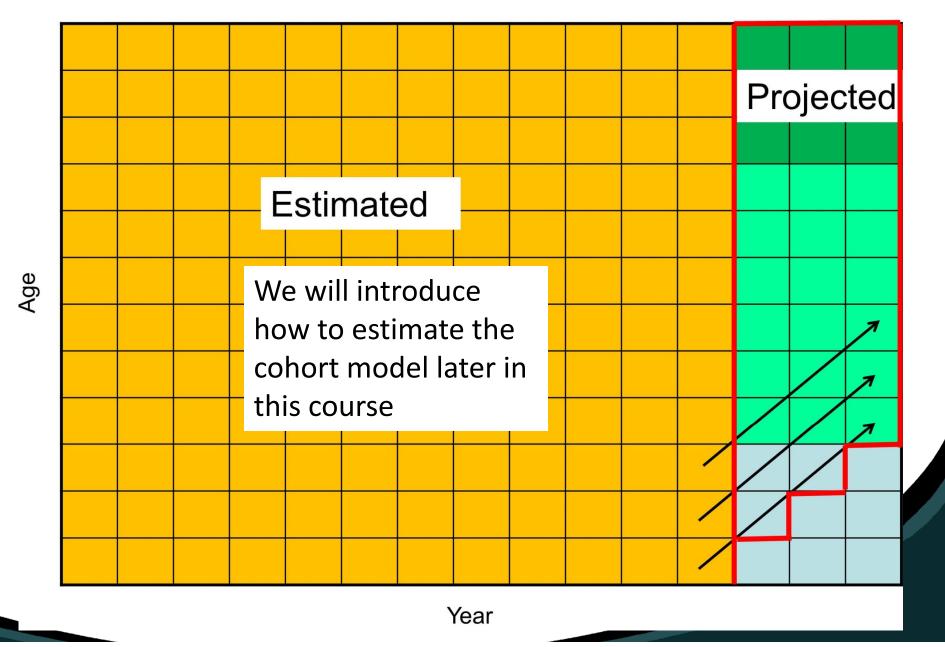
Cohort model

$$N_{a,y} = N_{a-1,y-1} \exp(-Z_{a-1,y-1})$$



Year

Cohort Model plus Projections

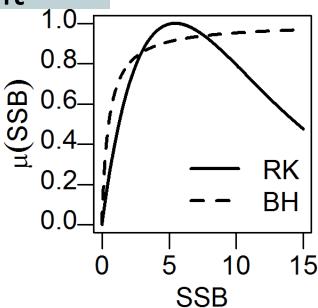


Reproduction

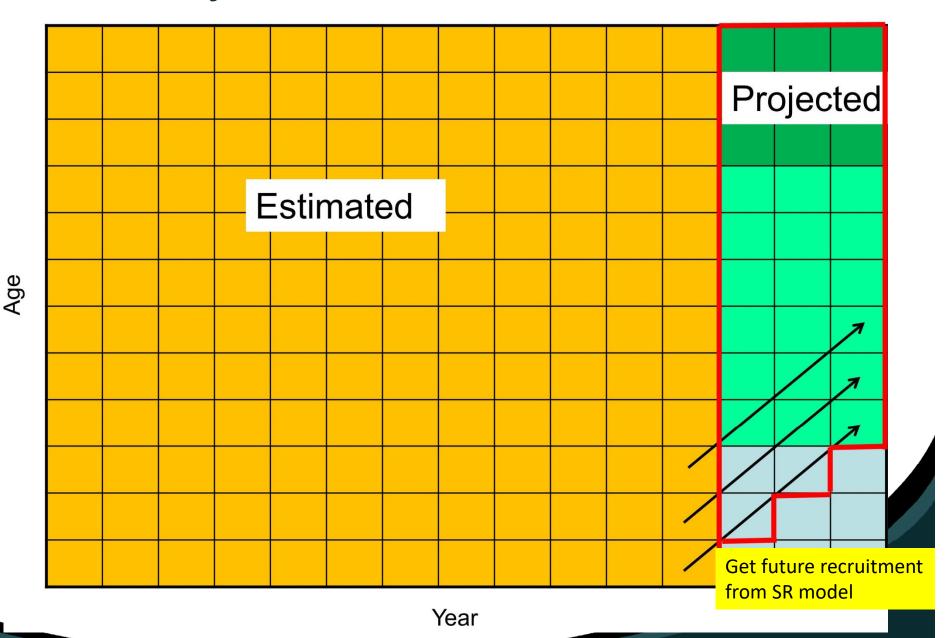
- Reproduction (aka recruitment) is modelled as a density-dependent function of parental population size.
- Known as the stock-recruit (SR) function in fisheries, μ(SSB)
- Common examples:
- Beverton-Holt: $\mu(SSB) = \frac{\alpha SSB}{\beta + SSB}$
- Ricker: $\mu(SSB) = \alpha SSBexp(-\beta SSB)$

Reproduction

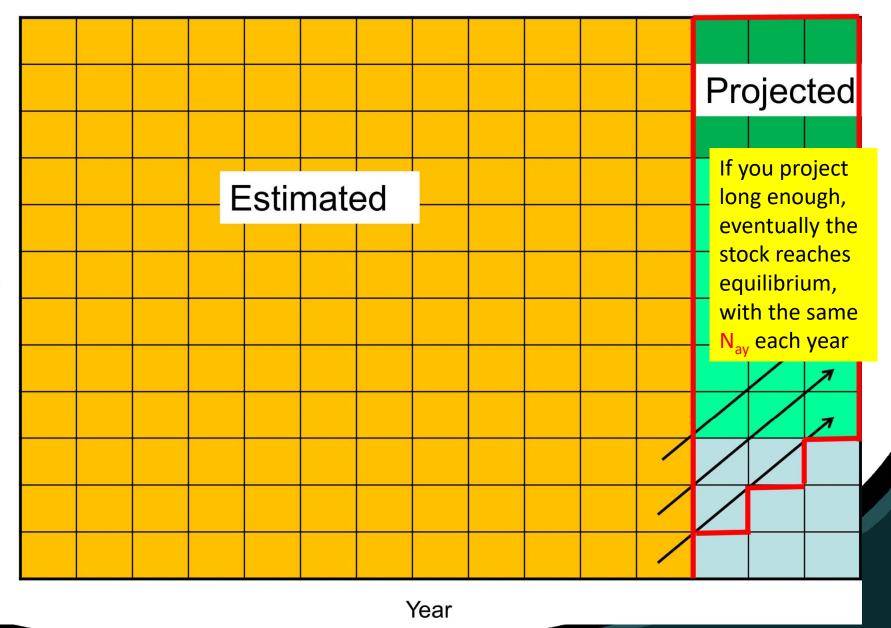
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Projections for Reference Points

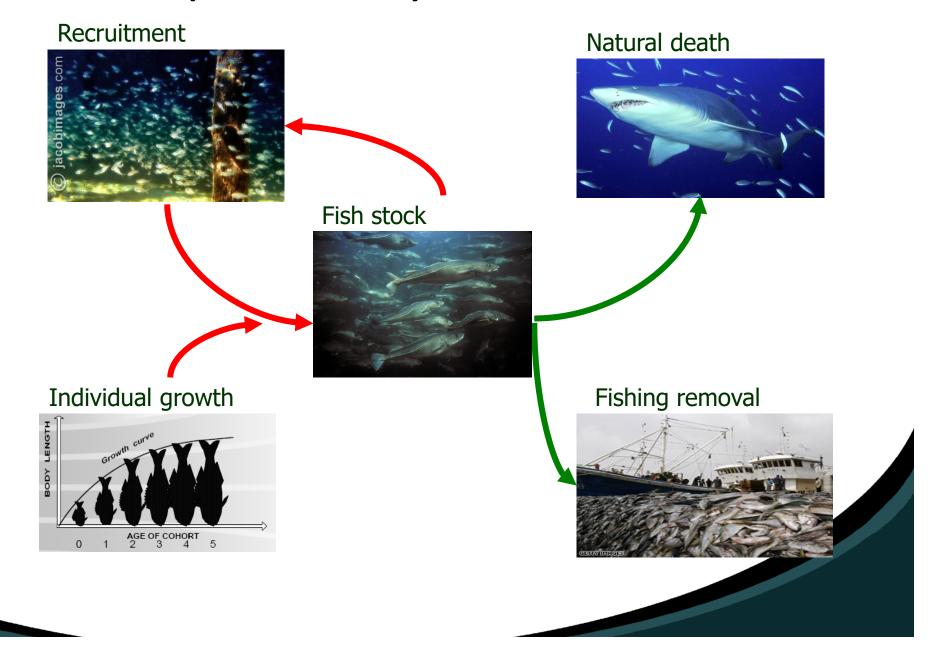


Projections for Reference Points



Age

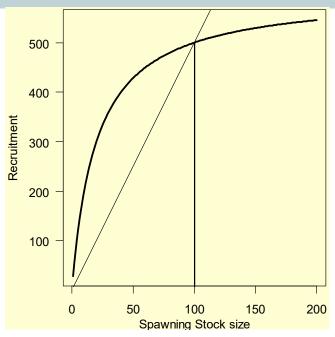
Population dynamics model



Equilibrium (long-term) results

- At equilibrium the production of R from SSB (i.e. the SR relationship) and the production of SSB from R (survival and growth) are the same
- $R_e(f) = \mu\{SSB_e(f)\} = SSB_e(f)/SPR(f)$
- $SSB_e(f)$ is the x solution to $\mu(x) = x/SPR(f)$

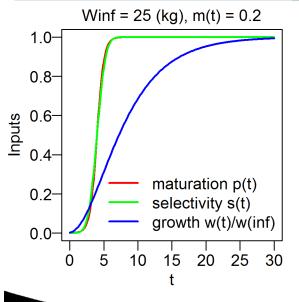
e subscript indicates equilibrium result

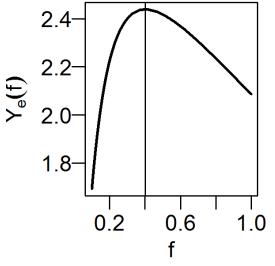


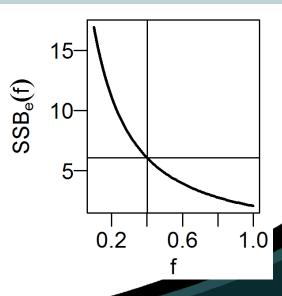
Compensatory
Mortality Property
(CMP): $SSB_e(f)$ is
unique when $\mu(x)/x$ is
strictly monotone
decreasing in x

Maximum sustainable yield (MSY)

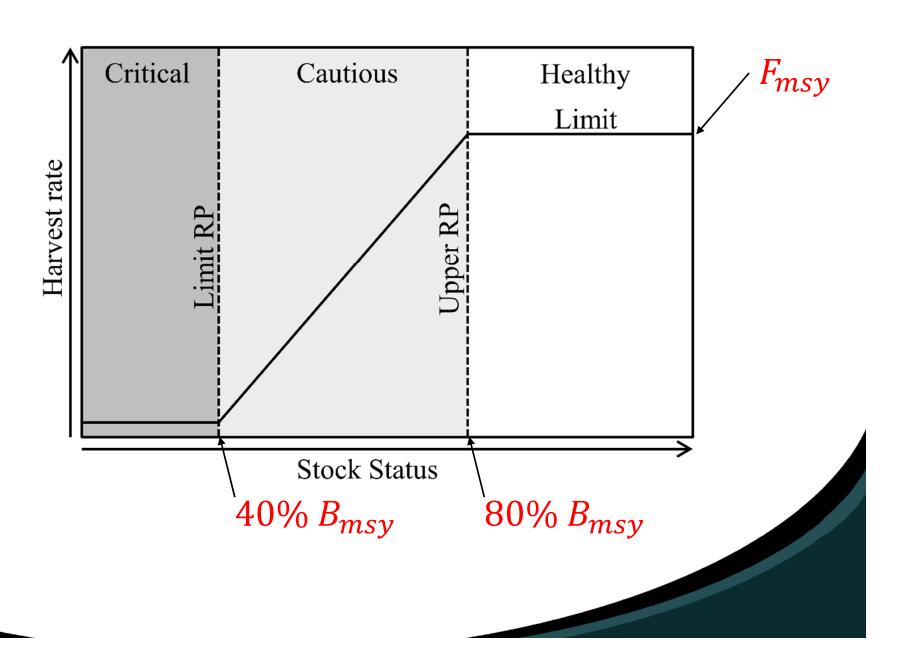
- Equilibrium yield: $Y_e(f) = R_e(f)YPR(f)$
- $F_{msy} = max_f Y_e(f)$
- $B_{msy} = SSB_e(F_{msy})$
- $Y_e(f)$ is usually concave at $f = F_{msy}$



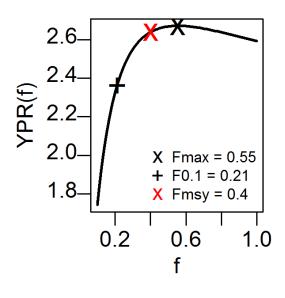


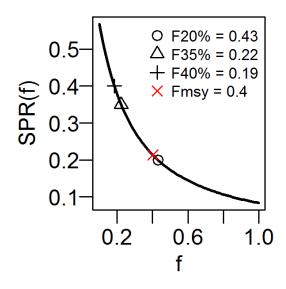


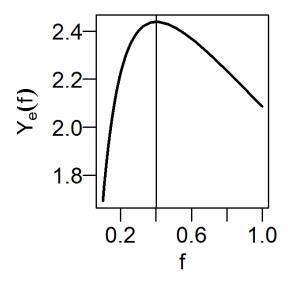
MSY RPs

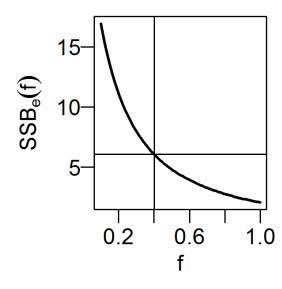


Reference Point Illustrations









Per-recruit RPs

- MSY RPs are often difficult to estimate reliably, primarily because of uncertainty about the SR function (e.g. ICES J. Mar. Sci. 70: 56–67).
- 'per-recruit' F RPs can be more readily calculated with available information
- based on only YPR(f) or BPR(f)
- Does not require a SR function