Biomass dynamics models

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David Miller and ICES staff (following Steve Cadrin)

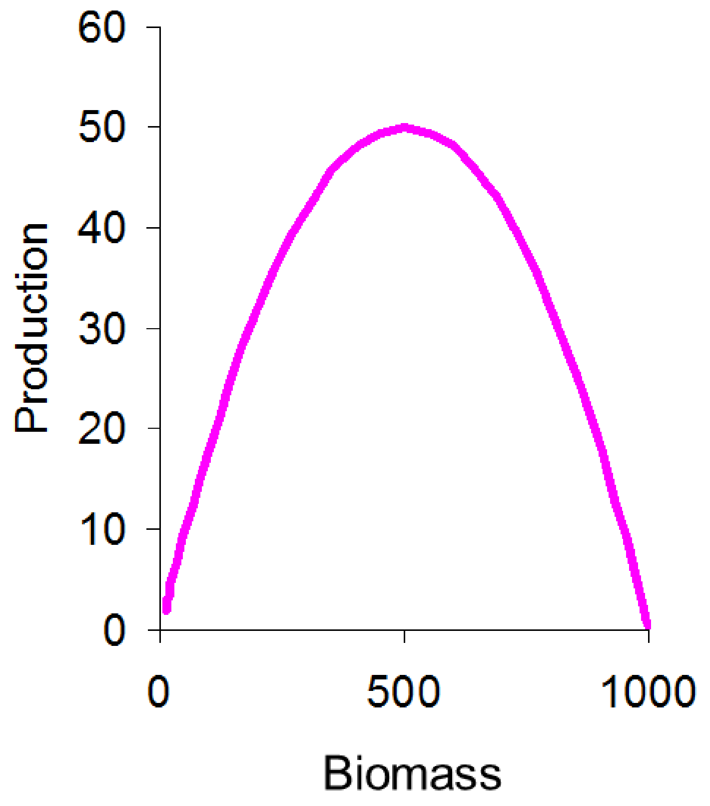
Ben Dipper, Marine Scotland Image Bank

Course programme

- Monday
  - Objectives of stock assessment
  - Data for stock assessment
  - Fitting models to data
  - ICES data
  - Evening icebreaker
- Tuesday
  - ICES Advice
  - Biological production & sustainable yield
  - **Biomass dynamics models**
- Wednesday
  - Simple demographic models
  - ICES data-limited assessments
  - Virtual Population Analysis (VPA)
  - Calibrated VPA
- Thursday
  - Dynamic pool models
  - Age-based Maximum Sustainable Yield (MSY)
- Friday
  - Statistical catch-at-age models
  - Integrated models

Outline of today's lecture

- Questions from this morning
- Modelling biological production
  - Exponential population growth
  - Limited population growth
- Biomass dynamics models:
  - Equilibrium methods
  - Time series fitting
- Assignment - Time series model
- Biomass Dynamics in R (Colin)



Revision: Biological and fishery production

- Population growth:

$$B_{t+1} = B_t + R_t + G_t - (f_t + m_t)$$

- Biological production: change in biomass

$$B_{t+1} - B_t = R_t + G_t - (f_t + m_t)$$

- Harvest equation (Russell 1931):

$$B_{t+1} = B_t + R_t + G_t - Y_t - m_t$$

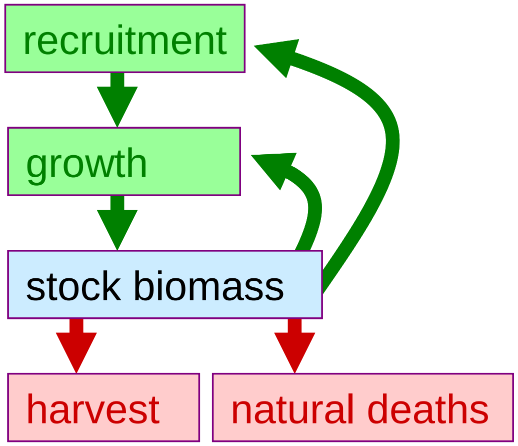
- Fishery production:

$$B_{t+1} - B_t + Y_t = R_t + G_t - m_t$$

- Sustainable Yield: Overfishing

$$B_{t+1} \geq B_t$$
$$Y_t \leq R_t + G_t - m_t$$

$$B_{t+1} < B_t$$
$$Y_t > R_t + G_t - m_t$$



Biological production

- Biological production: change in stock biomass (ignoring fishing mortality for now)

$$B_{t+1} - B_t = R_t + G_t - m_t$$

- Some possible hypotheses:
  - Recruitment: reproduction of new fish increases as stock size increases (more mothers -> more babies).
  - Growth: the sum of individual growth increments increases as stock size increases (more fish -> more population growth)

Exponential growth

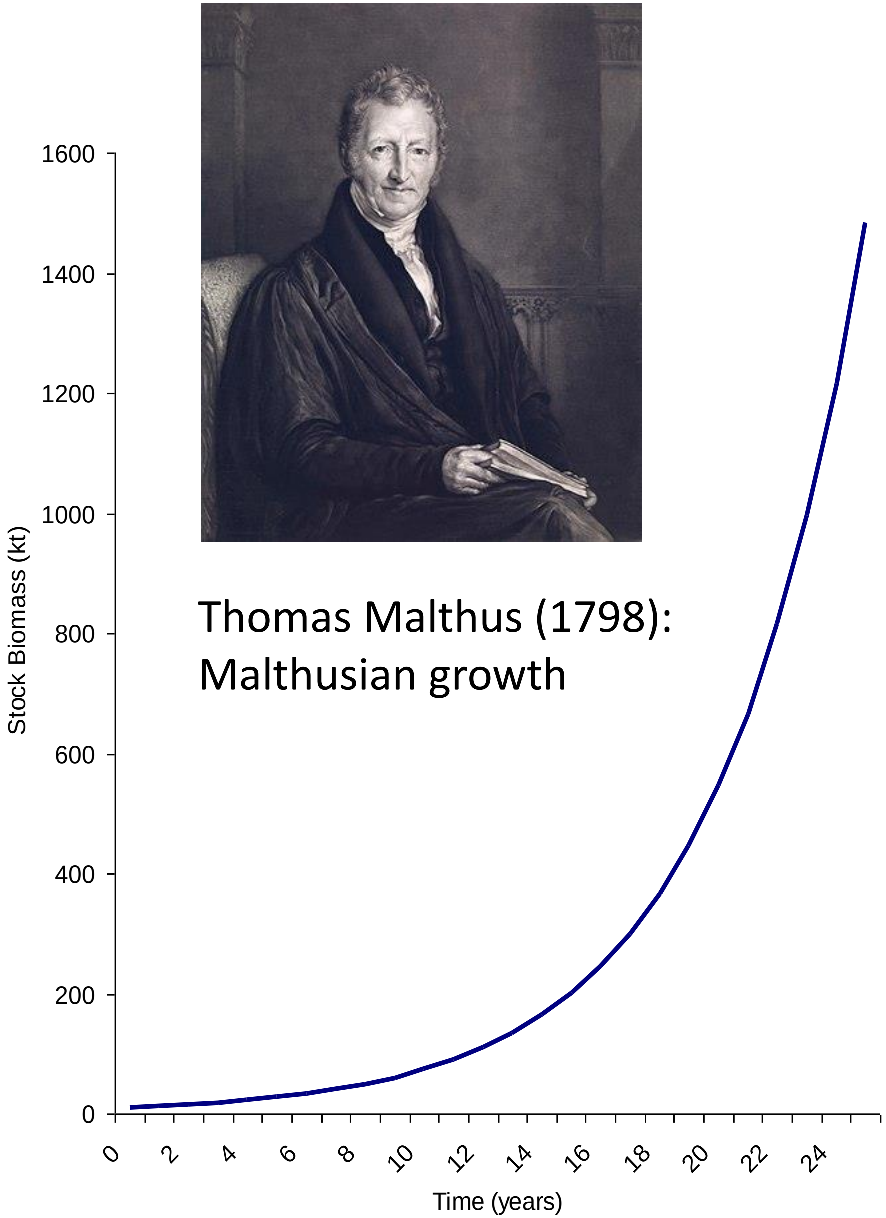
- Populations increase in proportion to their biomass (the rate of change is a function of stock size):

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

- The larger the population, the greater the growth increment
- *r* denotes the *per capita* rate of increase:

$$r = \frac{dB/_{dt}}{B}$$

Wikipedia

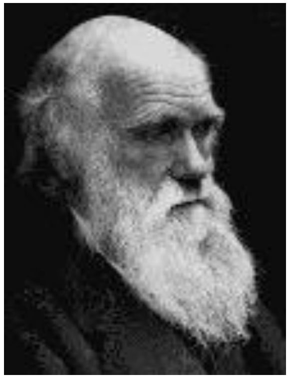


Thomas Malthus (1798): Malthusian growth

Exponential growth

- Exponential growth shows us the reproductive potential of populations
  - but does not adequately describe our general observations

Problems with exponential growth



- Darwin (1859): *"The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase:*
  - *it would be reasonable to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pairs of young in this interval;*
  - *if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair."*

Limited population growth

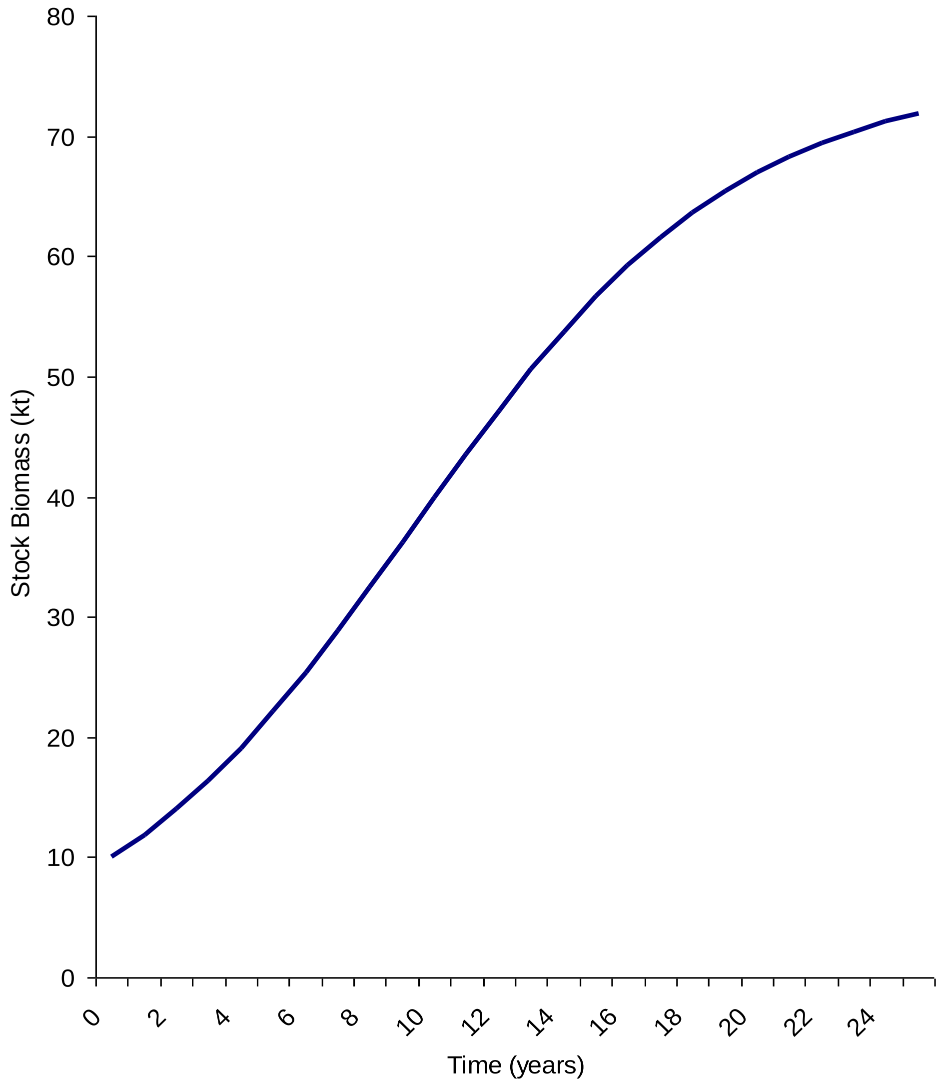
- Darwin (1859) realized that something was wrong with Malthus' model, because every population would have the capacity to increase until they covered the earth.
- He argued that as density increases, competition for limited resources reduces the population growth rate.

$$B_{t+1} - B_t = R_t + G_t - m_t$$

  - Recruitment *R*: reproduction of new fish may decrease with crowding.
  - Growth *G*: individual growth rates may decrease with crowding.
  - Removals due to natural mortality *m*: may increase with crowding

Logistic growth

- Populations increase proportional to their biomass, but the rate of increase slows as the population approaches its carrying capacity:
  - *r*: intrinsic growth rate
  - *K*: carrying capacity
  - Rate of change (production) is maximum when the population is at half of its carrying capacity



Density-dependent growth

- Assumes population growth decreases as population size (and density) increase

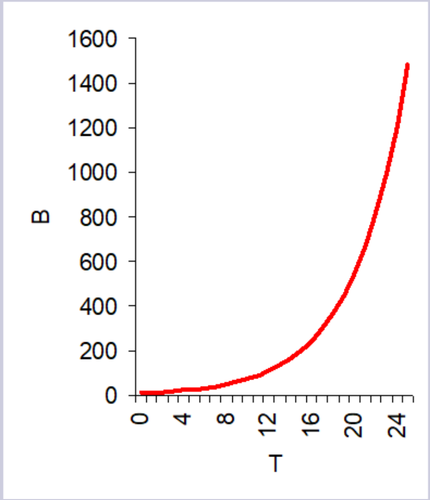
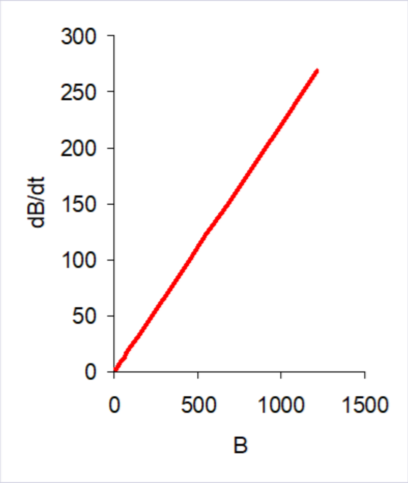
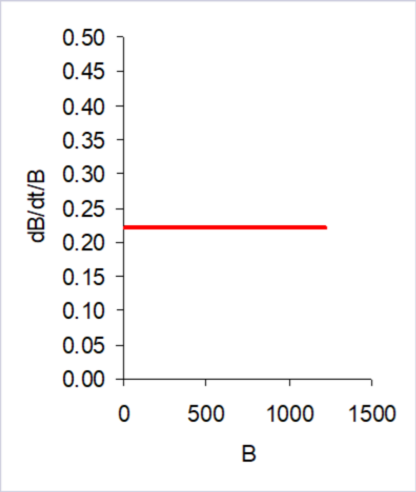
$$dB/_{dt} = rB - (r/_K)B^2$$

- In other words: the per capita rate of population growth decreases as a linear function of abundance

$$\frac{dB/_{dt}}{B} = r - (r/_K)B$$

- The growth rate is the intrinsic growth rate reduced by the effect of the population on itself through intraspecific competition
  - *r* is per-capita growth rate at extremely low densities
  - *K* is the density at which growth stops (d*B*/d*t*=0; carrying capacity)

Model comparisons

<table>
<tr><th>Model</th><th>Abundance</th><th>Rate of change</th><th>Per capita rate of change</th></tr>
<tr><td>Exponential growth</td><td>
</td><td>
</td><td>
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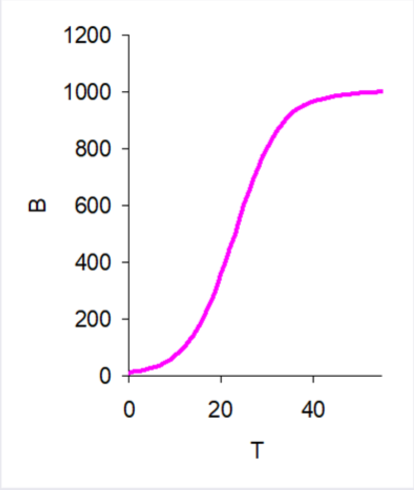
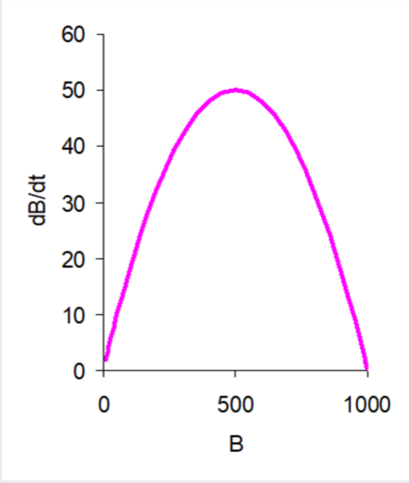
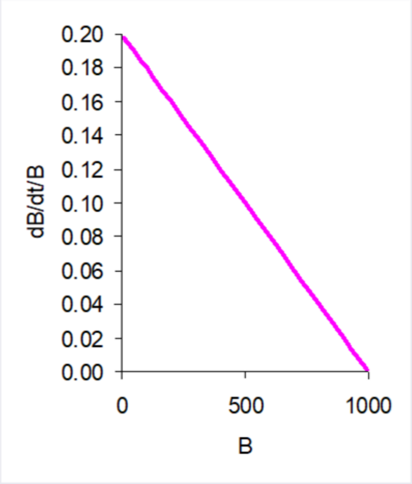
<tr><td>Logistic growth</td><td>
</td><td>
</td><td>
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Lagged density effects

- If decreasing birth rates and increasing mortality caused by increased density are delayed (by time to maturation for example), response to abundance will also be delayed:

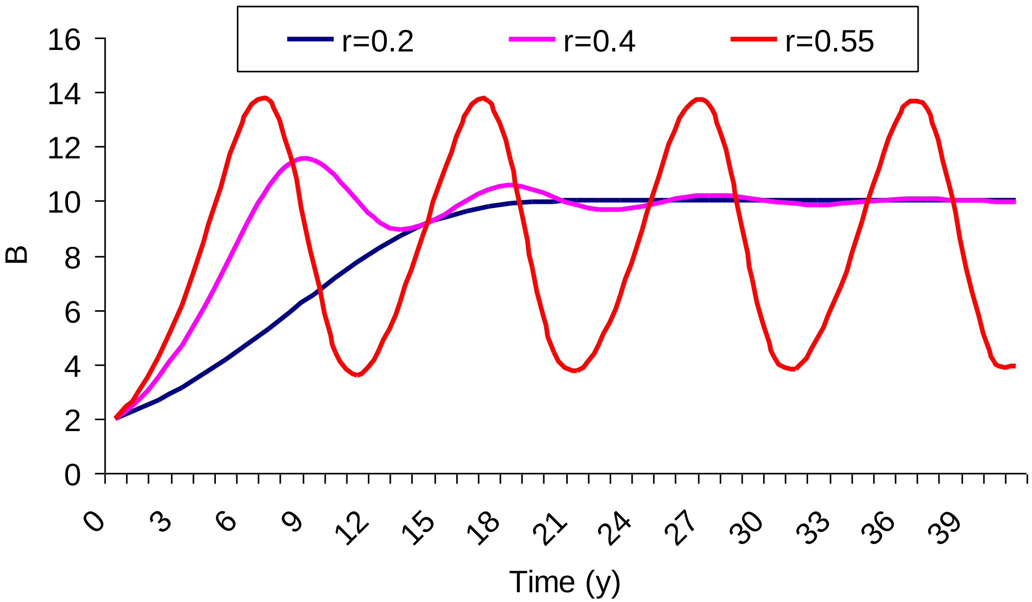
$$ {}^{dB}\!/_{dt} = rB_t - \left({}^{r}\!/_{K}\right)(B_{t-L})^2 $$

- where L is a lag between time of abundance and the compensatory response

Lagged density effects

- At a fixed time lag (L = 1) a range of r's behave differently.
  - At r = 0.2, growth is essentially logistic.
  - At r = 0.4, abundance initially exceeds the carrying capacity, but eventually settles into an equilibrium.
  - At r = 0.6, abundance quickly exceeds the carrying capacity, then crashes, then continues to boom and crash in regular cycles.

$$dB/_{dt} = rB_t - (r/_K)(B_{t-L})^2$$



Summary: population growth

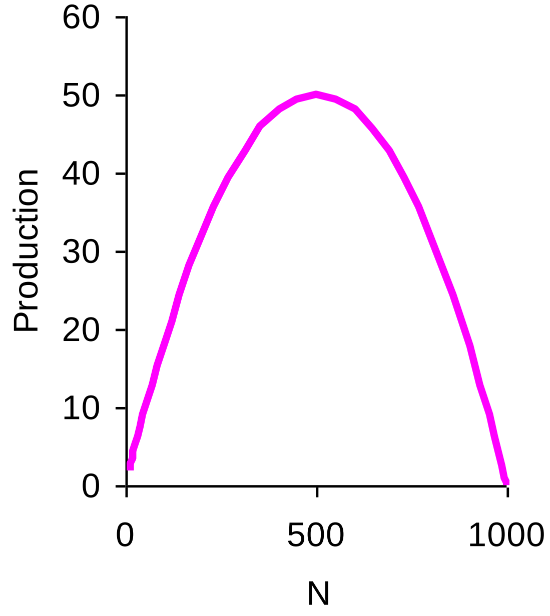
- Exponential growth (multiplicative growth without limit):

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

- Logistic growth (multiplicative growth with negative density dependence):

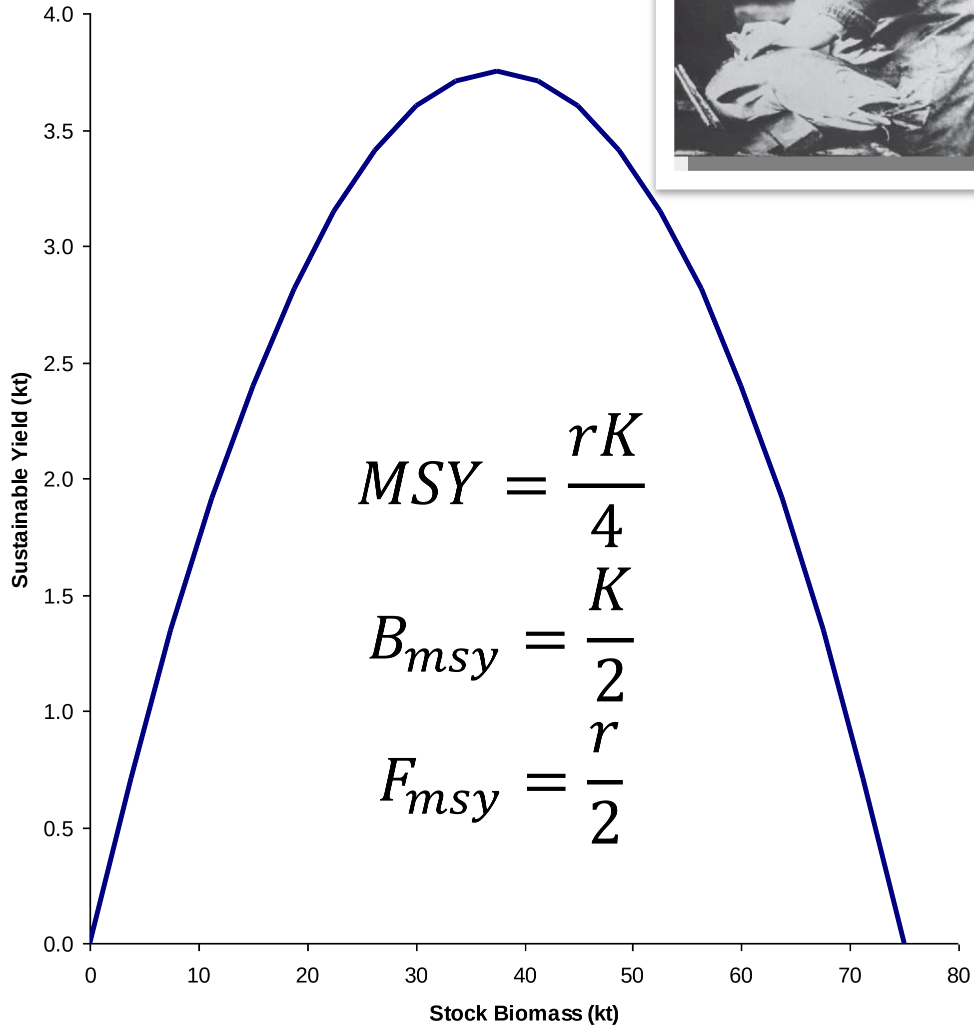
$$\frac{dB}{dt} = rB - \frac{r}{K}B^2$$

- Density dependence confers compensatory growth (increased production at lower densities), allowing sustainable fishing and maximum sustainable yield (MSY) at intermediate stock sizes and fishing mortalities.



Biomass dynamics models

- Graham's *Theory of Sustainable Fishing* (1935):
  - If removals can be replaced by stock production each year, the fishery is sustainable.
  - If stock size is maintained at half its carrying capacity, the population growth rate is fastest, and sustainable yield is greatest (Maximum Sustainable Yield MSY)



$$MSY = \frac{rK}{4}$$

$$B_{msy} = \frac{K}{2}$$

$$F_{msy} = \frac{r}{2}$$

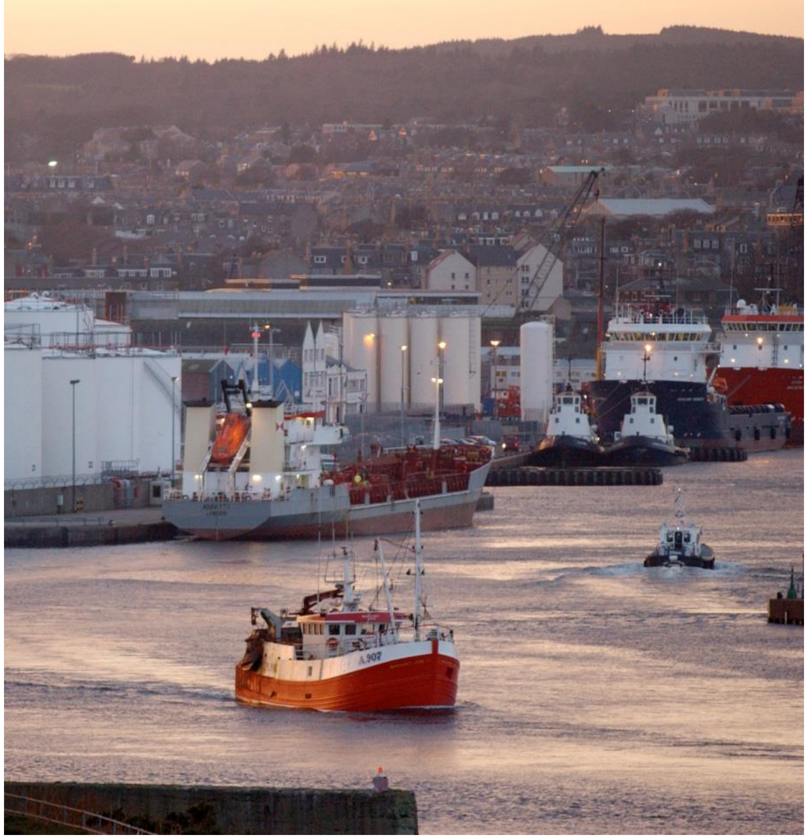
$$\frac{dB}{dt} = rB - \frac{r}{K}B^2 - Y$$

Revision: Fishery catch rates

- CPUE: catch per unit effort (*U*)
- Index of the magnitude of the average 'exploitable' population over the observed time (in biomass *B* or abundance *N*):

$$Y_t = F_t \bar{B}_t \qquad F_t = qE_t$$

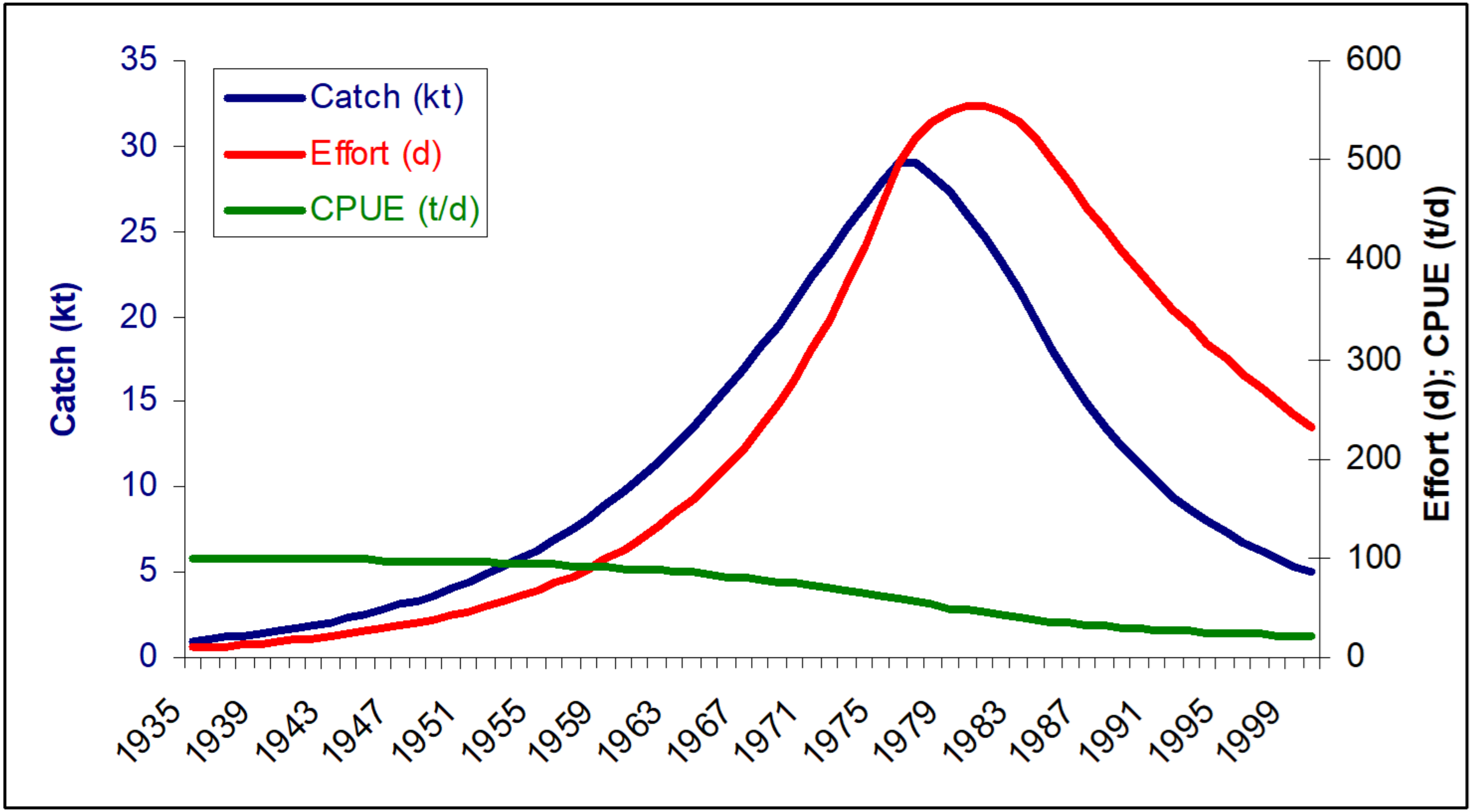
$$Y_t = qE_t \bar{B}_t \qquad \frac{Y_t}{E_t} = q\bar{B}_t$$



Keith Mutch, Marine Scotland Image Bank

- Greater catch rates indicate a larger exploitable biomass

Revision: Exploitation history



Biomass dynamics models

- Estimation Methods:
  - Assume Equilibrium:
    - Not reliable – can overestimate MSY
    - However, equilibrium behaviour is informative for long-term expectations
  - Linearized Models – improper error structure
  - Time Series Fitting – most reliable method

Equilibrium conditions

- Rewrite the production model $dB/dt = rB - \frac{r}{K}B^2 - Y$ as:

$$dB/_{dt} = \left(r - \frac{r}{K}B\right)B - FB$$

- At equilibrium, stock size doesn't change, so $^{dB}/_{dt} = 0$ and:

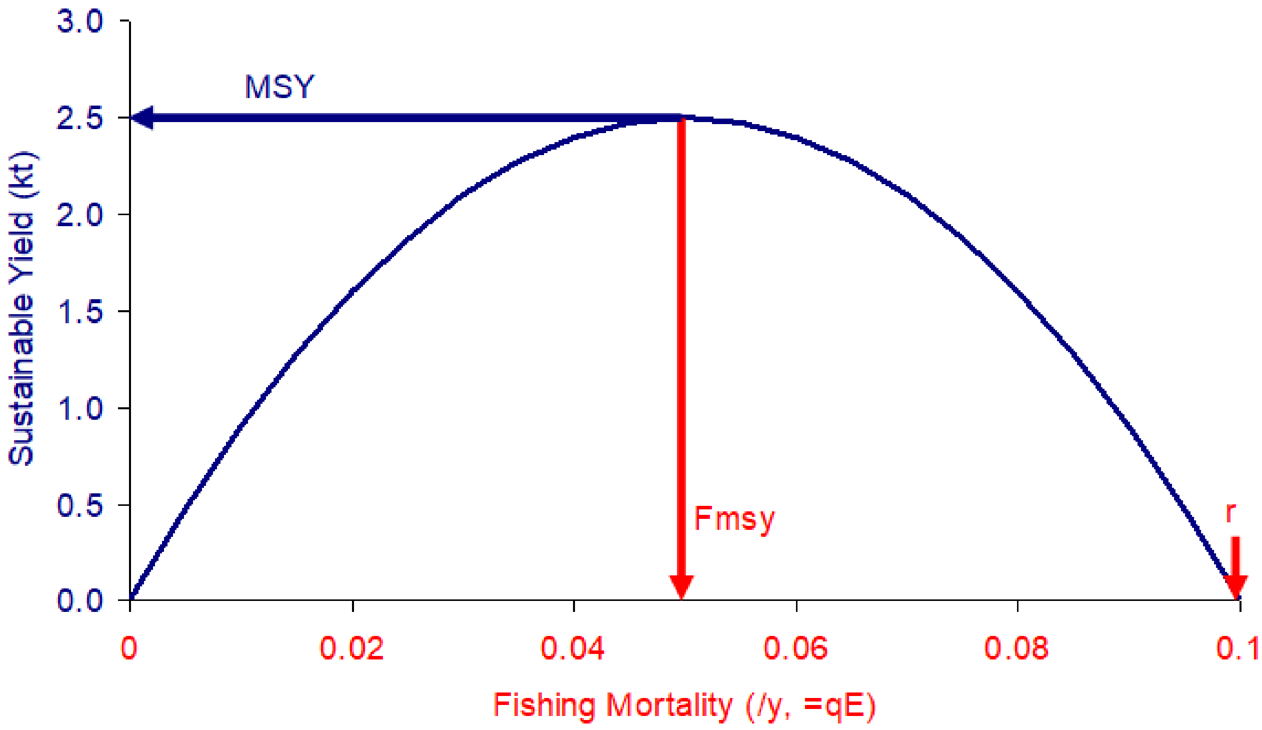
$$\left(r - \frac{r}{K}B\right)B = FB$$

- At a constant fishing mortality rate (*F*), biomass will reach an equilibrium of *B**, and catch will equal biological production:

$$\left(r - \frac{r}{K}B^*\right)B^* = FB^* \Rightarrow B^* = K - \left(\frac{K}{r}\right)F$$

Equilibrium conditions

- So for every F^*, there is an equilibrium biomass (B^*)
- This produces an equilibrium yield (Y^*) since $Y = FB$



MSY, B_{msy}, F_{msy}

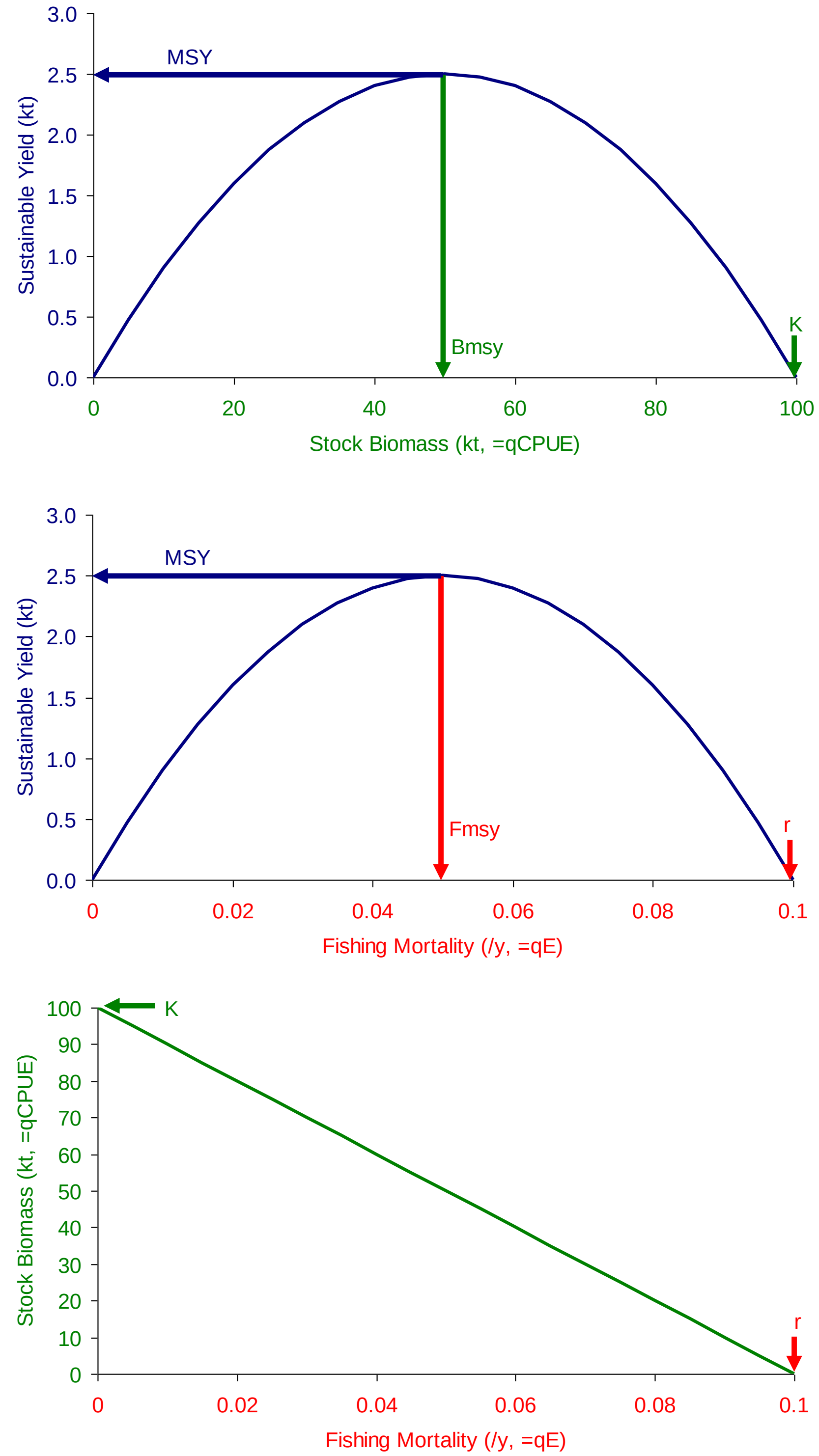
- Logistic Growth:

$$\frac{dB}{dt} = rB - \left(\frac{r}{K}\right)B^2$$

- Harvest Model:

$$B_{t+1} = B_t + rB_t - \left(\frac{r}{K}\right)(B_t)^2 - Y_t$$

- MSY (= $rK/4$) is the yield in a time period that equals maximum production
- B_{MSY} (= $K/2$) is the stock size (biomass) that produces MSY
- F_{MSY} (= $r/2$) is the fishing mortality (exponential rate) that produces MSY



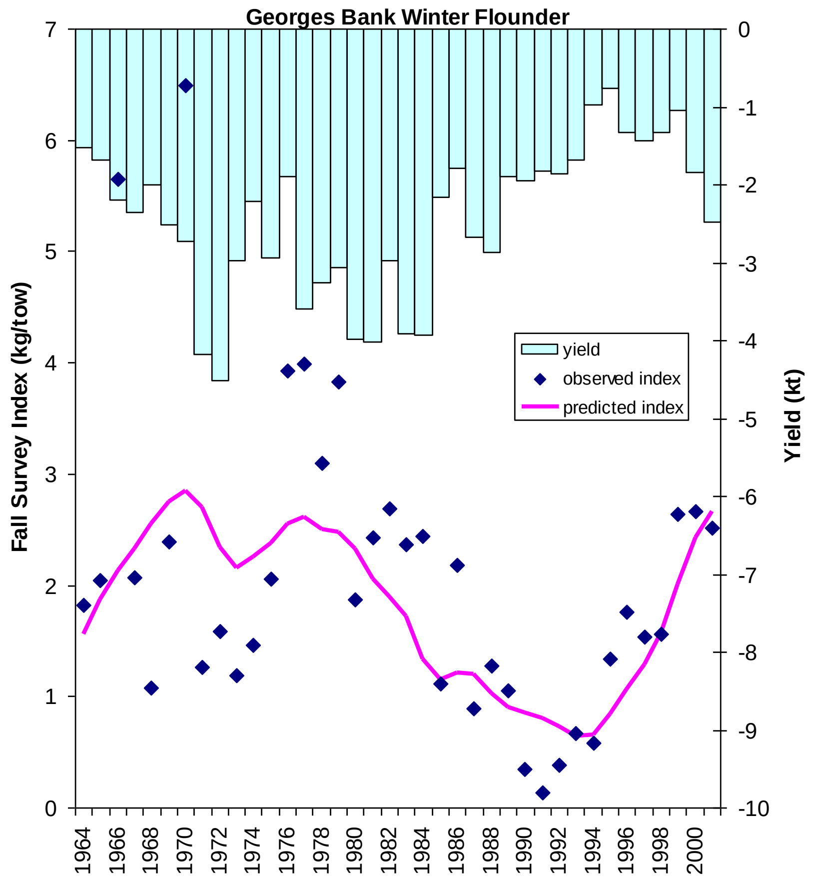
Time-series estimation

- Recent models can use observed yield and stock size indices (*I*) to estimate *B* by *smoothing and scaling*
- With logistic growth and observed catch we have a process equation and can calculate a time series of biomass

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

- If we have a times series of catch and relative biomass index (*I*), then:

$$I_t = qB_t$$



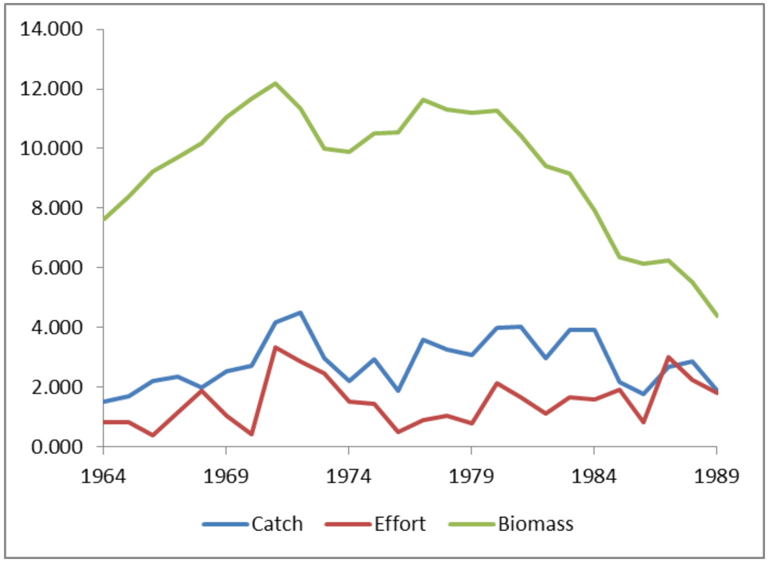
Nonlinear estimation

1. Input: time series of catch and survey index
2. Estimated parameters: r, K, q, B_1 (with starting guesses, r ~ 0.5, K ~ 8 x mean Y, B_1 ~ $K/2$, q ~ I_1/B_1)
3. Calculate predicted time series of biomass:
$$B_{t+1} = B_t + rB_t\left(1 - \frac{B_t}{K}\right) - Y_t$$
4. Calculate predicted survey observations: $I_t = qB_t$
5. Calculate residuals $\ln(I_{obs}/I_{pred})$ and residual sum of squares
6. Find values of r, K, q, B_1 that minimize RSS

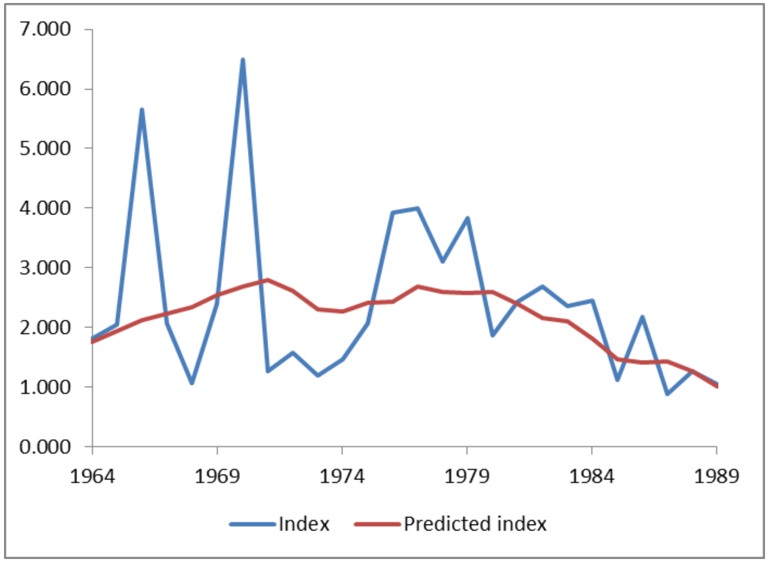
Parameter		Estimate	Starting value
r	Growth rate	0.345	0.500
K	Carrying capacity	59.430	22.703
q	Survey catchability	0.230	0.160
B1	Initial biomass	7.637	11.352

Year	Catch	Effort	Index	B	Predicted I	Residual	RSS
1964	1.517	0.834	1.820	7.637	1.755	0.036	5.228
1965	1.687	0.823	2.050	8.416	1.934	0.058	
1966	2.197	0.388	5.660	9.221	2.119	0.982	
1967	2.349	1.135	2.070	9.711	2.232	-0.075	
1968	1.999	1.868	1.070	10.165	2.336	-0.781	
1969	2.518	1.054	2.390	11.072	2.545	-0.063	
1970	2.716	0.418	6.490	11.662	2.681	0.884	
1971	4.183	3.320	1.260	12.180	2.800	-0.798	
1972	4.512	2.856	1.580	11.338	2.606	-0.500	
1973	2.976	2.480	1.200	9.991	2.296	-0.649	
1974	2.218	1.519	1.460	9.882	2.271	-0.442	
1975	2.937	1.426	2.060	10.507	2.415	-0.159	
1976	1.893	0.482	3.930	10.553	2.426	0.483	
1977	3.594	0.901	3.990	11.654	2.679	0.398	
1978	3.250	1.048	3.100	11.292	2.596	0.178	
1979	3.064	0.800	3.830	11.198	2.574	0.397	
1980	3.975	2.126	1.870	11.269	2.590	-0.326	
1981	4.012	1.651	2.430	10.444	2.401	0.012	
1982	2.980	1.108	2.690	9.402	2.161	0.219	
1983	3.908	1.656	2.360	9.153	2.104	0.115	
1984	3.931	1.604	2.450	7.916	1.819	0.298	
1985	2.163	1.931	1.120	6.352	1.460	-0.265	
1986	1.787	0.820	2.180	6.146	1.413	0.434	
1987	2.669	2.999	0.890	6.260	1.439	-0.480	
1988	2.859	2.251	1.270	5.523	1.269	0.000	
1989	1.891	1.801	1.050	4.392	1.010	0.039	

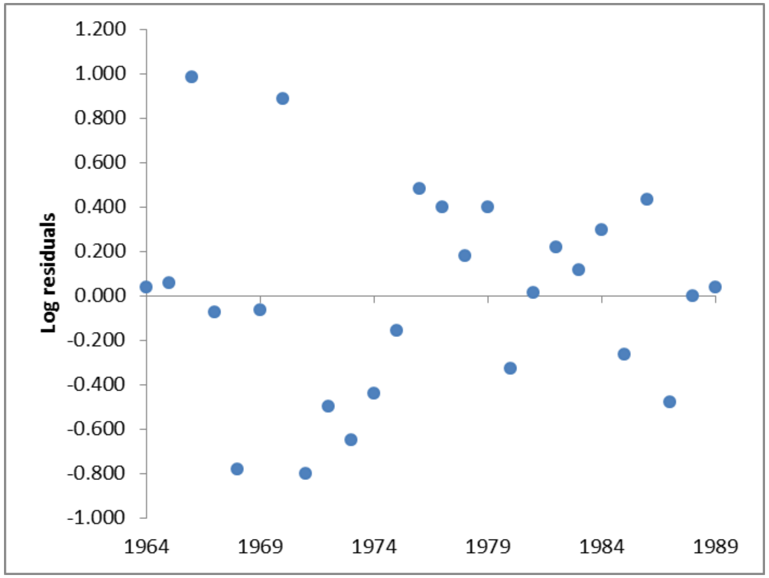
Nonlinear estimation



Catch, effort and estimated biomass



Observed and predicted index



Residual time-series

Assignment: Biomass dynamics

- Biomass dynamics analysis of catch and CPUE data for south Atlantic Albacore (Polachek et al. 1993)
  - See sheet "4_Biomass dynamics"
- For starting values, assume
  - B(1967) = 100kt
  - r = 0.5
  - K = 200kt
  - q = 0.5
- Time series fitting for biomass estimates
- Treat yield as the "catch" and CPUE as the "index"

	Yield (kt)	CPUE
1967	15.9	61.89
1968	25.7	78.98
1969	28.5	55.59
1970	23.7	44.61
1971	25	56.89
1972	33.3	38.27
1973	28.2	33.84
1974	19.7	36.13
1975	17.5	41.95
1976	19.3	36.63
1977	21.6	36.33
1978	23.1	38.82
1979	22.5	34.32
1980	22.5	37.64
1981	23.6	34.01
1982	29.1	32.16
1983	14.4	26.88
1984	13.2	36.61
1985	28.4	30.07
1986	34.6	30.75
1987	37.5	23.36
1988	25.9	22.36
1989	25.3	21.91

Assignment: Biomass dynamics

- Calculate biomass series (use max(function,0.001)

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

- Calculate predicted CPUE:

$$U_t = qB_t$$

- Calculate log residual: ln l(obs/exp)
- Calculate residual sum of squares: sum[ln l(obs/exp)^2]
- Solve for B_1, r, K, q by minimizing RSS
- What is the 1989 biomass estimate (compare to B_1 and B_{msy})?
- Extra Credit: calculate fishing mortality for the series and compare to F_{msy}

	Yield (kt)	CPUE
1967	15.9	61.89
1968	25.7	78.98
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1970	23.7	44.61
1971	25	56.89
1972	33.3	38.27
1973	28.2	33.84
1974	19.7	36.13
1975	17.5	41.95
1976	19.3	36.63
1977	21.6	36.33
1978	23.1	38.82
1979	22.5	34.32
1980	22.5	37.64
1981	23.6	34.01
1982	29.1	32.16
1983	14.4	26.88
1984	13.2	36.61
1985	28.4	30.07
1986	34.6	30.75
1987	[illegible]	23.3[illegible]
[illegible]	[illegible]	[illegible]
1989	[illegible]	21.9[illegible]

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