Some more mathematical formulation of stock dynamics

Purpose of slides

- Introduce the basics in mathematical representation of population dynamics in some detail:
  - Show how the models are all a a special form of the mass balance equation (Russels equation)
  - Stock production models
  - Cohort based models (generic length/age models)
    - Describe the general pattern observed
    - Derive the mathematical equation
- Source:
  - Haddon 2001: Chapter 1 & 2
  - Hilborn and Walters 1992: Chapter 3.4

Russel's mass balance formulation

$$\begin{pmatrix}\text{next}\\ \text{biomass}\end{pmatrix}=\begin{pmatrix}\text{last}\\ \text{biomass}\end{pmatrix}+(\text{recruitment})+(\text{growth})-\begin{pmatrix}\text{natural}\\ \text{mortality}\end{pmatrix}-(\text{catch})$$

- Russels contribution:
  - ".. the sole value of the exact formulation given above is that it distinguishes the separate factors making up gain and loss respectively, and is therefore an aid to clear thinking" (Russel 1931)
  - Recognized that a stock could be divided into animals that were in the fishable stock and those that were entering the fishable stock at any one time (recruitment)
  - Stock biomass has gains: Recruitment and growth
  - Stock biomass has losses: Natural and fishing mortality (catch)

Russel's equation: A mass balance equation

- $B_{t+1} = B_t + R_t + G_t - M_t - Y_t$
  - B_{t+1} stock size in weight at start of time t+1
  - B_t stock size in weight at start of time t
  - R_t weight of all recruits entering stock at time t
    - Recruits: Young fish "entering" the stock in each time period
  - G_t weight increase of fish surviving from t to t+1
  - M_t weight loss of fish that died from t to t+1
  - Y_t weight of fish captured from t to t+1

Stock production models

Russel's equation modified

- Russel's equation for biomass:

  $B_{t+1} = B_t + R_t + G_t - M_t - Y_t$
- In the absence of fishing:

  $B_{t+1} = B_t + R_t + G_t - M_t$
- The two sources of increase are called production:

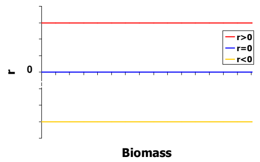
  Production = $(R_t + G_t)$
- Difference between production and natural mortality is called surplus production:

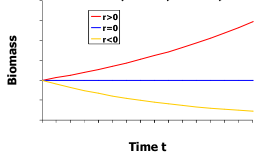
  Surplus production = $(R_t + G_t) - M_t$
- If the processes of recruitment, growth and natural mortality are constant we can write the Russel equation as:

  $B_{t+1} = B_t + rB_t$
  - r: intrinsic growth rate
    - Here recruitment, growth and mortality are all lumped into one number
      - $r > 0$, population will grow
      - $r = 0$, population remains constant
      - $r < 0$, population decreases with time

Population growth curves

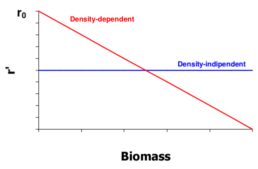
$$B_t = B_t + rB_t$$

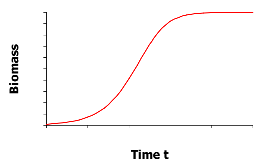




- Model limitations
  - No population increase or decreases continuously and there seems to be an upper bound due to food / space limitation, predation, competition. This model is thus not realistic to describe long term population change
  - Note this is an exponential model

Density dependent model





- Alter the exponential model by taking into account that population growth rates is a function of population size:
  - $r' = r_0 - r_1 B$
    - where ro is the population growth rate when the population size is small (mathematically NULL)
    - r_1 is a value that scale the rates with population size (B)

The logistic model 1

By mathematical derivation, taking into account a linear density dependent effect of birth and death rate, we can expand the exponential model:

$$B_{t+1} = B_t + rB_t$$

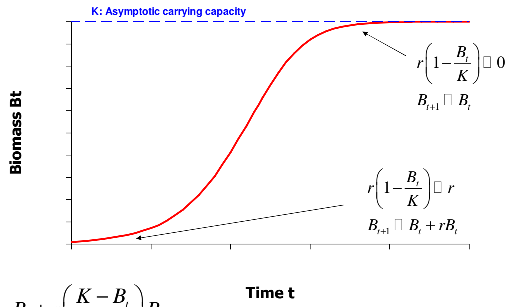
to the following form:

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

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

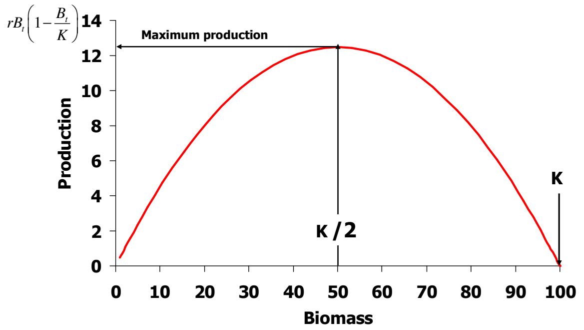
- K: The carrying capacity (often written as B_{max}).
- r: The intrinsic rate of growth (r):
  - is multiplied by the difference between the current population size and the carrying capacity ($K-B_t$ / K).

Population trajectory according to logistic model



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

Production as a function of stock size



Functional forms of surplus productions

- Classic Schaefer (logistic) form:

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

- The more general Pella & Tomlinson form:

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

  - Note: when p=1 the two functional forms are the same
  - If p <> 1, then the density dependence is no longer linear

General form of surplus production models

The Schaefer production model is related directly to Russels mass-balance formulation:

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

$B_{t+1} = B_t + P_t - Y_t$

$B_{t+1} = B_t + f(B_t) - Y_t$

- B_{t+1}: Biomass in the beginning of year t+1 (or end of t)
- B_t: Biomass in the beginning of year t
- P_t: Surplus production
  - the difference between production (recruitment + growth) and natural mortality
- $f(B_t)$: Surplus production as a function of biomass in the start of the year t
- Y_t: Biomass (yield) caught during year t

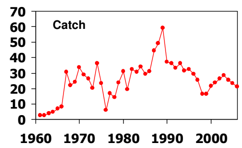
Production model: The model and data needs

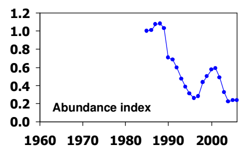
$$B_{t+1} = B_t + r\left(\frac{K - B_t}{K}\right)B_t - Y_t$$

$$CPUE_t = qB_t$$

- Need a time series of:
  - Total annual catch (Y_t)
  - Index of abundance ($CPUE_t$)
    - This index is most often obtained from data collected on the total effort in the commercial fisheries.
    - In rare cases independent scientific surveys are used in such analysis.

The data and the results





- The data needed:
  - Catch
  - Index of abundance
- The results:
  - Get an estimate of MSY
  - Get an estimate of Fmsy
  - Current stock status and fishing mortality
- The issue:
  - Is the model and are the estimates a true reflection of the population?
  - Are the data informative?

The reference points from a production model

$B_{MSY} = K/2$

$F_{MSY} = r/2$

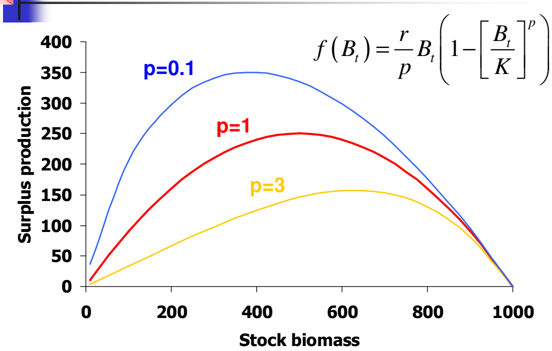
$MSY = F_{MSY} * B_{MSY} = r/2 * K/2 = rK/4$

$E_{MSY} = F_{MSY}/q = (r/2)/q = r/(2q)$

$F_t = C_t/B_t$

... just some word of caution

Model uncertainties: The true shape of the production



Model uncertainties: The cpue-biomass relationship

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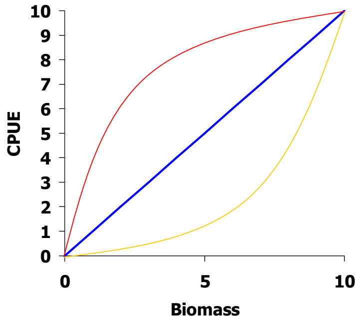

$$CPUE_t = f(B_t)$$

often assume

$$CPUE_t = qB_t$$

Model uncertainties

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- The assumption of stock production (and age based recruitment) models is that:
  - The carrying capacity (K), the production (r) and the MSY is on average constant over a long period of time
    - This assumption is highly debated at present, particularly in relation climatic and anthropogenic changes
    - A paradox:
      - It is sometimes argued that the longer the time series of data available (catch and cpue) the better the model estimates.
      - However, since K and r are likely changing over long time spans the problems of the model assumption of constant r and K is more likely to become violated when we use long time series
      - But short time series do not enough information to obtain the parameter estimates

Some other draw back of production models

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- The population is treated as a "lump":
  - Input
    - Total catch by weight
    - Catch per unit effort
  - Output
    - Total biomass estimates
- We know however that:
  - Fish grow in size with time, and thus pass through a multitude of life history stages
    - Larval
    - Juvenile
    - Adult
  - The number of fish must by nature reduce with time after birth
  - The size composition of the fisheries may change with time

FTP

Size/age based models
(cohort models)

Development of an cohort

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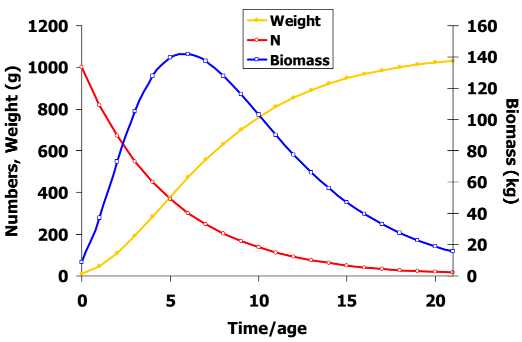

Cod: Length composition in survey, march 2002

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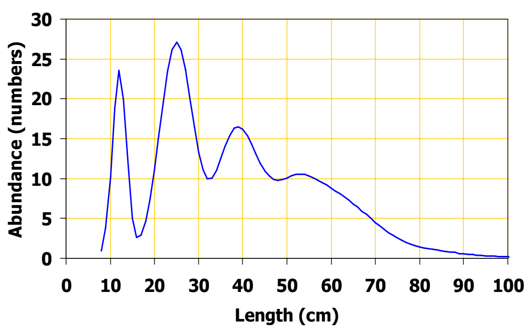

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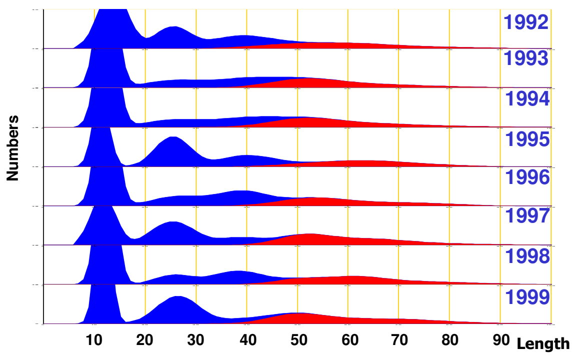
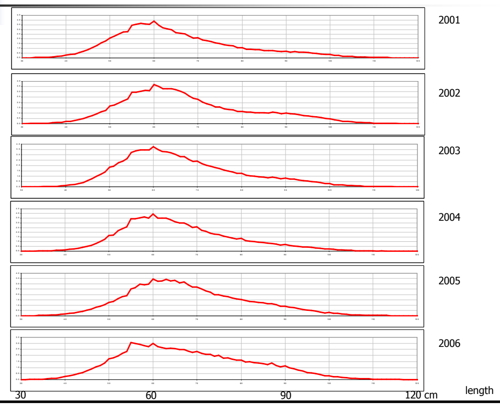
Cod: Time series of SURVEY length measurements



Cod – annual length distribution in the FISHERY



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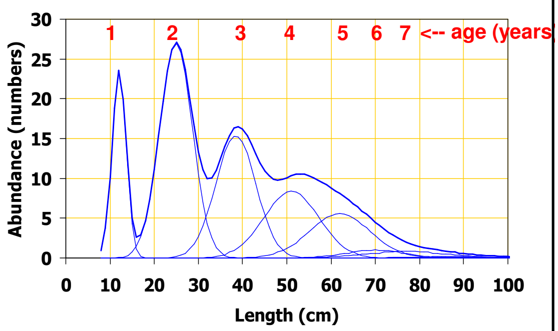
Cod: Length and age composition in survey, march 2002



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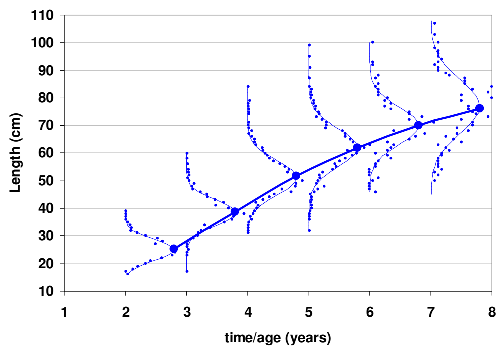
Cod: Cohort change in length with age



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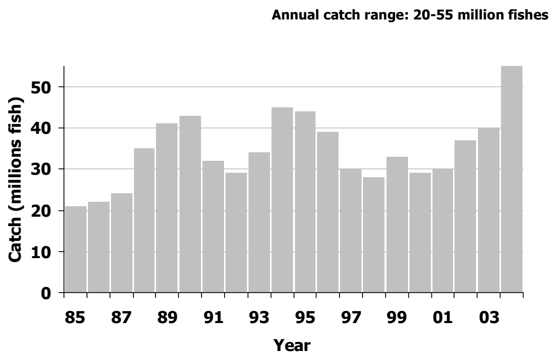
Haddock: Annual catch - 1985-2004



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Catch in numbers - 1985-2004 (millions)

Year	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Total
85	0	2	5	6	1	2	3	2	20
86	0	4	4	5	6	1	1	1	21
87	2	8	8	3	2	1	0	0	24
88	0	10	16	6	1	1	1	0	35
89	0	3	23	10	3	1	1	0	40
90	0	3	8	24	7	1	0	0	43
91	3	1	4	7	14	3	0	0	32
92	3	7	4	4	4	6	1	0	30
93	0	12	13	3	2	2	2	0	34
94	0	3	27	11	2	1	0	1	45
95	2	6	6	23	6	1	0	0	45
96	2	9	7	5	14	2	0	0	39
97	1	4	11	5	3	5	1	0	29
98	0	8	6	8	2	2	2	0	29
99	1	2	17	5	5	1	1	1	31
00	2	7	2	14	2	2	0	0	30
01	2	11	7	2	6	1	1	0	30
02	1	11	16	5	1	3	0	0	38
03	0	6	16	13	3	1	1	0	41
04	1	4	18	19	9	2	1	1	55

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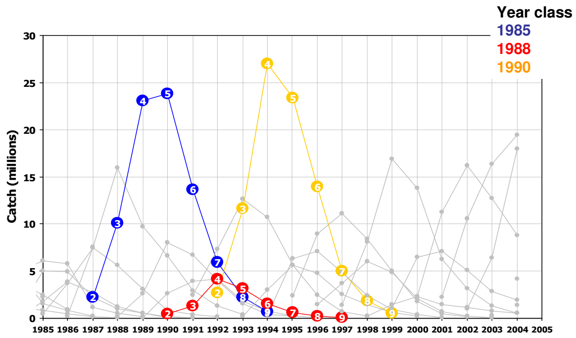
Catch by yearclasses



Note exponential decline in catches of older fish

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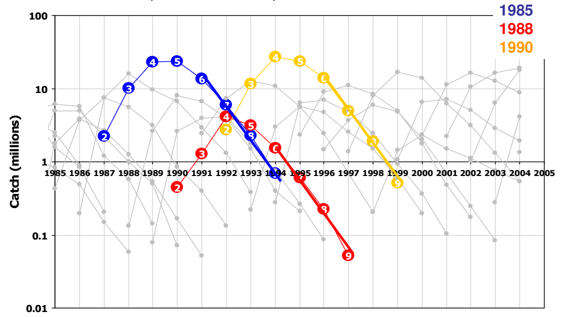
Catch by yearclasses on a log scale

The slope ≅ total mortality = Z



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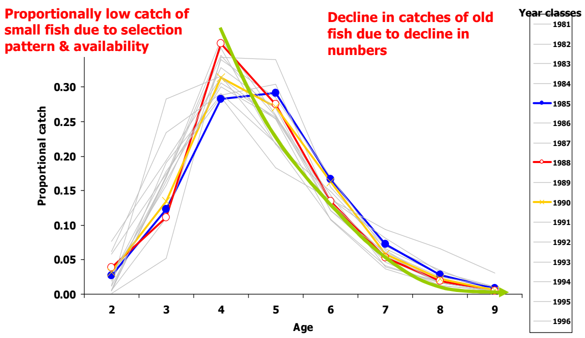
Proportional catch of different year classes by age



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Pattern observed

- The pattern observed in the catches:
  - Often have multiple cohorts in the fisheries at any given time
  - The contribution of different cohorts to the catches is quite variable
  - Variable year class size
  - Initial increase in numbers with size/age
  - Decline in numbers with size and age
- How do we extract information on the population and exploitation from such data?
  - Use mathematical models

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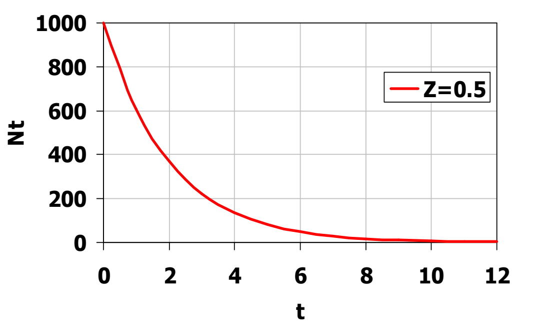
$N_t = N_0 e^{-Zt}$

The stock equation: Exponential population decline



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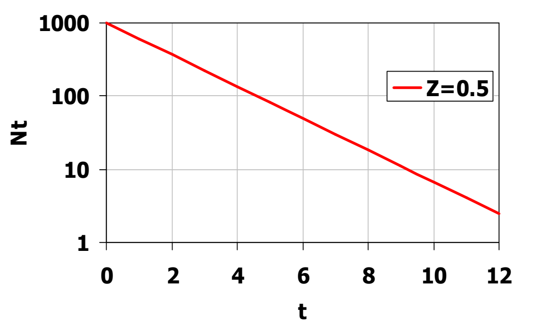
$\ln(N_t) = \ln(N_0) - Zt$

The stock equation: Logarithmic transformation



Russel equation modified 1

- Russel equation for <u>biomass:</u>

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

- Russel equation for <u>numbers</u>:

$$N_{t+1} = N_t + R_t - D_t - C_t$$

  - N_{t+1} stock size in numbers at start of time t+1
  - N_t stock size in numbers at start of time t
  - R_t number of recruits entering the stock at time t
  - D_t number of fish that died from t to t+1
  - C_t number of fish that are caught from t to t+1

    - What happened to the growth term??

Russel equation modified 2

- Russel equation for <u>numbers</u>:

$$N_{t+1} = N_t + R_t - D_t - C_t$$

- If we are considering <u>ONE</u> cohort only we can drop the recruitment term and have

$$N_{t+1} = N_t - D_t - C_t$$

$$\begin{pmatrix}\text{Numbers alive}\\ \text{at the beginning}\\ \text{of next time period}\end{pmatrix} = \begin{pmatrix}\text{Number alive}\\ \text{at the beginning}\\ \text{of this time period}\end{pmatrix} - \begin{pmatrix}\text{Numbers dying}\\ \text{naturally}\\ \text{this period}\end{pmatrix} - \begin{pmatrix}\text{Catch}\\ \text{this}\\ \text{period}\end{pmatrix}$$

- If we assume that the total number dying ($D_t + C_t$) are a proportion of those living we have:

$$N_{t+1} = N_t - mN_t = N_t(1 - m) = sN_t$$

  - m: proportion of fish that die during time interval t to t+1
  - s: proportion of fish that survive during time interval t to t+1
  - s+m = 1

Russel equation modified 3

- The equation:

$$N_{t+1} = N_t(1 - m) = N_t s$$

is an exponential model and the discrete version is:

$$N_{t+1} = N_t e^{-Z_t}$$

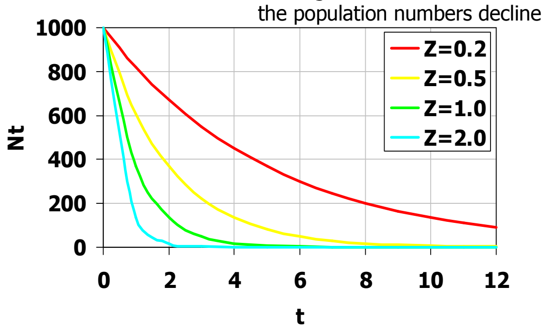
i.e. a negative exponential model

m & s: proportional coefficients (never bigger than one)

Z: instantaneous coefficient (can be bigger than one)

$N_t = N_0 e^{-Zt}$

The higher the Z the faster the population numbers decline



Cohort stock equation for each year

- Since mortality is not constant through out a cohorts life we work in smaller time steps:

$$N_{t+1} = N_t e^{-Z_t}$$

  - N_t: Number of fish at age time t
  - N_{t+1}: Number of fish at time t+1
  - Z_t: instantaneous mortality coefficient over time period t to t+1

Separation of fishing and natural mortality

- Since we are often interested in separating natural and fishing mortality we write:

$$N_{t+1} = N_t e^{-(M_t + F_t)}$$

  - M_t: natural mortality at time t
  - F_t: fishing mortality at time t

  - We will refer to this equation as the stock equation.

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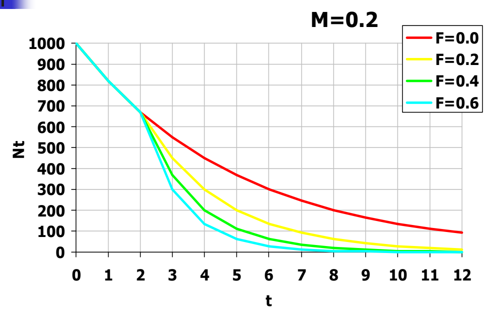
The effect of fishing

$$N_{t+1} = N_t e^{-(M_t + F_t)}$$



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Describing the catch 1

- The number of fish that die in each time interval is:

$$D_t = N_t - N_{t+1}$$

- Substituting with the stock equation we get:

$$D_t = N_t - N_t e^{-(M_t + F_t)}$$
$$= N_t \left(1 - e^{-(M_t + F_t)}\right)$$

$$\begin{pmatrix}\text{Numer of}\\ \text{fish that die}\\ \text{during the time}\end{pmatrix} = \begin{pmatrix}\text{Number of}\\ \text{fish alive in}\\ \text{the beginning}\end{pmatrix}\begin{pmatrix}\text{Proportion of}\\ \text{fish that die}\end{pmatrix}$$

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Describing the catch 2

- The number that die due to fishing mortality is the fraction (F_t/Z_t) of the number of fish that die, i.e.

$$C_t = \frac{F_t}{F_t + M_t}\left(1 - e^{-(F_t + M_t)}\right) N_t$$

$$\begin{pmatrix}\text{Numer of}\\ \text{fish fished}\\ \text{during the time}\end{pmatrix} = \begin{pmatrix}\text{Proportion of}\\ \text{fish that die}\\ \text{due to fishing}\end{pmatrix}\begin{pmatrix}\text{Proportion of}\\ \text{fish that die}\end{pmatrix}\begin{pmatrix}\text{Number of}\\ \text{fish alive in}\\ \text{the beginning}\end{pmatrix}$$

  - C_t: The number of fish caught over time t to t+1

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Describing the catch 3

- It can be shown that if we take the average* population size of the period t to t+1 (N_{bar}) the catch equation becomes:

$$C_t = F_t \bar{N}_t$$

  - The form of the stock equation is then however more complex

$$\bar{N}_t = N_i \left(\frac{1 - e^{-Z_i T_i}}{Z_i T_i}\right)$$

    - Where Ti is the time between t and t_i (often 1 year)

* More precisely: the integral

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Cohort analysis: Minimum measurements needed

- Used to estimate mortality (Z, F) and abundance (N)
  - Mortality (Z) can be estimated from both age and relative size frequency samples
    - survey or catch data by length
    - length based samples: Need to know growth (K and L_{inf})
  - For fishing mortality (F) we need to know M
    - F = Z – M
  - For abundance (N) we also need the total catch removed

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Age/size structured models

- Advantages
  - Populations do have age/size structure
  - Basic biological processes are age/size specific
    - Growth
    - Mortality
    - Fecundity
  - The process of fishing is age/size specific
  - Relatively simple to construct mathematically
  - Model assumption not as strict as in e.g. logistic models
- Disadvantages
  - Sample intensive
  - Data often not available
  - Mostly limited to areas where species diversity is low
  - Have to have knowledge of natural mortality
  - For long term management strategies have to make model assumptions about the relationship between stock and recruitment
  - Often not needed to address the question at hand