Mortality

Reading: Chapter 9 (9.3)

Exploring mortality:

- Continuous vs. discrete
- Natural mortality vs. fishing mortality
- Conditional mortality rates
- Type 1 vs. Type 2 fisheries
- Baranov’s Catch equation

Density-dependent mortality

- mechanisms

Mortality

The life history of a fish is a series of time intervals through which an individual survives several risks, including:

- being eaten (predation)
- starving (starvation)
- being harvested (fishing)
- dying from disease

- Risks rarely occur sequentially, but instead occur simultaneously
- And a fish can only die once (and once it’s dead, it’s dead!)

We therefore need to understand the dynamics of mortality
Many fishes demonstrate a Type III survivorship curve.

Exponential decay

\[ dN/dt = -ZN \]

- If we consider a time interval from \( t \) to \( t+1 \), the decline in numbers of fish over time usually follows a negative exponential model.

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If we integrate:

\[ dN/dt = -ZN \]

We obtain:

\[ N_t = N_0 e^{-Zt} \]

or

\[ N_{t+1} = N_t e^{-Z} \] (for a single time step)
The exponential decline in numbers over time is then expressed as:

\[ N_{t+1} = N_t e^{-Z} \]

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Now we have \( N_t = N_0 e^{-Zt} \) or \( N_{t+1} = N_t e^{-Z} \)

\( Z = \text{instantaneous rate of total mortality} \)

\( Z \) is calculated as the negative natural log of the slope of the plot of \( N_t \) vs. \( t \)

\[ \text{Slope} = e^{-Z} \]

\[ Z = -\ln(\text{slope}) \]
**Mortality**

The slope of $N_t$ vs. $t$ is also an estimate of the total survival rate ($S$)

$S = \frac{N_{t+1}}{N_t}$

So we can interchange $S$ and $e^{-Z}$

$N_{t+1} = N_t S \quad \rightarrow \quad N_{t+1} = N_t e^{-Z}$

Thus, $S = e^{-Z}$

and $Z = -\ln(S)$

where $0 \leq S \leq 1$ and $0 \leq Z \leq \infty$

Now, we can calculate the slope of a curve at any single point, but not along its entire length

But, we can linearize the curve by taking the natural log ($\ln$) of both sides of the equation:

$N_t = N_0 e^{-Zt}$

$\ln N_t = \ln N_0 - Zt$

Which is in our familiar straight line form ($Y = a + bX$)
Mortality

Estimating mortality from a linearized catch data (lnN vs. time/age) is referred to as: Catch Curve Analysis

Assumptions:
1. Equal natural mortality across ages
2. Equal vulnerability to capture
3. Constant recruitment across years

Mortality: F vs. M

The total instantaneous rate of mortality (Z) is the sum of mortalities from various sources (in fisheries we use 2 broad groups):

\[ Z = F + M \]

F = fishing mortality
M = natural mortality (many sources)

Mortality: F vs. M

![Graph showing mortality vs. age with different mortality rates]
**Mortality: F vs M**

We often think of F and M as competing sources of mortality

\[ Z = F + M \]

Since they are both acting at the same time, overall mortality will be less than the sum of independent sources of mortality

**Mortality: discrete vs. instantaneous**

Annual discrete rate of mortality (A)

\[ A = 1 - S \]
\[ S = 1 - A \]

Discrete survival rate = 1 - discrete mortality rate and vice versa

**Mortality: discrete vs. instantaneous**

Remember that S also = e^{-Z}, so 1-A = e^{-Z} and ln(S) = -Z

\[ \ln(\text{discrete survival rate}) = -(\text{instantaneous mortality rate}) \]
\[ \text{discrete survival rate} = e^{-\text{(instantaneous mortality rate)}} \]
Since \( S = 1 - A = e^{-Z} \)
\[ \text{discrete mortality rate} = 1 - e^{-\text{(instantaneous mortality rate)}} \]
Mortality: why use instantaneous rates?

They are additive

Similar to the APR on your savings account, the interest compounds

Future value = $P(1+r)^n$

If your APR is 5%, after two years your interest earned isn’t simply $5\% \times 2 = 10\%$

Example: $P = 100; r = 0.05; n = 2$
$FV = 110.25$
Actual Yield = 10.25%

Mortality: why use instantaneous rates?

$A = 20\%$ or 0.2
$A$ over 3 yrs $\neq 20 \times 3$, instead = 48.8%
Why?

$Z = -\ln (1-A) = -\ln (0.80) = 0.223$/yr
$0.223 \times 3 = 0.669$
then convert back to $A$

$A = 1 - e^{-Z} = 1 - e^{-0.669} = 0.488$
This is $A$ for a 3 year period
Mortality Rates
Glossary of symbols

**Discrete rates**
- A = total mortality rate
- S = total survival rate
- u = fishing mortality rate
- v = natural mortality rate

**Instantaneous rates**
- Z = total mortality rate
- F = fishing mortality rate
- M = natural mortality rate

- m = conditional fishing mortality rate
- n = conditional natural mortality rate

- C = total catch in numbers

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**Mortality: discrete vs. instantaneous**

TOTAL MORTALITY = HARVEST MORTALITY + NATURAL MORTALITY

**In discrete time**
- A = u + v

**In continuous time**
- Z = F + M

- A and Z = total mortality, but A ≠ Z
- u and F = fishing mortality, but u ≠ F
- v and M = natural mortality, but v ≠ M
Mortality: discrete vs. instantaneous

A includes conditional rates (rates in absence of all other risks) of fishing and natural mortality, minus their product.

\[ A = m + n - mn \]

remember: \[ A = 1 - e^{-Z} \]
so, \[ m = 1 - e^{-F} \] (conditional fishing mort.)
and \[ n = 1 - e^{-M} \] (conditional natural mort.)

Conditional rates (m and n) are discrete rates

Mortality: discrete vs. instantaneous

\[ A = m + n - mn = u + v \]

where u and v are the discrete rates of fishing (u) and natural (v) mortality

Therefore, m nearly always > u
n nearly always > v
Mortality

- Calculation of mortality rates will depend on the relationship between natural and fishing mortality

In a Type 1 fishery, natural mortality occurs at time of year separate from the period of harvest

Very short fishing season (with no natural mortality) Example: Alaskan king crab

Mortality

Type 1 fishery = no overlap in time between natural and fishing mortality

\[ u = m = 1 - e^{-F} \]

- discrete fishing mort \((u)\) = conditional fishing mort \((m)\)

then, \[ v = n \times (1 - u) \]

- discrete natural mort \((v)\) = conditional natural mort \((n)\) \times (1 – percent of fish harvested, not available to die naturally)

Mortality

In a Type 2 fishery (most common), natural and fishing mortality occur simultaneously, so \( u \neq m \)

\[ m = 1 - e^{-F} \]
\[ n = 1 - e^{-M} \]

\[ u = FA/Z \]
\[ v = MA/Z \]
Mortality

In a Type 2 fishery:

\[
\begin{align*}
\frac{Z}{A} &= \frac{F}{u} = \frac{M}{v}
\end{align*}
\]

- Using these equations we can convert from discrete time to continuous time and *vice versa*.

Mortality

\[
\begin{align*}
u &= \frac{F \cdot A}{Z} \quad v &= \frac{M \cdot A}{Z}
\end{align*}
\]

Proof:

\[
u + v = \frac{F \cdot A}{Z} + \frac{M \cdot A}{Z} = \frac{(F + M) \cdot A}{Z} = A
\]

Mortality: Baranov’s Catch equation

Average abundance during the interval is:

\[
\overline{N} = \frac{NA}{Z}
\]

Where \( N_{\text{bar}} \) = average population abundance and \( NA \) = total deaths.
Mortality: Baranov’s Catch equation

Total deaths =

\[ NA = Z\bar{N} \]

Total natural deaths =

\[ N_v = M\bar{N} \]

Total fishing deaths (or catch) =

\[ Nu = C = F\bar{N} \]

From this we get Baranov’s catch equation

\[ C = F\bar{N} = \frac{FNA}{Z} \]

Remember that:

\[ \bar{N} = \frac{NA}{Z} \]
Mortality: Baranov's Catch equation

Baranov's catch equation

\[ C = F\bar{N} = \frac{FNA}{Z} \]

Valuable because we can examine the effect of changing the rate of exploitation (F) on the total mortality rate (A)

Example:
- \( N_0=1000; F=0.4, M=0.2; S=0.549; A=0.451 \)
- The proportion of deaths due to fishing = \( 0.4/0.6 = 0.67 \)
- Catch = \( 1000 \times 0.451 \times 0.67 = 301 \)
- Natural deaths = \( 1000 \times 0.451 \times 0.33 = 150 \)
- Total deaths = 301 + 150 = 451
- \( N_{bar} = (1000 \times 0.451)/0.6 = 752 \)
- So Catch also = \( 0.4 \times 752 = 301 \)

Estimating M

- M is essential to assess a fish stock
- Hard to measure, no direct evidence like harvest
- Need to understand timing as well as magnitude
- Factors responsible often operate synergistically
Estimating M

So, how do we estimate M?

- Borrow from closely related species
- Predictive models relating M to von Bert parameters (K, L∞)
- Pauly (1980) related M to K, L∞, and temp
- Hoenig (1983) related M to max age, needs to be lightly exploited population
- Lorenzen (1996) related M to body weight
- Predictive models = good 1st guess

Estimating M

So, how do we estimate M from data?

- Catch curve analysis for non-harvested life stages
- Regress Z vs. F or effort (f)
- Predation models
- Tagging studies
Mortality: density-dependence

Fish populations produce more progeny than necessary to replace themselves. Why?

- Strong influence of variable environment on survival

But, populations can neither grow unbounded, nor can they continually produce less progeny than necessary

- Population stability is a function of both density-dependent and -independent processes

Mortality: density-dependence

- True population regulation requires density-dependence

- Processes (growth, survival, reproduction, habitat use) are density dependent if rates change with density

- Density dependent processes are compensatory if they result in slowed pop. growth at high densities and fast pop. growth at low densities
**Mortality: density-dependence**

If response of fish populations to variation in density is linear, then mortality is *density-independent*

- Mortality is thus a constant proportion and is **not** a function of density

**Mortality: density-dependence**

If response of fish populations to variation in density is *non-linear*, then mortality is *density-dependent*

- Mortality rate is a function of density (i.e., birth and death rates not constant proportions)

**Mortality: density-dependence**

- More likely in natural populations...density-independent until **threshold** density
Mortality: density-dependence

Density-dependent responses are commonly observed in fish populations:

Individual-level processes

- Fecundity (egg production)
- Growth rate
- Age or size at maturation

Population-level processes

- Predation

Empirical examples

Japanese anchovy
- Proportion mature↑, spawning frequency↓, batch fecundity↑ at low density

Orange roughy
- Proportion spawning↑, fecundity↑ at low density

North Sea plaice
- Strong density-dependent mortality due to functional response of shrimp predators

North Atlantic haddock
- High adult abundance = small juvenile size and small size of later adults, ↓recruitment

Figure 8-3. Density-dependent reductions in daily growth for tilapia in aquaculture ponds. Redrawn from data in Diets et al. (1991) and unpublished data.
Mortality: density-dependence

John Gulland once suggested that density-dependent processes affecting natural mortality can, for the most part, be ignored! Why?

- Maybe due to difficulty and frustration in measuring their cumulative effects and the inability of traditional stock assessment models to deal with compensation

Mortality: density-dependence

But, ignoring density-dependent changes in mortality is a double-edged sword...

- Biologist interested in conservation can ignore it, since compensatory density dependence that is unaccounted for causes impacts of harvest to be overstated.
- Harvester, however, requires that all possible compensatory mechanisms are accounted for in order to maximize yield

Mortality: density-dependent processes

- Dens-dep growth easiest to measure and incorporate into population models
- Dens-dep predation can be compensatory (predation rate ↑ at high prey density)
Mortality: density-dependent processes

- Dens-dep growth easiest to measure and incorporate into population models
- Dens-dep predation can be compensatory (predation rate ↑ at high prey density)
- Dens-dep predation can also be depensatory (predation rate ↑ at low prey density)

Mortality: depensation

mechanism?

Figure 8-4. Density-dependent increases in mortality for brown trout stocked into a stream (data from LeCren 1962).

Figure 8-6. Depensatory (declining) mortality with increasing density for age-1 perch from Oneida Lake. Redrawn from Forney (1974).
Mortality: depensation

- One potential mechanism is:
  
  **Predation** with constant number of predators:
  - As prey density ↓, %mortality ↑

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Mortality: density-dependent processes

**Compensatory** predation can result from:

- Increase in abundance of predators
- Concentration of predators in an area of high prey density

For example, concentration of bluefish on menhaden schools or mako sharks on bluefish schools

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Mortality: density-dependent processes

**Depensatory** predation caused by:

- Constant number and feeding rate of predators
- Predator preference

For example, in commercial fisheries, low stock levels increase prices and stimulate increased search effort
Mortality: density-dependent processes

Examples of compensatory mortality:

- Egg superimposition in salmon
- Territoriality by reef fish achieves same compensatory purpose (excludes potential spawners)
- Cannibalism is a very strong form of compensatory mortality
  - Intra- vs. inter-year class cannibalism

Potential sources of density-dependent mortality

- Life history processes affecting mortality rate that could be characterized as density-dependent

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<th>Density-Indep.</th>
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CPUE remains high due to aggregation of fish.