

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

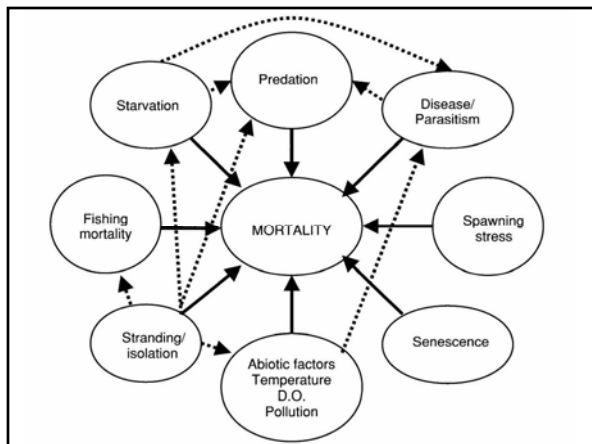
Mortality

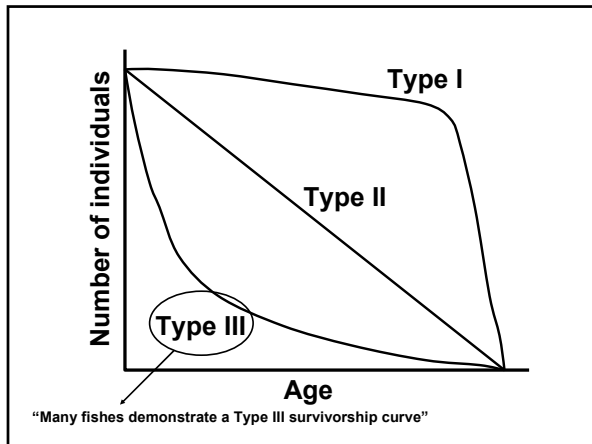
The life history of a fish is a series of time intervals through which an individual survives several risks, including:

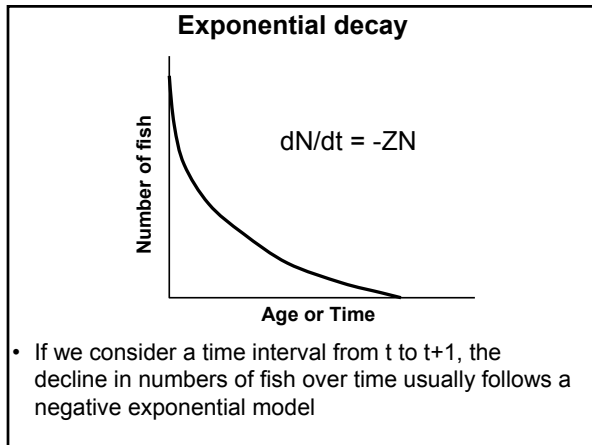
- > being eaten (predation)
- > starving (starvation)
- > being harvested (fishing)
- > dying from disease

- ❖ 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







Mortality

If we integrate:

$$dN/dt = -ZN$$

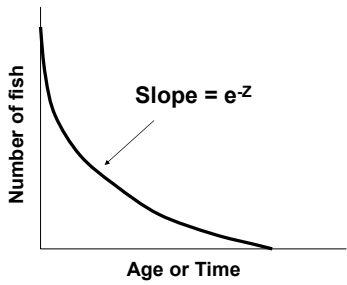
We obtain:

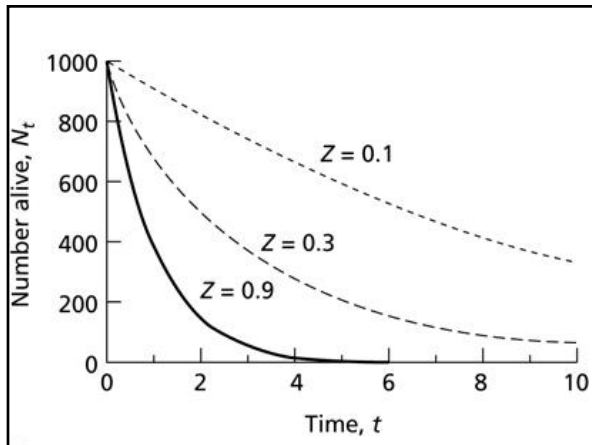
$$N_t = N_0 e^{-Zt}$$

or

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

The exponential decline in numbers over time is then expressed as: $N_{t+1} = N_t e^{-Z}$





Mortality

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

Z = instantaneous rate of total mortality

Z is calculated as the negative logarithm 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)**

= the number alive at the end of time t divided by the number alive at the start of time t .

$$S = N_{t+1}/N_t$$

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

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

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

$$\text{and } Z = -\ln(S)$$

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

Mortality

Now, calculating the slope of a curve is difficult

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

$$N_t = N_0 e^{-Zt}$$



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

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



Mortality

Estimating mortality from a linearized data (lnN vs. time) 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

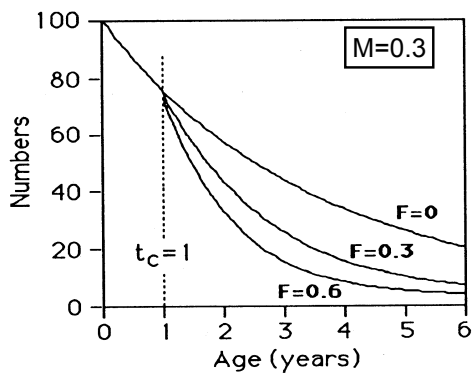
The total instantaneous rate of mortality (Z) is the sum of mortalities from various sources (in fisheries we use 2 broad groups):

$$Z = F + M$$

F = fishing mortality

M = natural mortality (many sources)

Mortality: F vs. M



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: F vs. M

Rewriting the general mortality equation we get:

$$N_t = N_0 e^{-(F+M)t}$$

$$N_t = N_0 e^{-Ft} e^{-Mt}$$

$$S_T = S_F S_M$$

Total survival rate is the product of the survival rates from each individual risk of mortality (fishing and natural)

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

Mortality: why use instantaneous rates?

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

$$\text{Future value} = P(1+r)^n$$

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

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%

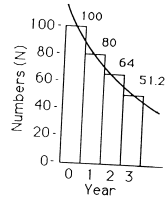
Why?

$Z = -\ln(1-A) = -\ln(0.80) = 0.223/\text{yr}$

$0.223 \times 3 = 0.669$

then convert back to A

$A = 1 - e^{-Z} = 1 - e^{-0.669} = 0.488$



Mortality Rates

Glossary of symbols

Discrete rates

A = total mortality rate

S = total survival rate

u = fishing mortality rate

v = natural mortality rate

m = conditional fishing mortality rate

n = conditional natural mortality rate

C = total catch in numbers

Instantaneous rates

Z = total mortality rate

F = fishing mortality rate

M = natural mortality rate

Mortality: discrete vs. instantaneous

$$\begin{aligned} &\text{TOTAL MORTALITY} \\ &= \\ &\text{HARVEST MORTALITY} \\ &+ \\ &\text{NATURAL MORTALITY} \end{aligned}$$

In discrete time $A = u + v$
 In continuous time $Z = F + M$

Mortality: discrete vs. instantaneous

In discrete time $A = u + v$
In continuous time $Z = F + M$

A and Z = total mortality, but $A \neq Z$
u and F = fishing mortality, but $u \neq F$
v and M = natural mortality, but $v \neq M$

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, $v = n * (1 - u)$

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

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

$$m = 1 - e^{-F}$$

$$n = 1 - e^{-M}$$

$$u = FA/Z$$

$$v = MA/Z$$

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In a Type 2 fishery:

$$\frac{Z}{A} = \frac{F}{u} = \frac{M}{v}$$

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

Mortality

$$u = \frac{F \cdot A}{Z} \quad v = \frac{M \cdot A}{Z}$$

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:

$$\bar{N} = \frac{NA}{Z}$$

Where N_{bar} = average population abundance and NA = total deaths

Mortality: Baranov's Catch equation

Total deaths =

$$NA = Z\bar{N}$$

Mortality: Baranov's Catch equation

Total natural deaths =

$$Nv = M\bar{N}$$

Total fishing deaths (or catch) =

$$Nu = F\bar{N}$$

Mortality: Baranov's Catch equation

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)

Mortality: Baranov's Catch equation

➤ 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 = $1000 \cdot 0.451 \cdot 0.67 = 301$
- Natural deaths = $1000 \cdot 0.451 \cdot 0.33 = 150$
- Total deaths = $301 + 150 = 451$
- $\bar{N} = (1000 \cdot 0.451) / 0.6 = 752$
- So Catch also = $0.4 \cdot 752 = 301$

$$C = F\bar{N} = \frac{FNA}{Z}$$

Estimating M

- ❖ M is essential for most stock assessments
- ❖ Hard to measure, no direct evidence like harvest
- ❖ Need to understand timing as well as magnitude
- ❖ Little information on factors responsible

Estimating M

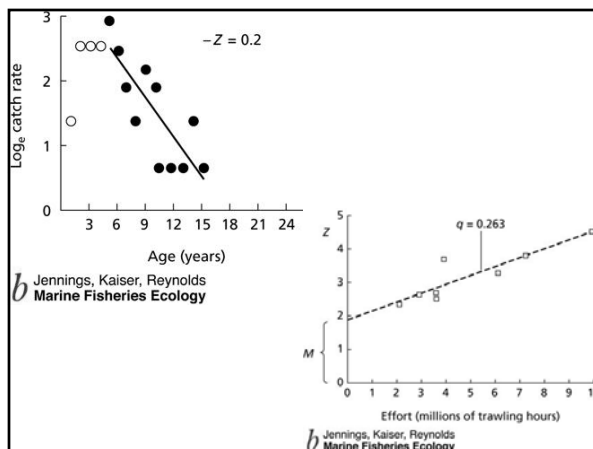
So, how do we estimate M?

- Borrow from closely related species
- Predictive models relating M to von Bert parameters (K, L_{∞})
- Pauly (1980) related M to K, L_{∞} , and temp
- Gunderson (1980) related M to gonad wgt/body wgt index
- Hoenig (1983) related M to max age, needs to be lightly exploited population
- 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



The evolution of $M = .2$

$M = ?$ $? \rightarrow ? \rightarrow ? \rightarrow ? \rightarrow ? \rightarrow ? \rightarrow ?$ EUREKA !

b Jennings, Kaiser, Reynolds
Marine Fisheries Ecology

Mortality: density-dependence

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

- > Strong influence of variable environmental 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

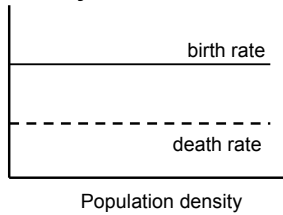
Mortality: density-dependence

- > 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

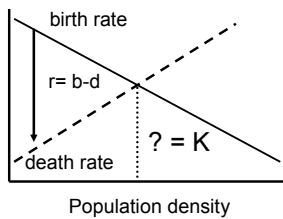
- Mortality is thus a constant proportion and is not a function of density



Mortality: density-dependence

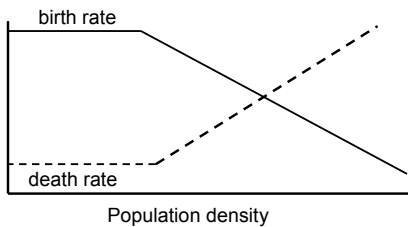
If response of fish populations to variation in density is non-linear, then mortality is density-dependent

- 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
- Growth rate
- Age or size at maturation

Population-level processes

- Predation

density-dependent growth

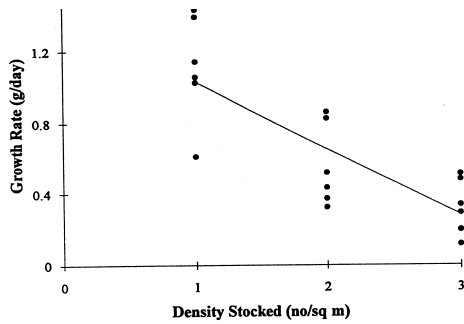


Figure 8-3. Density-dependent reductions in daily growth for tilapia in aquaculture ponds. Redrawn from data in Diana et al. (1991) and unpublished data.

Empirical examples

Japanese anchovy

- Proportion mature \uparrow , spawning frequency \downarrow , batch fecundity \uparrow at low density

Orange roughy

- Proportion spawning \uparrow , fecundity \uparrow 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, \downarrow recruitment

Mortality: density-dependence

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

- Maybe due to difficulty and frustration in measuring it and the inability of traditional stock assessment models to deal with it

Mortality: density-dependence

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

- Biologist interested in conservation can ignore it, since compensatory dens-dep mortality 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 \uparrow at high prey density)

Mortality: density-dependent processes

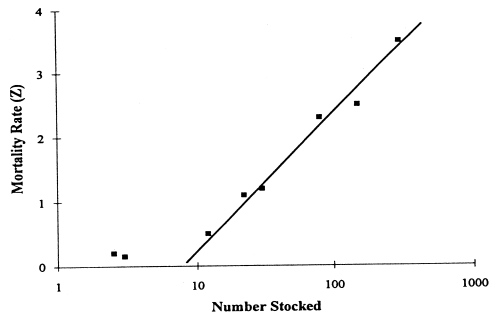


Figure 8-4. Density-dependent increases in mortality for brown trout stocked into a stream (data from LeCren 1962).

Mortality: density-dependent processes

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

Mortality: depensation

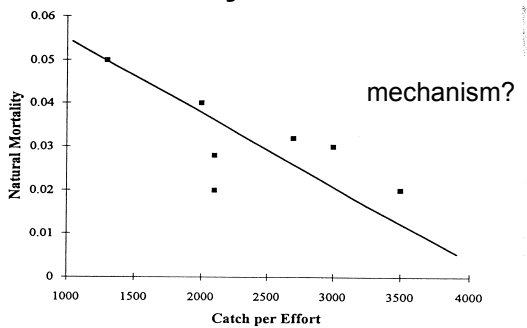


Figure 8-6. Depensatory (declining) mortality with increasing density for age-0 perch from Oneida Lake. Redrawn from Forney (1974).

Mortality: depensation

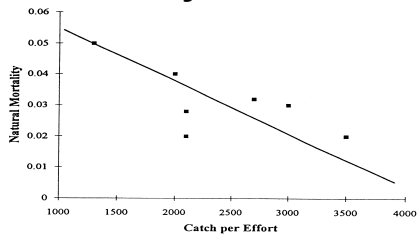


Figure 8-6. Depensatory (declining) mortality with increasing density for age-1 perch from Oneida Lake. Redrawn from Forney (1974).

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

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

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

Potential sources of density-dependent mortality

PROCESS	MORTALITY TYPE		
	Compensatory	Depensatory	Density-Indep.
Cannibalism	X	?	
Predation	X	X	X
Egg Superim	X		
Growth	X		X
Maturation	X	?	X

