4. ESTIMATION OF MORTALITY RATES

Chapter 3 dealt with growth, the positive aspects in the dynamics of a fish stock. This chapter deals with its negative counterpart, the death process or mortality (cf. Fig. 1.3.1.1). The growth was described with the aid of a model and a number of parameters, and so is the death process going to be. The key parameters used when describing death are called the "*mortality rates*".

This chapter deals with the definition of mortality, and it introduces some of the methods to estimate mortality rates which require input data from random samples representative of a certain part of the population, namely the exploited part. These methods do not require estimates of total catch from the population. On the other hand, they do not provide estimates of population size. Methods dealing with those aspects will be introduced in Chapter 5.

The easiest way to describe the change in numbers in a fish stock is often to follow the fate of fish spawned at approximately the same time, a cohort. We shall consider the mortality of a cohort as composed of the mortality caused by fishing and that due to all other causes lumped together as the "*natural mortality*". The latter covers events such as predation, disease and deaths due to old age.

4.1 THE CONCEPT OF A COHORT AND SOME BASIC NOTATION

A "*cohort*" is a batch of fish all of approximately the same age and belonging to the same stock (cf. Section 1.3.1). The concepts "day of recruitment of a cohort" and "recruitment" were introduced in Section 1.6. In all the following derivations we assume (with Beverton and Holt, 1957) that a cohort consists of "average fish" only. This means that all fish of a cohort are assumed to have the same age at a given time so that they all attain the "*recruitment age*", Tr, at the same time (cf. Section 1.6). In Chapter 3 we similarly used the average length of a cohort to describe growth. In the context of mortality rates we are interested in the number of survivors from a cohort as a function of time (cf. Fig. 1.3.1.1A).

The symbol "N(t)" is used to designate the "*number of survivors from a cohort attaining age t*". The age is usually measured in units of years. Thus, N(Tr) is the "*number of recruits*" to the fishery. Often the symbol "R" is used to designate the "*recruitment*", R = N(Tr). The actual choice of Tr is not critical, since all calculations are based on relative ages (age differences). In many applications we do not need to define the recruitment age. Tr is the minimum age at which the fish can enter the fishery, i.e. become liable to encounter with fishing gears (Beverton and Holt, 1957). The age at which they actually enter the fishery, Tc, is dependent on the mesh size. Tc is called the "*age at first capture*" and marks the beginning of the "*exploited phase*".

Fig. 4.1.1 illustrates the basic features of cohort dynamics. Due to mortality (fishing or natural causes) there is a continuous decrease in the number of survivors. At birth the cohort has age zero. From age 0 to Tr the cohort is in the "*pre-recruitment phase*". In the present context we are not concerned about what happens before age Tr. After age Tr the fish may be caught if a suitable small meshed gear is used. At age Tc the fish start to be caught with the mesh size actually in use. By definition we must have $Tr \leq Tc$.

In some applications we consider several cohorts at a time as illustrated by Fig. 4.1.2, where a situation with two cohorts per year during a period of two years is depicted. Fig. 4.1.2 is a parallel to the multi cohort case for growth which was illustrated in Fig. 3.2.1.1. If more than one cohort is considered at a time, the symbol N(t) is not sufficient, and some index to indicate the cohort is then required. However, in the following only one cohort at a time is usually considered, so the short symbol N(t) will do.

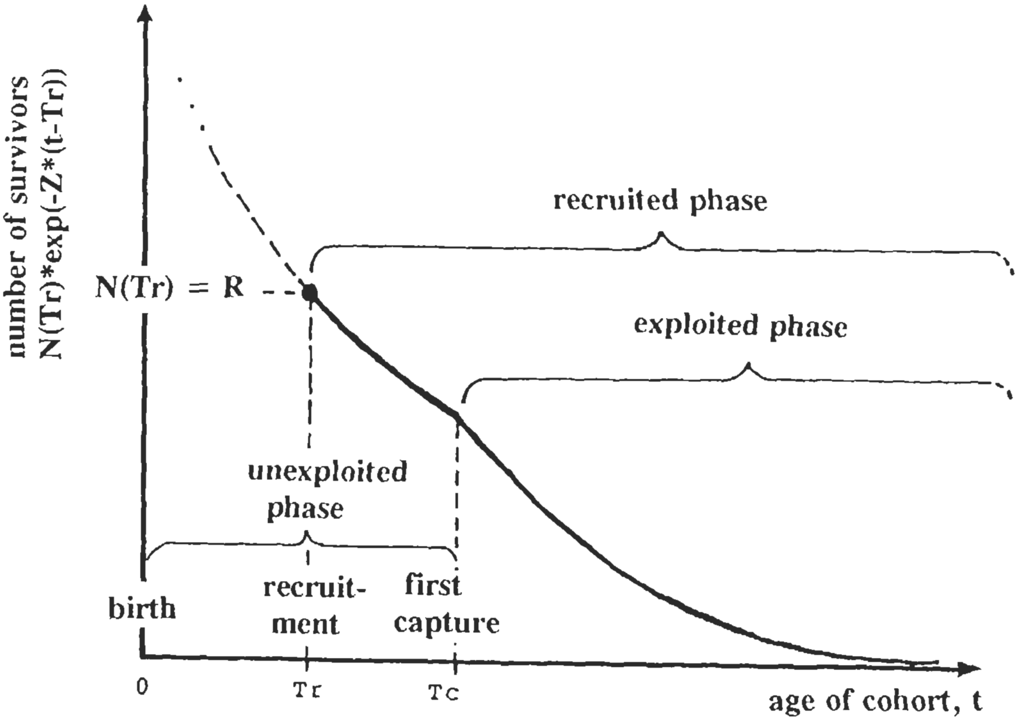


Fig. 4.1.1 Basic features of cohort dynamics

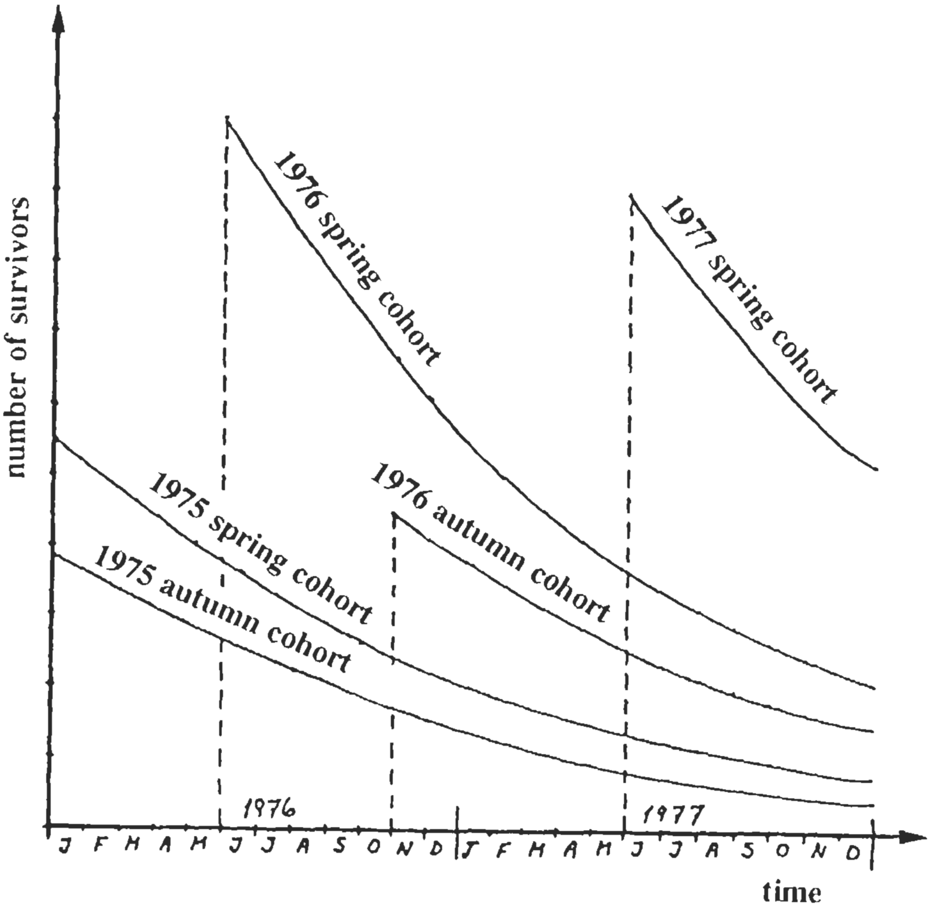


Fig. 4.1.2 Illustration of the situation with more than one cohort (compare Fig. 3.2.1.1)

As an example, consider the number of survivors at age t = 0.5 year, N(0.5), and the number of survivors one day later, N(0.50274) (1 day = 1/365 year = 0.00274 year). The number of specimens lost during that day is: N(0.5) - N(0.50274)

To designate the change in numbers during a relatively short time period (say, 1 day) we use the symbol ΔN:

$$\Delta N(0.5) = N(0.50274) - N(0.5)$$

Note that ΔN is negative because it represents a loss from the cohort. The rate of change in numbers is written:

$$\Delta N(t)/\Delta t$$

where Δt is the length of the time period (1 day in this case).

Suppose N(0.5) = 1000 and N(0.50274) = 997, then

$$\frac{\Delta N(0.5)}{\Delta t} = \frac{997-1000}{0.00274} = -1095 \text{ per year}$$

Obviously, the rate of change in numbers per year, ΔN/Δt, depends on the number of survivors, N. The more survivors there are, the more will die. The high number of deaths, 1095 per year, more than N(0.5), is due to the fact that it is calculated as if we started every day with N(0.5) = 1000 fish. ΔN/Δt is not dependent on Δt, as a reduction of Δt will reduce ΔN accordingly. Thus it is natural to assume ΔN/Δt to be proportional to N:

$$\frac{\Delta N(t)}{\Delta t} = -Z*N(t) \qquad (4.2.1)$$

where Z is the coefficient of proportionality.

For the example above: $\frac{\Delta N(0.5)}{\Delta t} = -Z*N(0.5)$ or $\frac{-3}{0.00274} = -1.095*1000$,

Z, becomes 1.095 per year. Z is called the "*instantaneous rate of total mortality*", the "*total mortality coefficient*" or simply the "*total mortality rate*". The unit of Z is "per year", or in general "per time unit". If Z remains constant throughout the life of the cohort it can be shown that Eq. 4.2.1 is mathematically equivalent to:

$$N(t) = N(Tr)*\exp[-Z*(t-Tr)] \qquad (4.2.2)$$

Eq. 4.2.2 is called the "*exponential decay model*" and (together with the growth equation) it is a corner-stone of the theory of exploited fish stocks (cf. Baranov, 1918; Thompson and Bell, 1934; Fry, 1949 and Beverton and Holt, 1957). Fig. 4.2.1 shows a family of exponential decay curves for different Z-values. The higher the value of Z the faster the decrease in numbers and the lower the maximum age.

It is usually easier to understand the concept of mortality and survival if the number of survivors at a certain moment is expressed as a percentage of the original number. The following table gives the percentages of survivors after one and two years respectively of two populations subject to two different total mortality rates, $Z = 0.5$ and $Z = 2.0$.

total mortality rate Z	percentage of survivors *)	
	after 1 year 100*N(Tr+1)/N(Tr)	after 2 years 100*N(Tr+2)/N(Tr)
0.5 2.0	61% 14%	37% 2%

*) Percentage of survivors = 100*exp(-Z*(t-Tr))
and t-Tr = 1 and 2 respectively

It is evident that $Z = 2.0$ represents a high mortality rate and that a cohort subjected to such a high rate of total mortality will have been practically exterminated in two years.

Table 4.2.1 and Fig. 4.2.2 show an example of the exponential decay of a cohort subject to a constant total motality $Z = 1.5$ per year. In order to simplify the example, it has been assumed that the cohort starts to be caught as soon as it is recruited to the fishery, so that Tr = Tc (cf. Fig. 4.1.1).

The number of survivors of the cohort of 100000 recruits, N(Tr), at a given time, t, can be calculated from Eq. 4.2.2 as shown in the second column of Table 4.2.1, for example:

`N(Tr+0.4) = 100000*exp(-1.5*(Tr+0.4-Tr)) = 100000*exp(-0.6) = 54881`

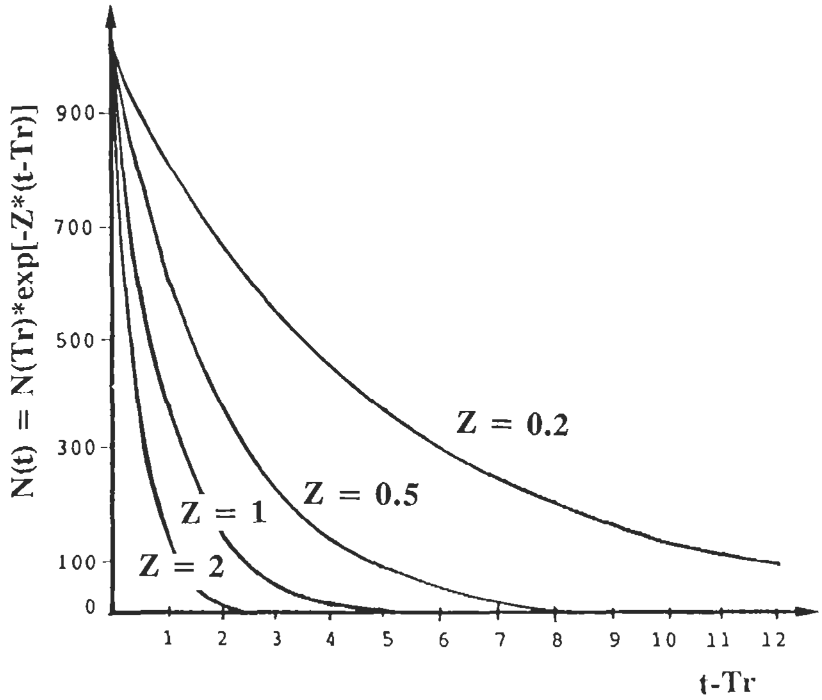


Fig. 4.2.1 **Exponential decay curves, for Z = 0.2, 0.5, 1 and 2 per year, with recruitment, N(Tr) = 1000 fish**

Table 4.2.1 **Exponential decay of a cohort with recruitment N(Tr) = 100000 and total (constant) mortality Z = 1.5 per year. It is demonstrated that the equation ΔN/Δt = -Z*N is fulfilled for various ages of the cohort (t). The corresponding graph is shown in Fig. 4.2.2. Δt is one day (= 1/365 year)**

age of cohort t years	number of survivors N(Tr)*exp(-Z*(t-Tr))	change in numbers during on day, ΔN	$-\frac{\Delta N}{\Delta t} * \frac{1}{N} = Z$
Tr	100000		
Tr+0.0+Δt	99590	-410	1.5
Tr+0.2	74081		
Tr+0.4	54881		
Tr+0.6	40657		
Tr+0.6+Δt	40490	-167	1.5
Tr+0.8	30119		
Tr+1.0	22313		
Tr+1.5	10540		
Tr+1.5+Δt	10497	-43	1.5
Tr+2.0	4978		
Tr+2.5	2351		
Tr+3.0	1111		
Tr+3.5	524.75		
Tr+3.5+Δt	522.60	-2.15	1.5
Tr+4.0	247.88		
Tr+5.0	55.31		
Tr+8.0	0.61		

As shown in the third column of Table 4.2.1, the decrease in numbers during one day changes during the life span of a cohort, because the total number of surviving fish becomes smaller every day. However, it can be demonstrated that Eq. 4.2.1

$$\frac{\Delta N(t)}{\Delta t} = -Z*N(t)$$

is fulfilled for different ages of the cohort, throughout its life span.

Ricker (1975) defines the "*survival rate*", S, as "the number of fish alive after a specified time interval, divided by the initial number, usually on a yearly basis".

The survival rate after one year is:

$$S = \frac{N(Tr+1)}{N(Tr)} = \frac{N(Tr)*\exp(-Z*(Tr+1-Tr))}{N(Tr)} = \exp(-Z)$$

Let t1 and t2 be two ages with t1 < t2. The total number of deaths during the time interval from t1 to t2 is

$$N(t1)-N(t2)$$

In Table 4.2.1 and Fig. 4.2.2, when t1 = Tr+0.4 and t2 = Tr+0.8 years, the number of deaths over this period is the difference between the number of survivors at t1, N(Tr+0.4) and t2, N(Tr+0.8): 54881-30119 = 24762.

Of these 24762 fish some died due to fishing and the rest died due to other causes (natural deaths).

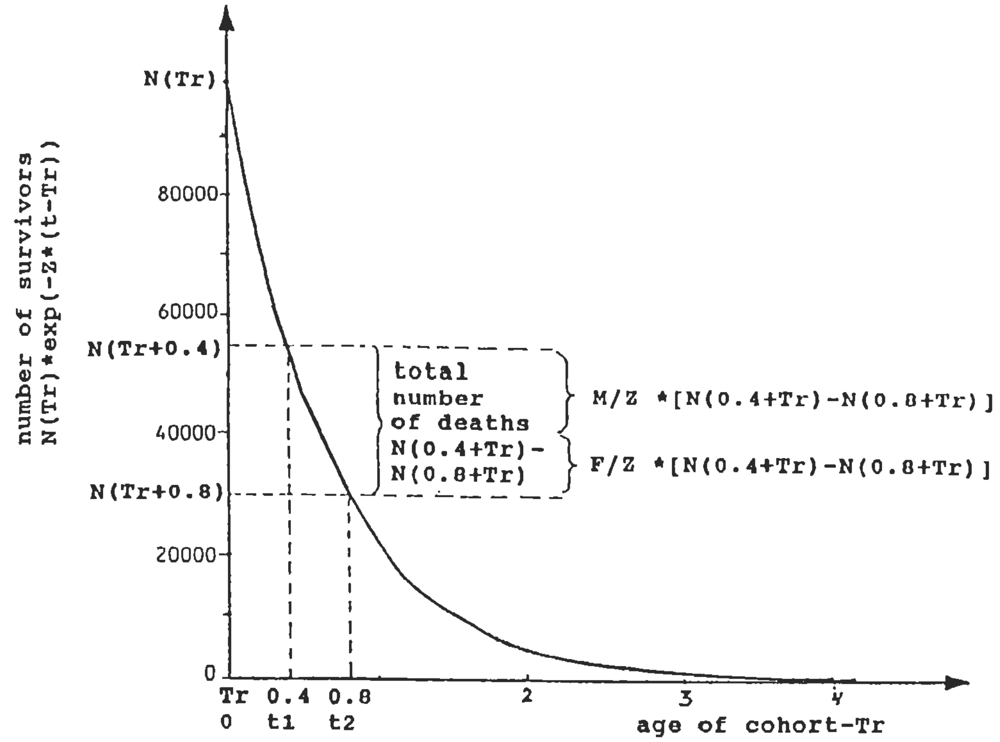


Fig. 4.2.2 **Exponential decay curve with N(Tr) = 100,000 recruits and Z = 1.5 (data from Table 4.2.1). Z remains constant for all ages, t**

Since we are interested in knowing the effect of fishing on fish stocks, we have to make a clear distinction between mortalities caused by fishing and those caused by other factors. Z is the coefficient of proportionality accounting for the total number of deaths. Similarly, the coefficient of proportionality for deaths due to fishing, called F, and due to natural mortality, M, can be assigned. F is called the "*fishing mortality coefficient*" and M is called the "*natural mortality coefficient*". These two coefficients can be added so that

$$Z = F+M \tag{4.2.3}$$

The total number of deaths can thus be split into a number dying due to fishing, the catch (C) and a number dying due to natural causes (D). The number dying due to fishing, the catch, during the time period from t1 to t2 is:

$$\boxed{C(t1,t2) = \frac{F}{Z}*[N(t1)-N(t2)] \qquad (4.2.4)}$$

Eq. 4.2.4 is called the "*catch equation*" (also called "*Baranov's equation*"), under the assumption of constant F and M (and thus constant Z) between ages t1 and t2 (Baranov, 1918). The fraction of deaths caused by fishing, F/Z, is called the "*exploitation rate*", E.

Correspondingly the number dying due to natural causes is:

$$D(t1,t2) = \frac{M}{Z}*[N(t1)-N(t2)] \tag{4.2.5}$$

Note that $N(t1)-N(t2) = C(t1,t2)+D(t1,t2)$ because $F/Z+M/Z = 1$.

In the example given above, based on Table 4.2.1 and Fig. 4.2.2, the total number of deaths was 24762, at a constant total mortality rate of Z = 1.5.

Now, suppose that between the ages t1 = Tr+0.4 and t2 = Tr+0.8 the fishing mortality coefficient was F = 0.6, and the natural mortality coefficient M = 0.9. The numbers of deaths due to fishing and due to natural causes can then be calculated as follows:

$$\begin{array}{llr}
C(Tr+0.4,Tr+0.8) & = (0.6/1.5)*(54881-30119) = & 9905 \\
D(Tr+0.4,Tr+0.8) & = (0.9/1.5)*(54881-30119) = & 14857 \\
\hline
N(Tr+0.4)-N(Tr+0.8) = & \qquad\qquad 54881-30119 \;\; = & 24762
\end{array}$$

In real life the mortalities usually vary with the age of the cohort. Small (young) fish are exposed to a greater natural mortality because more predators can eat them. On the other hand small fish may suffer less fishing mortality than large (old) fish because they either have not yet migrated to the fishing grounds or they escape through the meshes of the gear. However, if the time span from t1 to t2 is not too large it is considered a fair approximation to assume F and M to remain constant within this period.

The "catch equation" (Eq. 4.2.4) is one of the most important mathematical expressions in fisheries biology. For many applications, however, it is convenient to rearrange its terms, where the catch is related to the number present at the beginning of the time span, N(t1). To do so Eq. 4.2.2 is applied to N(t2):

$$N(t2) = N(Tr)*\exp[-Z*(t2-Tr)]$$ which is equivalent to

$$N(t2) = N(Tr)*\exp[-Z*(t1-Tr)]*\exp[-Z*(t2-t1)]$$ and to

$$N(t2) = N(t1)*\exp[-Z*(t2-t1)] \tag{4.2.6}$$

Inserting Eq. 4.2.6 into Eq. 4.2.4 gives:

$$\boxed{C(t1,t2) = N(t1)*\frac{F}{Z}*[1 - \exp(-Z*(t2-t1))] \qquad (4.2.7)}$$

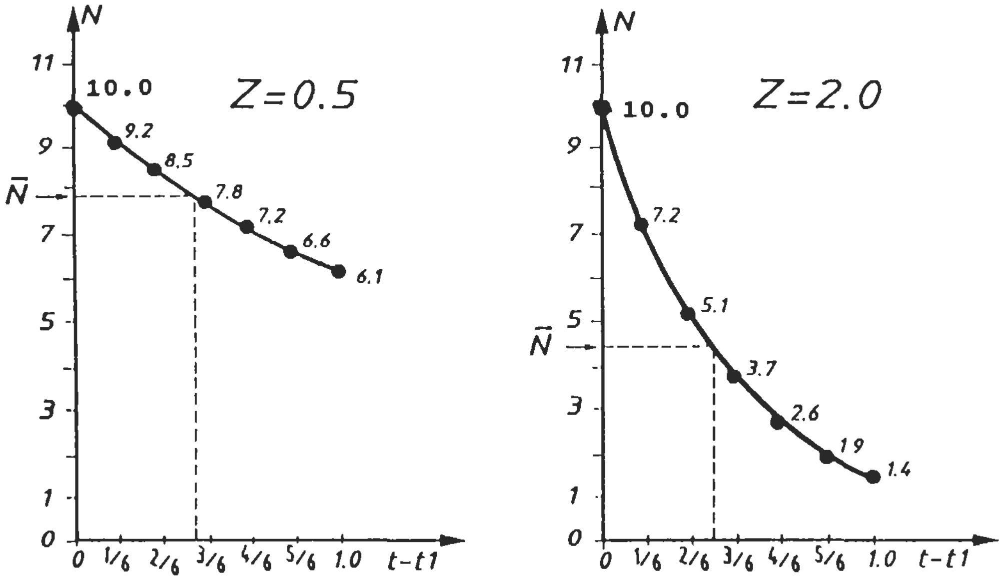
Eq. 4.2.7 is the most commonly used version of the catch equation. Another is convenient for special applications:

$$C(t1,t2) = (t2-t1)*F*\bar{N}(t1,t2) \tag{4.2.8}$$

where $\bar{N}(t1,t2)$ is the "*average number of survivors during the time period from t1 to t2*". To get consistency between Eq. 4.2.7 and Eq. 4.2.8 we must have:

$$\boxed{\bar{N}(t1,t2) = N(t1) * \frac{1 - \exp(-Z*(t2-t1))}{Z*(t2-t1)} \qquad (4.2.9)}$$

The mathematical proof of Eq. 4.2.9 is outside the scope of this manual. However, in Fig. 4.2.3 it is demonstrated that Eq. 4.2.9 conforms to the intuitive concept of "*average number*".



Z = 0.5	**Approximation: $\bar{N}$ = (10.0+9.2+8.5+7.8+7.2+6.6+6.1)/7 = 7.9** **Exact expression: $\bar{N}$ = 10.0*[1 - exp(-0.5)]/0.5 = 7.9**
Z = 2.0	**Approximation: $\bar{N}$ = (10.0+7.2+5.1+3.7+2.6+1.9+1.4)/7 = 4.5** **Exact expression: $\bar{N}$ = 10.0*[1 - exp(-2.0)]/2.0 = 4.3**

Fig. 4.2.3 **Illustration of Eq. 4.2.9:**
$\bar{N}$(t1,t2) = N(t1)*[1 - exp(-Z*(t2-t1))]/Z if t2-t1 = 1 year and Z = 0.5 or 2.0. Note that the larger the Z is the larger is the deviation between the approximation and the exact value

For the example used above (Fig. 4.2.2 and Table 4.2.1) we find:

$$\bar{N}(Tr+0.4,Tr+0.8) = 54881*\frac{1}{1.5*(0.8-0.4)}*[1 - \exp(-1.5*(0.8-0.4))] = 41269$$

$$C(Tr+0.4,Tr+0.8) = (0.8-0.4)*0.6*41,269 = 9905$$

which is also the answer we got from applying Eq. 4.2.4.

Eq. 4.2.8 has the advantage of being easy to interpret. It says that the number caught during the time period from t1 to t2 depends on:

1) The length of the time period
2) The fishing mortality
3) The average number of fish in the sea

and each of these statements is easy to accept.

If Δt = t2-t1 is very small, it can be shown that

$$C(t,t+\Delta t) = \Delta t*F*N(t) \qquad (4.2.10)$$

is approximately correct. If Δt is small the number of survivors will change very little during the period and N and N will be approximately equal. Eq. 4.2.10 then follows from Eq. 4.2.8. Eq. 4.2.10 is another version of the catch equation which is convenient for reasoning about the fishing mortality created by a single fishing operation, one trawl haul, for example, as will be demonstrated in Section 4.3.

Table 4.2.2 **Example of the dynamics of a cohort with different mortality rates during its life span**

start of period t1	end of period t2	natural mortality M	fishing mortality F	total mortality Z	comments
Tr	Tr+0.5	2.0	0	2.0	The cohort has been recruited to the fishing grounds but is not yet exploited. Exposed to great predation.
Tr+0.5	Tr+1.0	1.0	0.5	1.5	The cohort has migrated to fishing grounds, but 50% escape through the meshes. Predation mortality reduced.
Tr+1.0	Tr+7.0	0.5	1.0	1.5	The cohort under full exploitation (all fish are retained by the meshes.) Predation mortality further reduced.

To apply the exponential decay model (Eq. 4.2.2) and the catch equations, it is not necessary to assume that M, F and Z remain constant during the entire life span of the cohort. The life span may be divided into a number of shorter time periods within which mortalities are assumed to remain constant whereas they may vary from period to period. As an example, consider a cohort with a life span of seven years. The seven years may be divided into three periods with different mortality rates as shown in Table 4.2.2. Suppose that N(Tr) = 100000 then, using Eq. 4.2.6:

$$\begin{aligned}
N(t2) &= N(t1)*exp[-Z*(t2-t1)] \\
N(Tr+0.5) &= 100000*exp(-2.0*0.5) = 36788 \\
N(Tr+1.0) &= 36788*exp(-1,5*0.5) = 17377 \\
N(Tr+6.0) &= 17377*exp(-1.5*5.0) = 9.61 \\
N(Tr+7.0) &= 9.61*exp(-1.5*1.0) = 2.14 \\
N(Tr+8.0) &= 2.14*exp(-1.5*1.0) = 0.48
\end{aligned}$$

Thus, after seven years the cohort has died out. The number caught in the first period (from Tr to Tr+0.5) is zero because F = 0. The number caught in the second period (from Tr+0.5 to Tr+1.0) is (using Eq. 4.2.7):

$$C(Tr+0.5,Tr+1) = N(Tr+0.5)*\frac{F}{Z}*[1 - exp(-Z*0.5)] =$$

$$36788*\frac{0.5}{1.5}*[1 - exp(-1.5*0.5)] = 6470$$

Alternatively, Eq. 4.2.4 could have been used to calculate the number caught, C:

$$C(Tr+0.5,Tr+1.0) = \frac{F}{Z}*[N(Tr+0.5)-N(Tr+1.0)] = \frac{0.5}{1.5}*(36788-17377) = 6470$$

The third period is treated in a similar way. The results may be summarized as follows:

t1	t2	t2-t1	Z	N(t1)	F	C(t1,t2)
Tr	Tr+0.5	0.5	2.0	100000	0	0
Tr+0.5	Tr+1.0	0.5	1.5	36788	0.5	6470
Tr+1.0	Tr+7.0	6.0	1.5	17377	1.0	11583

In the subsequent sections various methods for the estimation of Z, F and M will be discussed.

(See **Exercise(s)** in Part 2.)

4.3 ESTIMATION OF Z FROM CATCH PER UNIT OF EFFORT DATA AND THE CONCEPT OF THE CATCHABILITY COEFFICIENT

The total mortality coefficient Z can be estimated when estimates of the number of fish in the cohort are available for two different moments during its exploited phase, t1 and t2. To calculate Z from such data Eq. 4.2.6 may be rewritten:

$$Z = \frac{1}{t2-t1} * \ln \frac{N(t1)}{N(t2)} \qquad (4.3.0.1)$$

For the estimation of Z with this formula, it is not necessary to know the absolute values of N(t1) and N(t2), only their ratio is required. Thus, if only an estimate of some quantity proportional to N(t) is available Eq. 4.3.0.1 can still be applied.

The catch per unit of effort (CPUE), for example, the numbers caught per trawl hour, is a quantity which can be assumed proportional to the number of fish in the sea, N. Intuitively, it is not hard to accept that if there are twice as many fish in the sea, twice as many will be caught per fishing operation. Let CPUE(t) be the number caught of a cohort per unit of effort at time t, then mathematically, the assumption is expressed:

$$CPUE(t) = q*N(t) \qquad (4.3.0.2)$$

where q is a parameter called the "*catchability coefficient*". The more efficient the gear is, the higher the value of q because q is a measure of the ability of the gear to catch fish.

CPUE data from research surveys

Assume that we have obtained CPUE data for a certain species with a research vessel during a trawl survey in different periods, t1 and t2, using the same gear without any modifications and thus with a constant catchability coefficient, q. In that case it follows from Eq. 4.3.0.2 that:

$$\frac{N(t1)}{N(t2)} = \frac{q*N(t1)}{q*N(t2)} = \frac{CPUE(t1)}{CPUE(t2)}$$

Inserting the above into Eq. 4.3.0.1 gives:

$$Z = \frac{1}{t2-t1} * \ln \frac{CPUE(t1)}{CPUE(t2)} \qquad (4.3.0.3)$$

Eq. 4.3.0.3 can be used to obtain an estimate of Z from time series of CPUE data from research surveys if age compositions have been obtained, either from reading ring structures in hard parts or from length-frequency analysis. When age data are available, the numbers of fish caught per unit of effort of each age group (cohort) can be determined directly. So when such numbers are available for a time series the numbers of a certain cohort present at different moments can be used in Eq. 4.3.0.3. Recall that the results of a length-frequency analysis, e.g. the Bhattacharya method (Section 3.4.1), also include estimates of the numbers of fish belonging to each cohort. If such numbers are available for the same cohort at different times, then the progressive decline in numbers represents the total mortality and Eq. 4.3.0.3 can be applied to obtain an estimate of Z. An illustration of this method is provided in Exercise 4.3, based on the data presented in Table 3.2.1.2.

CPUE data from commercial fisheries

Sometimes CPUE is derived as the average value over a longer period. This is the case when data are collected from a commercial fishery, where data are most often given on a quarterly or yearly basis. The model to be used is mathematically equivalent to Eq. 4.3.0.3, but conceptually it is slightly different. The parallel to Eq. 4.3.0.2 corresponding to a longer time period is:

$$\overline{CPUE}(t1,t2) = q*\bar{N}(t1,t2) \qquad (4.3.0.4)$$

This is the model relevant to data on commercial fisheries. The mean CPUE, $\overline{CPUE}(t1,t2)$, is usually calculated as the catch of a cohort during the period from t1 to t2 divided by the effort during that period. $\bar{N}(t1,t2)$ is the average number of survivors during the period from t1 to t2.

The theory behind Eqs. 4.3.0.2 and 4.3.0.4 will be used several times in the following chapters. We therefore will discuss the reasoning leading to these expressions.

Let f be the effort during one year (t2-t1 = 1). Eq. 4.3.0.4 may then be written:

$$C/f = q*\bar{N} \qquad (4.3.0.5)$$

When t2-t1 = 1 year we have a special version of Eq. 4.2.8:

$$C = F*\bar{N} \qquad (4.3.0.6)$$

Inserting Eq. 4.3.0.6 into Eq. 4.3.0.5 gives

$$F = q*f \qquad (4.3.0.7)$$

Eq. 4.3.0.7 can be shown to apply to any time period [t2,t1]. It is intuitively easy to accept. It says that the more effort (e.g. boat days) goes into the fishery, the higher will be the fishing mortality, or the fishing mortality is proportional to the effort. As Eq. 4.3.0.7 is so simple we could have taken that as the starting point for the derivation of Eq. 4.3.0.2 or Eq. 4.3.0.4.

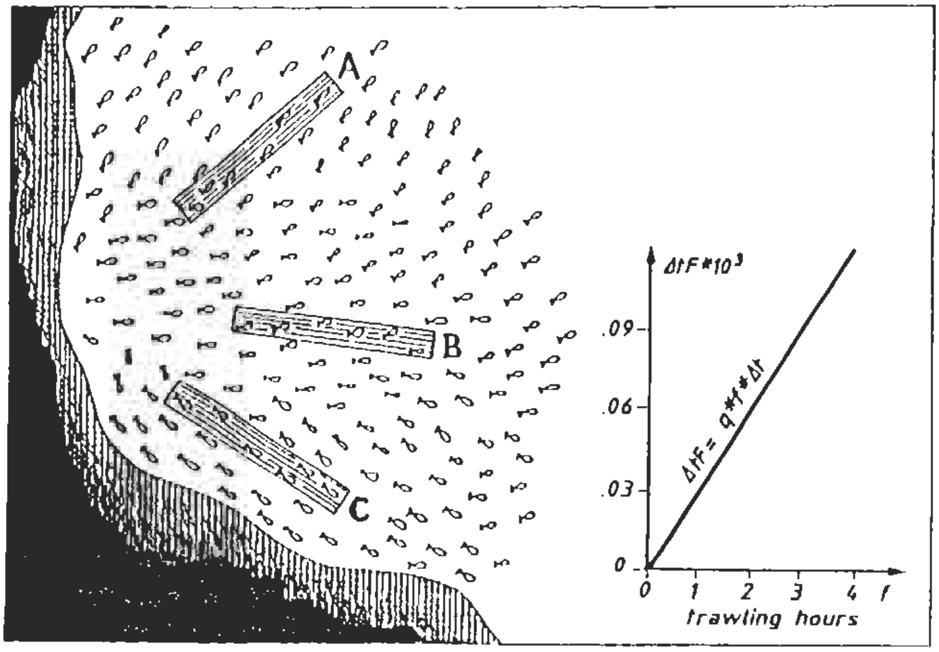


Fig. 4.3.0.1 **Illustration of Eq. 4.3.0.7: $F = q*f$, in the case of a catch, ΔC, which is small compared to the population, $\bar{N}$**

Fig. 4.3.0.1 illustrates Eq. 4.3.0.7 in a simplified system, consisting of 2 million fish uniformly distributed over a coastal area. The figure shows only 200 fish (1/10000 of the system).

The rectangle labelled "A" indicates the area swept by the trawl in, say, one hour = Δt. The catch in this short time, $\Delta C1$, consists of six fish. For simplicity, we assume that no fish dies due to natural causes during the towing period and that all fish encountered by the trawl are retained.

The catch, $\Delta C1$ created by a trawl haul must depend on the duration of the haul, Δt, and on the abundance of fish in the sea, N. The simplest model reflecting these intuitive assumptions is that of proportionality:

$$\Delta C1 = q*\Delta t*\bar{N} \qquad (4.3.0.8)$$

If we can accept this model for one haul there should be no problem in accepting it also for two hauls (say haul A and haul B):

$$\Delta C2 = q*\Delta t*f*\bar{N} \qquad (4.3.0.8')$$

where the effort, f = 2 hauls. Extending the model further with haul C to three hauls still gives no problems, because the abundance, N, will remain approximately constant as the three hauls will only remove a small part of the total population.

Combining Eq. 4.3.0.8′ with Eq. 4.2.10 gives (when ΔC is small):

$$\Delta C = q*\Delta t*f*\bar{N} = \Delta t*F*\bar{N} \qquad (4.3.0.8'')$$

which implies that $q*f = F$. Thus Eq. 4.3.0.7 is intuitively acceptable when ΔC is small.

It is less clear how effort and fishing mortality are related when we consider a longer time period during which the abundance cannot be assumed to remain approximately constant.

However, if a number of assumptions are met the equation also applies to cases where the catch, C, is large relative to the abundance, N, and where the time period, Δt, is long (say one year). In reality we often assume that these assumptions are being met.

The above reasoning applies in the case where the fish are uniformly distributed over the fishing grounds. However, this is rarely the case. For schooling fish (pelagics) the argument is simply wrong. When shooting the net at random the catch of a schooling fish species might be zero in nine out of ten tows, yet one tow might yield a very high catch. For demersal fish species the reasoning may be approximately correct although demersal fish also tend to aggregate in certain areas, which may or may not also be the fishable areas. The reasoning illustrated by Fig. 4.3.0.1 is behind the "*swept area method*" described in Chapter 13. That the reasoning is based on a relatively small catch and very few effort units, however, does not limit its applicability.

Now consider a system during a longer period. Fig. 4.3.0.2 shows such a (hypothetical) example, where in total more than half of the original number of fish are removed by fishing. Note that one unit of effort (one trawl haul) produces the same fishing mortality Δt*F, independent of the number of survivors (cf. Eqs. 4.2.10 and 4.3.0.8):

$$\Delta t*F \approx \frac{\Delta C(t)}{N(t)} \approx \frac{10}{64} \approx \frac{8}{54} \approx \frac{7}{46} \approx \frac{6}{39} \approx \frac{5}{33} \approx \frac{4}{28} \approx 0.15$$

where ≈ means "approximately equal to". One unit of effort (one trawl haul or tow) takes the same fraction from the stock. The fishing mortality is independent of the number of survivors, i.e., all hauls give equal Δt*F. Note also that Δt*F will remain constant only if the fish redistribute uniformly over the area after each removal by fishing.

Figs. 4.3.0.3A and B show an example in which Eq. 4.3.0.7, F = q*f, is not applicable, *viz.* when an increase in numbers produces also an increase of the area occupied by the stock. Then one effort unit (one trawl haul) would remove a smaller fraction of the stock and thus produce a smaller fishing mortality. Figs. 4.3.0.3A and C illustrate the way a stock must behave to conform to Eq. 4.3.0.7, namely that the area occupied remains constant for different stock numbers.

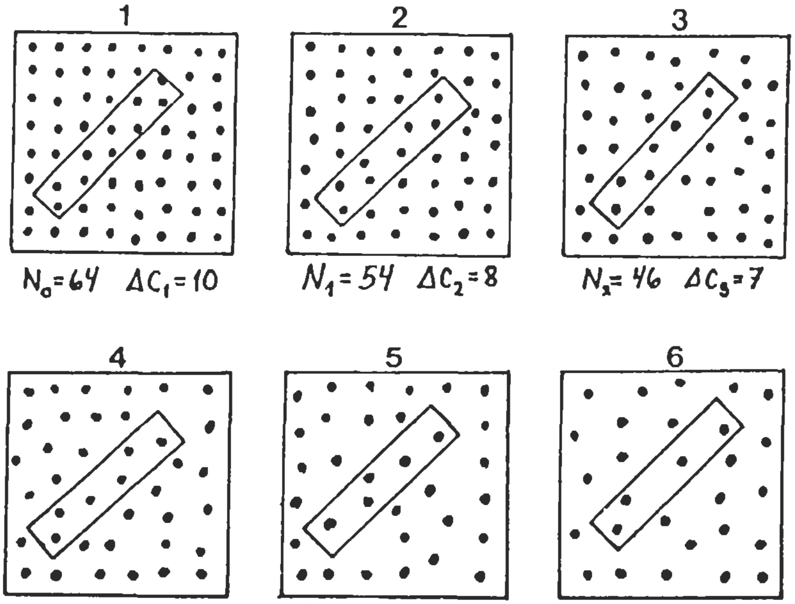


Fig. 4.3.0.2 **Illustration of Eq. 4.3.0.7, F = q*f, applied several times to a system during a longer time period. (For further explanation, see text)**

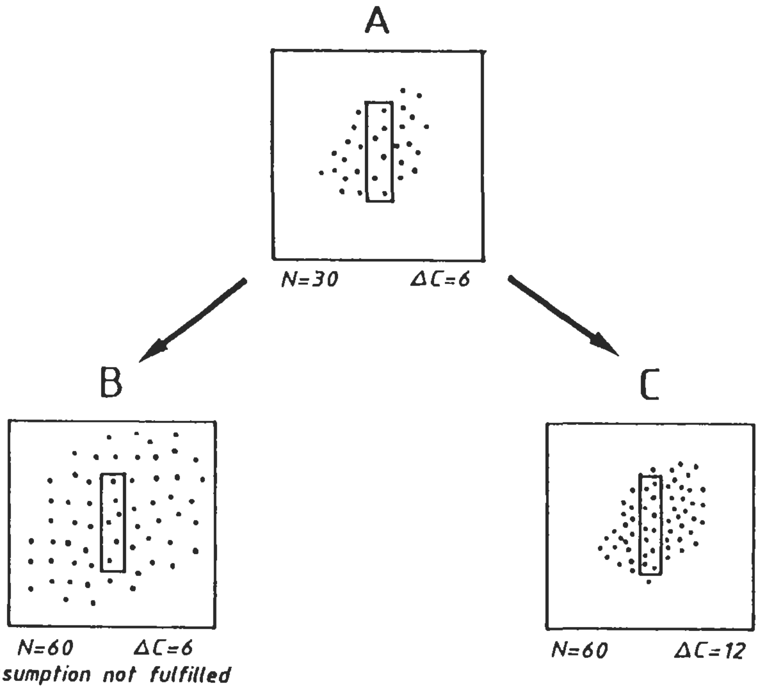


Fig. 4.3.0.3 **Illustration of one of the assumptions behind Eq. 4.3.0.7: F = q*f. (For further explanation, see text)**

4.3.1 Heincke's method

There are many ways of estimating Z from numbers in the catch. We shall describe one that dates as far back as 1913. Several other methods are described in Ricker (1975).

To introduce the method we start with a formula from common algebra:

$$\sum_{i=0}^{\infty} a^{i} = \frac{1}{1-a}, \text{ which is valid if } a < 1$$

If a = exp(-Z) then for Z > 0 it follows that a < 1 and consequently the following expression is valid:

$$\sum_{t=0}^{\infty} \exp(-Z*t) = \frac{1}{1-\exp(-Z)} \qquad (4.3.1.1)$$

When we multiply Eq. 4.3.1.1 by the same constant, N(0), on both sides of the equal sign we get:

$$\sum_{t=0}^{\infty} N(0)*\exp(-Z*t) = \frac{N(0)}{1-\exp(-Z)} \qquad (4.3.1.2)$$

Assuming total mortality, Z, to remain constant we have (cf. Eq. 4.2.6):

$N(t) = N(0)*\exp(-Z*t)$ and Eq. 4.3.1.2 can be written as

$$\sum_{t=0}^{\infty} N(t) = \frac{N(0)}{1-\exp(-Z)} \qquad (4.3.1.3)$$

It can be shown that Eq. 4.3.1.3 is equivalent to:

$$Z = -\ln \frac{N(1) + N(2) + N(3) + N(4) + \ldots\ldots}{N(0) + N(1) + N(2) + N(3) + N(4) + \ldots\ldots}$$

or

$$Z = -\ln\left[\sum_{t=1}^{\infty} N(t) / \sum_{t=0}^{\infty} N(t)\right] \qquad (4.3.1.4)$$

Eq. 4.3.1.4 is "*Heincke's formula*" (Heincke, 1913, in Ricker, 1975).

Eq. 4.3.1.4 should still hold if CPUE can be assumed proportional to the stock number so, replacing the N's by CPUE(t), Eq. 4.3.1.4 can be used in the form:

$$Z = -\ln \frac{\text{CPUE}(1) + \text{CPUE}(2) + \text{CPUE(age 3 and older)}}{\text{CPUE}(0) + \text{CPUE}(1) + \text{CPUE}(2) + \text{CPUE(age 3 and older)}}$$

where the CPUE of the oldest age groups is lumped. The reason for lumping them is that it is often so that age groups can be relatively easily separated for the first two or three (or perhaps four) age groups, whereas it is difficult to separate the older age groups (Ricker, 1975). Also it is sometimes neces-sary to exclude the youngest age group when it is not fully exploited by the fishery. In that case CPUE(0) should not be included in the denominator and CPUE(1) not in the numerator.

4.3.2 Robson and Chapman's method

Another method was introduced by Robson and Chapman, 1961 (in Ricker, 1975). They showed that the best estimate of Z from age composition data i.e. the numbers caught per age group, is:

$$Z = -\ln \frac{A}{B+A-1} \qquad (4.3.2.1)$$

where

$A = N(1)+2*N(2)+3*N(3)+ \ldots.$
$B = N(0)+N(1)+N(2)+N(3)+\ldots.$

The variance of the survival rate, S = exp(-Z), is

$$\text{VAR}(S) = S*\{(S-(A-1))/(B+A-2)\}$$

4.4 ESTIMATION OF Z FROM A LINEARIZED CATCH CURVE

A "*linearized catch curve*" is a graphical representation of the logarithms of numbers caught plotted against age.

The methods to be described in this section are essentially based on age composition data and as such they have been applied to temperate fish stocks. Because direct age reading is problematic for tropical fish stocks (see Section 3.2.1) the methods have to be converted into versions which take length composition data as input. This is possible when growth parameters are available so that lengths can be converted into ages by using the inverse von Bertalanffy equation (Eq. 3.3.3.3). The theoretical derivations start by using the age structured model, which will subsequently be converted into a corresponding length-structured model.

4.4.1 The constant parameter system

The linearized catch curve methods for estimating Z are based on the assumption of a "*constant parameter system*". This section is therefore used to explain this concept.

Consider, as an example, a fish stock during the period 1971-1975 with a life span of five years after recruitment. For simplicity we assume only one cohort per year, recruiting on

Table 4.4.1.1 **Illustration of the "constant parameter system" and the "variable parameter system". Note that the column of numbers in boxes consists of five different cohorts in the year 1971, whereas the diagonal of numbers in boxes consists entirely of the 1971 cohort. (For further explanation, see text)**

A: VARIABLE PARAMETER SYSTEM

age*/year t	COHORTS, number of survivors				
	1971 N(71,t)	1972 N(72,t)	1973 N(73,t)	1974 N(74,t)	1975 N(75,t)
0	$\boxed{2105}$	1111	9560	1869	1236
1	$\boxed{2575}$	$\boxed{736}$	405	3817	618
2	$\boxed{155}$	1097	$\boxed{281}$	142	1193
3	$\boxed{102}$	58	298	$\boxed{109}$	59
4	$\boxed{6}$	38	18	138	$\boxed{29}$

B: CONSTANT PARAMETER SYSTEM

age*/year t	COHORTS, number of survivors				
	1971 N(71,t)	1972 N(72,t)	1973 N(73,t)	1974 N(74,t)	1975 N(75,t)
0	$\boxed{2560}$	2560	2560	2560	2560
1	$\boxed{942}$	$\boxed{942}$	942	942	942
2	$\boxed{346}$	346	$\boxed{346}$	346	346
3	$\boxed{127}$	127	127	$\boxed{127}$	127
4	$\boxed{47}$	47	47	47	$\boxed{47}$

*) Age from recruitment data

1 January. The figures in Table 4.4.1.1A are the numbers of survivors per cohort and per age group on 1 January. Because we consider many cohorts simultaneously, an index to specify the year of recruitment of a cohort, y, is needed. N(y,t) is the number of survivors attaining age t from the cohort recruited at the start of year y-t. In this particular case t only takes the values t = 0,1,2,3 or 4. Note that a specific cohort can be followed diagonally across the Table. Every year the survivors of that cohort advance to a new age group. Each column, on the other hand, contains the numbers of survivors of five **different** cohorts on 1 January of a particular year.

Table 4.4.1.1A contains parts of nine different cohorts, of which only one is given for its entire life span (the 1971 cohort). It appears that recruitment, N(y,0), where y = 1971, 1972, 1973, 1974 and 1975, has varied from year to year. The 1971 cohort and the 1973 cohort are strong ones, whereas the 1972 cohort is a weak one ("strong" means that N(y,0) is considerably greater than the average recruitment).

Now, suppose that the recruitment, N(y,0), remains constant every year, as is the case in Table 4.4.1.1B. Assume further that also F and M remain constant, then the number of survivors and the numbers caught would be the same for all cohorts. An inspection of Table B shows that in this case the number of survivors per year during the life span of a cohort equals the number of survivors within a particular year for each age group. Thus, in the case of constant recruitment it does not matter whether we consider one cohort over its entire life span, or if we consider all the different cohorts (the entire stock) in one particular year. (The major part of the theory of Beverton and Holt (1957) is based on the assumption of constant recruitment.)

We know for sure that the assumption of a constant parameter system is never strictly fulfilled in real life. However, we are often in a situation which forces us to make assumptions, which are known to be crude approximations to reality. It often happens that only by making such assumptions we are able to carry out an analysis of available data, and it is better to do a crude analysis than none at all.

We speak of a "*pseudo-cohort*" when working with data from one year assuming these to resemble those of a cohort during its life span. Thus, the numbers 2105, 2575, 155, 102 and 6 in Table 4.4.1.1A form a pseudo-cohort, whereas the numbers 2105, 736, 281, 109 and 29 form a real cohort.

4.4.2 The linearized catch curve equation

Suppose that an estimate of the age composition of the catch during a year is available, i.e. pairs of observations:

age interval	numbers caught
t1-t2	C(t1,t2)
t2-t3	C(t2,t3)
t3-t4	C(t3,t4)
.	.
.	.

To develop a method to estimate Z from such data, the starting point is the catch equation (Eq. 4.2.7):

$$C(t1,t2) = N(t1)*\frac{F}{Z}*[1 - \exp(-Z*(t2-t1))]$$

Although the time interval from t1 to t2 is the first interval it will also be used in the following as the symbol for the general time interval, i.e. t2-t3, t3-t4, etc. Eq. 4.2.7 is not linear in t1 (or t2), so some transformation is required to make the analysis a linear regression (cf. Section 2.6). The first step is to replace N(t1) using Eq. 4.2.2 which gives:

$$C(t1,t2) = N(Tr)*\exp[-Z*(t1-Tr)]*\frac{F}{Z}*[1 - \exp(-Z*(t2-t1))]$$

The second step is to take logarithms on both sides. After rearranging the terms we get:

$$\ln C(t1,t2) = \ln N(Tr) + \ln \frac{F}{Z} + Z*Tr - Z*t1 + \ln[1 - \exp(-Z*(t2-t1))]$$

At least t1 now appears in one linear term (namely: -Z*t1). The terms ln N(Tr) + ln (F/Z) + Z*Tr form a constant, as N(Tr), Tr, F and Z are assumed to remain constant. To simplify the notation, this constant is named "d", and the equation then reads:

$$\ln C(t1,t2) = d - Z*t1 + \ln[1 - \exp(-Z*(t2-t1))] \qquad (4.4.2.1)$$

A linear expression in t1 has been obtained, except for the last term. Various methods suggest different ways of dealing with this term.

The first uses of this "*linearized catch curve equation*" date back to Edser (1908), Heincke (1913) and Baranov (1918) as reviewed in Ricker (1975). In the remaining part of Section 4.4 we shall discuss various special applications of Eq. 4.4.2.1.

4.4.3 The linearized catch curve based on age composition data

One of the methods commonly applied in temperate waters to estimate total mortality is the "*linearized catch curve method with constant time intervals*", which has been reviewed in Beverton and Holt (1956), Chapman and Robson (1960), Robson and Chapman (1961) and Ricker (1975).

If t2-t1 in Eq. 4.4.2.1 remains constant (e.g. when age groups are considered, so that t2-t1 = t3-t2 = t4-t3 = ... = 1 year), the non-linear term becomes a constant, which can be included in the intercept term. Thus, if the constant g is defined:

$$g = d + \ln[1 - \exp(-Z*(t2-t1))]$$

then Eq. 4.4.2.1 reads:

$$\ln C(t1,t2) = g - Z*t \text{ or}$$

$$\ln C(t,t+\Delta t) = g - Z*t \qquad (4.4.3.1)$$

Eq. 4.4.3.1 is the "*linearized catch curve equation with constant time intervals*", where the slope is -Z.

Example 13: Catch curve with constant time intervals, North Sea whiting

Table 4.4.3.1 shows an example of a linearized catch curve analysis based on age composition data. Most often such examples come from temperate waters where direct age reading is possible and where spawning is confined to a short period, once per year. This is also the case in this example which deals with whiting (*Merlangius merlangus*) caught in the North Sea.

Table 4.4.3.1 gives the annual age composition of whiting catches during the period 1974-1980 (from ICES, 1981a). The figures in Table 4.4.3.1 are numbers caught per year per age group (cohort), where

$C(y,t,t+1)$ = number caught in year y of age between t and t+1 years (in millions). For instance C(1976,3,4) = 159

For each year the total mortality, Z, (bottom row of Table 4.4.3.1) has been calculated using Eq. 4.4.3.1. These are linear regressions where x = age, y = ln C(y,t,t+1) and b = -Z. Thus, recruitment and other parameters are assumed to have remained constant from 1974 to 1980.

Table 4.4.3.1 Linearized catch curve analysis based on age composition data. Number caught per year by age group (in millions caught per year) of North Sea whiting. (From ICES, 1981a, see Fig. 4.4.3.1)

year y	1974	1975	1976	1977	1978	1979	1980	average	
age t	C(y,t,t+1)							1974-80	
0	599	239	424	664	685	478	330	488	not used
1	678	860	431	1004	418	607	288	612	
2	1097	390	1071	532	335	464	323	601	
3	275	298	159	269	203	211	243	237	used in analysis
4	40	54	75	32	69	86	80	62.3	
5	6	9	13	18	8	25	31	15.7	
6	1	8	3	5	5	3	8	4.7	
7+	(6)	(0)	(1)	(0)	(1)	(1)	(1)	1.4	
Z	1.88	1.16	1.36	1.25	1.33	1.40	1.12	1.28	

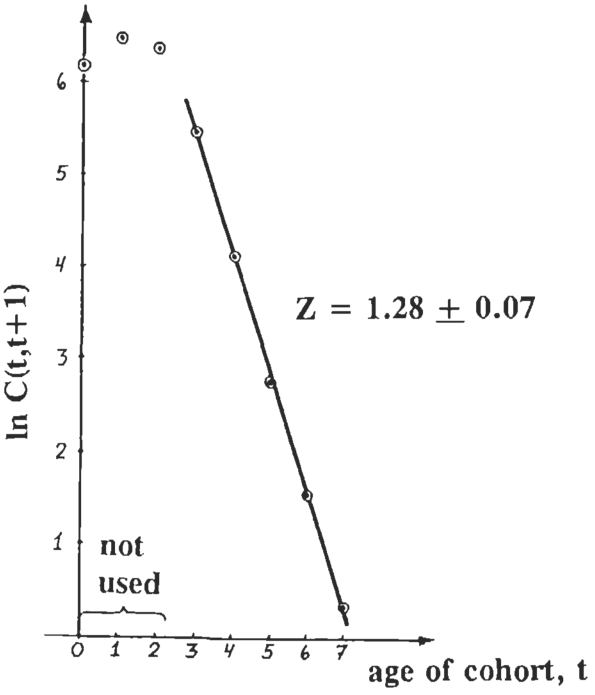


Fig. 4.4.3.1 **Linearized catch curve based on average age composition of North Sea whiting catches 1974-80 (ICES, 1981a)**

However, we could also calculate an overall estimate of Z for the seven year period by using the average number caught per age group, as shown in the last column of Table 4.4.3.1. By doing so we (more or less) circumvent the problem of assuming parameters to remain constant, as e.g. variation in recruitment is levelled out in the averaging process. Note that in this particular case the assumption of constant recruitment is not crucial. Except for the year 1974 the annual estimates of Z do not deviate much from the overall estimate.

Fig. 4.4.3.1 shows the graph for the estimation of Z based on the average age composition. As appears from Table 4.4.3.1 data for the three first age groups have been excluded from all the regression analyses, since they do not conform to the straight line (see Fig. 4.4.3.1). The reason is that these age groups are not under full exploitation. The fishing mortality is lower than that of the larger (older) fish because the fish of age groups 0 to 2 are so small that they escape through the meshes of the trawl-net. (The major part of the North Sea whiting are caught by trawls with codend mesh sizes from 70 mm to 110 mm.) Another reason for expecting a reduced fishing mortality on the small fish is that all of these may not yet have recruited to the fishing grounds and are still on the nursery grounds.

Thus total mortality, $Z = M+F$, does not remain constant for all age groups although this was one of the assumptions behind the linearized catch curve analysis. One way to circumvent the problem is to exclude those age groups we suspect not to be under full exploitation, as was done in this example. Which age groups to exclude is a somewhat subjective choice. Usually the points systematically deviating from the straight line are excluded. However, it is hard to give a general rule to decide when this deviation is sufficiently large to justify the exclusion of the point. As a rule of thumb: whenever you are in doubt about a point, exclude it. In the case of Fig. 4.4.3.1 it is easy to make the choice since the five points used provide a very convincing fit to the model.

In the estimations of Z's for each year (bottom row of Table 4.4.3.1) age group 7+ has been excluded as well (indicated by brackets). The reason is that the number of specimens of age 7 or more (7+ groups) in each year has been estimated from small samples only. Because few fish survive to age 7 these estimates are subject to great uncertainty. However, for the overall estimate of Z the age group 7+ has been used, because in this case the samples cover seven years and the sample size is accordingly larger.

Using the procedure described in Section 2.4 the 95% confidence limits of Z can be calculated:

$$Z = -\text{slope} = -b = 1.284 \qquad sy = 2.0316 \qquad sx = 1.5811$$

variance of the slope:

$$sb^2 = \frac{1}{n-2}*((sy/sx)^2 - b^2) = \frac{1}{5-2}*((2.0316/1.5811)^2 - 1.284^2) = 0.0005$$

$$sb = \sqrt{0.0005} = 0.0227$$

$sb*t_{5-2} = 0.0227*3.18 = 0.07$, so that the confidence interval becomes

$$[1.21,1.35] \quad \text{or:} \quad Z = 1.28 \pm 0.07$$

With the data of Table 4.4.3.1 the calculations could have been made on a cohort basis as well. Exercise 4.4.3 deals with this aspect.

(See **Exercise(s)** in Part 2.)

4.4.4 The linearized catch curve based on age compositions with variable time intervals

Let us return to the general linearized catch curve model (Eq. 4.4.2.1)

$$\ln C(t1,t2) = d - Z*t1 + \ln[1 - \exp(-Z*(t2-t1))]$$

In case the time intervals t2-t1, t3-t2, t4-t3, ... are not constant the non-linear term, ln[1 - exp(-Z*(t2-t1))] takes different values for different values of the time interval. As will appear from Section 4.4.5 this case is often relevant to tropical fish stocks. Two alternative ways of getting rid of the non-linear term have been suggested.

Cumulated catch curve equation

Jones and van Zalinge (1981) suggested to let t2 take a very high value (actually t2 = ∞ (infinity)). With t2 very large, the term exp(-Z*(t2-t1)) would be close to zero, consequently ln(1 - exp(-Z*(t2-t1))) = ln 1 = 0. Thus, if C(t,∞) designates all fish caught of age t and older, a linear relationship is achieved by

$$\ln C(t,\infty) = d - Z*t \qquad (4.4.4.1)$$

C(t,∞) is called the "*cumulated catch*", and Eq. 4.4.4.1 the "*cumulated catch curve equation*".

Linearized catch curve equation with variable time intervals

Van Sickle (1977) suggested a different approach which was further developed by Pauly (1983a). It is based on the observation that for small values of x, (x < 1.0):

$\ln[1 - \exp(-x)] = \ln(x) - x/2$ (approximately)

If Z*(t2-t1) is small it follows that approximately:

$$\ln[1 - \exp(-Z*(t2-t1))] = \ln[Z*(t2-t1)] - Z*(t2-t1)/2$$

Inserting this into Eq. 4.4.2.1 and rearranging terms gives:

$$\ln \frac{C(t1,t2)}{t2-t1} = d + \ln Z - Z*t1 - Z*(t2-t1)/2$$

Because t2-t1 must be small, it is called Δt. To simplify notation the constant c = d+ln Z is introduced. Then the equation reads:

$$\ln \frac{C(t,t+\Delta t)}{\Delta t} = c - Z*(t+\Delta t/2) \qquad (4.4.4.2)$$

which is linear in the interval midpoint, (t+Δt/2). Eq. 4.4.4.2 is the so-called "*linearized catch curve equation with variable time intervals*". Note that only the slope has significance to the present analysis. The intercept is not used.

The name of the equation might lead to the misunderstanding that the method is applicable only when data for total catches are available. However, Eq. 4.4.4.2 can still be used even if only the percentage composition of the catches is known, because from these we get the absolute catches by multiplying all the percentages by a constant. A multiplication of all the values for C in Eq. 4.4.4.2 by a constant, K, will change the intercept, c, but not the slope, Z, since

$$\ln \frac{K*C(t,t+\Delta t)}{\Delta t} = c - Z*(t+\Delta t/2)$$ is equivalent to:

$$\ln \frac{C(t,t+\Delta t)}{\Delta t} = c1 - Z*(t+\Delta t/2)$$ where

$$c1 = c - \ln K$$

Thus, if you have a sample from a fish population (for instance from a research survey or a market), but the total catch is unknown, you can use Eq. 4.4.4.2. Therefore the linearized catch curve analysis is often used for survey data, whereas cohort analysis (introduced in Chapter 5) is used for the analysis of total catch data. It should be noted that the example used in the next section to illustrate a linearized catch curve analysis based on length composition data (see Table 4.4.5.1) is a sample of only 3816 fish, which was not raised to the total catch.

4.4.5 The linearized catch curve based on length composition data

The method to be described here does not, as Eq. 4.4.3.1, assume a direct age reading but uses the von Bertalanffy growth equation to convert length into age. This model is discussed in Pauly (1983a, 1984a and b). It is often referred to as the "*length-converted catch curve*" or the "*linearized length-converted catch curve*".

To make the catch curve usable for length data it is in principle necessary to replace in Eq. 4.4.4.2 the t's (ages) by L's (lengths):

$$\ln \frac{C(t,t+\Delta t)}{\Delta t} = c - Z*(t+\Delta t/2)$$

However, what is actually done is to convert length data into age data, using the inverse von Bertalanffy growth equation (Eq. 3.3.3.2)

$$t(L) = t_0 - \frac{1}{K}*\ln(1 - \frac{L}{L_\infty})$$

The conversion of lengths into ages is fairly complex, because the amount of time needed for a fish to grow through a given length interval increases continuously as it gets older. Fig. 4.4.5.1 shows the transformation of length groups into age intervals. The growth curve used is the average growth curve for the entire cohort, from which large individual deviations can occur. These deviations are relatively small for small fish, but may be relatively large for large fish. In other words: the larger the fish, the longer time it will take to grow through a length group and therefore the relationship between length and age becomes more inaccurate for large fish. For example, it takes less than half a year for *Upeneus vittatus* to grow from 4 to 8 cm, but much more than a year to grow from 16 to 20 cm.

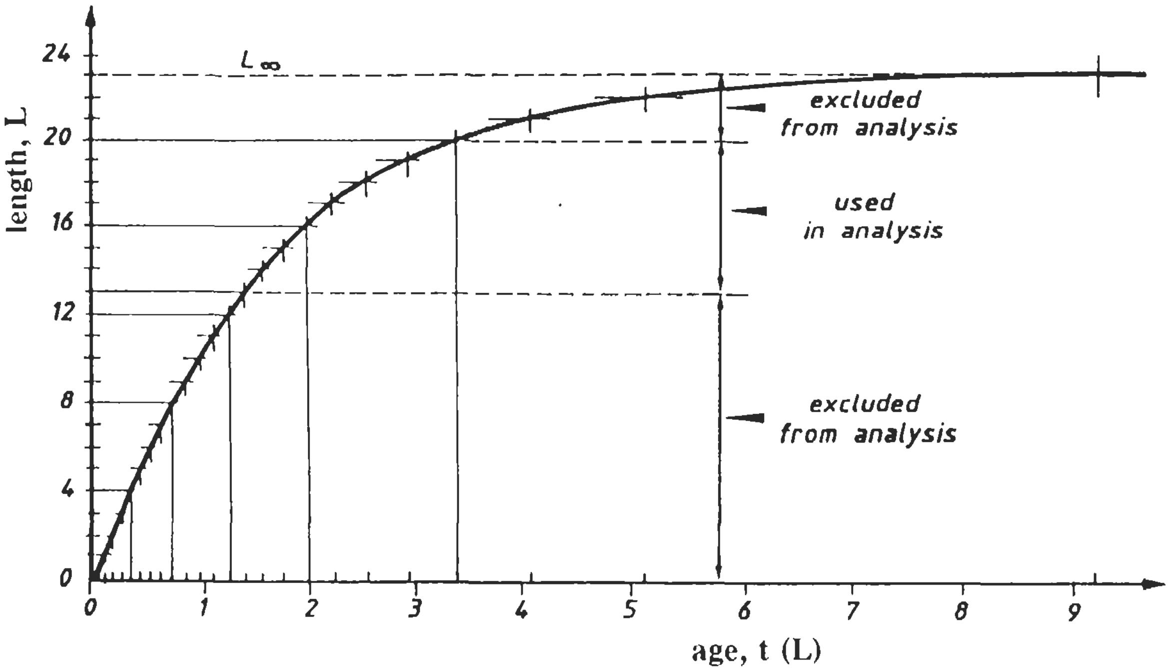


Fig. 4.4.5.1 Conversion of 1-cm length groups of *Upeneus vittatus* into age intervals, by the equation:

$$t(L) = t_0 - \frac{1}{K}*\ln(1 - L/L_\infty) \quad (t_0 = 0,\ K = 0.59 \text{ and } L_\infty = 23.1)$$

The biggest fish in the catch are often bigger because they grow faster, not because they are older as we assume in the inverse von Bertalanffy equation.

As an example consider the resolution of the length-frequency sample in Fig. 3.2.2.2 into normally distributed cohorts. The length group 15-16 cm, consists only of members of the 1983 spring cohort (as appears from Table 3.2.1.1), whereas the length group 45-46 cm contains three cohorts:

1. Fast growing members of the 1981 autumn cohort
2. Medium/fast growing members of the 1981 spring cohort
3. Medium growing members of the 1980 autumn cohort

The age corresponding to a certain length can be calculated, when t_0 is ignored or assumed to be 0.

Let age t correspond to L1 and age $t+\Delta t$ to L2:

$$L1 = L(t) \text{ and } L2 = L(t+\Delta t)$$

With this one-to-one correspondence between the age interval $[t,t+\Delta t]$ and the length interval [L1,L2] we can change the notation for the number caught:

$$C(t,t+\Delta t) = C(L1,L2)$$

In the present context Δt is the time it takes for an average fish to grow from length L1 to length L2, so we obtain Δt by subtracting the two inverse von Bertalanffy equations (Eq. 3.3.3.2) corresponding to L2 and L1 respectively and obtain:

$$\Delta t = t(L2) - t(L1) = \frac{1}{K}*\ln \frac{L\infty-L1}{L\infty-L2} \qquad (4.4.5.1)$$

It is now possible to calculate Δt directly from the growth parameters K and L_∞ and the corresponding L1 and L2, as well as, of course by subtracting t(L1) from t(L2).

The term $(t+\Delta t/2)$ of Eq. 4.4.4.2 can also be converted into an expression in length (L1 and L2), based on a suggestion by Pauly, *viz.*, that the age interval midpoint $(t+\Delta t/2)$ can be converted into a length-based midpoint by assuming that

$t(L1) + \Delta t/2$ is approximately equal to

$$t\left(\frac{L1+L2}{2}\right) = t_o - \frac{1}{K} * \ln\left(1 - \frac{L1+L2}{2L_\infty}\right) \qquad (4.4.5.2)$$

From these equations the so-called "*linearized length-converted catch curve*" can be derived:

$$\ln \frac{C(L1,L2)}{\Delta t(L1,L2)} = c - Z * t\left(\frac{L1+L2}{2}\right) \qquad (4.4.5.3)$$

This is a linear equation where

$y = \ln \frac{C(L1,L2)}{\Delta t(L1,L2)}$, $x = t\left(\frac{L1+L2}{2}\right)$ and the slope (b) is -Z.

Thus, given a set of length-frequency data and the growth parameters K and L∞ it is possible to obtain an estimate of Z.

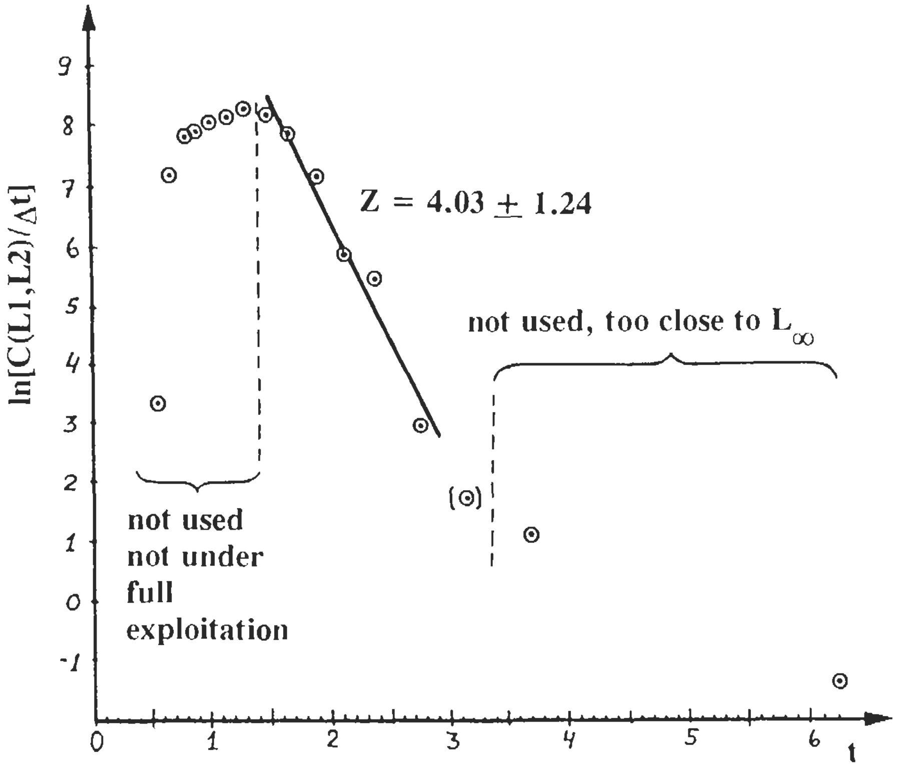


Fig. 4.4.5.2 **Linearized catch curve based on length composition data for *Upeneus vittatus* (from Ziegler, 1979) compare Table 4.4.5.1**

Example 14: Catch curve based on length composition data, *Upeneus vittatus*

An example of an application of Eq. 4.4.5.3 is given in Table 4.4.5.1 based on data for *Upeneus vittatus* (yellow-striped goatfish) from Manila Bay (Ziegler, 1979). The input data are the catch in numbers by length group (columns A and B) as well as values for L_∞ and K. Then t(L1) (column C) is calculated by Eq. 3.3.3.2 and Δt (column D) either from column C or by Eq. 4.4.5.1, while t((L1+L2)/2) = x (column E) is derived from column C or directly by Eq. 4.4.5.2 and $\ln(C(L1,L2)/\Delta t)$ = y (column F) from columns B and D.

The next step is to plot x against y (Fig. 4.4.5.2) and to decide which points should be used for a regression analysis, of which the slope b corresponds to -Z.

The confidence limits are calculated for various numbers of observations, so as to determine the best estimate of Z. (A similar procedure should be followed in Exercise 4.4.5.)

Table 4.4.5.1 Linearized catch curve based on length composition data for *Upeneus vittatus* from Manila Bay, Philippines (from Ziegler, 1979). L_∞ = 23.1 cm, K = 0.59 per year (see Fig. 4.4.5.1)

A	B	C	D	E	F	G	H
L1-L2	C(L1-L2)	t(L1) a)	Δt b)	$t(\frac{L1+L2}{2})$ c) (x)	$\ln \frac{C(L1,L2)}{\Delta t}$ (y)	Z	remarks
6- 7	3	0.510	0.102	0.56	3.38	-	not used; not under full exploitation
7- 8	143	0.612	0.109	0.67	7.18	-	
8- 9	271	0.721	0.116	0.78	7.76	-	
9-10	318	0.837	0.125	0.90	7.86	-	
10-11	416	0.961	0.134	1.03	8.04	-	
11-12	488	1.096	0.146	1.17	8.11	-	
12-13	614	1.242	0.160	1.32	8.25	-	
13-14	613	1.405	0.177	1.49	8.15	-	portion used in the regression analysis
14-15	493	1.579	0.197	1.67	7.83	-	
15-16	278	1.776	0.223	1.88	7.13	2.64	
16-17	93	2.000	0.257	2.12	5.89	3.61	
17-18	73	2.257	0.303	2.40	5.48	3.20	
18-19	7	2.560	0.370	2.74	2.94	4.03	
19-20	2	2.930	0.473	3.15	1.44	4.19	
20-21	2	3.404	0.659	3.70	1.11	-	not used; too close to L_∞
21-22	0	4.064	1.094	4.53	-	-	
22-23	1	5.160	4.047	6.19	-1.40	-	
23-24	1	-	-	-	-	-	

Details of the five regression analysis

L1-L2	slope b Z	no. of obs.	Student's distribution 95% t_{n-2}	variance of slope sb^2	confidence limits $Z \pm t_{n-2} * sb$
13-14	-	1	-	-	-
14-15	-	2	-	-	-
15-16	2.64	3	12.70	0.198	2.64 ± 5.65
16-17	3.61	4	4.30	0.283	3.61 ± 2.28
17-18	3.20	5	3.18	0.121	3.20 ± 1.11
18-19	4.03	6	2.78	1.198	4.03 ± 1.24
19-20	4.19	7	2.57	0.087	4.19 ± 0.76

a) Eq. 3.3.3.2
b) Eq. 4.4.5.2
c) Eq. 4.4.5.2

As was the case for the age-based linearized catch curve (compare Table 4.4.3.1), some of the observations have been excluded from the regression analysis in Table 4.4.5.1. The first seven length groups (6-13 cm) form the ascending part of the curve. These fish are considered not yet fully recruited to the fishery. The last four length groups are excluded as well, the reasons being:

1) Small numbers in the samples (as for the age-based linearized catch curve)

2) When approaching L_∞ the relationship between age, t(L), and length, L, becomes uncertain (compare with the problems with the von Bertalanffy plot discussed in Section 3.3.3).

Point two above is an important one for length-based linearized catch curves. It is a good reason for never using the largest length groups.

Let us go back to the example of Table 4.4.5.1. Only the length groups 13-20 cm are used in the analysis of the data. To assess the sensitivity due to the choice of points to be excluded, the slope b = Z has been calculated from 3 points, 4 points, ..., and 7 points as shown at the bottom of Table 4.4.5.1. The first Z is calculated for the lengths 13-16 cm, the next Z for lengths 13-17 cm, ..., etc. Confidence limits have been calculated using the method described in Section 2.4. In the present case the conclusion is that Z is somewhere between 4.03-1.24 = 2.8 and 4.03+1.24 = 5.2 per year, using the six intervals from 13 to 19 cm. For the length groups 16-20 cm, $Z*\Delta t > 1$ which is not small, therefore the approximation behind the linearized catch curve ($\ln[1 - \exp(-x)] = \ln x - x/2$, see Section 4.4.4) is a crude one in this case.

(See **Exercise(s)** in Part 2.)

4.4.6 The cumulated catch curve based on length composition data. (The Jones and van Zalinge method)

To convert the "cumulated catch curve" (Eq. 4.4.4.1) into an equation that can be used for a length-based analysis, the inverse von Bertalanffy equation (Eq. 3.3.3.2)

$$t(L) = t_0 - \frac{1}{K}*\ln(1 - \frac{L}{L_\infty})$$

is inserted into the cumulated catch curve equation (Eq. 4.4.4.1):

$$\ln C(t,\infty) = d - Z*t$$

which gives the following results:

$$\ln C(L,L_\infty) = d - Z*[t_0 - \frac{1}{K}*\ln(1-L/L_\infty)]$$

which can be converted into

$$\ln C(L,L_\infty) = d - Z*t_0 - \frac{Z}{K}*\ln L_\infty + \frac{Z}{K}*\ln(L_\infty-L)$$

The first three terms are constants which can conveniently be renamed:

$$a = d - Z*t_0 - \frac{Z}{K}*\ln L_\infty$$

The "*Jones and van Zalinge equation*" has thus been derived:

$$\ln C(L,L_\infty) = a + \frac{Z}{K}*\ln(L_\infty-L) \qquad (4.4.6.1)$$

where $C(L,L_\infty)$ stands for the cumulated catch of fish of length L and above. The slope estimated by the linear regression Eq. 4.4.6.1 is Z/K so that an estimate of Z is obtained from:

$$Z = K*\text{slope}$$

Example 15: The Jones and van Zalinge method, *Upeneus vittatus*

Table 4.4.6.1 and Fig. 4.4.6.1 show an application of Eq. 4.4.6.1 to *Upeneus vittatus* (the data used in the foregoing section). Note that the basic data also for this method is the sample - not the total catch (compare Sections 4.4.4-4.4.5). The results of the Jones and van Zalinge analysis using the length groups 13 and 19 cm are similar to the results from the linearized catch curve analysis (Table 4.4.5.1).

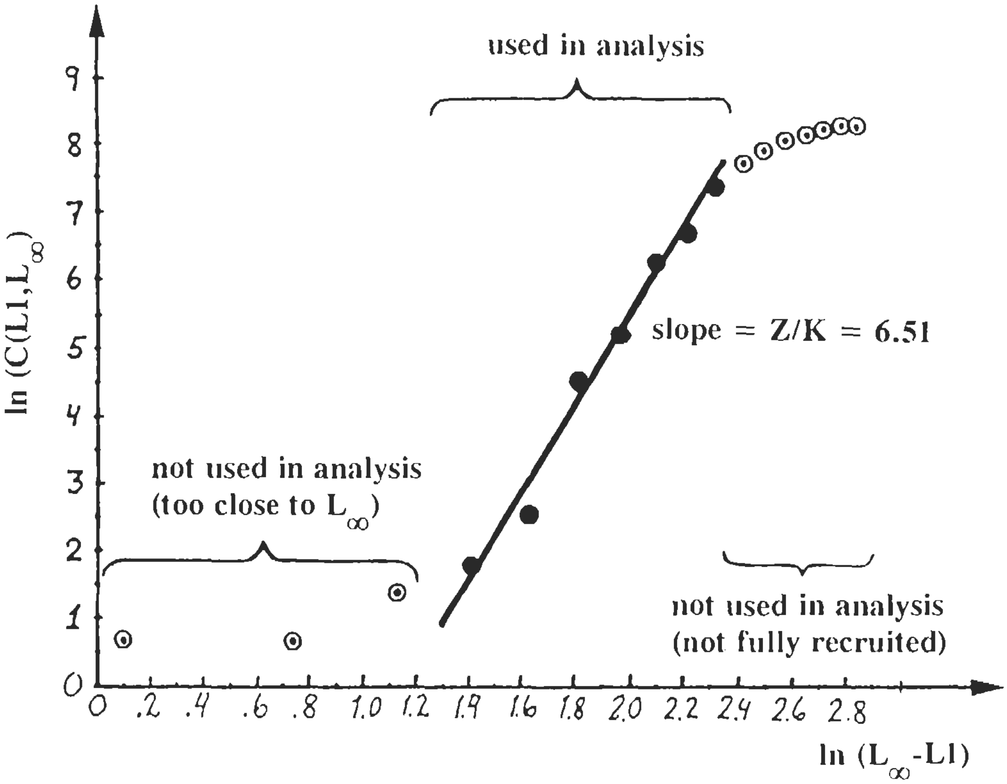


Fig. 4.4.6.1 Cumulated catch curve based on length composition data for *Upeneus vittatus*. The line drawn is estimated from seven points. Data from Table 4.4.6.1

(See **Exercise(s)** in Part 2.)

Table 4.4.6.1 Cumulated catch curve based on length composition data for *Upeneus vittatus* from Manila Bay, Philippines (from Ziegler, 1979). L_∞ = 23.1 cm, K = 0.59 per year (see Fig. 4.4.6.1)

L1-L2	catch $C(L1,L2)$	cumulated catch $C(L1,L_\infty)$	ln cumulated catch $\ln C(L1,L_\infty)$ (y)	$\ln(L_\infty-L1)$ (x)	slope Z/K	remarks
6-7	3	3816	8.25	2.84	-	not used, not under full exploitation
7-8	143	3813	8.25	2.78	-	
8-9	271	3670	8.21	2.71	-	
9-10	318	3399	8.13	2.65	-	
10-11	416	3081	8.03	2.57	-	
11-12	488	2665	7.89	2.49	-	
12-13	614	2177	7.69	2.41	-	
13-14	613	1563	7.35	2.31	-	portion used in the regression analysis
14-15	493	950	6.86	2.21	-	
15-16	278	457	6.12	2.09	5.61	
16-17	93	179	5.19	1.96	6.20	
17-18	73	86	4.45	1.81	5.98	
18-19	7	13	2.56	1.63	6.86	
19-20	2	6	1.79	1.41	6.51	
20-21	2	4	1.39	1.13	-	not used too close to L_∞
21-22	0	2	0.69	0.74	-	
22-23	1	2	0.69	0.10	-	
23-24	1	1	0.00	-2.30	-	

Details of the five regression analysis

L1-L2	slope*K Z	number of obs. n	Student's distrib. 95% t_{n-2}	variance of slope sb^2	confidence limits of Z $Z \pm K*t_{n-2}*sb$
13-14	-	1	-	-	-
14-15	-	2	-	-	-
15-16	3.30	3	12.71	0.131	3.30 ± 2.71
16-17	3.66	4	4.30	0.118	3.66 ± 0.87
17-18	3.53	5	3.18	0.047	3.53 ± 0.41
18-19	4.05	6	2.78	0.202	4.05 ± 0.74
19-20	3.84	7	2.57	0.110	3.84 ± 0.50

4.4.7 Summary of the linearized catch curve methods

Fig. 4.4.7.1 shows a summary of the versions of the linearized catch curve (Eq. 4.4.2.1) discussed in Section 4.4. These all originated from the catch equation (or Baranov's equation), Eq. 4.2.7. The following five models were introduced, three based on *age composition data*:

1) The linearized catch curve with constant time intervals.
   Eq. 4.4.3.1

2) The linearized catch curve with variable time intervals.
   Eq. 4.4.4.2 (generalizes Eq. 4.4.3.1)

3) The cumulated catch curve. Eq. 4.4.4.1

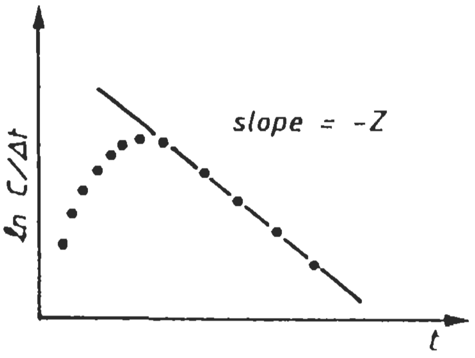
and two based on *length composition data*:

GENERAL LINEARIZED CATCH CURVE MODEL

$$\ln C(t1,t2) = d - Z*t1 + \ln[1 - \exp(-Z*(t2-t1))]$$

(Eq. 4.4.2.1)

Models based on age composition data	Δt = t2-t1 is constant **LINEARIZED CATCH CURVE EQUATION WITH CONSTANT TIME INTERVALS** $\ln C(t,t+\Delta t) = g - Z*t$ (Eq. 4.4.3.1)	
	Δt = t2-t1 is variable	
	Δt = small **LINEARIZED CATCH CURVE EQUATION WITH VARIABLE TIME INTERVALS** $\ln \frac{C(t,t+\Delta t)}{\Delta t} = c - Z*(t+\Delta t/2)$ (Eq. 4.4.4.2)	$\Delta t = \infty$ **CUMULATED CATCH CURVE EQUATION** $\ln C(t,\infty) = d - Z*t$ (Eq. 4.4.4.1)
Conversion of age into length	$\Delta t(L1,L2) = \frac{1}{K}*\ln \frac{L\infty-L1}{L\infty-L2}$ (Eq. 4.4.5.1) and $t+\Delta t/2 \approx$ $t_o - \frac{1}{K}*\ln(1 - \frac{L1+L2}{2L\infty})$ (Eq. 4.4.5.2)	$t(L) = t_o - \frac{1}{K}*\ln(1 - \frac{L}{L\infty})$ (Eq. 3.3.3.2)
Models based on length composition data	**LINEARIZED LENGTH CONVERTED CATCH CURVE** $\ln \frac{C(L1,L2)}{\Delta t(L1,L2)} = c - Z*t(\frac{L1+L2}{2})$ (Eq. 4.4.5.3)	**JONES AND VAN ZALINGE METHOD** $\ln C(L,L_\infty) = a + \frac{Z}{K}*\ln(L_\infty-L)$ (Eq. 4.4.6.1)



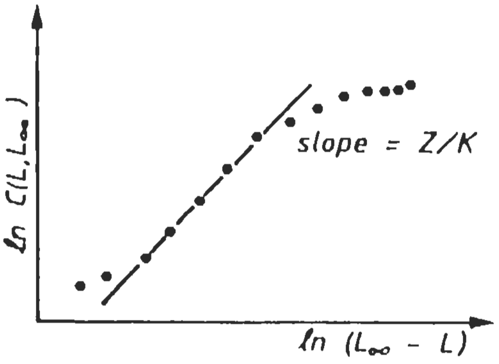


Fig. 4.4.7.1 Summary of models presented in Section 4.4

4) The linearized length-converted catch curve. Eq. 4.4.5.3, derived from Eq. 4.4.4.2

5) The Jones and van Zalinge method. Eq. 4.4.6.1, derived from Eq. 4.4.4.1

Sparre (1990) pointed out that there are problems with length-based stock assessment methods when growth is seasonal, and in particular the length-converted catch curve method. In the same issue of Fishbyte, Pauly (1990) describes a new method for the construction of length-converted catch curves, which takes the seasonality of growth into account. The bias in the estimation of Z for small short-lived species, which are exposed to strong seasonal fluctuations in growth due to changing environmental conditions, is to a large extent removed by this new method. It gives much lower values for Z than those obtained with the length-converted methods described in Sections 4.4.5 and 4.4.6.

4.5 BEVERTON AND HOLT'S Z-EQUATIONS

The first method dealt with in this section estimates Z from the mean length of the fish in the catch and the von Bertalanffy parameters K and L_∞. Thus, the data requirements are even less than those for the length-based linearized catch curve methods, for which the relative (not necessarily the abso-lute) size composition of the catch should be known (see Sections 4.4.4 to 4.4.6). The derivation of Beverton and Holt's Z equations, however, is somewhat more complicated from a mathematical point of view. In the following we attempt to explain and justify the methods by aid of a numerical example, skipping the mathematics. It is finally shown that even L_∞ can be estimated together with an estimate of Z/K.

Assume that samples of length compositions of catches have been collected from a fishery in 1960, 1970 and 1980, and that the results are those shown in Table 4.5.0.1. The example used here is a hypothetical data set, that is, a data set for which the true parameters are known. The length groups represent only that part of the stock which is under full exploitation (cf. discussion in Section 4.4.5), the part for which Z is assumed to remain constant for all length groups. Z may of course be different for the three years in question.

In addition, the von Bertalanffy parameters K and L_∞ must be known. For the example in Table 4.5.0.1 the parameters are:

$$K = 0.3 \text{ per year}, \; L_\infty = 100 \text{ cm}$$

Figs. 4.5.0.1A1 to 4.5.0.1A3 show the length distributions. The mean length $\bar{L}$ has a decreasing trend in time. Thus in 1980 fewer fish survived to a certain length compared to 1970 and 1960. If this change in mean length is caused only by a change in the fishing mortality on the stock it follows that:

$$(F \text{ in } 1960) < (F \text{ in } 1970) < (F \text{ in } 1980)$$

In other words, the lower the mean length in the catch, the higher is F. Under the assumption of a constant natural mortality, M, the same conclusion holds for the total mortality, $Z = F+M$.

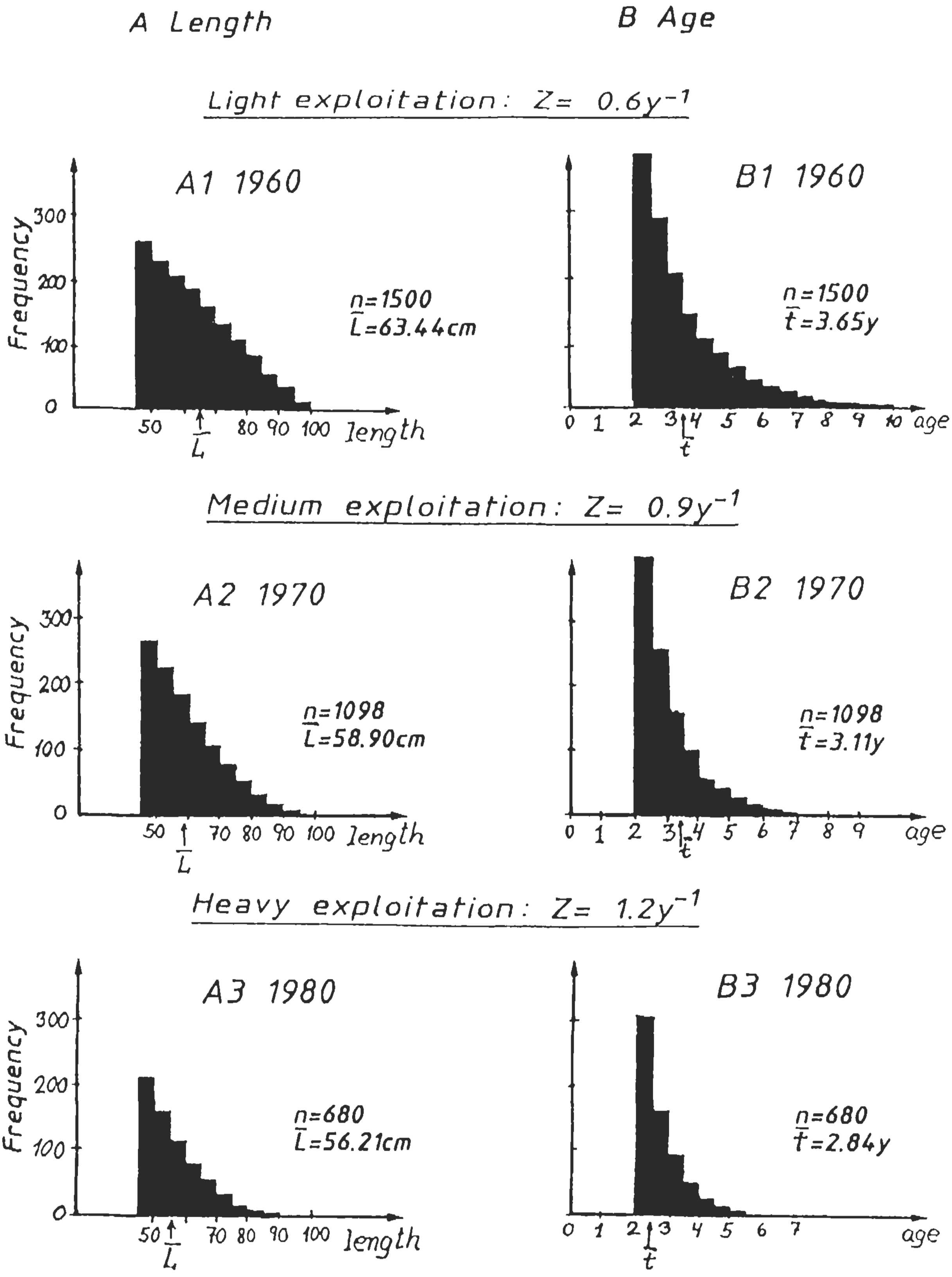


Fig. 4.5.0.1 Hypothetical example to illustrate Beverton and Holt's Z-equation (Eq. 4.5.0.1). K = 0.3, L′ = 45 cm and L_∞ = 100 cm

4.5.1 Beverton and Holt's Z-equation based on length data

Beverton and Holt (1956) showed that the functional relationship between Z and $\bar{L}$ is:

$$Z = K*\frac{L\infty-\bar{L}}{\bar{L}-L'} \qquad (4.5.1.1)$$

where $\bar{L}$ is the mean length of fish of length L′ and longer, while L′ is "*some length for which all fish of that length and longer are under full exploitation*". Note that L′ is the *lower limit* of the corresponding length interval. For the choice of L′, the same comments as those given in Section 4.4.2 and 4.4.6 can be applied. In the example the value of L′ = 45 cm has been chosen.

Table 4.5.0.1 Length composition samples of catches (hypothetical example to illustrate the method). Mean lengths are calculated as demonstrated in Section 2.1 (Table 2.1.2). L′ is some length for which all fish of that length and longer are under full exploitation

		year					
		1960	1970	1980	1960	1970	1980
		numbers caught			number * midlength		
length group L1-L2	mid-length $\frac{L1+L2}{2}$	C			$C * \frac{L1+L2}{2}$		
L′ = 45-50	47.5	256	268	212	12160.0	12730.0	10070.0
50-55	52.5	237	226	161	12442.0	11865.0	8452.5
55-60	57.5	211	180	116	12132.5	10350.0	6670.0
60-65	62.5	187	141	79	11687.5	8812.5	4937.5
65-70	67.5	161	105	52	10867.5	7087.5	3510.0
70-75	72.5	138	76	31	10005.0	5510.0	2247.5
75-80	77.5	113	50	17	8757.5	3875.0	1317.5
80-85	82.5	87	30	8	7177.5	2475.0	660.0
85-90	87.5	62	15	3	5425.0	1312.5	262.5
90-95	92.5	36	6	1	3330.0	555.0	92.5
95-100	97.5	12	1	0	1170.0	97.5	0.0
Total, n		1500	1098	680			
$\Sigma C*\frac{L1+L2}{2}$					95154.5	64670.0	38220.0
$\bar{L} = (\Sigma C*\frac{L1+L2}{2})/n$					63.44	58.90	56.21

The Z-values for the three years in the example become (compare Table 4.5.0.1 and Fig. 4.5.0.1A):

$$Z(1960) = 0.3*\frac{100.0-63.44}{63.44-45.0} = 0.6 \text{ per year}$$

$$Z(1970) = 0.3*\frac{100.0-58.90}{58.90-45.0} = 0.9 \text{ per year}$$

$$Z(1980) = 0.3*\frac{100.0-56.21}{56.21-45.0} = 1.2 \text{ per year}$$

The method is refined in Section 4.5.4.

(See **Exercise(s)** in Part 2.)

4.5.2 Beverton and Holt's Z-equation based on age data

As was the case for the linearized catch curve method the length-based Beverton and Holt formula has an age-based parallel. It is mentioned here mainly because it illustrates a basic feature about the Beverton and Holt theory (cf. Section 1.3).

The age compositions corresponding to the length compositions in Table 4.5.0.1 are shown in Table 4.5.2.1 and Fig. 4.5.0.1B. The same reasoning as was used for the mean length can be used for the mean age: the larger the fishing mortality the smaller is the mean age, $\bar{t}$, in the catch, or, the higher the mean age the smaller is F. This may be considered an implication of the functional relationship between age and length. However, the exact relationship between mean age and mean length is somewhat complicated. It should be noticed that the von Bertalanffy equation does not transform the mean age into the mean length, because the growth equation is not linear.

Table 4.5.2.1 Age composition of the samples given in Table 4.5.0.1

age group	1960	1970	1980
2.0- 2.5	390	399	308
2.5- 3.0	289	255	169
3.0- 3.5	214	162	92
3.5- 4.0	150	103	52
4.0- 4.5	118	66	28
4.5- 5.0	97	42	15
5.0- 5.5	64	27	8
5.5- 6.0	48	17	6
6.0- 6.5	35	11	2
6.5- 7.0	26	7	-
7.0- 7.5	19	4	-
7.5- 8.0	14	3	-
8.0- 8.5	11	2	-
8.5- 9.0	8	-	-
9.0- 9.5	6	-	-
9.5-10.0	4	-	-
10.0-10.5	3	-	-
10.5-11.0	2	-	-
11.0-11.5	2	-	-
sample size	1500	1098	680
Σ number*age	5475	3415	1931
mean age, $\bar{t}$	3.65	3.11	2.84

The age-based parallel to Eq. 4.5.1.1 is somewhat simpler. Beverton and Holt showed that:

$$Z = \frac{1}{\bar{t}-t'} \qquad (4.5.2.1)$$

where $\bar{t}$ is the mean age of all fish of age t′ and older, and where t′ is "*some age for which all fish of that age and older are under full exploitation*". For the example age, t′, corresponding to L′ = 45 cm is

$$t'_{45} = t_o - \frac{1}{K}*\ln(1-L/L_\infty) = 0 - \frac{1}{0.3}*\ln(1-45/100) = 1.99 \text{ years}$$

and

$$Z(1960) = \frac{1}{3.65-2.0} = 0.6 \quad \text{per year}$$

$$Z(1970) = \frac{1}{3.11-2.0} = 0.9 \quad \text{per year}$$

$$Z(1980) = \frac{1}{2.84-2.0} = 1.2 \quad \text{per year}$$

4.5.3 Beverton and Holt's Z-equation based on length-at-first-capture

A third version of the equation exists which is mathematically equivalent to Eq. 4.5.1.1, but conceptually different. Consider a "*gear selection curve*" for, say, a trawl-net as shown in Fig. 4.5.3.1. The vertical axis shows the percentage of the fish entering the gear (trawl) that is retained by the meshes. Lc, or L50%, is the length at which 50% are retained and 50% escape through the meshes. Note that Lc < L'. (In Chapter 6 we shall further discuss properties of selection curves.)

This version of the Beverton and Holt Z-equation reads:

$$Z = K*\frac{L\infty-\overline{Lc}}{\overline{Lc}-Lc} \qquad (4.5.3.1)$$

where Lc is the "*length at which 50% of the fish entering the gear are retained*" and $\overline{Lc}$ is the "*average length of the entire catch*".

Eq. 4.5.3.1 has proved useful in many cases where estimates of Lc and $\overline{Lc}$ are available, but where L and L' are not known.

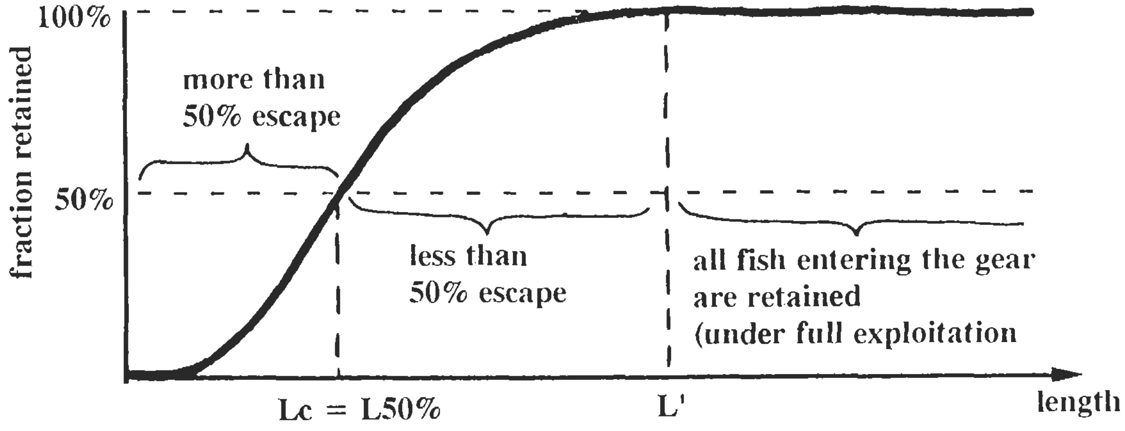


Fig. 4.5.3.1 Gear selection curve

4.5.4 The Powell-Wetherall method

Powell (1979), discussed in Wetherall *et al.* (1987), suggested a special application of Eq. 4.5.1.1 by which L_∞ and Z/K can be estimated. As L' can take any value equal to and above the smallest length under full exploitation, Eq. 4.5.1.1 can give a series of estimates of Z, namely one for each choice of L'. This makes it possible to turn Eq. 4.5.1.1 into a regression analysis with L' as the independent variable. A series of algebraic manipulations shows that Eq. 4.5.1.1 is equivalent to:

$$\bar{L}-L' = a + b*L' \qquad (4.5.4.1)$$

where

$$Z/K = -(1+b)/b \quad \text{and} \quad L_\infty = -a/b$$

or $b = -K/(Z+K)$ and $a = -b*L_\infty$

Thus, plotting $\bar{L}-L'$ against L' gives a linear regression from which a and b can be estimated and hence L_∞ and Z/K (see Fig. 4.5.4.1). Powell (1979) actually gave a whole suite of different formulas for Z/K, of which Eq. 4.5.4.1 represents the simplest approach. This method is especially suitable for situations where little or nothing is known about the fish stock in question. The estimation of L_∞ is especially useful (compare Section 3.3.2).

It should be remembered that like the Beverton and Holt formula (Eq. 4.5.1.1) the method is based on the assumption of a constant parameter system which reduces its applicability.

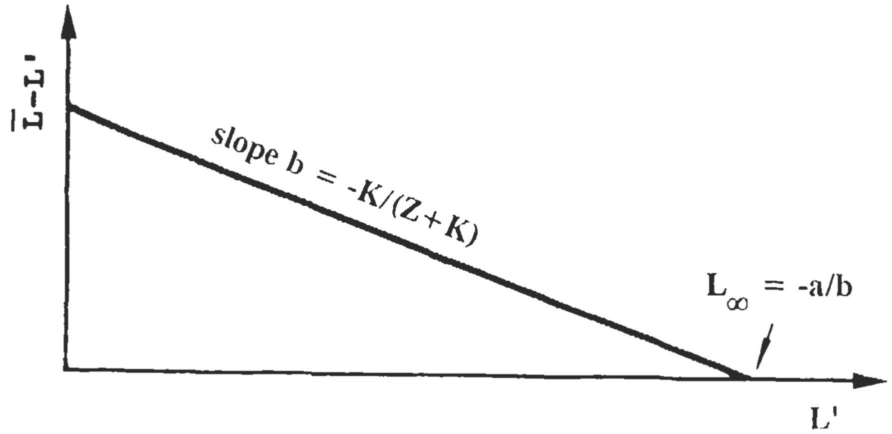


Fig. 4.5.4.1 Powell-Wetherall plot

Example 16: The Powell-Wetherall method

An example of the Powell-Wetherall method is given in Table 4.5.4.1 and Fig. 4.5.4.2. The calculation of $\bar{L}$ starts with the mid-length of the largest length class, in this case 46 cm.

The next value of $\bar{L}$ is calculated as follows: (46*3+44*10)/13 = 44.462. L' is the lower limit of each length-class. The values for $\bar{L}-L'$ are obtained by subtracting the corresponding value of L' from $\bar{L}$, for example 46.000-45 = 1.000 and 44.462-43 = 1.462. These values are then first plotted against L', in order to be able to judge which points lie on the straight line and should be included in the linear regression analysis. In this example the points corresponding to the largest sizes were excluded, because they represent very few fish. (Note, the same data set has been used to illustrate the estimation of the selection ogive from a catch curve, see Section 6.5.)

Computer programs

The program "BHZWET" in the LFSA package of microcomputer programs (Sparre, 1987) can execute the Powell-Wetherall analysis as well as the estimation of Z from Beverton and Holt's Z-equation. The "COMPLEAT ELEFAN" package of microcomputer programs (Gayanilo, Soriano and Pauly, 1988) and FiSAT also contain such programs.

Table 4.5.4.1 Powell-Wetherall method (see Fig. 4.5.4.2). The same data are used in Table 6.5.1

length interval L1-L2 (x) = L1	number caught C(L1,L2)	mean length of fish longer than L' $\bar{L}$	$\bar{L}$-L' (y)	
3-5	37	21.101	18.101	not used in analysis
5-7	56	21.291	16.291	
7-9	86	21.552	14.552	
9-11	129	21.917	12.917	
11-13	188	22.419	11.419	
13-15	258	23.101	10.101	
15-17	319	23.998	8.998	
17-19	352	25.108	8.108	
19-21	351	26.394	7.394	
21-23	324	27.801	6.801	
23-25	283	29.279	6.279	used in analysis
25-27	239	30.792	5.792	
27-29	196	32.320	5.320	
29-31	158	33.852	4.852	
31-33	123	35.392	4.392	
33-35	93	36.926	3.926	
35-37	69	38.447	3.447	
37-39	48	39.982	2.982	
39-41	31	41.516	2.516	
41-43	18	43.032	2.032	
43-45	10	44.462	1.462	not used
45-47	3	46.000	1.000	

intercept a: 11.671 confidence limits of a: [11.64 , 11.70]
slope b : -0.2349 confidence limits of b: [-0.2359 , -0.2340]

L_∞ = -a/b = 49.7 Z/K = -(1+b)/b = 3.26

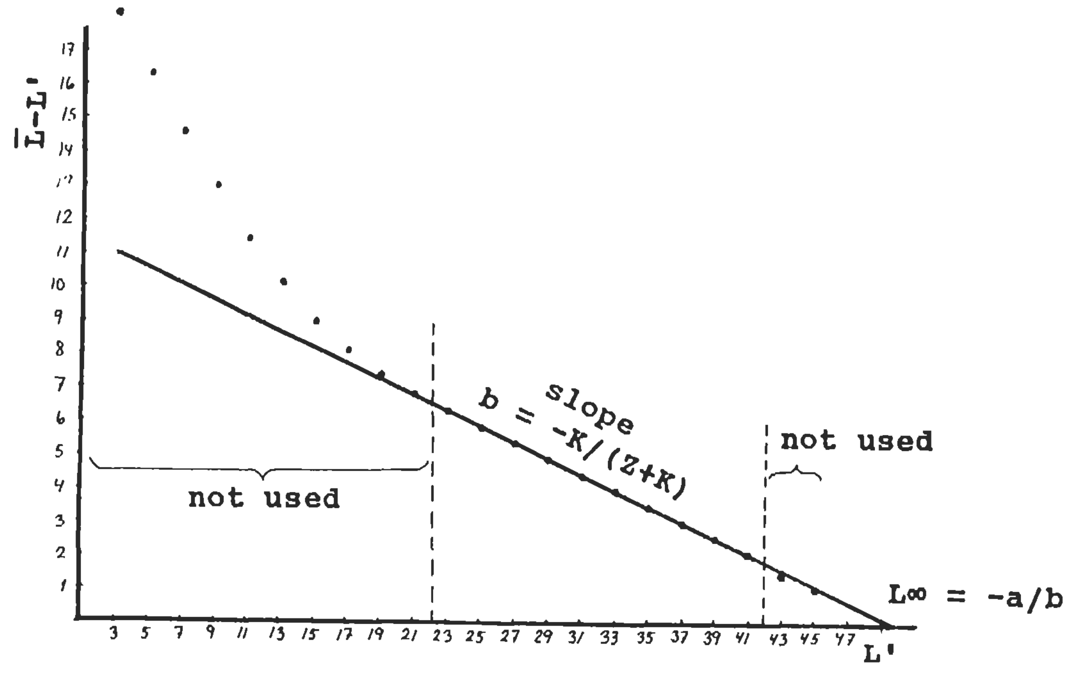


Fig. 4.5.4.2 Powell-Wetherall plot based on data from Table 4.5.4.1

4.6 A PLOT OF Z ON EFFORT FOR SEPARATE ESTIMATES OF F AND M

The estimate of Z derived by the methods described in the foregoing section can sometimes be used to obtain estimates of F, the fishing mortality and M, the natural mortality. This is possible if pairs of estimates of Z and effort are available for a number of time periods covering a wide range of efforts.

Let Z(y) and f(y) be the total mortality and the effort in year y. The method (Paloheimo, 1958, 1961 and 1980) is based on Eq. 4.2.3: $Z = F+M$, and the assumption that effort and fishing mortality are related in the simple manner of Eq. 4.3.0.7: $F(y) = q*f(y)$, where q is the catchability coefficient. Inserting Eq. 4.3.0.7 into Eq. 4.2.3 gives:

$$Z(y) = M + q*f(y) \qquad (4.6.1)$$

With Z as the dependent variable and f as the independent variable Eq. 4.6.1 becomes a linear regression with slope q and the natural mortality, M, as the intercept. The fishing mortality for the time period y, F(y), is derived from:

$$F(y) = Z(y) - M$$

Example 17: Estimation of M and q of a tropical fish

Table 4.6.1 and Fig. 4.6.1 show an application of Eq. 4.6.1 to *Selaroides leptolepis* in the Gulf of Thailand (from Boonyubol and Hongskul, 1978). In this case Z is calculated by Eq. 4.5.3.1, i.e. the observations are Lc, the 50% retention length, and $\overline{Lc}$, the mean length of all fish in the catch. Effort is given in units of millions of trawling hours per year. Fig. 4.6.1 shows the plot of Z on effort.

Using linear regression we find:

slope : q = 0.2532
intercept: M = 2.034 per year

Confidence limits are calculated as described in Section 2.4:

Table 4.6.1 Data for estimation of M and q for *Selaroides leptolepis* in the Gulf of Thailand (from Boonyubol and Hongskul, 1978)
K = 1.16 per year, Lc = 10.0 cm, L_∞ = 20.0 cm

year y	effort a) f(y)	mean length $\overline{Lc}$ cm	$Z = K*\frac{L\infty-\overline{Lc}}{\overline{Lc}-Lc}$ (Eq. 4.5.3.1)
1966	2.08	13.25	2.41
1967	2.08	13.01	2.69
1968	3.50	12.99	2.72
1969	3.60	13.07	2.62
1970	3.80	12.37	3.73
1971	-	- no data	-
1972	7.19	12.30	3.88
1973	9.94	12.01	4.61
1974	6.06	12.60	3.30

a) effort in units of millions of trawling hours

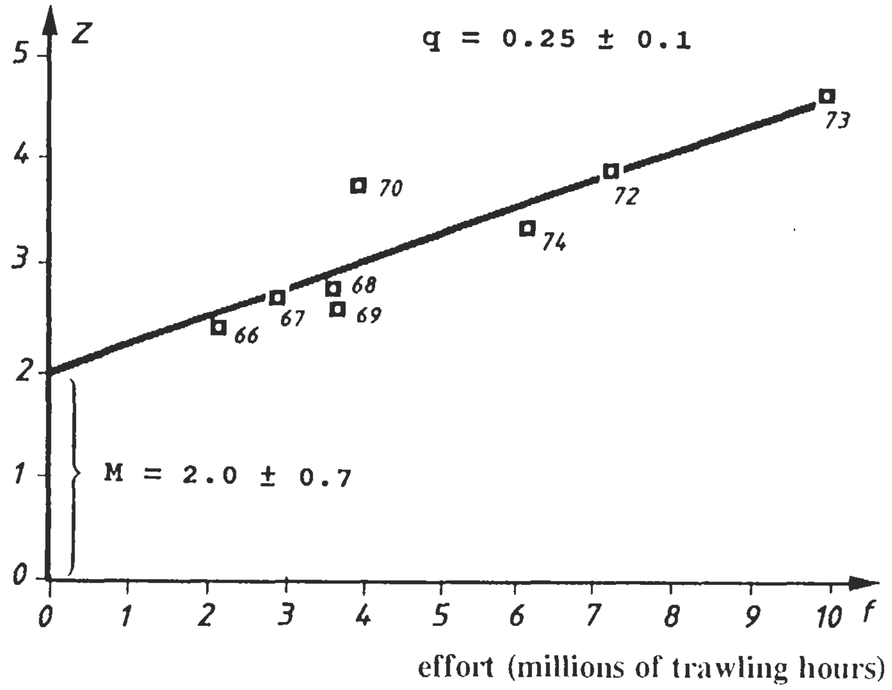


Fig. 4.6.1 Plot of total mortality, Z, on effort, f, for estimation of natural mortality, M, and catchability coefficient, q. Based on data from Table 4.6.1 (from Boonyubol and Hongskul, 1978)

$$sq^2 = \frac{1}{n-2} * \left[\left[\frac{sy}{sx} \right]^2 - q^2 \right] = \frac{1}{6} * \left[\left[\frac{0.7724}{2.7423} \right]^2 - 0.2532^2 \right] = 0.002533$$

$$sq = 0.0503$$

$$sM^2 = sq^2 * \left[\frac{n-1}{n} * sx^2 + \bar{x}^2 \right] =$$

$$0.002533 * (\tfrac{7}{8} * 2.7423^2 + 4.7813^2) = 0.07457 \qquad sM = 0.2731$$

The 95% confidence limits for q and M are

$$q\text{: } [q - sq*t_{n-2} \text{ , } q + sq*t_{n-2}] =$$

$$[0.253 - 0.0503*2.45 \text{ , } 0.253 + 0.0503*2.45] = [0.13, 0.38]$$

$$M\text{: } [M - sM*t_{n-2} \text{ , } M + sM*t_{n-2}] =$$

$$[2.03 - 0.2731*2.45 \text{ , } 2.03 + 0.2731*2.45] = [1.36, 2.70]$$

The estimates of M and q obtained this way are not precise. For example, they are based on the assumption that effort is proportional to fishing mortality, i.e, that q is constant - an assumption which can always be questioned due to an increasing trend in fishing efficiency. One trawling hour in 1970 may not create the same fishing mortality as a trawling hour in 1980 because fishing vessels in 1980 were often better equipped (more efficient gears, larger engines, etc.) than the vessels in 1970. If this is the case in the example of Fig. 4.6.1 the more recent observations should be moved to the right hand side to compensate for the increased efficiency. This would correspond to expressing the effort in units of 1966 trawling hours per year. The effect on the regression analysis would be a smaller slope and a larger intercept, i.e. the estimate of M would be larger and that of q smaller.

Note also that the application of the method is only possible if there is a clear change in effort during the period considered (cf. Exercise 4.6). If effort (the independent variable) remains constant during the period we should not be able to fit a line to the points.

In Section 4.7 we shall continue the discussion of natural mortality, and two alternative simple methods for estimation of M will be suggested. All simple methods for estimation of natural mortality are questionable and it is recommended always to assess the reasonability of any estimate by comparing results of alternative methods and estimates of M for similar species.

(See **Exercise(s)** in Part 2.)

4.7 NATURAL MORTALITY

One method of estimating the natural mortality coefficient, M, was introduced in Section 4.6. Many other procedures have been suggested in the literature. Most of them, perhaps all, rank no higher than "guesstimates" or "qualified" guesses. Some of these methods are widely used and others may be so in the future. They therefore merit discussion.

Recall that the natural mortality is the mortality created by all other causes than fishing, e.g., predation including cannibalism, diseases, spawning stress, starvation, and old age. Predation and starvation mortalities and several others are linked to the ambient ecosystem. The same species may have different natural mortality rates in different areas dependent on the density of predators and competitors whose abundance is influenced by fishing activities.

As direct measurements of M are often impossible to obtain, it has been attempted to identify quantities which can be assumed proportional to M and which are easier to measure (or estimate).

The von Bertalanffy curvature parameter, K, has been demonstrated to be linked to the longevity of the fish (Beverton and Holt, 1959) and longevity is related to mortality (Tanaka, 1960; Holt, 1965 and Saville, 1977) (see Eq. 4.5.2.1). Other methods involving longevity are treated in Section 4.7.1.

As a rough generalization, fish species with a high K-value have a high M-value, and species with a low K-value have a low natural mortality. A slow growing species (low K) simply cannot bear high natural mortality - if it did it would soon become extinct. Beverton and Holt (1959) found that values of the ratio M/K mostly lie in the range of 1.5 to 2.5.

Natural mortality must also be linked to L_∞ or the maximum weight of the species, W_∞, since large fish have fewer predators than small fish. It has been suggested that M can be predicted from the body size for certain groups of animals (Taylor, 1960, for bivalves and Peterson and Wroblewski, 1984, for pelagic fish).

Rikhter and Efanov (1976) (Section 4.7.3) demonstrated that fish with a high natural mortality mature early in life, compensating for the high M by starting to reproduce earlier. It can also be mentioned that Gunderson and Dygert (1988) found a relationship of M with the ratio of gonad weight to somatic weight. This is reasonable because fish with a high mortality may compensate by producing more eggs.

Further, as most biological processes go faster at higher temperatures (of course within certain limits) one could imagine the natural mortality to be related to the environmental temperature. Pauly's empirical formula (Section 4.7.2) describes M as a function of K, L_∞ and T, the ambient temperature.

4.7.1 Natural mortality and longevity

Intuitively, we would consider longevity as something more closely related to mortality than K, L_∞ or ambient temperature. The basic concept of mortality coefficients was discussed in Section 4.2 (e.g. Fig. 4.2.1). Alagaraja (1984) suggested another way of illustrating the concept of the mortality coefficient. He tentatively defined the natural life span of fish species (or the *longevity*) as the age at which 99% of a cohort had died if it had been exposed to natural mortality only (i.e. if Z = M). If Tm stands for longevity and M1% stands for the natural mortality corresponding to a 1% survival, then:

$$M1\% = -\ln(0.01)/Tm \qquad (4.7.1.1)$$

Table 4.7.1.1 shows a collection of M-values defined by the 99% life span as well as the corresponding 99.9% life span.

Table 4.7.1.1 can be used for a first rough evaluation of a mortality estimate in conjunction with a modal progression analysis (in particular for tropical species). If, for example, from the modal progression analysis (cf. Section 3.4.2) you find significant numbers (more than 1%) of three year old fish in the catch samples you should not accept a total mortality Z larger than 1.5. If you find very few (less than 1 per mille) you may accept a total mortality up to 2.3.

Table 4.7.1.1 M-values for various life spans

Tm	(months)	3	4	5	6	7	8	10	12	
M1% M0.1%	per year	18 28	14 21	11 17	9 14	8 12	6.9 10.4	5.5 8.3	4.6 6.9	
Tm	(years)	2	3	4	5	6	8	10	15	20
M1% M0.1%	per year per year	2.3 3.5	1.5 2.3	1.2 1.7	0.92 1.38	0.77 1.15	0.58 0.86	0.46 0.77	0.31 0.69	0.23 0.63

As longevity is usually as difficult to observe as the natural mortality the relationship between mortalities and life span does not provide any easier way to estimate M, but it presents the concepts in a way which may be easier to grasp. How easy it is to estimate the longevity of a certain species depends on how difficult it is to determine the age of the oldest specimens. If the age of the oldest specimens can be read from the hard parts and if the stock is unexploited it is relatively easy to get an estimate of Tm.

The above aspects were discussed by Hoenig (1983), who also developed a model for estimation of Z from observations on longevity. This model is basically the same as the Alagaraja (1984) model, but applies to Z rather than to M. Hoenig gave the following equation based on observations of Z and Tm and linear regression analysis:

`ln Z = a + b*ln Tm` with

`a = 1.46` and `b = -1.01` for fish
(based on 84 stocks of 53 species) and

`a = 1.23` and `b = -0.832` for molluscs
(based on 28 stocks of 13 species)

The above results were based mainly on data from unexploited stocks. Hoenig suggests Tm to be estimated from the mean age of "the oldest specimens" in a sample. This approach, however, is somewhat problematic as the estimate of Tm then depends on the sample size and on the proportion of the sample that is considered to represent "the oldest specimens".

Finally it should be emphasized that the usual assumption, that natural mortality remains constant for all age (size) groups within a species, is highly unrealistic for certain age (size) groups. Naturally, a small fish is exposed to a larger predation mortality than a big fish, simply because small animals have more predators than large animals. This difference in predation mortality (which is perhaps the dominating source of natural mortality for small fish) may be quite big.

When estimating predation mortalities from multispecies cohort analysis combined with work on stomach contents, the ICES Multispecies Working Group (ICES, 1986; Gislason and Sparre, 1987), found a factor of about 10 between the mortalities of 0-group fish and 2-group fish in the North Sea. (see also Section 10.2.)

4.7.2 Pauly's empirical formula

Pauly (1980b) made a regression analysis of M (per year) on K (per year), L_∞ (cm) and T (average annual temperature at the surface in degrees centigrade), based on data from 175 different fish stocks, and estimated the empirical linear relationship:

$$\ln M = -0.0152 - 0.279*\ln L_\infty + 0.6543*\ln K + 0.463*\ln T \qquad (4.7.2.1)$$

Table 4.7.2.1 shows values of M (per year) calculated by "*Pauly's formula*" for various combinations of L_∞, K and T. It should be kept in mind that Eq. 4.7.2.1 gives an estimate of M belonging to the category of "qualified guesses".

Eq. 4.7.2.1 may be correct for the "average fish", but may be way off the mark for any particular fish stock. The formula indicates that:

Table 4.7.2.1 Natural mortality (per year) calculated by Pauly's formula for various combinations of L_∞, K and T

	T = 5 C°				T = 25 C°			
$\overline{L}$	K 0.1	0.5	1.0	2.0	0.1	0.5	1.0	2.0
10	0.24	0.7	1.1	1.7	0.51	1.5	2.3	3.6
80	0.14	0.38	0.6	1.0	0.29	0.8	1.3	2.0
200	0.10	0.30	0.47	0.7	0.22	0.6	1.0	1.6

1. Small fish have high natural mortalities
2. Fast growing species have high natural mortalities
3. The warmer the ambient water the higher the natural mortality

The implication is that any other aspect which may influence the natural mortality is considered "random noise around the regression line" (Eq. 4.7.2.1). Other aspects are, for example, the behaviour (schooling, pelagic/demersal), the reproduction physiology, the ecosystem (abundance of predators). Pauly (1983) suggests to account for schooling in Eq. 4.7.2.1 by multiplication by 0.8 so that for schooling species the estimate becomes 20% lower:

$$M = 0.8 * \exp[-0.0152 - 0.279 * \ln L_\infty + 0.6543 * \ln K + 0.463 * \ln T] \quad (4.7.2.2)$$

It should also be kept in mind that the quality of the input data to the regression analysis from which Eq. 4.7.2.1 was derived, can be questioned. To arrive at Eq. 4.7.2.1 Pauly needed "observations" of M, which as discussed in the foregoing are difficult to obtain. Any M value which was used for the estimation of Eq. 4.7.2.1 can be questioned. Therefore it is recommended only to use one decimal when presenting the result of Eq. 4.7.2.1. For some species the result seems to be twice or half of what it should be. However, when no other information on M is available as is most often the case one should not hesitate to apply Eq. 4.7.2.1 or the Rikhter and Efanov formula discussed in Section 4.7.3. Usually, it is only for unexploited stocks (M = Z) that we are able to estimate M.

Note that Pauly's formula is based on data for fish stocks only, and that the result depends on how you measure the length of the fish (total length, fork length, standard length, etc.). As Pauly's equation gives only a rough estimate of M we can ignore this detail. Do not use Pauly's formula for crustaceans, molluscs or cephalopods or any other invertebrates, as the formula does not cover these groups.

4.7.3 Rikhter and Efanov's formula

Beverton and Holt (1959) investigated a relationship between longevity, Tm, and the Lm/L_∞ ratio, where Lm is the length at first spawning. Holt (1962) noted that it was generally accepted that the Lm/L_∞ ratio was about 2/3 (average 0.64 with minimum and maximum values of 0.3 and 0.9).

Continuing these investigations in comparative dynamics for high latitude stocks, Rikhter and Efanov (1976) showed a close association between M and Tm50% the age when 50% of the population is mature (also called "*the age of massive maturation*"):

$$M = 1.521/(Tm50\%^{0.720}) - 0.155 \text{ per year} \quad (4.7.3.1)$$

They also suggested that Tm50% should be equal to the "optimum age" defined as the age at which the biomass of a cohort is maximal.

Eq. 4.7.3.1 gives these values for Tm50%:

Tm50%	4 months	8 months	1 year	5 years	10 years
M	3.2	1.9	1.4	0.3	0.1