

6 Mortality

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■ 6.1 INTRODUCTION

Mortality is a concept that describes the rate at which individuals are lost from a population. This concept is central to understanding the ecology of populations, particularly their dynamics, and is essential to managing fish stocks. Each species has developed mortality patterns, with specific distribution over life stages and age-groups. High mortality is common at the egg or larval stages, largely due to abiotic conditions, but the lethal effects of abiotic conditions usually become minor when the larvae become mobile. In the early stages of external feeding, limited food may directly influence mortality. If the fish survives, limited food becomes only an indirect source of mortality by retarding growth and lengthening the time spent searching for food, which makes the fish more vulnerable to predation. Later in life, fishing may be an important source of mortality. Knowledge about the patterns and causes of mortality helps fisheries scientists understand inter- and intraspecific interactions and interactions between the population and its abiotic environment.

When studying fish populations from a consumptive outlook, mortality has traditionally been separated into natural and fishing sources. Natural mortality combines death by disease, starvation, predation, inadequate environmental conditions, and old age; most of these causes are interdependent, so the distinctions are arbitrary. Fishing mortality combines harvest and any effect directly linked to the fishing process (e.g., bycatch in commercial fishing gear or death after catch and release). Describing and estimating total, natural, and fishing mortalities is often a challenge in natural populations given sampling limitations and inability to meet fully the assumptions of most estimation procedures.

■ 6.2 BASIC CONCEPTS

Mortality represents the number of individuals that die during a certain time interval. If, for instance, N_t individuals are present in a population at the start of an interval of length \hat{I}_t , and N_{t+1} survive to the end of the interval, then $(N_t - N_{t+1}) / \hat{I}_t$ equals interval absolute mortality. When comparing populations over time or space, interval absolute mortality can be uninformative because population sizes may

differ. A more useful expression is obtained by representing $(N_t - N_{t+1})/\hat{I}_t$ as a fraction of N_t , and as such, interval absolute mortality becomes interval mortality rate (A ; $[(N_t - N_{t+1})/\hat{I}_t]/N_t$) and comparable over populations. The interval mortality rate represents the fraction of individuals present at the start of an interval that actually dies during the interval. Traditionally, A has been taken to represent a 1-year \hat{I}_t but may be defined to represent any \hat{I}_t time interval.

Theory and empirical observations suggest that the number of fish in a cohort does not decline linearly through a time interval. Instead, it declines approximately exponentially at a rate proportional to the number alive at any point in time (Figure 6.1). This pattern of decrease indicates that $A = [(N_t - N_{t+1})/\hat{I}_t]/N_t$ is not constant over time because it is affected by a changing N_t . An alternative method for expressing mortality is the instantaneous mortality rate (Z ; Table 6.1), which linearizes the exponential pattern of A through a logarithmic transformation; thus, $(\log_e N_t - \log_e N_{t+1})/\hat{I}_t = Z$ for any \hat{I}_t . We note that as \hat{I}_t approaches zero, Z and A converge because Z represents the death rate at an instant, whereas A represents the death rate at the end of an interval; as the interval becomes small and its width approaches zero, an instant and an interval become indistinguishable.

For example, if by the end of a 1-year interval $A_{\text{annual}} = 0.80$ and, thus, $Z_{\text{annual}} = -\log_e(1 - 0.80) = 1.61$, then the instantaneous monthly mortality rate $Z_{\text{month}} = 1.61/12 = 0.134$ and interval monthly mortality rate $A_{\text{month}} = 1 - e^{-Z_{\text{month}}} = 0.125$. Similarly,

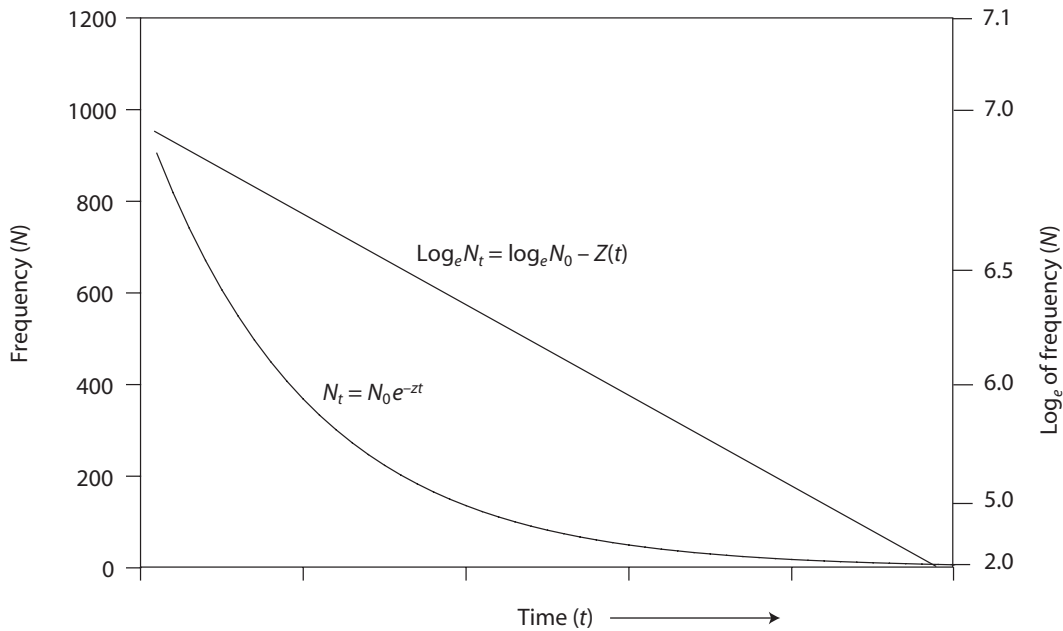


Figure 6.1 Catch curves are based on the assumption that a cohort will decline in frequency at a rate that is proportional to the abundance of the cohort at each instant in time. A \log_e transformation of frequency (N_t) changes an exponential curve into a straight line, which can be described using least-squares regression. The slope of the regression line, Z , represents the instantaneous mortality rate; the intercept (N_0) represents the estimated density at time zero.

Table 6.1 Parameters descriptive of mortality rates and relations among parameters. Symbols are as follows: interval mortality rate (A); instantaneous mortality rate (Z); interval fishing mortality (I); interval natural mortality (v); instantaneous natural mortality (M); instantaneous fishing mortality (F); conditional natural mortality (n); and conditional fishing mortality (m).

Mortality rates	Total	Fishing	Natural
Interval	$A = \mu + v = 1 - e^{-Z}$	$\mu = FA/Z = vF/M$	$\mu = MA/Z = \mu M/F$
Instantaneous	$Z = F + M = -\log_e(1 - A)$	$F = \mu Z/A = \mu M/v$	$M = vZ/A = vF/\mu$
Conditional interval	$A = m + n - mn$	$m = 1 - e^{-F}$	$n = 1 - e^{-M}$

$Z_{\text{week}} = 1.61/52 = 0.0310$ and $A_{\text{week}} = 0.0305$; $Z_{\text{day}} = 1.61/365 = 0.00441$ and $A_{\text{day}} = 0.00442$. Note that A and Z become alike as interval width decreased from a year to a day. Also, note that the additive property of instantaneous rates allows flexibility to interpolate or predict mortality for intervals other than the ones estimated and to estimate the number of individuals surviving to any point in time (Box 6.1).

Box 6.1 Basic Mortality Computations

Take for example a hypothetical fish population consisting of a single age-group. At the start of a 12-month interval, the age-group consists of 1,000 individuals, and at the end it has been reduced by mortality to 700. For this example,

interval absolute mortality = $N_0 - N_{12} = 1,000 - 700 = 300$;

interval mortality rate = $(N_0 - N_{12})/N_0 = (1,000 - 700)/1,000 = 0.300$; and

instantaneous mortality rate = $Z_{12} = -\log_e(1 - [N_0 - N_{12}]/N_0) = -\log_e(1 - [1,000 - 700]/1,000) = 0.357$.

Now, suppose we wish to know the fraction of the population remaining, the number of individuals, and the number of deaths at the end of 4 and 8 months intervals. For this, Z_{12} must be partitioned into 4-month (Z_4) and 8-month (Z_8) estimates as

$Z_4 = 4(Z_{12}/12) = 0.119$, and

$Z_8 = 8(Z_{12}/12) = 0.238$.

Interval mortality rates during the 4-month (A_4) and 8-month (A_8) intervals are then calculated as

$A_4 = 1 - e^{-Z_4} = 1 - e^{-0.119} = 0.112$, and

$A_8 = 1 - e^{-Z_8} = 1 - e^{-0.238} = 0.212$.

Numbers of individuals remaining (survival) after 4 months (N_4) and 8 months (N_8) are represented by

$N_4 = N_0 - (N_0 A_4) = 1,000 - (1,000 \cdot 0.112) = 888$, and

$N_8 = N_0 - (N_0 A_8) = 1,000 - (1,000 \cdot 0.212) = 788$.

The number of deaths during each interval is therefore 112 in the first 4-months, 100 between month 4 and month 8, and 88 between month 8 and month 12.

Interval and instantaneous mortality rates are also defined for fishing and natural mortalities. The sum of interval natural (ν) and fishing (μ) mortalities adds up to A , whereas the sum of instantaneous natural (M) and fishing (F) mortalities adds up to Z (Table 6.1). Interval mortality A and instantaneous mortality Z are associated as $A = 1 - e^{-Z}$ (Table 6.1); however, $\nu = 1 - e^{-M}$ and $\mu = 1 - e^{-F}$ only when natural and fishing mortalities occur in separate intervals, which is infrequent in freshwater fisheries. When they occur in the same interval, $1 - e^{-M}$ and $1 - e^{-F}$ are also defined as n and m , respectively, and referred to as conditional interval mortality because they estimate potential deaths during the interval had it been the only acting mortality. When n and m occur simultaneously, they compete for the same fish and do not add up to A ; instead, $A = m + n - mn$ (Table 6.1).

The effect of harvest on the total mortality of a population can be either additive or compensatory (Nichols et al. 1984). Additive mortality implies that an increment in fishing mortality leads to an equal increment in total mortality. Compensatory mortality implies that an increment in fishing mortality leads to a smaller or no increment in total mortality because natural mortality adjusts downwards to compensate for reduced density. Populations near carrying capacity are more likely to be regulated by density-dependent processes and display compensatory mortality. Hence, a population may exhibit additive mortality at low density and compensatory mortality at high density (section 6.8).

■ 6.3 CATCH-CURVE MODELS

Catch curves and their use in estimating mortality rates of fish populations have a history dating back to C. G. J. Petersen in the late nineteenth century. Most fisheries scientists are familiar with classic catch curves that graphically depict the decline in the number of older fish in a sample; however, the term catch curve applies to any analysis where the change in number of fish over age-classes is considered. This section will discuss common and historical approaches to using catch-at-age data to estimate mortality rates. Catch-curve techniques require several assumptions, including constant recruitment and mortality over years and equal catchability for all ages under consideration. If recruitment is constant, and the analysis is restricted only to ages fully recruited to the gear, then observed declines in abundance of successive age-classes would be due solely to mortality. We will discuss these assumptions and how to deal with situations in which one or more assumptions are not met.

6.3.1 Relative Abundance of Consecutive Age-Classes

In this approach, a single random sample comprising several age-groups is examined. The relative abundance of fish in consecutive age-classes is used to estimate mortality rates. These methods should not be used with catch data from a single sampling season (i.e., a standing age-frequency distribution) unless annual mortality and recruitment are thought to be reasonably constant and all age-groups considered are nearly equally vulnerable to the sampling gear.

6.3.1.1 *Heincke's Method*

In the early twentieth century, fisheries biologists readily took advantage of new techniques for aging marine fishes to examine mortality rates of exploited stocks. If it was assumed that equal numbers of fish were produced each year (i.e., recruitment was constant), then the ratio of the number of fish collected from two consecutive year-classes served as an estimate of interval mortality rate,

$$A = 1 - \frac{N_{t+1}}{N_t}. \quad (6.1)$$

Heincke (1913; cited in Ricker 1975) noted that old fish were less common in a random sample of a population than were young fish, and therefore more weight should be placed on the numbers of young fish when estimating mortality rates. Heincke's method calculated A and its standard error, SE_A , as

$$A = n_0/N, \text{ and} \quad (6.2)$$

$$SE_A = \sqrt{\frac{A(1-A)}{N}}, \quad (6.3)$$

where n_0 was the number of fish in the youngest age considered and N the sum of all fish considered (Box 6.2). Note that it is not important to have accurate ages of fish older than the age-group that serves to start the age series (Ricker 1975). Although this method is used infrequently, it is appropriate when old fish cannot be accurately aged, or when the circumstances prevent the sacrifice of large (likely old) fish to obtain hard bony structures for aging.

6.3.1.2 *Robson and Chapman's Method*

When the age of every fish in a large random sample is known with reasonable certainty, then a simple approach presented by Robson and Chapman (1961), and discussed by Ricker (1975) and Van Den Avyle and Hayward (1999), can be used to estimate survival rate (S) and its standard error (SE_S) as

$$S = \frac{T}{N + T - 1}, \text{ and} \quad (6.4)$$

$$SE_S = \sqrt{S \left(S - \frac{T-1}{N+T-2} \right)}, \quad (6.5)$$

where N is the total number of fish fully recruited to the gear and T is derived from the distribution of vulnerable ages in the sample as shown in Box 6.3. Robson

Box 6.2 Heincke's Method of Estimating Annual Mortality

From a reservoir, a large random sample of spotted bass was collected with electrofishing gear, and fish age was determined by inspecting otoliths. The number of fish in each age-class is given below.

Age (years)	1	2	3	4	5	6	7+
Number	257	407	147	32	17	5	4

There was some disagreement over the ages of the four largest and oldest fish, but they were all at least 7 years of age, so the data were coded accordingly. The low catch of age-1 fish relative to age-2 fish suggested that age-1 fish were not fully recruited to the electrofishing gear. When the calculations were limited to age-2 and older fish, annual mortality calculated with equation (6.2) was

$$A = \frac{n_0}{N} = \frac{407}{407 + 147 + 32 + 17 + 5 + 4} = \frac{407}{612} = 67\%,$$

and its standard error was

$$SE_A = \sqrt{\frac{A(1-A)}{N}} = \sqrt{\frac{0.67(1-0.67)}{612}} = 1.9\%$$

Using the same equation, the estimated annual mortality rate for age-3 and older fish was 72%. Alternatively, mortality rates between consecutive years could have been calculated using equation (6.1). For instance, annual mortality between age 2 and age 3 is

$$A_{2-3} = 1 - \frac{N_3}{N_2} = 1 - \frac{147}{407} = 64\%,$$

and between age 3 and age 4 is

$$A_{3-4} = 1 - \frac{N_4}{N_3} = 1 - \frac{32}{147} = 78\%.$$

Both of these approaches are very sensitive to violations of the assumption of constant recruitment. If recruitment is known to vary widely, other mortality estimation techniques should be considered.

and Chapman's method is a discrete-time model (Jensen 1985) that estimates interval survival using maximum-likelihood estimation. The assumptions regarding constant survival, constant recruitment, and equal vulnerability also apply to this method. In fact, Robson and Chapman (1961) stated that the age-frequency distribution from a single sample provides no insight whatsoever into the force of mortality acting on the population unless it can be stated that recruitment and mortality do not vary among years and among ages. Robson and Chapman (1961)

Box 6.3 Robson and Chapman's Maximum-Likelihood Estimate of Survival

Assume that all the fish in a large sample were aged and the numbers of fish in each age-class were tallied, as below. Along with constant (or near constant) recruitment and survival rates, the assumption of equal vulnerability to capture must be met. A cursory examination of the catch-at-age data suggests that the two youngest age-groups were not fully vulnerable, or recruited, to the gear (i.e., the curve does not truly begin to descend until age 3); therefore, the analysis will apply to only age-3 and older fish. The first step is to code each age, starting with zero for the youngest age considered fully recruited.

Age (years)	1	2	3	4	5	6	7	8	9	10
Catch (N_x)	90	164	162	110	55	41	20	14	7	5
Coded age (x)	–	–	0	1	2	3	4	5	6	7

An unbiased estimator of the annual survival rate (S) is

$$S = \frac{T}{N + T - 1},$$

where N is the total number of fish fully recruited to the gear ($N = 162 + 110 + 55 + 41 + 20 + 14 + 7 + 5 = 414$), and T is derived from the distribution of vulnerable ages in the sample, $T = \sum (xN_x) = 0(162) + 1(110) + \dots + 7(5) = 570$. Therefore,

$$S = \frac{570}{414 + 570 - 1} = 0.580.$$

The precision of this survival rate estimate is assessed by calculating its standard error, SE_S , as

$$SE_S = \sqrt{S \left(S - \frac{T-1}{N+T-2} \right)} = \sqrt{0.580 \left(0.580 - \frac{570-1}{414+570-2} \right)} = 0.018.$$

Note that the precision of this survival estimate is a function of the number of fish examined. Approximate 95% confidence intervals (CI) on the survival rate estimate are

$$CI_{0.95} = S \pm 1.96() = S \pm 1.96(0.018) = 0.58 \pm 0.035.$$

Annual mortality rate (A) is $1 - S$, or 0.42 ± 0.035 .

provided two useful alternatives to equations (6.4) and (6.5). First, they modified equations (6.4) and (6.5) to allow for estimation when only some of the youngest age-groups are aged and the remaining age-groups are pooled; this procedure sacrifices potential information available from the sample but may enhance accuracy and precision of predictions. Second, they provided a modified equation to apply to catch curves derived using age-length keys: when age-length keys are applied (i.e., the fish that are aged represent subsamples from fixed length-groups),

additional variation is introduced into the survival estimate, and equation (6.5) must be modified to calculate the variance.

6.3.2 Linearized Catch Curves

If fish density declines at a rate proportional to the number of fish present at each point in time, density will decline exponentially (Figure 6.1). Most fish populations exhibit this decline, and this characteristic allows estimation of instantaneous and interval mortality rates. If the \log_e of frequency is plotted in relation to time, the slope of a line fit to those observations will be the instantaneous mortality rate (Z). The instantaneous mortality rate can assume values ranging from 0 to slightly over 4, which correspond to interval mortality rates between zero and nearly 100%.

If all fish in a large random sample are aged, and natural logarithms of the catch at each age are taken, the slope of a regression line fit to the descending right limb of the catch curve should represent Z (Figure 6.2). Such plots are widely used by fisheries scientists to estimate mortality rates. Although the mathematics involved in estimating the slope of the catch curve are clear-cut (Box 6.4), there are a number of concerns or assumptions that need to be addressed when using

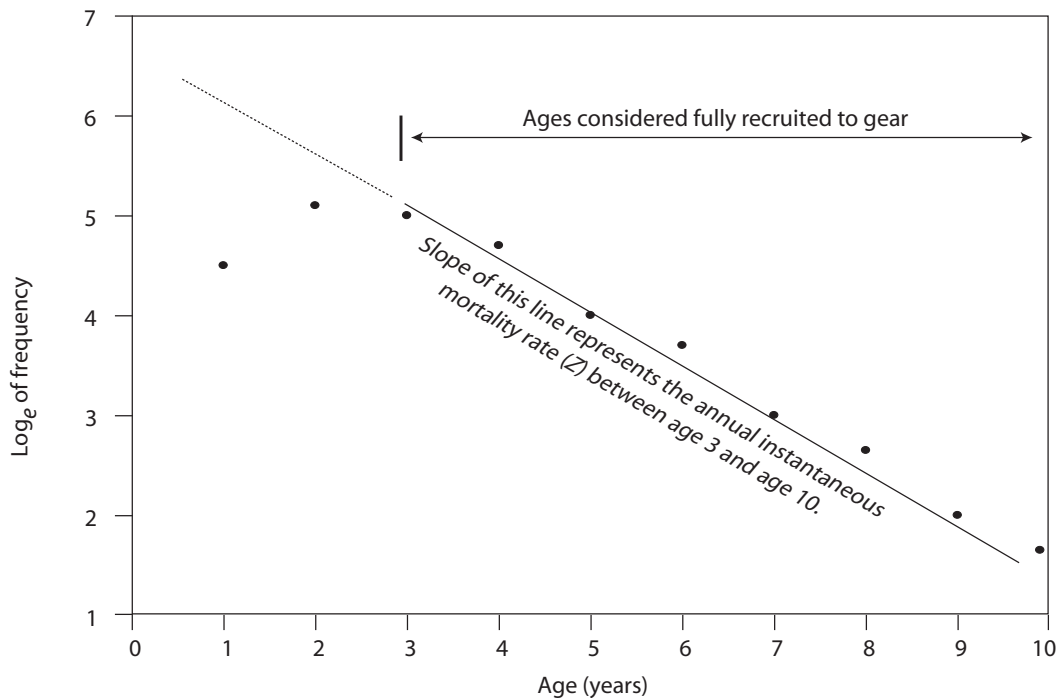


Figure 6.2 Hypothetical catch curve for a freshwater fish population sampled with electrofishing gear. The dashed line represents the expected catch of fish at age 1 and age 2. Catch-curve analysis would be limited to the descending right-hand portion of the curve between ages 3 and 10. See Box 6.4 for further explanation.

catch curves. Partial recruitment of the youngest age-classes to the gear is common, and estimates of mortality must be restricted to those ages considered “fully recruited” to the gear. In Figure 6.2, the catch curve has an ascending left-limb corresponding to lower than expected catches of age-1 and age-2 fish. The low catches of young fish could be due to the bias of electrofishing gear toward larger fish (i.e., only the largest age-1 and age-2 fish were vulnerable to capture). Perhaps young fish were less likely to occupy the shoreline habitat sampled with electrofishing gear. Similar vulnerability issues are also possible when using other gears, such as gill nets, trap nets, and trawls. Alternatively, the ascending left limb of the catch curve could have been caused by the production of weak year-classes in the 2 years preceding the sample. Without repeated sampling in subsequent years, it is impossible to determine which explanation (gear bias or poor recruitment) is most feasible.

Constant recruitment is the exception rather than the rule in many fish populations; however, moderate and random variations in recruitment will not change the general form of a catch curve, and mortality rates can still be estimated (Ricker 1975). In practice, reasonable estimates of annual mortality can usually be derived from catch curves for species such as crappies that often exhibit erratic recruitment (Allen 1999). A common scenario is that depicted by the catch curve in Figure 6.3A, which shows recruitment of largemouth bass varying erratically among years. In these situations, successive years of data can be pooled (Figure 6.3B), and the influence of erratic recruitment can be dampened. Data are combined if it can be assumed that the population is in a state of equilibrium except for random variations in recruitment (Ricker 1975). Pooling several years of data may also resolve the problem of small sample size, particularly for the oldest age-classes. Extreme variation in catch-curve mortality estimates is possible when the few representatives of the oldest age groups are included (Van Den Avyle and Hayward 1999), and it is customary to truncate the analysis at the oldest age-group with at least five representatives. In Figure 6.3A, only 102 fish were collected in the 1992 sample, and the frequency of fish in the oldest age-class (age 7) was less than 5. Pooling data from two consecutive years (Figure 6.3B) reduced the scatter of points around the catch curve and allowed estimation of annual mortality out to age 7. Alternatively, the information provided by each age-group may be weighted according to their representation in the sample (section 6.3.4).

Modest fluctuations in recruitment are acceptable when constructing catch curves, if the fluctuations are random in nature and not serially correlated over time. However, steadily decreasing or increasing recruitment can confound catch-curve analyses. For instance, the introduction of a forage fish to boost prey abundance for piscivores may have the unintended consequence of reducing recruitment of those same piscivores (Johnson and Goettl 1999). Similarly, the phenomenon of reservoir aging may cause long-term shifts in community composition and thereby recruitment (Agostinho et al. 1999). In a population experiencing steadily declining recruitment, a catch curve constructed from a single random sample will underestimate annual mortality. Conversely, steadily increasing recruitment would cause overestimation of annual mortality. Systematic changes

Box 6.4 Mortality Rates from the Slope of Regression Line

The catch-at-age data shown in Box 6.3 and Figure 6.2 are repeated here, along with the natural logarithms of the number at each age.

Age (years)	1	2	3	4	5	6	7	8	9	10
Number	90	164	162	110	55	41	20	14	7	5
Log _e number	4.50	5.10	5.09	4.70	4.01	3.71	3.00	2.64	1.95	1.61

The catch-curve analysis is limited to those ages considered fully recruited to the gear (age 3 and older). At least five fish in the oldest age-class are present, so the mortality rate will apply to ages 3–10. Using least-squares regression, the slope of the line describing the relation between log_e of number (y-variable) and age (x-variable) can be calculated longhand, by means of a spreadsheet, or with the following SAS program:

```
Data A;
Input Age Catch @@;
If Age < 3 then delete;
LogN = Log (catch);
Cards;
1 90 2 164 3 162 4 110 5 55 6 41 7 20 8 14 9 7 10 5;
Proc Reg Data = A; Model LogN = Age;
Run;
```

The SAS output consists of an analysis of variance (ANOVA) table and estimates of the slope, as follows.

Table Regression procedure (log_e unweighted data) for catch-at-age data. Abbreviations are as follows: mean square error (MSE) and coefficient of variation

$$CV = 100 \left(\sqrt{\frac{MSE}{\bar{X}}} \right), \text{ where } \sqrt{MSE} = \text{Root MSE in SAS output.}$$

Analysis of Variance					
Source	df	Sum of squares	Mean square	F-value	P > F
Model	1	10.97660	10.97660	1072.55	<0.0001
Error	6	0.06140	0.01023		
Corrected total	7	11.03801			
R ²	0.9944	Root MSE	0.10116		
Adjusted R ²	0.9935	Dependent mean	3.33739		
CV	3.03123				

Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	6.66033	0.10758	61.91	<0.0001
Age	1	−0.51122	0.01561	−32.75	<0.0001

The slope of the line (−0.51122) is listed under the heading “Parameter Estimates” for the variable “age.” The slope of the line represents the instantaneous annual mortality rate, Z . The antilog (e^{-Z}) of the instantaneous mortality rate is the annual survival rate (S) or 60%, and mortality (A) is $1 - S$, or 40%. The standard error of the slope (SE_Z), obtained from the SAS program or equation (6.6), was 0.01561. Thus, the 95% CIs for Z are

$$CI_{0.95} \text{ of } Z = Z \pm t_{(0.05, n-2)} SE_Z.$$

Eight ages were used in the catch curve; therefore, there are $8 - 2$ df. Thus,

$CI_{0.95}$ of $Z = 0.511 \pm 2.447(0.0156) = 0.473$ and 0.549 , and
 $CI_{0.95}$ of $A = 1 - e^{-0.473} = 0.377$ and $1 - e^{-0.549} = 0.422$.

These results suggest that one would be 95% confident that the true mortality rate was between 38% and 42%, and the best estimate would be 40%. Note that the precision of this estimate is a function of the number of age-groups present. When these data were analyzed using the Chapman–Robson method (Box 6.3), the estimated annual mortality rate was slightly higher (42%).

The following SAS program performs weighted regression analysis on the above data, deflating the importance of older, rare fish in the sample. In this example, each observation is weighted by the predicted number of fish in each age-class as suggested by Maceina and Bettoli (1998). The first regression procedure calculates predicted values of $\log_e(\text{catch})$ for each age and outputs them to a second data set, where they are used as weights in the second regression procedure.

```

Data A;
Input Age Catch @@;
If Age < 3 then delete;
LogN = Log (catch);
Cards;
1 90 2 164 3 162 4 110 5 55 6 41 7 20 8 14 9 7 10 5
;
Proc Reg Data = A; Model LogN = Age; Output out = B Predicted = W;
Proc Reg Data = B; Model LogN = Age; Weight W;
Run;

```

The SAS output for the first regression procedure is the same as above; the ANOVA results and slope estimate for the weighted regression procedure are as follows:

Table Regression procedure (\log_e weighted data) for catch-at-age data.

Analysis of Variance					
Source	df	Sum of squares	Mean square	F-value	P > F
Model	1	32.14136	32.14136	968.34	<0.0001
Error	6	0.19915	0.03319		
Corrected total	7	32.34051			
R^2	0.9938	Root MSE	0.18219		
Adjusted R^2	0.9928	Dependent Mean	3.74851		
CV	4.86026				
Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	6.66128	0.10002	66.60	<0.0001
Age	1	-0.51139	0.01643	-31.12	<0.0001

In this example, the slope of the weighted regression (-0.51139) is almost identical to the slope for the unweighted regression line (-0.51122), although that is not always the case. It is usually desirable to estimate mortality rates over the greatest number of age-classes, but the oldest ages are often represented by fewer than five individuals. Use of weighted regression may allow relaxing the “requirement” that the oldest age-class should always be represented by at least five individuals because the influence of the oldest age-classes on the regression line will be reduced.

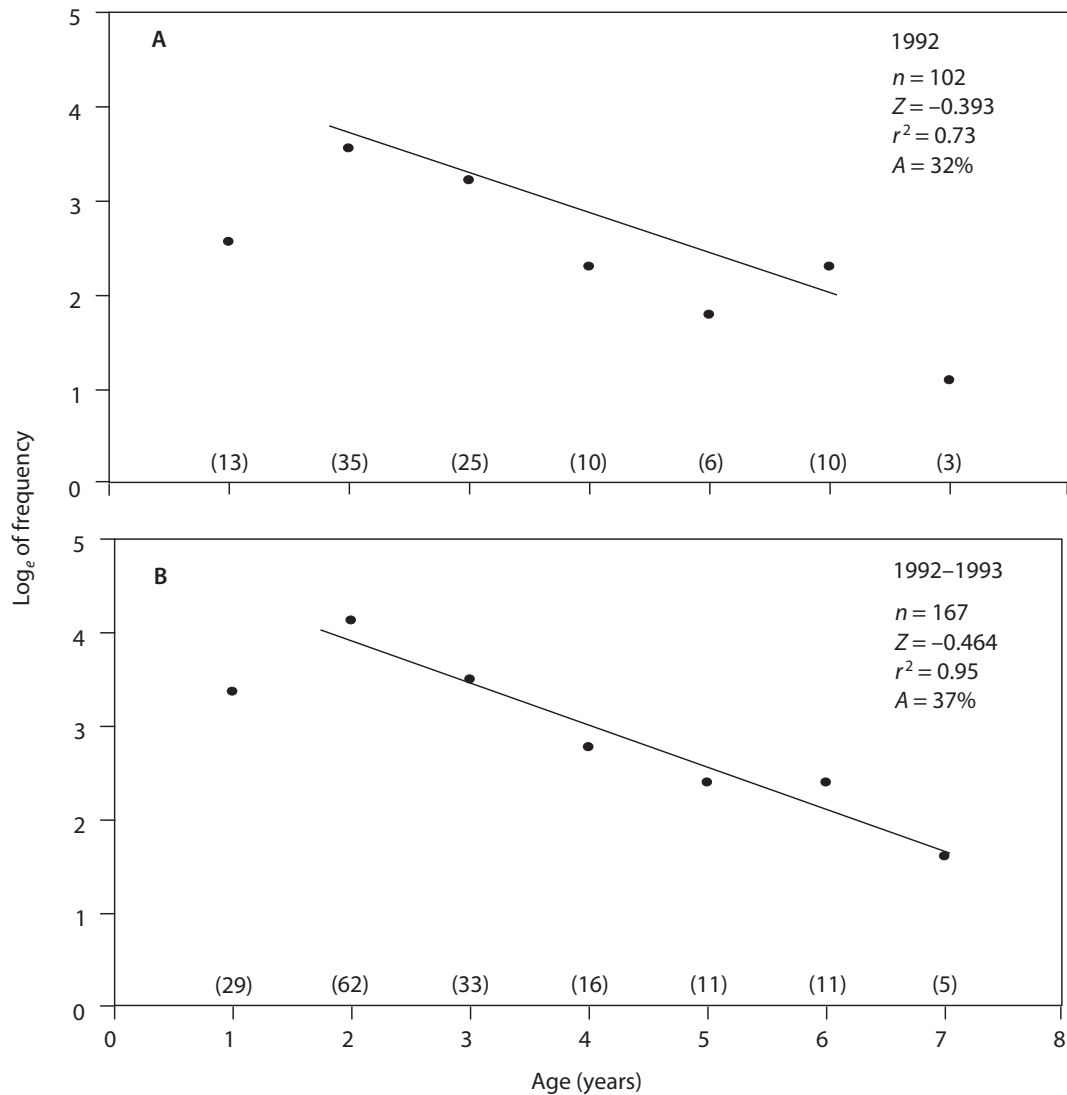


Figure 6.3 Catch curves for largemouth bass collected in (A) one year and (B) two consecutive years in Normandy Reservoir, Tennessee. Numbers in parentheses are the catch at each age. Pooling catch-at-age data over two consecutive years did not appreciably change the estimate of annual mortality; however, the influence of erratic recruitment was dampened and age-7 fish could now be included in the analysis, both of which contributed to an increased r^2 . The estimate of interval mortality rate is given as A .

(or lack thereof) in recruitment could be identified by examining historical trends in abundance of age-0 fish. For instance, many agencies rely on annual fall trap-netting to index the abundance of age-0 and age-1 crappies, and long-term databases may be readily available (Chapter 4). If trends in recruitment are detected, mortality rates could be estimated after adjusting for variable recruitment (Box 6.5) or by analysis of cohort catch curves (section 6.3.5).

Box 6.5 Adjusting Catch-at-Age Data for Unequal Recruitment

Trap-netting of white crappies in a midwestern reservoir in the spring of 2001 provided information on the standing age structure for the 281 fish collected representing six age-classes. Previous studies indicated that all ages were recruited to the trap nets, so the goal was to calculate instantaneous mortality between ages 1 and 6. The catch-at-age data clearly indicated that recruitment varied widely among years, and therefore one of the assumptions of catch-curve analysis was violated. It was assumed that the trap-net catches accurately indexed recruitment variability, and these data were used to create an index of year-class strength (I_i) for each i year as $I_i = r_i/r_L$, where r_i = number of age-0 fish collected with trap nets in year i , and r_L = lowest number of age-0 fish collected during the time series. The index was used to adjust the representation of each year-class N_i in spring 2001 to a constant recruitment as N_i/I_i .

Table Adjusting for non-constant recruitment.

Metric	Year-class					
	2000	1999	1998	1997	1996	1995
Unadjusted standing age distribution estimated by trap-netting in 2001 (N_i)	150	28	5	69	12	17
Number of age-0 fish collected annually with trap nets (r_i) between 1995 and 2000	1,665	556	111	2,330	445	1,220
Index of year-class strength ($I_i = r_i/r_L$)	15	5	1	21	4	11
Adjusted catch (N_i/I_i)	10	5.6	5.0	3.3	3.0	1.5

Plots of the adjusted and unadjusted data relative to age would show that the adjusted data have less scatter around the regression line. In this example, the slope of the adjusted catch-curve line was $Z = -0.34$, translating into $A = 29\%$.

Many freshwater sport fish populations are maintained or augmented by stocking age-0 fish, which can confound catch-curve analysis. In situations where consistent numbers and sizes of fish are stocked annually, and no natural reproduction occurs, the assumption of constant recruitment might be easily met. Conversely, estimating mortality rates using catch curves is confounded when rates, sizes, and frequency of stockings vary, as depicted in Figure 6.4; in such instances, other estimation approaches should be investigated (Box 6.5 and section 6.3.5).

It should be apparent from the comments above that catch curves require fairly large samples of at least several hundred individuals, particularly for long-lived species. Accurate aging in most locales requires the use of otoliths, and if it is important to limit the number of individuals sacrificed, age-length keys can be used to estimate the number of fish at each age from subsampled data (Bettoli and Miranda 2001).

Biases in catch-curve mortality estimates due to unequal recruitment can often be identified and sometimes rectified (e.g., by pooling several years of data). However, variation in mortality rates among age-classes may be difficult to detect and hard to remedy. Ricker (1975) described different shapes, or functional forms,

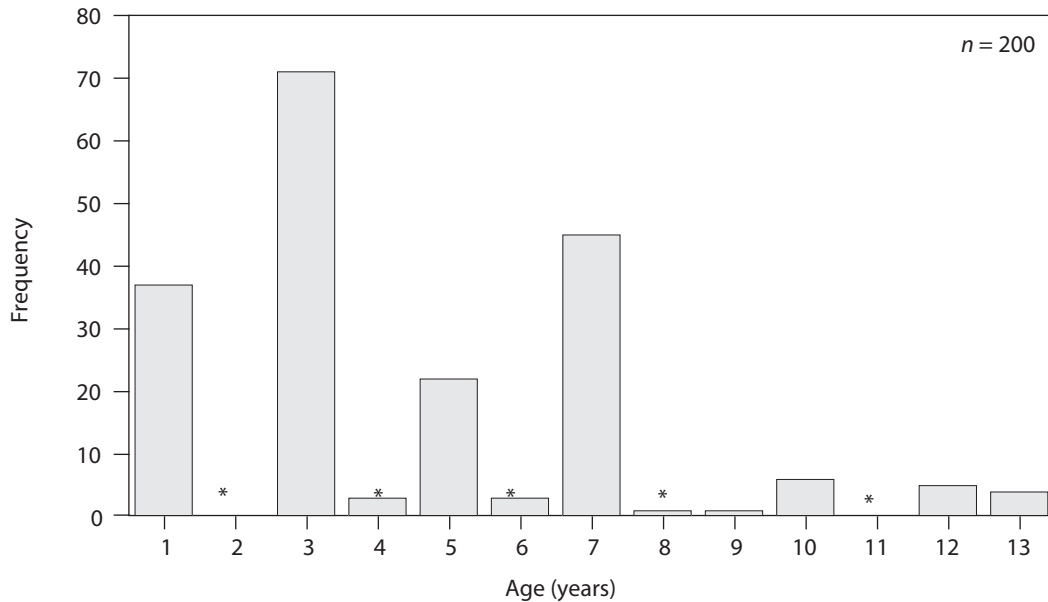


Figure 6.4 Frequency-at-age data for a standing age distribution of walleyes in Dale Hollow Reservoir, Tennessee–Kentucky, December 1999 (Vandergoot and Bettoli 2001). Asterisks denote years when no walleyes were stocked. In years when walleyes were stocked the number of fish stocked varied, which confounds the use of catch curves to estimate annual mortality.

of catch curves derived from empirical data and how forces of natural mortality and fishing mortality may shape the curves. In situations where larger (older) fish are exploited at higher rates than are small fish, the possibility exists that higher rates of fishing mortality are compensated by falling rates of natural mortality (Allen et al. 1998), resulting in no substantial change in total mortality rates over all ages fully recruited to the gear.

When natural mortality is constant, a catch curve for a heavily exploited population with a minimum-length-limit harvest regulation in effect might increase in slope beyond some age due to intense exploitation past the length limit (Figure 6.5). Such biases, caused by violation of the constant-mortality assumption, can be reduced if the catch curve is split into the unexploited and exploited segments and analysis applied to each segment independently. For instance, if a walleye population is being fished under a 40-cm length limit, the catch-curve analysis could be applied separately to those age-classes smaller than 40 cm (Z would represent M if catch–release mortality and illegal harvest were low), and those larger than 40 cm (Z would represent $M + F$ if it was assumed that all legal-sized fish were exploited equally).

6.3.3 Precision of Catch-Curve Mortality Estimates

The precision of the instantaneous mortality rate Z derived from regression of abundance as a function of age is assessed by calculating its variance (S_z^2), which is the variance of the slope of the regression line (Neter et al. 1990):

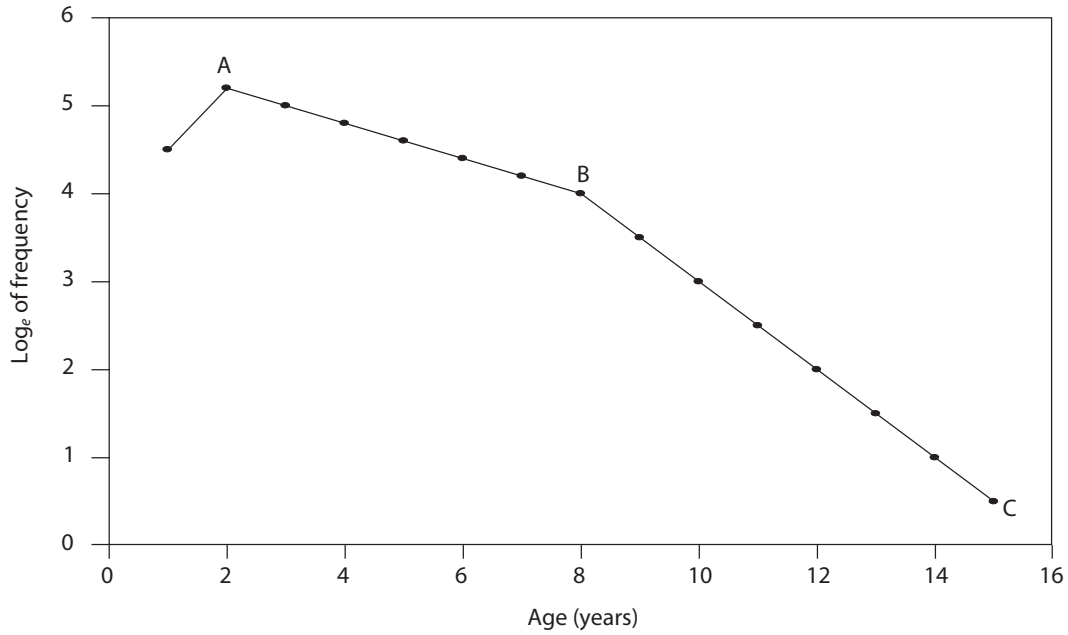


Figure 6.5 Catch curve for a hypothetical population that experiences constant recruitment and constant natural mortality but an increase in fishing mortality past age 8. Separate estimates of Z should be calculated for fish age 2 through age 8 (line A-B) and for fish age 8 through age 15 (line B-C).

$$S_z^2 = \frac{\text{MSE}}{\sum X_i^2 - ([\sum X_i]^2/n)}, \quad (6.6)$$

where MSE is the mean square error term from the regression model, X_i are the ages used in constructing the catch curve, and n the number of i ages included in regression. The square root of S_z^2 represents the standard error of the slope (S_z), and 95% confidence limits would be

$$\text{CI}_{0.95} \text{ of } Z = Z \pm t_{(0.05, n-2)} S_z. \quad (6.7)$$

The proper t -value is that for a two-tailed test. The statistical software package SAS (SAS Institute 1998), as well as others, provides estimates of the standard errors of the slopes when performing regression analysis. Note that the precision of Z increases with the number of ages i included in the analysis and decreases as the scatter of points along the regression line increases. In only rare instances will the slope not be declared different from zero; such outcomes should not preclude calculation and reporting of mortality rates (Maceina and Bettoli 1998).

Testing whether two instantaneous mortality rates differ is equivalent to testing for inequality of slopes. Although the mathematics are cumbersome, the null hypothesis that the slopes are equal can be tested using an F -test generated by a SAS program (Box 6.6).

Box 6.6 Comparing Instantaneous Mortality Rates from Catch Curves

Comparing instantaneous mortality rates (Z) for two or more populations is equivalent to comparing the slopes of the catch-curve regression lines. Below are catch-at-age data for two populations that fully recruited to the gear at age 2.

Age (years)	1	2	3	4	5	6	7	8	9
Lake 1	433	818	243	67	48	5	30	42	22
Lake 2	305	491	155	100	30	49	16	6	

The SAS program to calculate and compare the slopes of the catch-curve regression lines is given below.

```

Data A;
Input Lake Age Catch @@;
LnCatch = log(catch);
If Age < 2 then delete;
Cards;
1 1 433 1 2 818 1 3 243 1 4 67 1 5 48 1 6 5 1 7 30 1 8 42 1 9 22
2 1 305 2 2 491 2 3 155 2 4 100 2 5 30 2 6 49 2 7 16 2 8 6
;
Proc SORT; By Lake;
Proc REG; Model LnCatch = Age; By Lake;
Proc GLM; Class Lake; Model LnCatch = Age Lake Age*Lake; Run;

```

The output is given as follows:

Table Catch-curve regression (\log_e catch) for Lake 1.

Analysis of Variance					
Source	df	Sum of squares	Mean square	F-value	P > F
Model	1	8.94246	8.94246	7.02	0.0380
Error	6	7.63908	1.27318		
Corrected total	7	16.58154			
R^2	0.5393	Root MSE	1.12835		
Adjusted R^2	0.4625	Dependent mean	4.01440		
CV	28.10766				
Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	6.55225	1.03737	6.32	0.0007
Age	1	-0.46143	0.17411	-2.65	0.0380

Table Catch-curve regression (\log_e catch) for Lake 2.

Analysis of Variance					
Source	df	Sum of squares	Mean square	F-value	P > F
Model	1	12.18239	12.18239	72.74	0.0004
Error	5	0.83743	0.16749		
Corrected total	6	13.01981			
R^2	0.9357	Root MSE	0.40925		
Adjusted R^2	0.9228	Dependent mean	3.95749		
CV	10.34116				

Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	7.25554	0.41649	17.42	<0.0001
Age	1	-0.65961	0.07734	-8.53	0.0004

Table The general linear model (GLM) procedure for comparison of regressions (\log_e catch) of lakes 1 and 2 ($n = 15$). Sum of squares abbreviated as SS.

Source	df	SS	Mean square	F-value	P > F
Model	3	21.13693771	7.04564590	9.14	0.0025
Error	11	8.47650657	0.77059151		
Corrected total	14	29.61344429			
R^2	0.713762	Root MSE	0.877833		
CV	22.01277	\log_e catch mean	3.987838		

Source	df	Type I SS	Mean square	F-value	P > F
Age	1	20.08252514	20.08252514	26.06	0.0003
Lake	1	0.39457442	0.39457442	0.51	0.4892
Age*Lake	1	0.65983816	0.65983816	0.86	0.3746

Source	df	Type III SS	Mean square	F-value	P > F
Age	1	21.11299343	21.11299343	27.40	0.0003
Lake	1	0.26295830	0.26295830	0.34	0.5709
Age*Lake	1	0.65983816	0.65983816	0.86	0.3746

The instantaneous mortality rates (i.e., slopes of the catch-curve regression lines) for lakes 1 and 2 were -0.46143 and -0.65961, respectively; thus, annual mortality rates were 37% and 48%. Direct your attention to the Type III sum of squares (SS). The null hypothesis that the two slopes were similar is tested with the F-value associated with the Age*Lake interaction term ($F = 0.86$). At 1 and 11 df, the significance of the test is $P = 0.3746$. Thus, we accept the hypothesis that the slopes were similar.

6.3.4 Weighted Catch-Curve Analysis

Regression lines fit for catch curves give equal weight to each observation. For example, in the sample of largemouth bass in Figure 6.3B, a frequency of five age-7 fish carried as much weight when fitting the line as a frequency of 62 age-2 fish. However, it is sometimes desirable to weight each observation according to the amount of information it contains (Steel and Torrie 1980). Weighted linear regression will deflate the influence of older and rarer fish (Maceina 1997). A SAS program to perform weighted catch-curve regression is given in Box 6.4. In our largemouth bass example with the 2 years of data (Figure 6.3B), the weighted regression using the predicted $\log_e(\text{catch})$ at each age as the weighting factor yielded a slope Z of -0.479 , which translates to an A of 38%, in this case similar to the unweighted estimate of 37%.

6.3.5 Cohort Catch Curves

When ancillary data suggest that recruitment, mortality rates, or both are varying enough to render standard catch-curve analysis unreliable, mortality rates can be estimated by following a year-class, or cohort, over time. Although this approach avoids the need for assuming constant recruitment, the assumption of constant mortality is still required if mortality is estimated by regressing catch at age over more than two ages or years.

All of the preceding catch-curve examples have discussed estimating annual mortality rates based on a single, large random sample that represents a standing age structure or a pooling of several annual samples that represents an average standing age structure. However, catch curves can also be constructed to estimate cohort mortality over short time frames by use of multiple samples. For instance, if a cohort of hatchery fish is marked before stocking, subsequent sampling of marked fish should reveal a decline in its abundance over time. If the catch data are \log_e transformed and plotted against days poststocking, the slope of the line will represent the instantaneous daily mortality rate, which can then be expanded to estimate mortality on a weekly, monthly, or annual basis, as in the example of brown trout in Figure 6.6. Similarly, in a study of age-0 largemouth bass mortality, Timmons et al. (1980) collected fish in shoreline rotenone samples weekly through the summer and fall and fit a catch curve to the declining catch per unit effort. Weekly instantaneous mortality rate was -0.226 , which translated into a weekly interval mortality rate of 20%.

Correspondingly, annual mortality for individual year-classes can be estimated by examining declining abundance in annual samples (Box 6.7). In many situations in which routine monitoring efforts provide samples of fish that are subsequently aged, long-term databases are available to perform these analyses.

■ 6.4 LENGTH-BASED MODELS

Length-based models do not use estimates of age directly; instead they use growth parameters such as the L_∞ (asymptotic length) and K (rate at which L_∞ is approached) parameters from the von Bertalanffy or other growth models (Chapter

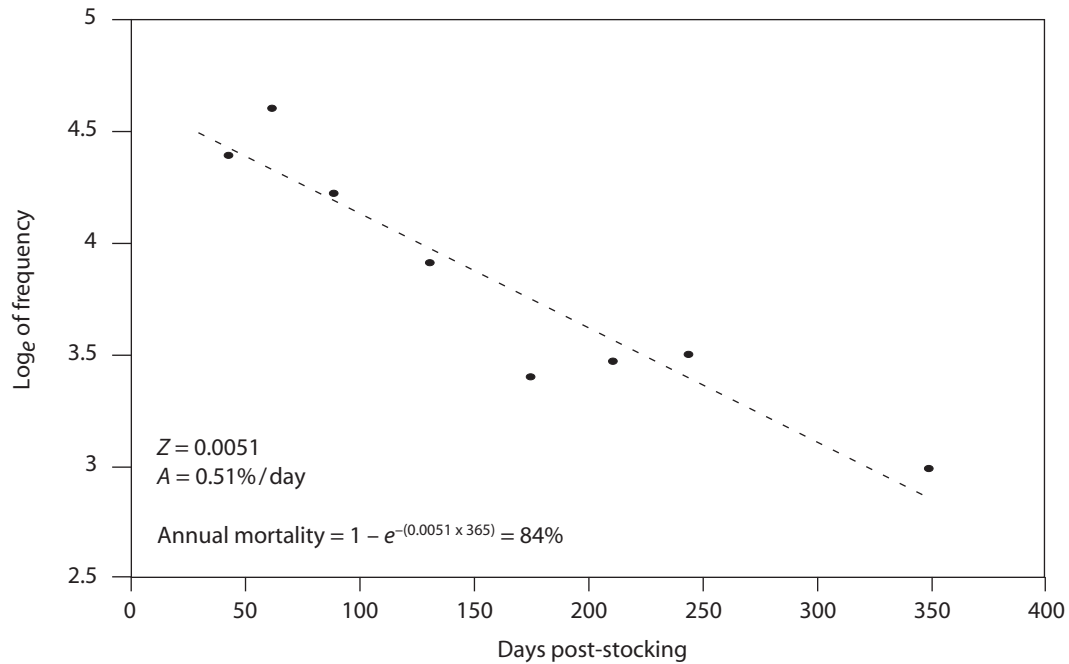


Figure 6.6 Catch curve for microtagged brown trout ($N = 17,322$) stocked into the Watauga River, Tennessee, March 1998, and subsequently sampled using electrofishing gear on eight dates (Bettoli 1999). Note that the daily instantaneous mortality rate (Z) and the daily interval mortality rate (A) are similar because the size of the interval is small. During a 32-week (224 d) creel survey that began when the fish were stocked, it was estimated that 4,612 of these brown trout were harvested during the survey period; thus, the interval exploitation rate (μ) was 4,612/17,322, or 27%. The total mortality rate (A) over that same interval was $1 - e^{-(Z \times 224\text{ d})} = 68\%$. Thus, the interval natural mortality rate (μ) was $A - \mu = 41\%$.

5) to convert length to age. Like catch-curve models, assumptions of length-based models include (1) recruitment is constant within the period covered by the length distribution, or at least recruitment has varied in a random fashion, (2) mortality is constant over ages, (3) only lengths fully recruited to the gear are included (equivalent to the descending portion of a catch curve), (4) growth is constant and adequately described by the growth model, and (5) the sampling gear adequately represents the standing length distribution. Another assumption made by length-based models is that recruitment into the smallest length considered for analysis is constant through time each year, so that the shape of the length distribution and mean length does not vary seasonally. This last assumption is violated in populations that exhibit seasonal instead of continuous recruitment but may be avoided by taking multiple samples within the year and pooling them before analysis (Ralston 1989) or by limiting analysis to longer (i.e., older) fish for which length at age is generally more variable and recruitment spread out over a year. Given these stringent assumptions, length-based estimates should be used when only a rough approximation will do or there is no better option.

Box 6.7 Cohort Catch Curves

Spring electrofishing samples at 40 sites in Normandy Reservoir indicated that recruitment by spotted bass varied more than twofold among years (Sammons and Bettoli 1998); therefore, analysis of cohort catch curves was employed. The catch from the 1992 cohort in annual samples taken between 1993 and 1998 was as follows.

Sample year	1993	1994	1995	1996	1997	1998
Age (years)	1	2	3	4	5	6
Number	65	66	27	6	4	1

These and other data suggested that fish were not fully recruited to the gear until age 2. The Chapman–Robson estimator (Box 6.3) was used to estimate annual survival, S , and ages 2 through 6 were assigned coded ages of 0 to 4. Thus, $N = 104$; $T = 55$;

$$S = \frac{T}{N + T - 1} = 0.35,$$

$SE_S = 0.046$, and

$$CI_{0.95} = 0.35 \pm 1.96(SE_S) = 0.35 \pm 0.090.$$

Alternatively, the slope of the catch curve could be calculated to estimate Z . The low catch of age-6 fish restricted the analysis to ages 2 through 5. Natural logarithms were taken of the catch data, and a regression line was fit to the points, yielding a slope of -0.99 and a SE of 0.14 . Thus, annual survival for ages 2 through 5 was $S = e^{-0.99} = 0.37$. Although this estimate was similar to the 35% Chapman–Robson estimate, the CIs (calculated with equation [6.7]) were broad (20–68%) because of the small number of age-classes in the regression model. In this example, the Chapman–Robson estimate and variance are clearly superior to the regression estimate.

6.4.1. Estimates from Average Length

The rationale behind these methods is that as mortality increases, the average length of fish in a population is expected to decrease. Various models have been developed to convey this relation (reviewed by Hoenig et al. 1983), but the most common is that attributed to Beverton and Holt (1956):

$$Z = K \frac{L_{\infty} - L_{mean}}{L_{mean} - L_x}, \quad (6.8)$$

where K and L_{∞} are von Bertalanffy growth parameters, L_x the length above which all fish are equally vulnerable to capture by the collection gear, and L_{mean} the mean length of fish larger than L_x .

A similar method but based on median length instead of mean length was developed by Hoenig et al. (1983):

$$Z = \frac{0.693K}{Y_{median} - Y_x}, \quad (6.9)$$

where $Y_{\text{median}} = -\log_e(1 - L_{\text{median}}/L_{\infty})$; $Y_x = -\log_e(1 - L_x/L_{\infty})$; and L_{median} is the median length of fish above L_x . Hoenig et al. (1983) indicated that estimates based on the median length were more robust because median length is less sensitive to variability in growth and year-class strength than is mean length. Box 6.8 shows how equations (6.8) and (6.9) are applied to estimate mortality.

Approximate variances for Z in equations (6.8) and (6.9) were derived by Hoenig et al. (1983) but are not reproduced here because of their length. Alternatively, variances may be derived by bootstrapping from the expected distributions of K , L_{∞} , L_x , L_{mean} , and L_{median} . Bootstrapping (Efron and Tibshirami 1998; Haddon 2001) is a method for estimating variance based on resampling from the statistical distribution of each variable included in the computation of Z .

6.4.2 Estimates from Length-Frequency Distributions

When a length-frequency distribution is available a catch curve may be constructed through conversion of lengths to age relative to L_{∞} . Pauly (1984) developed a length-converted catch-curve procedure that consists of regressing the logarithm of the number of fish in the i th length interval (N_i , dependent variable) against the relative age t'_i of fish in the interval:

$$\log_e(N_i) = a - bt'_i, \quad (6.10)$$

where $t'_i = -\log_e(1 - [L_{\text{mid}}/L_{\infty}])$, and L_{mid} is the midpoint of the i th length interval. The slope of this regression (b) represents $1 - (Z/K)$, and thus $Z = K(1 - b)$. An example is given in Box 6.8. A variance equation for Z has not been derived; however, the variance may be estimated by bootstrapping from the distributions of K and b .

When estimates of L_{∞} and K are not available, several methods may be used to derive approximations. First, dividing the mean length of the three largest fish known from the population stock by 0.95 may adequately approximate L_{∞} when the population is not too heavily exploited (Pauly 1984). Second, L_{∞} may be estimated from the maximum length of fish observed (L_{max}) with an empirical equation derived by Froese and Binohlan (2000; $\log_e L_{\infty} = 0.044 + 0.984 \log_e L_{\text{max}}$; length in centimeters). Note that L_{∞} is smaller than L_{max} because L_{∞} represents a population mean, whereas L_{max} represents the largest fish. Third, L_{∞} may be approximated through regression of L_x (L_x = lower limit of each length interval in the length-frequency distribution) on $L_{\text{mean}} - L_x$ (L_{mean} = mean length of fish larger than L_x in the length-frequency distribution) as suggested by Wetherall et al. (1987):

$$(L_{\text{mean}} - L_x) = a - bL_x, \quad (6.11)$$

where $L_{\infty} = -a/b$. Once an estimate of L_{∞} is obtained by one or more of these methods, K may be estimated by rearranging the growth equation, and if an estimate of length at time t (L_t) is available and t_0 is assumed equal to zero,

$$K = \frac{-\log_e(1 - [L_t/L_{\infty}])}{t}. \quad (6.12)$$

Box 6.8 Mortality Estimation with Length-Based Models

We use a largemouth bass data set from Columbus Lake, Mississippi, to illustrate mortality computations from length-based models. The von Bertalanffy model parameters (K and L_∞) were available from a parallel study in Columbus Lake and were $K = 0.226$ and $L_\infty = 636$ mm (see Chapter 5 for calculations). All largemouth bass 150 mm or longer were considered equally vulnerable to the collection gear (electrofishing); thus, $L_x = 150$. The mean and median length of fish 150 mm or longer in the data set were $L_{\text{mean}} = 260$ and $L_{\text{median}} = 255$. Therefore, based on equation (6.8),

$$Z = K(L_\infty - L_{\text{mean}})/(L_{\text{mean}} - L_x) \\ = 0.226(636 - 260)/(260 - 150) = 0.773.$$

Based on equation (6.9),

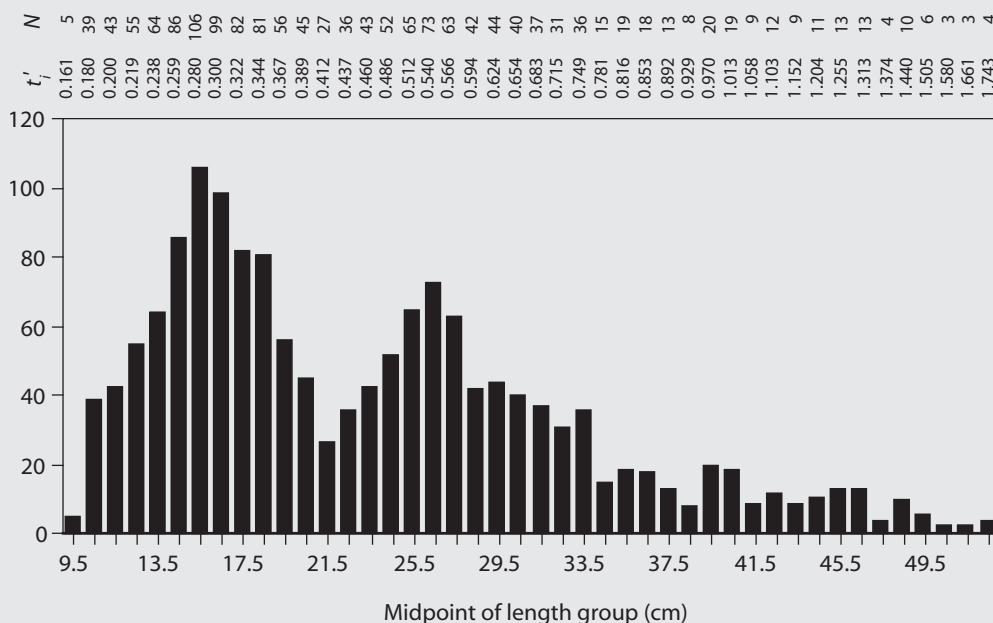
$$Z = 0.693K/([- \log_e \{1 - L_{\text{median}}/L_\infty\}] - [- \log_e \{1 - L_x/L_\infty\}]) \\ = 0.693(0.226)/[- \log_e (1 - 255/636) - (- \log_e (1 - 150/636))] = 0.644.$$

Mortality can also be estimated using a length-converted catch curve (Pauly 1984). The length-groups in the length-frequency distribution of the largemouth bass population in Columbus Lake (see figure in this box) are converted to relative age t'_i and regressed on \log_e of the number of fish in the i th length interval as in equation (6.10):

$$\log_e(N_i) = a - bt'_i \\ = 4.97 - 2.27t'_i.$$

Then, $Z = K(1 - b) = 0.226[1 - (-2.27)] = 0.739$. Regression was limited to length-groups 15 cm and greater.

Figure Length-frequency distribution of the largemouth bass population in Columbus Lake. The number of fish in each length-group is represented by N , and t'_i is as defined in equation (6.10).



■ 6.5 MARK-RECAPTURE MODELS

Mortality can be measured directly by marking individual fish. Historically, mark-recapture models have been developed to estimate abundance, which naturally leads to methods for estimating mortality (i.e., reductions in abundance); however, more recently, the focus of mark-recapture models has shifted towards estimation of mortality (Lebreton et al. 1992). Although an extensive literature on mark-recapture models exists (see reviews by Ricker 1975; Seber 1982; Lebreton et al. 1992; Schwarz and Seber 1999), we describe only three approaches for estimating Z . Additional details about the use of mark-recapture models to estimate abundance are given in Chapter 8.

Our presentation is brief because tagging is not extensively used to assess mortality of fish populations, mostly due to the cost and the practical difficulties related to tagging a representative sample of a population and obtaining unbiased recovery data. Major commercially or recreationally exploited fish stocks are usually large and distributed over a wide area. Thus, mark-recapture estimates depend on tagging large numbers of fish and often cooperation from fishers to find and report marked fish. In the past, mark-recapture estimation has sometimes failed because too few fish have been tagged or because fishers and other members of the industry have been reluctant to report recoveries (Hilborn and Walters 1992; Miranda et al. 2002).

Mark-recapture models make many assumptions about the tagged sample and untagged population. Assumptions include (1) the tagged sample is representative of the entire population; (2) there is no tag loss or it can be accounted for (e.g., Seber 1982; Fabrizio et al. 1996); (3) mortality rates are not influenced by tagging; (4) all tagged fish within a tagged cohort have constant mortality and recovery probabilities in a given period; (5) mortality and recovery probabilities do not depend on age and are the same for the tagged sample and untagged population; (6) F and M are additive and independent; (7) M is constant within and between periods; (8) fishing mortality imposed by a user group is constant for the period of the year that the fishery is operating; and (9) tagging takes place over a short period (although there are models that account for continuous tagging; see Ricker 1975 and Seber 1982). These assumptions are not made by all models, and not all models make the same assumptions.

6.5.1 Single Tagging Event

If fish are tagged only once, mortality may be estimated from the decline of tagged individuals. Estimates of losses may be obtained by recapturing tagged fish at various time intervals or by relying on the fishery to catch and report tagged fish. The former approach is applicable if it is possible to tag a large proportion of the population, so that the expectation of collecting tagged fish in subsequent samples is reasonably high. The latter approach is applicable when there is a high likelihood that tags will be recognized and reported by commercial or recreational fishers. Both approaches assume that effort is constant, or at least known, so that catch in a given period can be standardized per unit of effort. Whichever method is used, declines in number of tagged fish can be equated to declines in number

of fish in a cohort and analyzed with the various catch-curve techniques described earlier. For example, the fraction of fish bearing a tag for any two successive periods of recaptures will indicate interval mortality rate:

$$A_i = 1 - \frac{r_{i+1}}{r_i}, \quad (6.13)$$

where r_i = number of fish recaptured during period t_i , and r_{i+1} = number of fish recaptured during period t_{i+1} (Box 6.9). When recaptures are available from a series of periods, a regression of either (1) \log_e of the fraction of fish caught bearing a tag or (2) \log_e of the number caught per unit of effort, as a function of time, would produce a decreasing slope equivalent to Z :

$$\log_e(r_i/n_i) = a - bt_i, \text{ or} \quad (6.14)$$

$$\log_e(r_i/f_i) = a - bt_i, \quad (6.15)$$

where n_i = number of fish caught in t_i , f_i = fishing effort in t_i , a = regression parameter, and b = slope parameter representing Z . Which approach is used will depend on the data available and the assumptions that are appropriate. The assumption of constant recruitment is no longer relevant because the user is dealing with a single group of fish of known initial abundance.

6.5.2 Multiple Tagging Events

Whereas a single tagging event assumes constant survival to estimate mortality, multiple tagging events allow relaxation of this assumption. Studies based upon two tagging events followed by one recapture event (Ricker's method, Ricker 1975; Seber 1982) can account for variable mortality if recruitment is assumed constant. A triple-catch study is based upon two tagging events with recaptures collected during the second tagging event and during a third sampling event (Bailey 1951; Ricker 1975). A triple-catch study can account for variable recruitment (which includes immigration) and variable mortality (which includes emigration). Multiple mark-recapture data are best handled by a model proposed independently by both Jolly (1965) and Seber (1965) that accounts for variable recruitment and mortality. The Jolly-Seber model is more general and powerful than any of the other methods and can estimate population size and recruitment in addition to mortality using four or more mark-recapture periods; estimates are limited to sizes of fish that were tagged. Example applications for Ricker's method are given by Ricker (1975), triple-catch method by Fairfield and Mizroch (1990) and Evans and Lockwood (1994), and Jolly-Seber method by Hightower and Gilbert (1984), Law (1994), and Fabrizio et al. (1997). Below, we describe the Ricker and Jolly-Seber methods for estimating mortality.

Ricker (1975) and Seber (1982) describe similar methods for determining mortality from tagging in two successive years. With both methods, tagging occurs at the start of two periods (e.g., seasons or years) using tags that distinguish between the two tag groups. With Ricker's method, recaptures are taken during both years from

fishers. If mortality is assumed constant over years, then mortality is estimated by equation (6.13). Thus, only one marking followed by two recapture periods are needed. If mortality cannot be assumed constant over years, Ricker's method estimates mortality in period 1 as

$$A_1 = 1 - \frac{r_{12}m_2}{r_{22}m_1}, \quad (6.16)$$

with variance

$$V(A_1) = A_1^2 \left(\frac{1}{r_{12}} + \frac{1}{r_{22}} + \frac{1}{m_1} + \frac{1}{m_2} \right), \quad (6.17)$$

where m_1 = fish marked at the start of time 1, m_2 = fish marked at start of time 2, r_{22} = fish marked and recaptured in time 2, and r_{12} = fish marked in time 1 and recaptured in time 2. Seber's method also uses equation (6.16), but r_{12} and r_{22} are measured through samples taken soon after the second release. Both of these methods assume that natural mortality is constant over ages. The equations for both methods are the same because the expectation of the ratio r_{12}/r_{22} is unchanged through time 2. For Ricker's method, it is not essential that all recaptured fish be reported, only that reporting rate is constant over years. Both Seber and Ricker provide equations modified to compensate for small number of recaptures. An example application of Ricker's method is given in Box 6.9.

The Jolly-Seber method estimates mortality by evaluating changes in population size, including increases (recruitment and immigration) and decreases (deaths and emigration), from multiple mark-recapture samplings on an open population. Thus, estimates of mortality represent death only when emigration is zero. Fish are captured and marked during brief collection periods (e.g., days), and in between are longer periods (e.g., months) in which recapturing is not attempted and no tags are released. During the first collection period, fish are marked with numbered tags that distinguish individuals, and during the last period, fish are checked for marks. During intermediate periods, fish are checked for marks, unmarked individuals are tagged, and marked individuals are noted and released. Categories of marked and recaptured are tallied by collection period as shown in Table 6.2. Then, the interval mortality rate between collection period i and collection period $i + 1$ is estimated as

$$A_i = 1 - \frac{\beta_{i+1}}{\beta_i - r_i + m_i}, \quad (6.18)$$

where the number of marked fish in the population at the time of the i th sample, β_i , equals $r_i + m_i k_i / r_i$, and r_i , m_i , k_i , and r_i are as defined in Table 6.2. Seber (1965) proposed a modified estimator of β_i , $\beta_i^* = r_i + 1 + (m_i + 1)k_i / (r_i + 1)$ for a small number of recaptures. Variance equations are given by Seber (1982) and by programs listed in Table 6.3. We illustrate application of the Jolly-Seber method in Box 6.9.

Box 6.9 Total Mortality Estimation from Marked Recaptures

Single tagging event

In late winter 1995, before intense fishing began, 1,596 crappies were tagged in Sardis Reservoir, Mississippi. Of these, 655 were recaptured and reported by anglers during the first year after tagging, 225 in year 2, 89 in year 3, and 34 in year 4 (in this example, recaptures have been preadjusted for tag loss and nonreporting; Miranda et al. 2002). Following equation (6.13), where r_i = number of fish recaptured during period t_i ,

$$A_i = 1 - (r_{i+1}/r_i),$$

$$A_1 = 1 - (225/655) = 0.66,$$

$$A_2 = 1 - (89/225) = 0.60, \text{ and}$$

$$A_3 = 1 - (34/89) = 0.62.$$

Alternatively, regression of $\log_e(r_i/f_i)$ as a function of t_i (equation [6.15] assuming constant $f_i = 1$, where f_i = fishing effort in t_i) yields

$$\begin{aligned} \log_e(r_i/f_i) &= a - bt_i \\ &= 7.4 - 0.98t_i, \end{aligned}$$

which indicates $Z = -0.98$ and thus $A = 0.62$.

Multiple tagging events

Crappies were tagged at the beginning of two consecutive years in Lake Sham. In all, 1,700 crappies were marked in year 1 (m_1) and 1,500 in year 2 (m_2). In year 1, 430 crappies were recaptured (r_{11}); in year 2, 360 of the crappies tagged earlier that same year were recaptured (r_{22}), and 249 tagged the previous year (r_{12}). If annual mortality can be assumed constant, then A for year 1 (and year 2) may be estimated with equation (6.13) as $A_1 = 1 - (249/430) = 0.42$. However, if mortality is suspected to vary over years, then A_1 and $V(A_1)$ may be estimated with Ricker's method (equations [6.16] and [6.17]) as

$$A_1 = 1 - \frac{r_{12}m_2}{r_{22}m_1} = 1 - \frac{249 \times 1,500}{360 \times 1,700} = 0.39,$$

$$\text{and } V(A_1) = A_1^2 \left(\frac{1}{r_{12}} + \frac{1}{r_{22}} + \frac{1}{m_1} + \frac{1}{m_2} \right) = 0.39^2 \left(\frac{1}{249} + \frac{1}{360} + \frac{1}{1,700} + \frac{1}{1,500} \right) = 0.0012.$$

Estimation of mortality for year 2 would require a third year of marking and recaptures.

6.5.3 Other Mark–Recapture Methods

Many Jolly–Seber-type models have been developed in recent years (Buckland 1982; White 1983; Burnham et al. 1987; Cormack 1989; Lebreton et al. 1992; Pradel et al. 1997; Schwarz and Seber 1999). In particular, Pollock and Mann (1983) extended the Jolly–Seber model to enhance application to fisheries by accounting for differential mortality over age-groups. Advances in computer technology have facilitated development of these models and allowed a number of extensions such as constraining of the model parameters (e.g., fixing mortality

A 5-year tagging program was completed to monitor mortality (as well as population size and recruitment, which are not shown in this example) of largemouth bass in Lake Travesty. Fish were marked and recaptured annually during a 2-week collection period in spring each year, and results were analyzed with the Jolly–Seber method.

Table Five-year history of marking and recaptures (recaptures were preadjusted for tag loss) in a largemouth bass fishery. See Table 6.2 for explanation of symbols.

t_i	m_i	r_{ji}				$r_{\cdot i}$	k_i
		t_{1i}	t_{2i}	t_{3i}	t_{4i}		
1	643						
2	489	43				43	43
3	712	28	31			59	40
4	630	12	16	48		76	31
5		3	9	19	37	68	
$r_{\cdot i}$		86	56	67	37		

Computations of annual interval mortalities are made with equation (6.18) as shown below. As an example,

$$A_i = 1 - \frac{\beta_{2+1}}{\beta_2 - r_{\cdot 2} + m_2} = 1 - \frac{484}{418 - 43 + 489} = 0.44.$$

Table Computations of annual interval mortalities. The number of marked fish in the population at the time of the i th sample is given by β_i .

t_i	m_i	$r_{\cdot i}$	r_i	k_i	β_i	A_i
1	643	86	0	0	0	0.35
2	489	56	43	43	418	0.44
3	712	67	59	40	484	0.47
4	630	37	76	31	604	
5			68			

between 0 and 1) and setting selected parameters constant (e.g., mortality over time). Parameters can also be modeled as functions of ordinary variables, with a regression equation built into the recapture model; thus, mortality can be made dependent on environmental conditions or capture rates dependent on measures of effort. Maximum likelihood estimation of model parameters and associated probabilities is facilitated by computer power, superseding traditional deterministic estimates. Treatment of these computer models is beyond the scope of this chapter; however, we list many in Table 6.3.

Table 6.2 Classification of marked and recaptured fish in a Jolly–Seber-type model with five mark–recapture periods. Only marking takes place in the first period, mark and recapture in periods two through four, and only recaptures in the last period. Time period is t_i ; m_i represents the number of fish marked in t_i ; r_{ji} the recaptures in time period t_i of fish marked at an earlier t_j ; $r_{i\cdot}$ the total number of recaptures that were originally tagged in t_i ; $r_{\cdot i}$ the total number of recaptures in t_i regardless of when they were tagged; and k_i the total number of recaptures made after t_i of fish marked before t_i . Application is illustrated in Box 6.9.

t_i	m_i	r_{ji}				$r_{i\cdot}$	k_i
		t_{1i}	t_{2i}	t_{3i}	t_{4i}		
1	m_1						
2	m_2	r_{12}				$r_{\cdot 2}$	$r_{13} + r_{14} + r_{15}$
3	m_3	r_{13}	r_{23}			$r_{\cdot 3}$	$r_{14} + r_{15} + r_{24} + r_{25}$
4	m_4	r_{14}	r_{24}	r_{34}		$r_{\cdot 4}$	$r_{15} + r_{25} + r_{35}$
5		r_{15}	r_{25}	r_{35}	r_{45}	$r_{\cdot 5}$	
$r_{i\cdot}$		$r_{1\cdot}$	$r_{2\cdot}$	$r_{3\cdot}$	$r_{4\cdot}$		

6.6 SEPARATION OF FISHING FROM NATURAL MORTALITY

Fisheries scientists may need to know the proportionate effects of several components of mortality. Most commonly, we wish to isolate the effect of fishing from the effect of all other influences on mortality, a group often lumped together as natural mortality. It is possible to obtain estimates of fishing and natural mortality independently. Most commonly, and given $Z = F + M$ (Table 6.1), Z and F are measured and M estimated as the difference. However, this approach results in estimates of M that are not independent of F . At least six different approaches may be used to estimate M , F , or both, including (1) regression of Z as a function of fishing effort to estimate M , (2) catch-curve analysis to estimate M , (3) mark–recapture to estimate F , (4) direct census to estimate F , (5) production modeling to estimate M , and (6) meta-analysis to estimate M , F , and Z .

6.6.1 Regression of Z as a Function of Fishing Effort to Estimate M

Natural mortality (M) is commonly estimated as the difference between Z and F . For unfished populations or segments of populations, M equals Z and may be estimated using methods described earlier. As unfished populations are rare, other approaches must be used. Changes in fishing effort can lead to changes in Z , and the relation between fishing effort and Z can be used to achieve the separation of F and M (Paloheimo 1958). Thus, with Z as the dependent variable and fishing effort as the independent variable, the slope of the line becomes a catchability coefficient and the intercept (i.e., when effort is zero) becomes M (Figure 6.7). This method requires a minimum of two x – y pairs, but more is better.

There are at least three drawbacks for this method. First, because the independent variable (i.e., fishing effort) is estimated with considerable error, a basic

Table 6.3 Selected computer programs for analyzing mark–recapture data from multiple tagging events in open populations. Many of these programs include the ability to fit customized log-linear and constrained maximum log-likelihood models and impose arbitrary temporal, group, and covariate constraints to select the best model.

Program	Description	References
BAND2	Estimates number of animals that must be marked to achieve a specified level of precision for mortality estimates.	Wilson et al. (1989)
BROWNIE	Estimates mortality and recovery rates for two age-classes (e.g., juvenile and adult) in open populations.	Brownie et al. (1985)
CAPQUOTA	Estimates expected coefficients of variation of mortality and capture probability.	Pollock (1981)
CONTRAST	Compares estimates of mortality when variances and covariances are available (analogous to means comparisons in ANOVA).	Hines and Sauer (1989)
ESTIMATE	Estimates mortality and recovery rates for one-age-class (e.g., juvenile or adult) open populations. More flexible than BROWNIE but not as flexible as MARK.	Brownie et al. (1985)
JOLLY	Estimates mortality and capture probability for one-age-class open populations. Widely used but not as flexible as MARK.	Pollock et al. (1990)
JOLLYAGE	Similar to program JOLLY, it estimates mortality and capture probability for two-age-class open populations.	Pollock et al. (1990)
MARK	Estimates mortality and capture probability for open populations. Allows a wider class of encounter histories and constraints than do other programs and was developed primarily for mortality estimation. It will handle various mark–recapture models, the joint live-recapture and dead-recovery models, robust-design models, and multi-strata models. It is the newest and potentially most complete package.	White and Burnham (1999)
MULT	Estimates mortality and recovery rates with additional models for estimating reporting rate.	Conroy et al. (1989)
POPAN	Estimates mortality and capture probability for open populations.	Arnason and Schwarz (1999)
RELEASE	Estimates mortality and goodness-of-fit tests for a large class of mortality models for open populations. Originally developed to estimate survival for a large suite of fish mark–release experiments	Burnham et al. (1987)
SURGE	Estimates mortality and allows easy implementation of linear models.	Pradel and Lebreton (1993); Cooch et al. (1996)
SURPH	Estimates mortality using mark–recapture data as a function of environmental and experimental effects. These effects may apply to a population (such as ambient temperature) or an individual (such as body length).	Smith et al. (1994)
SURVIV	Estimates mortality with multinomially distributed data. SURVIV is very flexible and used heavily as a research tool. However, one needs a FORTRAN compiler to run program and a healthy appetite for programming to get things to work. Not recommended for novices.	White (1992)
TMSURVIV	Estimates mortality and capture probability and the proportion of “transients” in open populations.	Pradel et al. (1997)

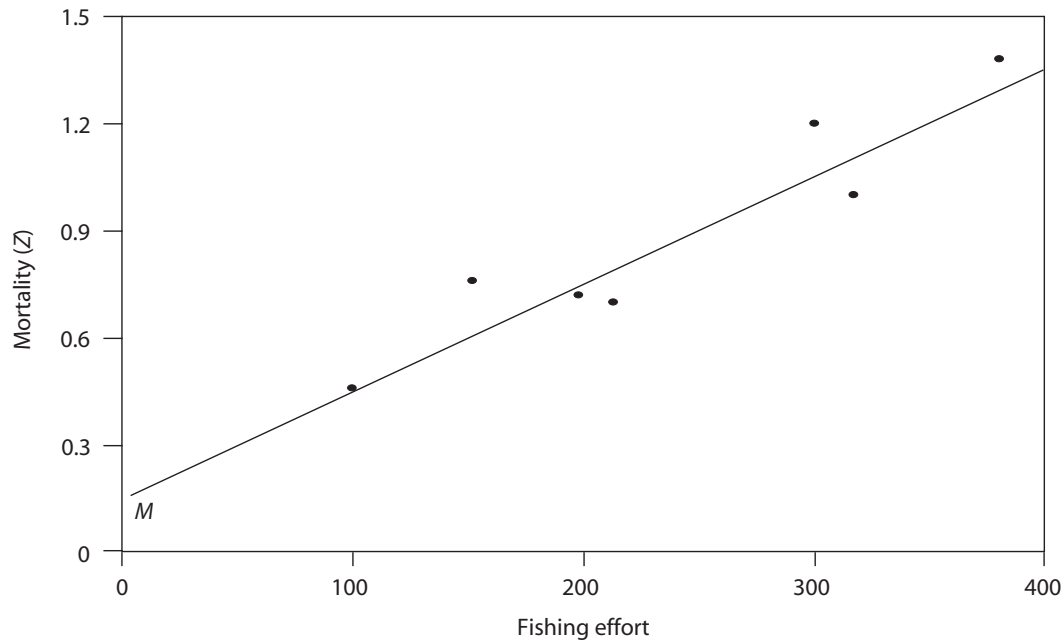


Figure 6.7 Separation of fishing (F) and natural (M) mortality by regression of Z as a function of fishing effort. The intercept of regression represents M .

assumption of regression analysis is violated. The effect is to flatten the slope because, as the measurement error in the independent variable increases, any relationship between the dependent and independent variables becomes indistinguishable, driving the slope toward zero. Flattening of the slope can produce an overestimate of the intercept and thus M . Second, this method is applicable only when the relation between effort and Z is linear (i.e., catchability is constant). Conceivably, the same fishing effort may not encounter the same catchability in different years because of changes in population density or gear efficiency. Third, an unreliable estimate of the y -intercept (i.e., M) will result if the fishing effort does not vary greatly; ideally, estimates of Z would be available over a wide range of fishing effort, including very low levels.

6.6.2 Catch-Curve Analysis to Estimate M

Under limited conditions, the linearized catch-curve analysis described in section 6.3.2 may be used to estimate M . Conceivably, some of the age-groups available for analysis may not be available to the fishery. The slope of a line fitted through these points may be interpreted as M . For instance, in situations where a length-limit regulation exists and catch-and-release mortality and illegal harvest are virtually zero, fishing mortality for protected fish is in effect zero. Hence, any estimates of Z will constitute estimates of M for fish in those protected lengths.

6.6.3 Mark–Recapture to Estimate F and M

Estimates of F can be derived from tagged fish recaptured by fishers if concurrent estimates of Z are available. Estimation procedures depend on whether one or multiple release periods are employed. Various methods are available (reviewed by Seber 1982), but we limit our presentation to methods counterpart to those identified for estimating Z in section 6.5. An additional assumption is that fishers report tagged fish; violation results in an underestimate of F . Various methods have been designed to adjust for underreporting (Zale and Bain 1994; Hearn et al. 1999), but none of the underreporting adjustments are fully satisfactory (Miranda et al. 2002).

If fish are tagged in only one marking period, fishing mortality may be estimated from the proportion of tagged individuals captured in the fishery. This approach is applicable when there is a high likelihood that tags will be recognized and reported by commercial or recreational fishers. Equation (6.13) estimated A as the fraction of fish bearing a tag in two successive periods of recaptures. If the number of fish bearing tags in the first period (m_1) and the number of tagged fish captured by fishers in this period (f_1) are known, the interval fishing mortality, μ , can be estimated as

$$\mu_1 = \frac{f_1}{m_1}, \quad (6.19)$$

and $F = \mu Z/A$. A variance equation for (6.19) was given by Ricker (1975) and Jagielo (1991). If μ is assumed constant over several recapture periods, a weighted estimate of mean exploitation is obtained as

$$\mu = \frac{f_1 + f_2 + \dots + f_{n-1}}{m_1(1 + S_1 + S_2^2 + \dots + S_{n-1}^{n-1})}, \quad (6.20)$$

where S_i is the survival in each period. These computations are illustrated in Box 6.10.

If fishing mortality cannot be assumed constant, and mark–recapture is conducted over two or more periods, estimates of μ_i for each period i can be obtained by making successive estimates with equation (6.19). If mark–recapture is continued for three or more periods, estimates of μ_i for each period i can be estimated as (Ricker 1975)

$$\mu_i = \frac{f_{i.} f_{.i}}{m_i k_i}, \quad (6.21)$$

where m_i is the number of fish marked at the start of period i , $f_{i.}$ is the number of fish marked in year i caught by fishers over all years, $f_{.i}$ is the number of marked

Box 6.10 Fishing Mortality Estimation from Marked Recaptures

Single tagging event

Consider the 1,596 crappies tagged in Sardis Reservoir and used in Box 6.9 to illustrate computation of total mortality. Recall that 655 were recaptured and reported by anglers during the first year after tagging, 225 in year 2, 89 in year 3, and 34 in year 4 (in this example, recaptures have been preadjusted for tag loss and nonreporting; Miranda et al. 2002). Following equation (6.19),

$$\mu_1 = \frac{f_1}{m_1} = \frac{655}{1,596} = 41\%,$$

where m_1 = number of fish bearing tags in the first period and f_1 = number of tagged fish captured by fishers in this period. If μ can be assumed constant over the 4 years of tag returns, a weighted estimate of mean exploitation can be obtained with equation (6.20) as

$$\mu = \frac{f_1 + f_2 + \dots + f_{n-1}}{m_1(1 + S_1^1 + S_2^2 + \dots + S_{n-1}^{n-1})} = \frac{655 + 225 + 89 + 34}{1,596(1 + 0.34 + 0.40^2 + 0.38^3)} = \frac{1,003}{2,482} = 40\%.$$

Multiple tagging events

The 5-year tagging program for largemouth bass in Lake Travesty described in Box 6.9 provided data to estimate exploitation. Fish were marked and recaptured annually during a 2-week collection period in spring each year, and anglers were asked to report tagged fish they harvested. The 4-year history of tag reports is summarized below (recaptures were preadjusted for tag loss and nonreporting).

fish caught each year i , regardless of when they were marked, and k_i is the number of marked fish caught after year i of fish marked before year i . When mark-recapture occurs over three or more periods, equation (6.21) is preferred over successive estimates with equation (6.19) because equation (6.21) incorporates more recapture information.

Some relatively new approaches integrate changes in fishing effort with traditional multiperiod mark-recapture data to estimate F and M , and possibly tag-reporting rate, from a data matrix like the one illustrated at the bottom of Box 6.10. Hoenig et al. (1998) describe two approaches, one that estimates F and M from the pattern of effort over the course of a year or other period and another that estimates them from the pattern of effort over years. Brooks et al. (1998) develop a method to separate F from M in situations where two user groups (e.g., commercial and recreational fisheries) are exploiting a fish population. Separation of M and F is made possible by differences in recapture rates and seasonal

Table Tag reports for the largemouth bass fishery in Lake Travesty. The symbol m_i represents the number of fish tagged in year i ; f_i is the number of fish marked in year i caught by fishers over all years; $f_{.i}$ is the number of marked fish caught each year i , regardless of when they were marked; k_i the total number of tagged fish caught after year i of fish tagged before year i .

<i>Recaptures by anglers of fish marked in year i</i>							
Year and $f_{.i}$	m_i	1	2	3	4	f_i	k_i
1	643	89				89	173
2	489	60	63			123	202
3	712	19	35	92		146	212
4	630	5	20	41	75	141	141
$f_{i.}$	173	118	133	75			

Computations of annual exploitation estimated with equation (6.21) are as follows.

$$\mu_1 = \frac{f_{1.} f_{.1}}{m_1 k_1} = \frac{173(89)}{643(173)} = 14\%,$$

$$\mu_2 = \frac{118(123)}{489(202)} = 15\%,$$

$$\mu_3 = \frac{133(146)}{712(212)} = 13\%, \text{ and}$$

$$\mu_4 = \frac{75(141)}{630(141)} = 12\%.$$

effort between users. Hearn et al. (1998) present a method for estimating F and M from twice-a-period tagging (e.g., twice per year over several years). Tagging takes place before a heavy fishing episode and once again at the end of this episode; M and F are sorted out by comparing rates of returns from the two markings, over years.

Radio tags may also be used to estimate Z , M , and F in large-bodied species. For instance, Hightower et al. (2000) applied telemetry to estimate natural mortality of striped bass. The general approach was to locate repeatedly live and dead radio-tagged fish at fixed time intervals. The rate of decline in the number of live fish located over time provided information to estimate Z , whereas locations of dead fish provided information to estimate M . Fishing mortality may be estimated indirectly by subtraction or directly if the circumstances allow for inventorying harvest of radio-tagged fish. A key advantage of this approach is the information gained about the timing and causes of mortality. Telemetry studies are labor

intensive but may be pertinent to estimating mortality in closed populations, particularly where the effort can fulfill other information requirements (e.g., movement pattern or habitat use).

6.6.4 Direct Census to Estimate F

Fishing mortality can be derived from estimates of μ and Z (Table 6.1). Values of μ may be obtained through mark-recapture (section 6.6.3) or through direct census of harvest and population size. Direct census of harvest (H) involves estimating the total number of fish taken by the fishery during a time period (reviewed by Malvestuto 1996; and Fabrizio and Richards 1996), and direct census of the population (N) involves estimating the average population size during the same period (reviewed by Seber 1982; and Schwarz and Seber 1999). These two censuses estimate exploitation as $\mu = H/N$. Instantaneous fishing mortality is then estimated as $F = \mu Z/A$.

The phenomenon of catch-and-release mortality in recreational fisheries has received much attention in recent decades. When catch-and-release mortality is low or negligible, conventional estimates of F and M will not be grossly affected. For instance, catch-and-release mortality was 3% for cutthroat trout in the Yellowstone River (Schill et al. 1986) and 2% for common snook in southern Florida waters (Taylor et al. 2001). However, high levels of catch-and-release mortality will confound what otherwise might be a straightforward measurement of F and M . For instance, 67% of striped bass died after being caught and released in a Tennessee reservoir during summer (Bettoli and Osborne 1998), and reef fishes such as red snapper often experience high (>30%) catch-and-release mortality (Gitschlag and Renaud 1994). Catch-and-release mortality represents unaccounted fishing mortality, and high levels of catch-and-release mortality will inflate estimates of natural mortality. When M is high, the success of harvest regulations depends on the level of catch-and-release mortality (Waters and Huntsman 1986).

If estimates of release rates (P_r) and catch-and-release mortality (P_m) are available, these can be used to adjust exploitation rate (μ') as

$$\mu' = \mu + P_r P_m \frac{\mu}{1 - P_r}. \quad (6.22)$$

For example, suppose that a reward-tag study estimated $\mu = 40\%$. If a concurrent creel survey indicated that 50% of fish caught are released, and an independent study indicated that 10% of the fish released do not survive, the adjusted exploitation rate would be 44%.

6.6.5 Production Modeling to Estimate M

Csirke and Caddy (1983) estimated M from the relation between yield and Z . This method assumes a parabolic relation between Z and yield, and represents an extension of the traditional Graham-Schaefer production model (Ricker 1975). If

total catch (yield) and Z are known for a series of years (at least three, more is better), yield (Y_i) can be modeled in terms of Z_i with a quadratic equation as

$$Y_i = b_0 + b_1 Z_i - b_2 Z_i^2. \quad (6.23)$$

This equation corresponds to a parabola with a convex-downward curvature. When $F = 0$, yield becomes zero and Z becomes M , so that equation (6.23) becomes

$$Y = b_0 + b_1 M - b_2 M^2 = 0 \quad (\text{when } F = 0). \quad (6.24)$$

Solving for M ,

$$M = (-b_1 + [b_1^2 - 4b_0b_2]^{0.5}) / 2b_2. \quad (6.25)$$

Figure 6.8 provides an example application. A limitation of this method is the assumption of a parabolic relation between Y and Z . The model may be made more realistic by using new formulations of the basic parabola model (several models are reviewed by Quinn and Deriso 1999). Another limitation is that to produce reliable regression coefficients there must be enough contrast in the values of Z .

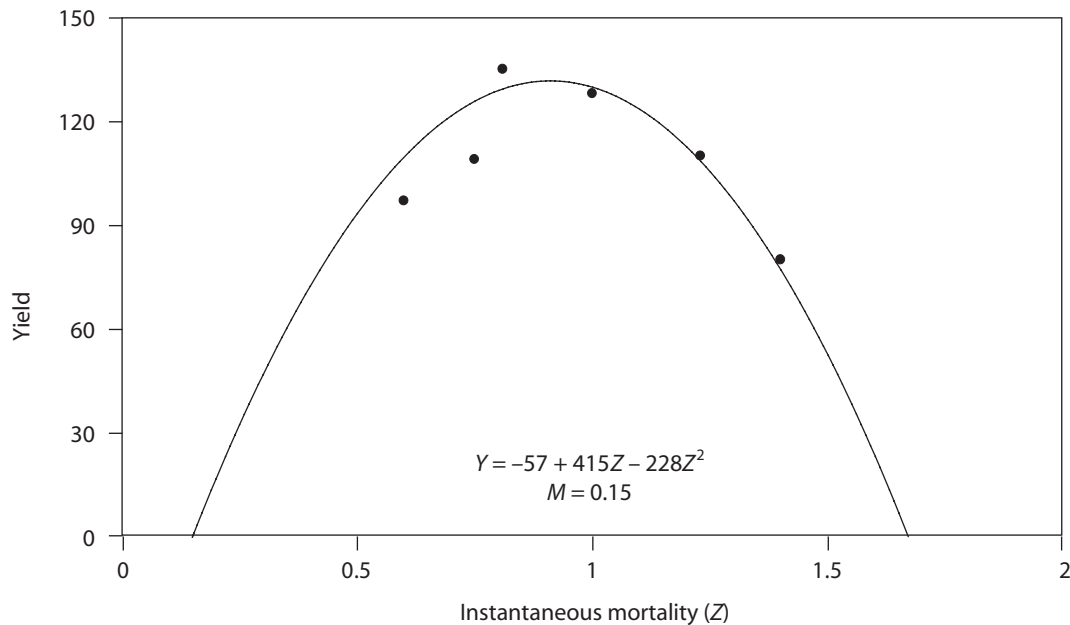


Figure 6.8 Estimating M from the relation between Z and yield (Y), assuming a traditional Graham-Schaefer-type curve. When $F = 0$, yield becomes zero and Z becomes M .

6.6.6 Meta-Analyses to Estimate M , F , or Z

Meta-analysis is a method for objectively synthesizing information from the literature and subjecting that information to statistical analysis (Wolf 1986). Unlike traditional literature reviews, the methodology of meta-analyses is clearly presented so that others can see how decisions were made. Meta-analysis has clearly defined procedural steps to translate the findings of different research to a common parameter defined statistically.

Meta-analyses can be used to develop empirical regression equations predictive of mortality. Natural mortality is consistently related to factors such as growth rate, ultimate body size, fecundity, age at sexual maturity, and temperature. For example, fish populations with slow growth tend to have low M values; a slow-growing species or population simply cannot bear high natural mortality without becoming extinct. Likewise, fishing mortality is related to factors such as fishing effort and diversity of target species. Meta-analyses make use of these natural associations between mortality and allied variables to develop regional or wide-ranging, single or multispecies, predictive models. Selected examples are listed in Table 6.4.

Given that sources of mortality are difficult to sort out, empirical models derived through meta-analyses are sometimes used to estimate mortality components. For example, Campana (1987) used Pauly's meta-analysis (Table 6.4) to

Table 6.4 Selected meta-analyses that use associations between mortality and allied variables to develop regional or wide-ranging predictive models.

Meta-analysis	Reference
In high-latitude stocks, there was a close association between M (annual) and the age (years) when 50% of the population was sexually matured (Tm_{50}). The equation was $M = 1.52Tm_{50}^{-0.72} - 0.155$.	Rikhter and Efanov (1976)
With data on 10 species the relation between M (annual) and gonadosomatic index (GSI = gonad weight/total weight) was estimated as $M = 4.64GSI - 0.37$.	Gunderson (1980)
Annual natural mortality (M) was analyzed for 175 stocks, including 84 freshwater and marine species of tropical to polar distribution. A predictive equation was derived for M based on the von Bertalanffy growth parameters K (annual), L_{∞} (cm), and T (mean annual surface temperature, °C). The equation was $M = -e^{0.0152 + 0.654\log_e K - 0.279\log_e L_{\infty} + 0.463\log_e T}$.	Pauly (1980)
Instantaneous total mortality (Z) was modeled relative to longevity (Y_{\max} = mean age of "the oldest specimens" in a sample). Unfortunately, longevity can be as difficult to estimate as mortality; thus, the value of such relations is limited. The equation was $Z = e^{-1.01\log_e Y_{\max} + 1.46}$.	Hoenig (1983)
For 40 largemouth bass populations in North America, M (annual) was related to the average number of degree-days (DD) above 10°C in a year as $M = 0.000159DD + 0.197$.	Beamesderfer and North (1995)
Wilde determined that the fraction of fishing mortality due to tournaments (TM; %) was related to water temperature (T ; °C) in 45 events: $TM = 0.10427^{T^{1.683}}$.	Wilde (1998)

estimate M for haddock, and Ebbers (1987) used the model to estimate M for largemouth bass. The user of models derived through meta-analyses should recognize the limitations of the models. Because mortalities and their predictors are often difficult to estimate, and come from a variety of studies using different techniques, quality of the models derived through meta-analyses may be questionable. Moreover, the models predict only average mortality for a given population characteristic, or a set of characteristics in the case of multivariate models, whereas the study population may fall above or below the mean. Pascual and Iribarne (1993) evaluated the predictive power of several empirical models and found that error around mortality predictions was high. Thus, estimates from models derived through meta-analysis can be unreliable and should be used only as rough approximations in preliminary analyses or exploratory modeling that seek only relative solutions.

■ 6.7 REFERENCE POINTS

Managing a fishery requires adjusting input and outputs to obtain a desired outcome. Reference points are targets or limits that help guide such adjustments. Target reference points represent a desirable condition toward which a population may be guided to obtain a desired outcome; limit reference points represent a danger zone to be avoided.

6.7.1 Reference Points Based on F

The relationship between yield-per-recruit (y -variable) and F (x -variable) is generally depicted as a dome-shaped curve. The peak of the curve has a slope of zero and identifies the F that produces the maximum yield-per-recruit (F_{\max} ; Quinn and Deriso 1999). This target reference point is often difficult to estimate because of the flat-topped shape of the yield-per-recruit curve. An easier target reference point to estimate is $F_{0.1}$, which estimates the fishing mortality at which the slope of the dome-shaped yield-per-recruit curve is 10% of its value at the origin. This value is always less than F_{\max} and therefore more conservative.

6.7.2 Reference Points Based on M

In unfished or lightly fished populations, mortality limit reference points may be established based on M . For surplus-production models, Gulland and Boerema (1973) proposed a simple empirical formula (i.e., $MSY = 0.5MB_0$) to establish maximum sustainable yield (MSY) in terms of the unfished standing stock (B_0) and the natural mortality at which the slope of a dome-shaped yield curve is zero. Their assumption relies on the symmetrical Schaefer yield model to assume that MSY will occur at 0.5 the unfished standing stock and that $F_{MSY} = M$. Because there is little evidence that $F_{MSY} = M$, this equation has been generalized to $MSY = pMB_0$, with p equal to 0.5 or other fraction. In general, p should be higher for long-lived species (low M) than for short-lived ones (high M). Patterson (1992) suggested

that for small pelagic species, a p near 0.5 (i.e., $F_{MSY} = 0.5M$) should be sustainable. Caddy (1998) suggested that p should decrease as M increases, so that $p = 0.8 - 0.9$ for long-lived ($M = 0.1 - 0.2$) terminal predators and $p = 0.4 - 0.5$ for short-lived ($M = 1.1 - 1.4$) small prey species.

6.7.3 Reference Points Based on Z

Because partitioning mortality into F and M is often difficult, there are advantages in expressing mortality limit reference points in terms of Z . For surplus-production models, Caddy and Defeo (1996) used time series of paired annual Z and catch to approximate the Z values that resulted in MSY. For age-structured models applied to recreational fisheries management, Miranda (2002) derived limits on Z based on size objectives for the fishery stated in terms of mean length or a size structure index. The relation between Z and mean length of fish was described by a decaying exponential curve (equation [6.8]). This curve suggested that to preserve fisheries with large fish requires maintaining a low Z , although exact levels depended on growth rate. The relation between Z and proportional stock density (PSD; Anderson and Neumann 1996) was described with the model (Miranda 2002)

$$Z = - \frac{\log_e (PSD/100)}{t_Q - t_S}, \quad (6.26)$$

where t_S = number of years it takes fish to grow to stock size and t_Q = number of years to quality size (size is defined according to species by Anderson and Neumann 1996). Thus, fast-growing populations can withstand higher mortality to maintain a target PSD. Equations (6.8) and (6.26) can be used to establish reference points based on threshold size objectives for the fishery (Box 6.11).

■ 6.8 COMPENSATORY AND ADDITIVE MORTALITY

Additive mortality assumes that an increment in F or M results in an equal increment in Z . When increments in F or M lead to disproportionate or no increment in Z , mortality is compensatory (Figure 6.9). Populations near carrying capacity are more likely regulated by compensatory processes and populations at low density by additive processes (Bartmann et al. 1992). Hence, a population may exhibit additive mortality at low density and compensatory mortality at high density, but a continuum of escalating partial compensation between completely additive and completely compensatory mortality is possible (Nichols et al. 1984; Conroy and Krementz 1990).

Adult fishes probably experience lower levels of compensatory mortality than do higher vertebrates because fish are better able to adjust their growth rate to food availability, lengthening the period they can survive with limited food (Weatherley and Gill 1987; Shuter 1990). Nevertheless, compensatory mortality may result from cumulative effects. During periods of reduced growth through

Box 6.11 Establishing Target Mortality Caps in Length-Based Fisheries Management

Consider, for instance, that in the Columbus Lake example (Box 6.8) a fishery management objective is for largemouth bass in the population (and thus perhaps the angler's creel) to average 300 mm total length or better (average length estimate includes only fish fully vulnerable to the collection method). If Z is excessive, whether due to F or M , few fish will live to old age (= large size), and thus the management objective cannot be met. Given the existing growth conditions described by the von Bertalanffy growth model ($K = 0.226$ and $L_\infty = 636$ mm), the length above which all largemouth bass are considered equally vulnerable to electrofishing ($L_x = 150$ mm), and the target mean length ($L_{\text{mean}} = 275$ mm), the limit Z may be estimated with equation (6.8) as

$$Z = 0.226 \frac{636 - 275}{275 - 150} = 0.65.$$

Alternatively, if the management objective for the largemouth bass population is expressed in terms of PSD instead of mean length, a limit on Z can be estimated with equation (6.26). Assume that the target PSD is 50 and that it takes 1.1 year for the average largemouth bass in the population to grow from stock to quality size (i.e., $t_Q - t_S = 1.1$); then

$$Z = - \frac{\log_e(50/100)}{1.1} = 0.63.$$

These Z values represent limit reference points above which the management objective cannot be achieved. The limit is intended to prevent overfishing that renders the size distribution of a population undesirable from a fishery perspective. The limit is not a target for management, but instead it helps managers define the upper cap of mortality. If the cap is approached, additional emphasis must be placed on monitoring the fishery. If the cap is exceeded, Z must be immediately reduced through cuts in F that are equal to or larger than the excess Z .

intra- or interspecific competition for resources, other stressors (e.g., disease, parasitism, or predation) may act synergistically to cause density-dependent mortality. Cushing (1981) suggested that predation acts in a density-dependent manner in some pelagic marine fish stocks. Allen et al. (1998) found that mortality was additive in largemouth bass populations but could be compensatory in crappies and northern pike. For crappies, empirical data showed no relation between μ and A at low levels of μ but a positive slope at mid- to high levels of μ ; for northern pike, there was no relation between μ and A .

The existence of compensatory mortality can be examined by plotting independent estimates of A and μ to identify potential trends like those shown in Figure 6.9. Such estimates may be obtained from existing data or by experimentally manipulating μ through harvest restrictions. A plot of F on Z would be problematic because computation of F involves Z (i.e., $F = \mu Z / A$), and thus Z would be included in both axes. The relation between A and μ is expected to be direct and linear if mortalities were completely additive. Conversely, the plot is expected to be slopeless or nearly so if mortalities were completely compensatory. Burnham

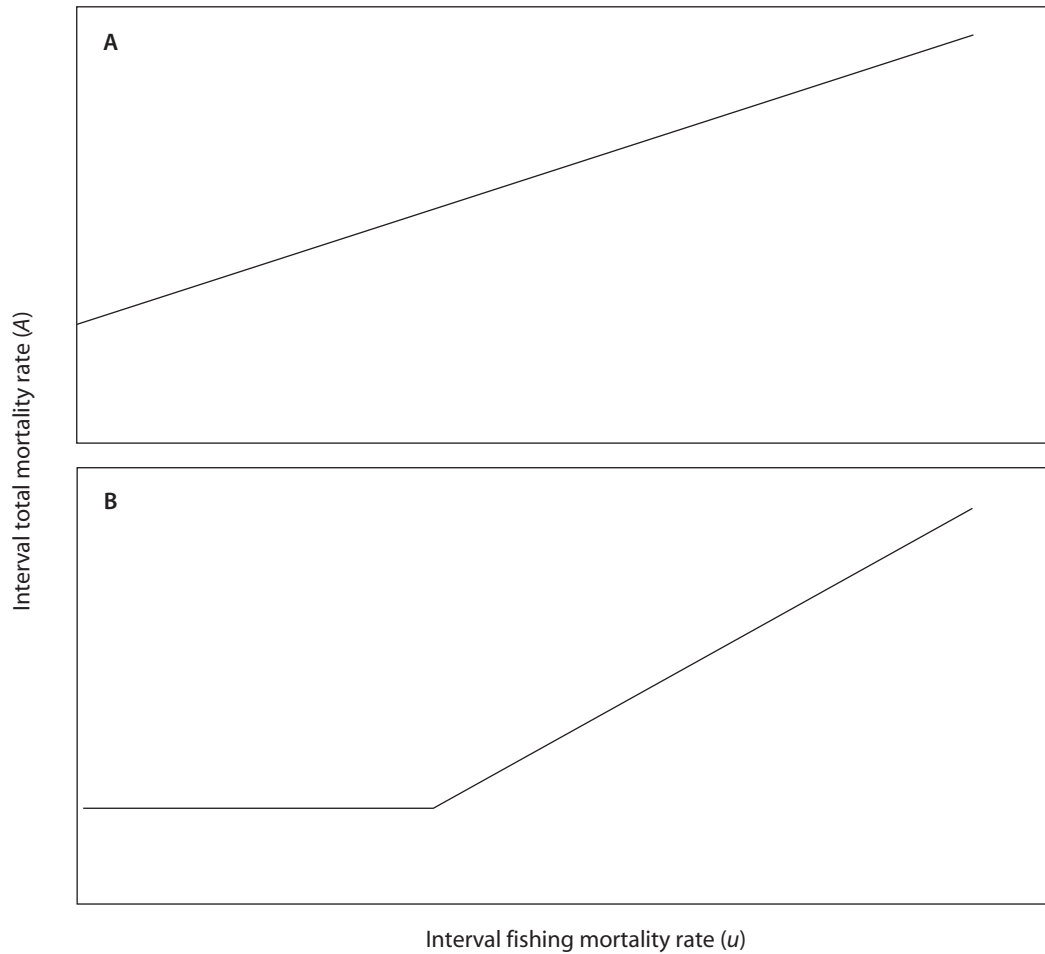


Figure 6.9 Conceptual models of the relation between μ and A under (A) additive, and (B) compensatory mortality. The flat portion of the curve in (B) implies natural mortality is changing and compensating for increased fishing mortality.

and Anderson (1984) present statistical models to test whether mortality conforms to either of these extremes or some intermediary level of compensation.

6.9 PERSPECTIVES ON BIASED AND IMPRECISE MORTALITY ESTIMATES

It should be apparent from the preceding sections that estimating mortality with sufficient accuracy and precision is not easy. Even the simplest estimation models require data that are difficult and expensive to collect, apart from having to rely on collection methods that have numerous biases. The models make various assumptions, which are often disregarded by Mother Nature and ignored by fisheries scientists. The saving attribute is that mortality has well-defined lower and upper limits, 0 and 100%, that conveniently bound the estimates. Given these

difficulties, it is appropriate to end this chapter with our views on how to deal with the uncertainties associated with mortality estimates.

Uncertainties result from inaccurate and imprecise estimates (i.e., estimates that have error). Accuracy refers to how close an estimate of mortality matches the true value, whereas precision refers to how close repeated estimates of mortality would agree with each other (Chapter 3). Error encompasses both the imprecision and inaccuracies of estimates. Uncertainty about accuracy of mortality estimates is created by error in estimating variables that affect the computation of mortality, such as fish age, size structure, growth rate, harvest rate, tag retention, and tag reporting. Error arises from imperfect representation of the population by the sampling process, inability to meet the assumptions of the estimating model, and lack of complete knowledge about the functioning of populations (e.g., additive versus compensatory mortality). Uncertainty due to poor precision results from the high variability associated with population variables that include sampling and natural components. Sampling error is introduced by the sampling gear, timing, and procedures; this error can be reduced through improved collection methods, proper sampling design, and increased sample sizes. Natural variability results from normal population fluctuations; although this variability does not constitute error, measures of error normally include natural variability. Francis and Shotton (1997) and Charles (1998) provide good reviews with more refined classifications of uncertainties.

Uncertainty in mortality estimates can be reduced by confronting the questions of accuracy and precision. Accuracy of estimates may be verified by comparing multiple estimates made with different methods (e.g., mark-recapture, length-based, and catch-curve models) or by evaluating estimates relative to covarying population or environmental parameters to examine if they follow expected trends (e.g., high *Z* values are unlikely when fishing effort is low, unless habitat is of poor quality). If two estimates are similar, the fisheries scientist may begin to feel confident about the quality of the estimates and use the average of the two values. Commonly, the estimates are not so similar, and the fisheries scientists ignores the least certain one, takes the average of the two, or develops two recommendations based on each of the estimates. If the estimates were highly different, averaging should be avoided because there is a good possibility that one of them is wrong and averaging would lead to an undesirable estimate (Schnute and Hilborn 1993). When only a single estimate is available and its accuracy is not confirmed by covarying variables, a second estimate should be sought.

Collecting ample, good data with proven protocols under acceptable sampling designs can increase precision. For example, to perform catch-curve analyses a reasonable sample size of aged fish could be about 200 for a heavily exploited, short-lived freshwater species with few age-classes or 500 or more for a species with 10 or more age-classes in the population (Sampson and Yin 1998; Ciepielewski 1999). However, except in cases where every death can be counted, estimates will still contain error. The variability inherent in every estimate should not be ignored by working exclusively with a point estimate. Instead, confidence intervals should be estimated and further application of the mortality esti-

mate must involve the range of values within the confidence band. Confidence limits mix estimation error and natural variability, which is pertinent given that management will be applied to naturally stochastic populations occupying unpredictable environments.

Further analysis may involve appraisal of the effect of uncertainty on possible outcomes and decision making. This step may take the form of an informal qualitative evaluation or a quantitative assessment using simple or complex models. Qualitative evaluations often involve making conservative allowances for uncertainties through arbitrary safety factors. Much attention has been given in the literature to establishment of precautionary reference points for F (e.g., $F_{0.1}$ and other F limits; Caddy 1998). Brown and Patil (1986) provide an example of a qualitative evaluation of uncertainty to establish levels of F . Quantitative evaluations may evaluate the outcome of models relative to the statistical distribution of mortality and other (if any) variables in the model (i.e., sensitivity analysis; Saltelli et al. 2000). These evaluations help identify the range of possible outcomes given the uncertainty of the variables included in the model; however, models can introduce additional uncertainty because they are unlikely to simulate accurately a population's dynamics.

■ 6.10 CONCLUSIONS

We have presented numerous conceptual and mathematical models of mortality in the preceding sections; however, mortality in fish populations should be more than an abstract concept. Knowledge of mortality rates is fundamental to understanding the dynamics of exploited fish populations, and when compared to rates of recruitment and growth, mortality rates are often the easiest to manage using harvest regulations. Size limits, slot limits, creel limits, closed seasons, and gear restrictions are all examples of regulations typically used to modify fishing mortality (Noble and Jones 1999). When you consider that promulgating regulations and evaluating the subsequent response of freshwater fish populations to new regulations is commonplace, it is surprising that mortality rates are not estimated more routinely or scrutinized more intensely by fisheries scientists.

The most common methods used by inland fisheries scientists to calculate mortality are linearized catch curves or Chapman–Robson's catch curves. Although some of the methods presented here have seen little use outside the marine literature, numerous freshwater sport fish and commercial fish populations are exploited in the same manner as marine stocks. For instance, crappie fisheries are almost exclusively catch-and-harvest fisheries (i.e., catch and release of legal-sized fish is unusual), as are most fisheries for paddlefish, catfishes, bluegill, walleye, and sauger. Instead of large fishing fleets operating in marine systems, inland fishers operate singly but with no less determination and zeal. The populations that are exploited by marine and freshwater fishers are also identical with respect to what is important to know about them and what fisheries scientists can do to conserve or enhance these populations. It should also be apparent that many

datasets lend themselves to several different analytical procedures that can produce different estimates of varying accuracy and precision. When estimates agree, confidence in them will be high; however, when they disagree, they provide direction and justification for future efforts.

The greatest difficulty in estimating mortality is partitioning total mortality into fishing and natural mortality. Whereas estimates of total mortality are abundant, rates of exploitation are difficult to obtain and are known for comparatively few populations; natural mortality rates are available for even fewer populations. The need for accurate estimates of all three rates will grow more acute as more fisheries scientists take advantage of recent advances in population models, whose outputs are critically sensitive to mortality rates.

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