$$\hat{N} = \frac{C}{1-\hat{p}^s}, \tag{6.17}$$

where C is the total catch over all sample periods $\left(\sum_{t=1}^{s} C_t\right)$, s is the number of sample periods, and $\hat{p}$ is the probability that a fish escapes capture during a sample period (i.e., $\hat{p} = 1-\hat{q}$, where $\hat{q}$ is the catchability coefficient as defined before). To calculate $\hat{N}$, we must first estimate $\hat{p}$ from experimental data using the equation

$$\frac{\hat{p}}{\hat{q}} - \frac{s\hat{p}^s}{(1-\hat{p}^s)} = \frac{\sum_{t=1}^{s}(t-1)C_t}{C}. \tag{6.18}$$

Using an example from Seber (1982), we have the following catches made from three consecutive sampling efforts: C_1 = 165, C_2 = 101, and C_3 = 54. First, estimate $\hat{p}$ by iteratively solving equation (6.18):

$$\frac{\hat{p}}{\hat{q}} - \frac{3\hat{p}^3}{(1-\hat{p}^3)} = \frac{(1-1)165+(2-1)101+(3-1)54}{320} = 0.65.$$

We then find $\hat{p}$ = 0.58. Using equation (6.17), calculate $\hat{N}$ = 320/(1– 0.58^3) = 400. Charts originally published by Zippin (1956) and partially reproduced in Seber (1982) can be used to help solve equation (6.18).

A 95% confidence interval for N can be calculated as $\hat{N} \pm 1.96\sqrt{V(\hat{N})}$, where

$$V(\hat{N}) = \frac{\hat{N}(1-\hat{p}^s)\hat{p}^s}{(1-\hat{p}^s)^2 - (\hat{q}s)^2\hat{p}^{s-1}}. \tag{6.19}$$

For our example, $V(\hat{N}) = 691.1$, and the confidence interval is 348–452.

One limitation of the Zippin method is that a large proportion of the population must be sampled to obtain reasonably accurate and precise estimates. This is especially restrictive as the population size decreases; thus, for small populations, it may be necessary to mark fish to simulate removal or to otherwise hold the collected fish for eventual release in order to avoid depleting the population. In cases in which catchability varies among individuals in the population, perhaps in relation to sex, age, or size (Thompson and Rahel 1996), it may be necessary to identify distinct segments of the population and estimate the size of each segment separately. White et al. (1982) described removal–depletion estimation methods useful in cases in which capture probability $(\hat{q})$ may change between sampling efforts.

6.3.2 Estimation of Mortality Rates

Sources of mortality in fish populations are usually placed into one of two categories: natural mortality, including losses to predation, diseases, and weather, or fishing mortality, which is mortality due to harvest (Table 6.2). The combined effect of natural and fishing mortalities is termed total mortality. For exploited stocks, we usually regard the life span of the fish as having a prerecruitment phase, when only natural mortality occurs, and a postrecruitment phase, when fishing and natural mortality occur. In this context, recruitment refers to the addition of fish to the exploited portion of the stock.

6.3.2.1 Estimation of Total Mortality

Methods used to estimate mortality rates vary in relation to assumptions that are made regarding temporal patterns of reproduction and survival rates. The simplest estimation procedures are based on three assumptions: (1) reproduction is constant from year to year; (2) survival is equal among all age-groups; and (3) survival is constant from year to year. Under these assumptions, the population will be in steady state; that is, the number of fish added equals the number dying annually, and the population's age composition would be stable. Hence, information on the population's age composition at any point in time would be representative of mortality rates over a much broader interval. A more realistic model for mortality of inland fish stocks would allow for annual variation in reproduction and survival rates. These variations would produce an unstable age structure in the population, meaning that samples would have to be collected annually for several years (at least) to estimate mortality rates.

For a population having a stable age distribution, the number of fish alive at any age could be described by the curve shown in Figure 6.1. The curve could also represent the decline in abundance of one year-class (or cohort) throughout its life, given the assumption of equal mortality among age-groups. The curve in Figure 6.1 is based on a mathematical model that assumes a constant proportion (Z) of the population (N) dies per unit of time (t):

$$\frac{dN}{dt} = -ZN. \tag{6.20}$$

Upon integration, we obtain an exponential equation for predicting the number of fish, among those currently present, that will still be present at some specified future time:

$$N_t = N_0 e^{-Zt}, \tag{6.21}$$

Table 6.2 Types of mortality rates and relationships among them.

Mortality rates	Symbol	Relationships
Instantaneous		
Total	Z	$A = 1 - e^{-Z}$
From fishing	F	$F = Z - M$
From natural causes	M	$M = Z - F$
Actual		
Total	A	$A = u + v$
From fishing (exploitation rate)[a]	u	$u = FA/Z$
From natural causes[a]	v	$v = MA/Z$

[a] Relationships shown are for cases in which the ratio of fishing mortality to natural mortality is similar throughout the year.

where N_t is the number alive at time t, N_0 is the number alive initially (at time t_0), Z is the force of total mortality (also known as the instantaneous total mortality rate), and t is the time elapsed since t_0.

Although any unit of time can be used with the above model, years are most commonly used so that the number of fish alive at any age t can be computed as a function of the number alive initially and the force of total mortality. If we let t = 1 year, the probability (S) that a fish survives the year can be expressed as

$$S = \frac{N_1}{N_0} = e^{-Z}, \qquad (6.22)$$

and the complement of survival, the annual mortality rate (A), is equal to $1 - S$ or $1 - e^{-Z}$.

In many applications, the exponential model is used to estimate the annual mortality rate of fish that are age 1 and older, and it sometimes is not applied until ages 2, 3, or older. Additionally, because many management efforts are focused on the postrecruitment phase of the species' life span, the exponential model has traditionally been used to describe mortality beginning with the youngest age-group that is exploited in the fishery. When the model includes the youngest exploited age-group, the assumption of constant reproduction is modified to become an assumption that the number of fish alive at the age first considered in the model is constant from year to year. If this age coincides with the age at recruitment, the assumption is one of constant recruitment.

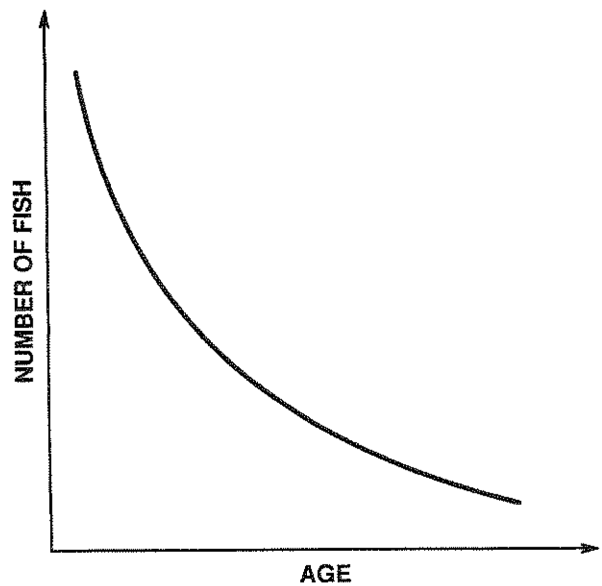

Figure 6.1 Relationship between the number of fish alive and fish age for a population that has a stable age distribution and a constant proportion dying per unit of time.

Total mortality rates are often estimated from the age structure in samples taken from a population. If we assume that recruitment and survival rates are equal across years, the population age structure would be stable, and a random sample taken from the population at any time would always show the same age composition (allowing for random variation among samples). Thus, relationships among numbers of fish at specific ages in the sample can be used to estimate mortality rates.

In practical applications, it is first necessary to assure that the sample is representative of the entire population. Most sampling gears, including those used in commercial operations, are selective for certain sizes or ages of fish, and they would produce biased estimates. A typical problem is that young fish are underrepresented in the sample because either they are too small to be effectively sampled by the experimental gear or they occur in a different habitat than that sampled. In these cases, age-groups that are not fully vulnerable to the sampling gear are excluded from the mortality computations.

The simplest methods of estimation assume that mortality is equal among ages (in addition to the assumptions of constant recruitment and mortality among years). Consider the following hypothetical sample, for which we have data from a population in which the annual survival rate (S) is 0.60.

Age	1	2	3	4	5	6	7	8	9
Number sampled	100	180	140	84	50	30	18	11	6

It is obvious that age-1 fish are underrepresented in the sample, and closer inspection also shows that age-2 fish were inadequately sampled (i.e., 140/180 exceeds the actual survival rate). Thus, ages 3–9 would be used in further computations.

A more realistic situation is one in which we have the sample, but the survival rate is unknown (it is, of course, the object of the investigation). One way to evaluate gear selectivity in this case is to plot the number collected versus age. This plot should be similar to Figure 6.1, but in the example given above, we would find that the youngest age-groups fall below the line expected from the exponential model (Figure 6.2). An alternative method is to plot the sample results on semilog paper (Figure 6.3). This latter plot is known as a catch curve. Because we assume that recruitment is constant and that $N_t = N_0 e^{-Zt}$ (equation 6.21), a plot of the logarithms of the numbers sampled at each age (N_t) versus age (t) should be a descending straight line with a slope of $-Z$. In Figure 6.3 we see that the numbers collected for age 3 and older form a straight line whereas the points for ages 1 and 2 lie below an extension of this line, indicating they were not adequately sampled. The catch curve can be used to estimate mortality rates. By taking the natural log of both sides of equation (6.21), we obtain

$$\log_e(N_t) = \log_e(N_0) - Z(t), \qquad (6.23)$$

which is of the form $Y = a + bX$, with $Y = \log_e(N_t)$ and $X = t$. Linear least-squares regression can then be used to estimate the annual instantaneous total mortality rate, Z. For example, assume we have collected the following data.

Age (t)	1	2	3	4	5	6
Number (N_t)	100	150	95	53	35	17

For ages 2–6, we regress $\log_e(N_t)$ versus t and obtain a slope of -0.54. Thus, $\hat{Z} = 0.54$, and $\hat{S} = 0.59$ (from $S = e^{-Z}$). By assuming constant recruitment and survival over time and equal survival among ages, we have determined that 59% of fish ages 2–6 survive annually (hence, total annual mortality is 41%).

The accuracy and precision of this estimate are affected by the number of age-groups included and the representativeness of the sample. Age-groups having fewer than five fish in the sample usually are excluded from the regression because of the extreme variation that could be introduced by the collection of, or failure to collect, a few individuals. This typically occurs for the oldest age-groups. In practice, the data set is truncated beginning with the youngest age-group having fewer than five fish in the sample. Because regression techniques are used, data for at least three age-groups that are fully vulnerable to the gear are required; precision will increase with the number of age-groups included. Confidence limits for Z are equal to the confidence limits for the slope of the regression; methods for computation are included in most statistical texts.

An alternative approach to constructing catch curves can be used when annual recruitment to a population is thought to vary substantially. This involves developing multiple catch curves, each based on a single cohort. Sometimes, despite varying annual recruitment, cohort mortality rates can be similar. The average of Z values derived from multiple catch curves should be more representative of the population but will require more years of data.

Other models that can be used to estimate survival in stable age populations are based on ratios among numbers of the various ages of fish collected. A method described by Robson and Chapman (1961) estimates survival as

$$\hat{S} = \frac{T}{n + T - 1}, \qquad (6.24)$$

where n is the total number of fish in the sample, beginning with the first age that is fully vulnerable to the sampling gear, and T is determined from the age distribution of the sample.

First, the sample data are coded so that the number collected in the first fully vulnerable age is labeled N_0, the number in the next oldest group is N_1, and so on, so that N_k is the number of fish in the oldest age-group in the sample. For our example, we have the following data.

Age	2	3	4	5	6
Coded age (x)	0	1	2	3	4
Number (N_x)	150	95	53	35	17

Mathematically,

$$T = \sum_{x=0}^{k} x(N_x) = 0(N_0) + 1(N_1) + 2(N_2) + 3(N_3) + 4(N_4),$$

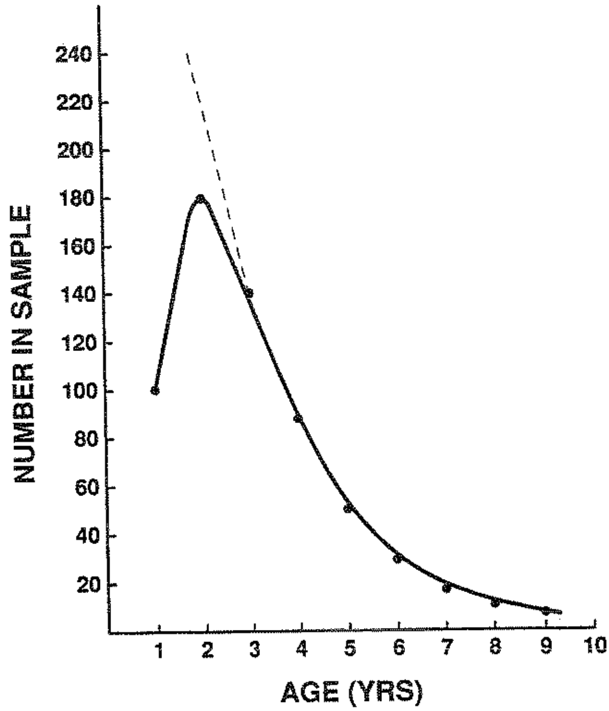

Figure 6.2 Plot of number of fish collected versus fish age. Figure illustrates underrepresentation of age-1 and age-2 fish relative to numbers expected from an exponential model (dashed line).

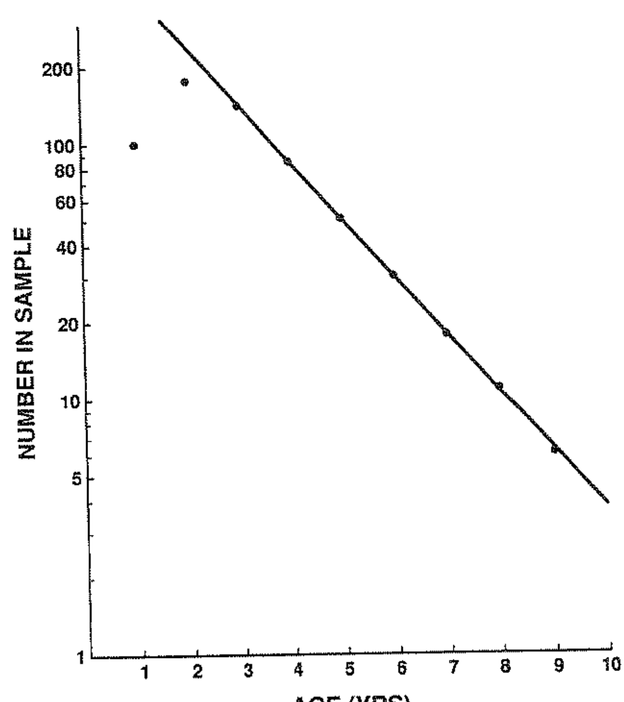

Figure 6.3 Catch curve illustrating the linear relationship between the number of fish collected and fish age when sampling results are plotted on a semilog scale. Ages 1 and 2 were underrepresented in the sample.

which, for the example, is

$$T = 0(150) + 1(95) + 2(53) + 3(35) + 4(17) = 374.$$

Hence, from equation (6.24), we have

$$\hat{S} = \frac{374}{350 + 374 - 1} = 0.52.$$

The variance of this estimator is

$$V(\hat{S}) = \hat{S}\left(\hat{S} - \frac{T-1}{n+T-2}\right), \tag{6.25}$$

which, for our example is

$$V(\hat{S}) = 0.52\left(0.52 - \frac{374-1}{350+374-2}\right) = 0.0018.$$

Methods for estimating mortality rates in populations that do not have stable age distributions can require considerable amounts of data and may be mathematically complicated.

6.3.2.2 Separation of Natural and Fishing Mortality

For exploited fish populations, it is often important to account for the influences of natural and fishing mortality separately. The total instantaneous mortality rate (Z) can be partitioned into instantaneous rates of fishing mortality (F) and natural mortality (M) from the relationship $Z = F + M$. Equation (6.21) can be modified as

$$N_t = N_0 e^{-(F+M)t} = N_0 e^{-Ft} e^{-Mt}. \tag{6.26}$$

Likewise, the actual total mortality rate (A) can be expressed as the sum of two components,

$$A = u + v, \tag{6.27}$$

where u is the expectation of death from fishing (also known as the rate of exploitation) and v is the expectation of death from natural causes. For cases in which fishing and natural mortality are similarly apportioned throughout the year, it is possible to equate

$$\frac{Z}{A} = \frac{F}{u} = \frac{M}{v}. \tag{6.28}$$

Upon rearrangement we find that

$$u = FA/Z, \quad \text{and} \tag{6.29}$$

$$v = MA/Z. \tag{6.30}$$

These relationships are useful if it can be reasonably assumed that the number of fish harvested in any given time period (perhaps a month) relative to the total number harvested annually is similar to the ratio of the number dying naturally in the same given period divided by the total number dying annually from natural causes.

Separation of total mortality into fishing and natural components is accomplished usually by first estimating total and fishing mortality and then estimating natural mortality as the difference. The exploitation rate, u, can be calculated by estimating the population size at the beginning of some time interval and then counting the number of fish harvested by fishers in the ensuing period. Provided that there is no immigration or other additions to the population, the number harvested divided by the initial population size is an estimate of u. If the number harvested is monitored for 1 year, the value of u estimates the annual exploitation rate. The precision and accuracy of the estimate are a function of methods used to estimate population size and number harvested.

Another way to estimate u is to release a known number of tagged fish at one point in time and then determine the proportion of tagged fish harvested in a year. Counts of number harvested are often obtained from anglers who report their catches of tagged fish; in many cases, monetary rewards are offered by management agencies to encourage complete reporting of harvested fish. The validity of tag reward procedures is based on assumptions that tagging does not affect the fish's vulnerability to angling or other sources of mortality, that the tagged fish are representative of the target population, that tags are not lost by the fish, and that all harvest of tagged fish is reported. Precision of the estimate is primarily a function of the number of fish tagged and released.

Another approach for estimating mortality components is based on the relationship $Z = M + F$. The instantaneous fishing mortality rate (F) can be related to the amount of fishing effort (f) as

$$F = qf, \tag{6.31}$$

where q is a catchability coefficient.

Because $Z = M + F$, we can substitute for F and obtain

$$Z = M + qf, \tag{6.32}$$

which is equivalent to a linear equation with slope q and intercept M. A hypothetical relationship between Z and f is illustrated in Figure 6.4. Thus, if we have annual estimates of Z and corresponding values of annual fishing effort, it is possible to estimate M using least-squares regression. The method requires several years of data (a minimum of three) and assumes that the catchability coefficient is constant over time and equal among age-groups. The time-specific annual estimates of Z could be obtained from age-specific catch data as described earlier in this section. The basis of this approach is that if natural mortality (M) is constant, any annual variation of total mortality (Z) will be due to variation in only fishing mortality (F), which, in turn, varies only in relation to effort (f).

6.3.2.3 Age-Specific Mortality

Virtual population analysis is a method commonly used to estimate age-specific fishing mortality rates (F_t), age-specific catchability (q_t), and annual recruitment for exploited populations. The material presented in this section is based on the more complete treatment of the topic by Hilborn and Walters (1992). Also known as cohort analysis, because parameters are estimated for individual cohorts, virtual population analysis has the advantage of being free of the sometimes unrealistic assumptions associated with previously described estimation procedures. Consider a population that is fished during only a brief period at the end of each year. For most of the year, only natural mortality would operate on the population. During the fishing period we could ignore natural mortality and consider only fishing mortality to be important, thereby separating the two types of mortality into distinct phases over time. If N_t is the number of fish alive in a cohort at the beginning of a year, and N_{t+1} is the number alive at the start of the next year (after the current year's fishing season), a model for cohort size during this interval is

$$N_t = N_{t+1} + C_t + D_t, \tag{6.33}$$

where C_t is the number of fishing deaths and D_t is the number of natural deaths that occurred between t and $t + 1$.

Natural deaths are considered proportional to the number in the cohort at the start of the 1-year period (N_t) such that

$$D_t = N_t v, \tag{6.34}$$

where v is the portion of N_t expected to die from natural causes before the start of the next fishing season. By rearranging equation (6.33) and substituting $N_t v$ for D_t, we obtain

$$N_t = \frac{N_{t+1} + C_t}{1 - v}. \tag{6.35}$$

Assumptions of virtual population analysis are that the expectation of death from natural causes (v) is known for all age-groups within cohorts and that an oldest living age-group (called the terminal age-group, for which $N_{t+1} = 0$) can be identified and is consistent over all cohorts.

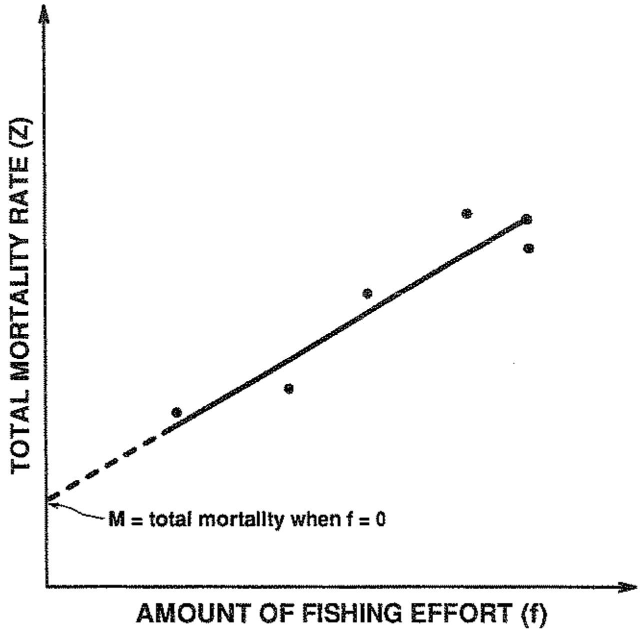

Figure 6.4 Illustration of a straight line (solid) fit to 5 years' estimates of fishing effort (*f*) and total instantaneous mortality (*Z*). The point at which an extension of this line (dashed) intercepts the vertical axis estimates the instantaneous natural mortality rate (*M*).

Assume that a population recruits to a fishery at age 2 and has a terminal age of 6 (i.e., 7-year-old fish are never caught). Next, consider the hypothetical catch-at-age data provided for a single cohort of that population (Table 6.3) and assume that v is 0.3 for all age-groups. Beginning with the terminal age-group and working backwards, numbers of fish in the cohort at the beginning of each year (N_t) can be successively back-calculated from equation (6.35): for age 6, $N_t = (0 + 112)/0.7 = 160$; for age 5, $N_t = (160 + 2{,}245)/0.7 = 3{,}436$; and so on. The cohort size each year just before the fishery begins is $N_t - D_t$, readily determined as $N_t(1 - v)$. Exploitation rate (u) for each age-group in the cohort is calculated as $C_t/(N_t - D_t)$, and F for each age-group is calculated as $F_t = -\log_e(1 - u)$. If age-specific effective fishing effort (f_t) is known, then the catchability coefficient of each age-group (q_t) can be calculated as

$$q_t = \frac{F_t}{f_t}. \qquad (6.36)$$

Values of q_t given in Table 6.3 assume 150 units of effective fishing effort for each age-group. Note that values of F_t and q_t could not be calculated for the terminal age-group. The number of fish from this cohort (spawned in 1992) that recruited to the fishery in 1994 was 22,903 according to this analysis. The information in Table 6.3 from catch-at-age data are typically developed for many cohorts in the population to gain insight into the dynamics of F, q, and annual recruitment.

Often, it is inappropriate to consider annual losses from a cohort due to fishing and natural mortality as separate in time. When both mortality sources are operating simultaneously, changes in number (N) over time (t) proceed according to the equation

$$N_{t+1} = N_t e^{-(F+M)}, \tag{6.37}$$

which is identical to equation (6.26) except t is 1 year. Catch during any one year can be represented as

$$C_t = \frac{F}{F+M}(N_t - N_{t+1}). \tag{6.38}$$

To perform virtual population analysis in this setting, we would like to solve for N_t in terms of N_{t+1}, C_t, and M, as done previously in equation (6.35) when periods of natural and fishing mortality were separated in time. If we first solve for F we have

$$F = -\log_e \frac{N_t}{N_{t+1}}, \tag{6.39}$$

and if we then substitute the right side of this equation for F in equation (6.38) we get,

$$C_t = \frac{M}{\log_e N_t - \log_e N_{t+1}}(N_t - N_{t+1}). \tag{6.40}$$

Although this is not exactly what we wanted, equation (6.40) can be used to determine values for N_t, when N_{t+1}, C_t, and M are known. The equation is solved iteratively by substituting values of N_{t+1}, C_t, and M until equality is obtained. Situations in which M operates solely during one part of the year and in combination with F during another part can be handled by appropriately combining the two approaches that have been described.

Table 6.3 Hypothetical catch-at-age data and calculations associated with virtual population analysis. It was assumed that the natural mortality rate (v) was 0.30. Values of the age-specific catchability coefficient, q_t, were calculated under the assumption that effective fishing effort, f, was 150 units for each age-group.

Year	Age (t)	Catch (C_t)	Cohort size at start of year (N_t)	Cohort size when fishing begins	Exploitation rate (u_t)	Instantaneous rate of fishing mortality (F_t)	Catchability coefficient (q_t)
1999	7	0	0	0			
1998	6	112	160	112	1.00		
1997	5	2,245	3,436	2,405	0.93	2.66	0.018
1996	4	4,545	11,401	7,981	0.57	0.84	0.006
1995	3	3,937	21,911	15,338	0.26	0.30	0.002
1994	2	992	32,719	22,903	0.04	0.04	<0.001