

Processes that regulate population size can be categorized as density dependent or density independent. Density-dependent factors, such as food availability, predation, cannibalism, diseases, parasites, and availability of spawning sites, vary with population size. These factors usually operate in a compensatory manner, so that extremes in population size are moderated by their action. For example, with increasing fish population density, food availability per fish declines, leading to slower growth and poorer condition of the surviving fish. These responses may, in turn, lead to increased vulnerability to predation or cause delayed sexual maturation, which would cause a decline in population size because of reduced rates of survival and reproduction. A low population density could lead to rapid growth and maturation, relatively high survival and reproduction, and increased population size.

Density-independent processes are not affected by population density. Factors such as water temperature, river flows, lake levels, drought, and other features of the environment may affect a population in ways that are not influenced by the number of fish present.

The relative importance of density-dependent and density-independent factors in regulating population size can vary among ecosystems and life stages of a species. In systems where the environment is relatively stable or undergoes recurring long-term cycles, density-dependent processes tend to produce an equilibrium level about which the population varies in response to density-independent environmental factors. Because oceans and large lakes provide relatively constant environments they often support fish populations that are regulated in this manner. An exception to this relative constancy is the well-known El Niño effect, which can substantially alter the thermal environment. Ecosystems with relatively unstable and unpredictable physical characteristics have fish populations that are regulated to a greater extent by density-independent factors. Examples of these systems are streams, rivers, and some reservoirs, which are subject to influence by storms, drawdowns, and temperature changes as well as other weather factors.

For many freshwater fishes, the period of reproduction, including spawning and egg incubation, occurs during a relatively short period in spring when weather conditions, water levels, turbidity, and other factors can be unstable. Hence, egg hatching success and the resultant number of young produced may be a function of density-independent factors. Survival of juveniles and adults is generally thought to be regulated primarily by density-dependent processes, although in many freshwater situations the most pronounced influence of increased population size is reduced growth. Subsequently, reduced growth can lead to increased mortality from predation because smaller fish are more vulnerable. Older fish are better capable of surviving or avoiding extremes of physical environmental factors than are eggs and larvae.

Most freshwater fish populations are characterized by considerable variation in the number of young produced annually. Such variation is most pronounced for species with brief spawning periods or those that spawn in variable, unpredictable environments. The extent to which variation in reproduction influences the adult population depends on the rate of survival of the group of fish spawned in a given year (termed a cohort or year-class) and the age structure of the population.

The overall population abundance of a long-lived species will show relatively less annual variation than will a short-lived species subjected to the same annual variation of reproduction.

A key requirement for management of a fishery is knowledge of the processes and factors that control survival of young fish to the age at which they are mature or reach a desired size. The relative abundance of a year-class (termed "year-class strength") at any early developmental stage may show no obvious relationship to either the abundance of the spawning population that produced it or the number of fish that eventually is added to the adult population; therefore, knowledge of the processes that regulate the dynamics of year-classes during their development is required to prescribe effective management programs.

The idea that year-class strength is established during some specific, relatively distinct phase of a species' life cycle has been applied to fish populations. The term critical period is defined as the time when natural regulatory factors determine the eventual abundance of a cohort. The concept that a critical period exists during the early life of fishes is consistent with the belief that natural processes of population regulation have their greatest influence on the youngest life stages.

The critical period has usually been postulated to occur during early larval development, at a time when the fish become reliant on exogenous food (Cushing and Harris 1973). Initially, larvae use energy contained in the yolk sac to develop functional mouth parts and become capable of swimming and foraging for food. At the point of transition to external food, larval energy reserves are low, and the fish are vulnerable to weather extremes, food shortages, and predation. Hence, biologists have often concluded that the number of fish surviving to juvenile and adult stages is functionally determined during the larval stage.

It is possible that a critical period may occur at later developmental stages. In temperate inland waters, seasonal changes in food availability can lead to a critical period during the first winter of life. This has been demonstrated for juvenile largemouth bass in reservoirs and ponds (Shelton et al. 1979; Miranda and Hubbard 1994a, 1994b; Ludsin and DeVries 1997). Young largemouth bass initially feed on zooplankton and other small aquatic invertebrates but switch to larger invertebrates and small fish as they grow. Individuals in a cohort that initially grow faster can realize an even greater growth and survival advantage because of their increased size and greater flexibility in prey use. During fall and winter, prey abundance can decline to an extent that food becomes limiting, especially to the smallest individuals that have the least flexibility in prey selection. Consequently, these individuals can have reduced condition and suffer greater losses to predators, disease, and other stresses. In these examples, population regulation is a function of density-dependent processes, but the intensity of their influence is expected to vary with severity of fall and winter weather conditions. In a study of smallmouth bass, Watt (1959) showed convincingly that age-0 fish that had not attained a critical size by October would not survive the winter.

Knowledge of the existence and timing of a critical period during a species' life cycle can provide guidance for making management decisions. Using largemouth bass as an example, one can see that in systems regulated like those de-

scribed above, management efforts should not be directed at increasing the number of young during the fall because survival is regulated by food availability during winter. A more effective approach might be to use procedures that would enhance growth in summer and fall, thereby increasing overwinter survival. It is also clear from this example that estimates of cohort abundance should be made after, not before, the critical period if one intends to use the data to forecast year-class strength in a fishery.

### 6.2.2 Effects of Fishing on Population Dynamics

Unexploited stocks are typified by a high proportion of old fish, slow individual growth rates, and low rates of total annual mortality (Clady et al. 1975; Goedde and Coble 1981). The presence of old fish in poor body condition is often reflective of little or no exploitation. When unexploited populations are opened to fishing, length- and age-frequency distributions typically shift toward smaller and younger fish, mean age declines, and total mortality increases. For stocks that are naturally regulated by density-dependent processes, it is also expected that individual growth rates of surviving fish would increase after exploitation because of reduced intraspecific competition (Backiel and Le Cren 1967). At initial stages of exploitation, a population usually is relatively stable because the abundance of adult fish is not reduced to an extent that reproduction is affected. In fact, it is possible that the reduction in numbers of larger, older fish could lead to increased survival of young because of reduced cannibalism (Ricker 1954). Management objectives in these cases usually are directed at maximizing the recreational or economic benefit that can be obtained from each fish newly added to the population by reproduction. However, if harvest is further increased, the reproductive potential of the population may be reduced to an extent that the adult population declines substantially. At such times, management goals are adjusted to help assure adequate reproduction in the population.

Angler catch rates (number or weight of fish caught per unit of effort) often are high for newly exploited stocks but decline rapidly thereafter. Redmond (1974) estimated that during the first 3 d that five Missouri lakes (9–83 ha) were opened to angling, 39–66% of the largemouth bass populations was removed by anglers. Similarly, Goedde and Coble (1981) showed that 1 month's angling in a recently opened Wisconsin lake (5 ha) reduced the number of harvestable-size pumpkinseed, yellow perch, largemouth bass, and northern pike by 74, 86, 53, and 46%, respectively. High initial exploitation rates are partly a function of intense angling pressure, but unexploited stocks may contain a large proportion of naive fish that are highly vulnerable to exploitation.

The effects of exploitation on the abundance of mature fish in a population is determined by the extent to which rates of mortality and replacement by reproduction are altered. For a population that is not fished, all growth and reproduction are balanced by natural mortality (Ricker 1975), and the population size is expected to remain close to some equilibrium level. With the addition of harvest, mortality increases, and the number of mature fish is reduced. The long-term effects of harvest on the population are a function of the new rates of mortality,

growth, and reproduction. An excessive rate of harvest may tip the balance, and fishing may steadily reduce a population to a level at which harvest is no longer economical or possible. More commonly, however, a new equilibrium population level is reached because the decreased abundance of mature fish (from harvest) allows the remaining fish to respond with (1) a greater rate of growth, (2) a reduced rate of natural mortality, or (3) greater rates of reproduction and survival of young (Ricker 1975). Fisheries managers use estimates of these rates and population size to determine appropriate levels of harvest for fish stocks.

Ricker (1954) developed generalized models of the relationships between abundance of adult fish (stock size) and the number of new fish surviving to reach an exploitable size or age (termed recruitment) for stocks that are regulated by density-dependent factors. Because populations vary in age structure, fecundity, and relative importance of density-dependent and density-independent mortality factors, there are many ways that populations can respond to a reduction in the number of adults. The possibilities range from direct proportionality between the number of adults and recruitment to total independence of these two measures. Stock–recruitment models have proven useful, primarily in marine fisheries, for predicting population responses to changes in exploitation and for estimating optimum levels of harvest. Application of stock–recruitment models to freshwater fisheries has been less common.

### 6.2.3 Quantification of Dynamics

A stock is the biological unit of interest in studies of fish population dynamics. Stocks are expected to respond differently to exploitation because of differences in growth or mortality rates. They can often be defined as geographically isolated, and biologists generally attempt to gather information for distinct stocks and manage each separately. The term stock is almost synonymous with biological usage of the term population, which is defined as a collection of interbreeding organisms having its own birth rate, death rate, sex composition, and age structure. The major distinction is that stock refers to the biological unit that is exploited; it may be a subset of a larger population or a collection of species that is exploited as a single unit.

Delineation of stocks and descriptions of their reproduction, behavior, and genetic characteristics are major areas of study in fisheries management; such studies are necessary to define the extent to which management actions may influence a particular fishery. Stocks of many inland fish species are easily defined spatially—populations that occur in isolated lakes or are geographically distant obviously represent different stocks. Marine fisheries managers often face a difficult task of stock identification because of species' life histories that include extensive migrations that lead to mixing of stocks. It is also difficult in some freshwater situations to know if a particular species within a body of water comprises one or more stocks. This problem is most common in large river systems, where the potential for evolution of distinct stocks is greater than it is in most lakes. Migratory behavior of adults may lead to aggregations of individuals from several stocks in one location. In this situation, management actions influencing the

species' abundance and mortality at this location would affect several stocks simultaneously; conversely, management actions directed toward improving survival at one stock's spawning grounds might not have the expected influence on the overall abundance of adults because recruitment from other stocks is unaffected.

Traditionally, the most important biological statistics of fish populations have been population size, total mortality rates at successive ages, the fractions of total mortality attributable to natural mortality and fishing mortality, individual growth rates, recruitment rates, and the rate of surplus production (Ricker 1975). These parameters are needed to determine the greatest amount of biomass that can be harvested from a stock on a sustained basis.

For recreational fisheries typical of inland waters, management objectives usually are far more complicated than simply maximizing harvest, which suggests that managers need to collect information beyond the statistics listed above. Fisheries that illustrate this need emphasize catch-and-release, fishing-for-fun, or trophy angling, where success is measured in terms of recreational enjoyment rather than biomass harvested. Management objectives of inland fisheries frequently address the need for maintaining "balance" in systems regulated by density-dependent processes. Here, the size distribution of fish available to anglers can be more important than total harvest or yield. In such cases, aesthetic and economic values of a given fishery may not be related simply to stock biomass, meaning that other measurements will be needed to monitor management success. These measurements might include estimates of the number of trips or hours fished by anglers, economic benefits derived from a fishery, number of hours required to catch a trophy fish, number of fish caught and released, number of fishing licenses sold, and various indices of condition of the fish population itself. Methods for conducting angler surveys to determine fishing effort, catch rates, and harvest have been reported by Malvestuto (1996), and procedures for determining social and economic values are described in Smith (1983), Weithman (1986), and Chapter 8.

## 6.3 METHODS OF ESTIMATING POPULATION PARAMETERS

### 6.3.1 Estimation of Population Size

Estimates of population size often provide the information needed for making fisheries management decisions. Research or survey programs that track fluctuations in numbers of fish in a stock are used to identify influences of environmental factors and human exploitation and ultimately identify effective management strategies. As such, population monitoring activities often make up a significant proportion of a fisheries biologist's workload. This section introduces three commonly used methods of population estimation: counts on sample plots, mark and recapture, and decline in catch per unit effort. Otis et al. (1978), Seber (1982), White et al. (1982), Brownie et al. (1985) contain information on more advanced models.

### 6.3.1.1 Counts on Sample Plots

An estimate of population size can be obtained by determining the average density of animals per unit area in sample plots and multiplying this value by the total area covered by the population. Seber (1982) outlined three main steps in developing a sampling scheme of this type.

1. The size and shape of the sample area, or plot, should be determined. This choice will be a function of the behavior of the animals to be evaluated, physical features of the habitat, and practical constraints associated with the sampling gear. Plots can cover a standardized area and be shaped as squares, circles, or rectangles, termed quadrats, or plots could consist of nonoverlapping strips running through the population area, termed transects.
2. The number of plots to be sampled should be established in advance. Sampling of more than one plot is necessary to estimate sampling variance, and the desired level of precision of the population estimate can be used to determine the number of plots required.
3. The sample plots should be located randomly so that valid statistical estimates of sampling error can be calculated.

This method of estimation is used primarily when all members of the target population within each sample plot can be counted with reasonable certainty. For example, plots could be established by using nets to block off sections of a small stream, and fish could be counted following removal with toxicants or electrofishing. Another example is the use of a seine to block a standardized quadrat along the shoreline of a lake or reservoir, followed by application of toxicants, such as rotenone, to facilitate removal and counting of the fish.

Counts of fish made per unit of time or volume can also be used to estimate population size, provided that the steps outlined above are followed. For example, counts of larval fish or plankton samples can be expanded to estimate population size provided that samples are collected randomly and have a standard sample volume.

An estimate of the population size ( $N$ ) in an area can be calculated from the individual plot counts as follows:

$$\hat{N} = \frac{A}{a} \bar{n}, \quad (6.1)$$

where  $A$  is the size of the study area,  $a$  is the size of the plot (same unit of measure as  $A$ ), and  $\bar{n}$  is the average number of animals counted per sample plot. The variance,  $V(\hat{N})$ , of the population estimate is calculated as follows:

$$V(\hat{N}) = \frac{A^2}{a} \frac{V(n)}{s} \frac{(A - s \cdot a)}{A}, \quad (6.2)$$

where  $V(n)$  is  $\sum_{i=1}^s (n_i - \bar{n})^2 / (s-1)$ ;  $n_i$  is the number of animals counted in the  $i$ th plot; and  $s$  is the number of plots used (Cochran 1977).

An approximate 95% confidence interval for the true population size can be calculated as  $\hat{N} \pm (t_{s-1, 0.05}) (\sqrt{V(\hat{N})})$ .

In designing a study, it is important to predetermine a desired level of precision to be achieved for estimates of important parameters. A convenient way of expressing the precision is to calculate a coefficient of variation, CV, which is defined as the square root of the variance of an estimate divided by the estimate itself. Thus, CV is a unitless measure of the relative amount of variation about an estimate. When using counts from sample plots to estimate population size, we define the coefficient of variation to be  $CV = \sqrt{V(\hat{N})} / \hat{N}$ . A coefficient of variation of 0.20 or less is usually judged to be adequate.

The number of plots sampled is a principal determinant of the precision of population estimates from simple random sampling designs. Prior to conducting fieldwork, a researcher should determine the number of plots that need to be sampled to achieve the target level of precision (Cochran 1977).

The above sampling procedures are termed simple random sampling when all potential sampling plots, transects, or intervals within their respective population areas or times have an equal chance of being included in the sample. Thus, every animal in the population has an equal chance of being included in the sample provided that the members of the population are randomly or uniformly distributed throughout the area. Fish populations, however, are rarely distributed randomly and more typically are aggregated in certain areas or times. In such cases, estimates from equation (6.1) are not biased but have poor precision because of extreme variability in counts among plots. If fish distribution patterns are known prior to conducting a population study, precision may be improved by subdividing the study area into zones, or strata, expected to have different fish densities and selecting sample plots at random within each stratum. This is termed stratified random sampling.

### 6.3.1.2 Mark and Recapture

The simplest mark-recapture technique of population estimation requires one sample period in which fish are collected, marked, and released and another period in which fish are collected and examined for marks. This method is the Petersen index (alternatively known as the Lincoln index), which is based on the assumption that the proportion of marked fish in the second sample estimates the proportion of marked fish in the total population. The estimator of population size is

$$\hat{N} = \frac{MC}{R}, \quad (6.3)$$

where  $M$  is the number of fish initially marked and released,  $C$  is the number of fish collected and examined for marks in the second period, and  $R$  is the number of recaptures (i.e., previously marked fish) found in  $C$ . This estimate applies to the population present during the first sample period, not the recapture period.

The Petersen index can give biased estimates of population size when the number of fish sampled is low, but several modifications of equation (6.3) have been proposed to help correct this bias. Bailey's (1951) modification is

$$\hat{N} = \frac{M(C+1)}{(R+1)}, \quad (6.4)$$

with variance

$$V(\hat{N}) = \frac{M^2(C+1)(C-R)}{(R+1)^2(R+2)}. \quad (6.5)$$

Bailey's modification is used in cases in which sampling during the recapture period is conducted with replacement, meaning that each fish is returned (replaced) to the population after it is examined for marks and thus is eligible to be included in the sample again. Chapman (1951) recommended using

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1, \quad (6.6)$$

with variance

$$V(\hat{N}) = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}. \quad (6.7)$$

This model is used when sampling during the recapture period is done without replacement, as in cases in which anglers examine their catch for marks or when all fish collected in the recapture period are marked in a way different from the first mark and then released. Differences among population estimates obtained from equations (6.3), (6.4), and (6.6) would probably be of little significance in making fishery management decisions if the number of fish recaptured ( $R$ ) exceeds 7.

Several important conditions or assumptions must be met to obtain valid estimates using the Petersen index or its modifications: (1) marked fish do not lose their marks prior to the recapture period; (2) marked fish are not overlooked in the recapture sample; (3) marked and unmarked fish are equally vulnerable to capture in the recapture period; (4) marked and unmarked fish have equal mortality rates during the interval between the marking and recapture sample periods; (5) following release, marked animals become randomly mixed with the unmarked ones or recapture effort is distributed in proportion to the number of animals in different parts of the population area; and (6) there are no additions to the population during the study interval.

Assuring that these conditions are satisfied is one of the most difficult aspects of estimating population size with the Petersen method. Any factor causing underrepresentation of marked fish in the second sample will lead to overestima-

tion of the population size. This could result from poor mark retention, failure to recognize all recaptures in the second sample, impaired survival of marked fish, and immigration of new (thus unmarked) animals before the recapture sampling. Conversely, any factor leading to overrepresentation of marked fish in the second sample, caused perhaps by increased susceptibility of marked animals to capture, will result in underestimation of the true population number.

Several methods may be used to establish confidence intervals for Petersen-type population estimates. These have been thoroughly developed for the most common sampling design—one in which sampling is done without replacement during the recapture period. For this design, the random variable is the ratio  $R/C$ , which estimates  $M/N$  for the population, and the distribution of  $R/C$  is hypergeometric. Unfortunately, neither tables nor explicit formulas are available for determining exact confidence intervals for the hypergeometric distribution. Consequently, various approximations based on the binomial, Poisson, or normal distributions have been used, depending on the magnitude of  $R/C$  and the values of  $M$ ,  $C$ , and  $R$  for a particular study (Seber 1982).

Precision and accuracy of Petersen estimates are affected by the numbers of fish marked and subsequently checked for marks. Charts prepared by Robson and Regier (1964) can be used to determine values of  $M$  and  $C$  required to produce Petersen population estimates expected to differ from the true population number by no more than 50%, 25%, or 10% at the 95% level of confidence. They recommend the 50% level for preliminary surveys, 25% for management studies, and 10% for research evaluations. Use of the charts requires an initial guess of population size. A particular combination of  $M$  and  $C$  can be chosen as a function of the relative costs associated with marking fish and sampling for recaptures.

Mark-recapture methods of population estimation that use two or more sample periods for marking animals are termed multiple-census procedures. The simplest of these was originally described by Schnabel (1938). Fish are collected from the population, marked, and released for a series of samples; the numbers of recaptures and unmarked fish collected in each sample are recorded. Assumptions of the method are identical to those of the Petersen index except that no mortality is allowed during the study. Because of this requirement, the multiple census is most appropriate when sampling periods are closely spaced and restricted to a relatively short overall period so that the occurrence of mortality would not have a great influence on the validity of the population estimate. Table 6.1 illustrates typical data and computational procedures for this method.

The Schnabel population estimation formula is

$$\hat{N} = \frac{\sum_{t=1}^n C_t M_t}{\sum_{t=1}^n R_t}, \quad (6.8)$$

where the subscript  $t$  refers to the individual sample period and  $n$  is the number of periods.

**Table 6.1** Data records and calculations for Schnabel (1938) multiple-census population estimate.

Sample period ( <i>t</i> )	Number of fish captured			Total number of marked fish released prior to sample period ( <i>M</i> )	<i>C</i> × <i>M</i>
	Marked ( <i>R</i> )	Unmarked	Total ( <i>C</i> )		
1	0	150	150	0	0
2	22	203	225	150	33,750
3	26	86	112	353	39,536
4	53	150	203	439	89,117
5	38	80	118	589	69,502
6	28	53	81	669	54,189
7	87	150	237	722	171,114
Total	254				457,208

For our example (Table 6.1),

$$\hat{N} = \frac{\sum_{t=1}^7 C_t M_t}{\sum_{t=1}^7 R_t} = \frac{457,208}{254} = 1,800.$$

Confidence limits are determined by first computing the variance of  $(1/N)$  because the inverse of  $N$  is more normally distributed than is  $N$  itself:

$$V(1/\hat{N}) = \frac{\sum_{t=1}^n R_t}{(\sum_{t=1}^n C_t M_t)^2}. \quad (6.9)$$

We next determine a 95% confidence interval for  $(1/N)$  as  $(1/\hat{N}) \pm 1.96\sqrt{V(1/\hat{N})}$  and compute the inverses of the limits to find the confidence interval of  $N$  itself. For our example,  $1/\hat{N} = 1/1,800 = 0.000556$ , and

$$V(1/\hat{N}) = \frac{254}{(457,208)^2} = 1.215 \times 10^{-9}.$$

From these, the 95% confidence interval for  $(1/N)$  is 0.000488–0.000624, and by calculating the inverses of these limits, we obtain a confidence interval for  $N$  of 1,602–2,049.

For cases in which the total number of recaptures in the study is small, say less than 25, we do not expect  $(1/N)$  to be normally distributed. We then must calculate confidence limits by alternative methods. This can be done by using tables of the Poisson distribution (see Ricker 1975) to determine 95% limits for the total number of recaptures and then substituting these values into the denominator of equation (6.8) to determine limits for  $N$ .

### 6.3.1.3 Removal Methods

Population size can be estimated from data on fishing effort and catch rates. Several estimators have been developed, all of which are based on the theory that the number of fish caught per unit of effort will progressively decline as members of the population are removed. The most common methods assume that (1) all members of the target population are equally vulnerable to capture, (2) vulnerability to capture is constant over time, and (3) there are no additions to the population or losses other than those due to fishing during the study interval. Additionally, one must be able either to quantify fishing or sampling effort or to create a sampling situation in which equal effort is expended in consecutive sampling periods. Examples of ways that effort could be quantified include hours spent electrofishing, angler trips, vessel-days, seine hauls, or gill nets fished.

The Leslie and DeLury methods are used in cases in which sampling effort may vary among periods. These models, which are part of a general class of methods described by Schnute (1985), have been used mainly for large populations for which there is low probability that an individual fish will be caught during a single unit of effort. Typical applications have included commercial fisheries for which data on sampling effort and catch are obtained by monitoring the fishers, but Leslie models have recently been applied to reservoir stock assessments (Maceina et al. 1993, 1995).

The Leslie method of estimation assumes that the number of fish caught per unit effort during some time interval,  $t$ , is proportional to the number of fish present at the beginning of the interval:

$$\frac{C_t}{f_t} = qN_t, \quad (6.10)$$

where  $C_t$  is the catch during period  $t$ ,  $f_t$  is the amount of fishing effort during period  $t$ ,  $N_t$  is the number of fish present at beginning of period  $t$ , and  $q$  is the catchability coefficient.

Because the method assumes that the population is closed to additions or losses other than fishing, we can express  $N_t$  as a function of the original population size ( $N_0$ ) minus the total number of fish caught and removed ( $K_t$ ) prior to time  $t$  as

$$N_t = N_0 - K_t. \quad (6.11)$$

We can substitute this expression for  $N_t$  into equation (6.10) and obtain

$$\frac{C_t}{f_t} = qN_0 - qK_t, \quad (6.12)$$

which is a linear relationship of the form  $Y = a + bX$ , where  $Y = C_t/f_t$  and  $X = K_t$ . A plot of catch per effort ( $C_t/f_t$ ) versus cumulative catch ( $K_t$ ) will approximate a straight line with slope (actually, the absolute value of the slope) equal to  $q$  and intercept of  $qN_0$ . We can use linear least-squares regression methods to estimate the slope and intercept, and then estimate the original population size as

$$\hat{N}_0 = \frac{\text{intercept}}{|\text{slope}|} = \frac{qN_0}{q}. \quad (6.13)$$

When the fraction ( $q$ ) of a population that is taken by a given unit of fishing effort is small, say less than 0.02 (<2% of the population), DeLury's modification of the Leslie model is preferred. The DeLury method also is based on the premise that catch per effort is proportional to population size (equation (6.10) and assumes a closed population (other than losses due to removal), but uses a different expression of population decline:

$$N_t = N_0 e^{-qE_t}, \quad (6.14)$$

where  $E_t$  is the cumulative total effort expended prior to period  $t$ , and other variables are defined as before. This implies that the population declines in proportion to total effort, whereas the Leslie method assumes that the decline is a function of the total catch.

Substituting the expression of  $N_t$  from equation (6.14) into equation (6.10), we get  $C_t / f_t = qN_0 e^{-qE_t}$ . By taking the natural log of both sides, we obtain

$$\log_e(C_t / f_t) = \log_e(qN_0) - qE_t, \quad (6.15)$$

which is also of the form  $Y = a + bX$ , with  $Y = \log_e(C_t / f_t)$  and  $X = E_t$ . So in this method, we can plot the natural log of catch per effort versus cumulative effort and again use linear least-squares regression to estimate the slope and intercept. The estimate of population size is

$$\hat{N}_0 = \frac{e^{\text{intercept}}}{|\text{slope}|}. \quad (6.16)$$

Confidence limits for population estimates obtained from the Leslie and Delury methods are calculated from intermediate statistics obtained when performing the least-squares regression, and they may be determined using Ricker (1975). Because regression techniques are used, these methods of estimation require a minimum of three sample periods. Precision can be improved by increasing the number of sample periods, but the influences of immigration or natural mortality on accuracy of the estimates could become significant if the duration of the study is extended.

Removal methods of population estimation are also used in situations in which the catchability of fish is high and equal effort is expended in each sample period. The most common example of this is sampling small streams, where sections are blocked off with nets, and fish are collected by making consecutive passes with electrofishing gear (e.g., Thompson and Rahel 1996). Each pass represents one sample period. Fish captured during each period can be released outside the sample reach or marked and then released back into the sampling area. Marking in this case can be used to remove fish from consideration in subsequent samples. A model for population estimation was described by Zippin (1956, 1958) as

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

where  $C$  is the total catch over all sample periods ( $\sum_{t=1}^s C_t$ ),  $s$  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

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

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

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

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