8 Abundance, Biomass, and Production

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■ 8.1 INTRODUCTION

Fisheries scientists face a challenge in that virtually all methods of fish capture or observation are selective. Further, most fish capture methods can be applied to only a fraction of the entire area of interest. Thus, measures such as catch per unit effort (C/f) or catch per area can only be regarded, at best, as being proportional to the true population abundance (see Chapter 7). The methods presented in this chapter are designed to address these problems and provide estimates of absolute abundance or "true" fish density. In general, these methods require additional sampling beyond that required to estimate relative abundance. As such, careful consideration should be given to whether relative measures of abundance are adequate or if the need for estimates of absolute abundance justifies the additional cost.

In many cases, relative abundance is sufficient to answer important research or management questions. One example is when the principal goal is to determine if abundance has changed over time. As long as vulnerability to the gear remains constant over time, trends in C/f can accurately indicate changes in abundance (see Chapter 7). In such cases, the extra effort required to determine absolute abundance is better spent in sampling more sites. In general, estimates of absolute abundance are needed when catchability is likely to vary across time or between sampling sites, confounding comparisons of C/f across space or time. Absolute abundance estimates are also important when harvest quotas are being computed.

Whether relative or absolute measures of abundance are desired, it is critical to define the population of interest carefully. In many cases, some part of the population is excluded from consideration because of limitations of the sampling gear. For example, population estimates of yellow perch in midsummer conducted by means of gill nets would likely not include age-0 fish because they would not be

vulnerable to the gear. Similarly, care must be taken in defining the spatial extent of the target population. Sometimes one is interested in the population in only a particular stream reach, whereas in other situations, the desired scale is an entire watershed, which would likely need to be subsampled.

Another consideration common to both relative and absolute measures of abundance is the precision and accuracy required for the task. Accuracy, bias, and precision are defined in Chapter 3. Applying these concepts to population estimates, it is important to recognize that failures to meet assumptions often reduce both accuracy and precision. Therefore, we emphasize methods for checking assumptions in addition to the methods commonly used to provide point estimates and measures of variability.

◾ 8.2   DIRECT OBSERVATION METHODS

In some situations, direct observation of all fishes in a given area (sampling site) is possible, providing a complete census of the area searched. This approach has been applied in small streams (Hankin and Reeves 1988) or in other situations where fish are tightly constrained. Likewise, counts of fish in hydroacoustic surveys are often assumed to represent all individuals within the hydroacoustic beam path. In situations in which counts are assumed to be accurate and complete, the total population is estimated as the product of the mean density in the sites sampled times the total area. The precision of total population estimates depends principally on the variability between sampling sites (Hankin and Reeves 1988) and the sampling design used (e.g., stratified random sampling). Methods of computing the variance for several sampling designs are presented in Chapter 3 and can be applied directly to data collected through complete censuses at selected sites. One specialized design not included in Chapter 3 is hydroacoustic surveys for which counts are collected along the path of the boat (i.e., along a transect). If data are collected along a single transect, specialized statistical methods are necessary to calculate the variance of the population estimate because of the autocorrelation between counts at adjacent points. (Foote and Stefansson 1993; Vondracek and Degan 1995). If two or more randomly placed transects are followed, however, each transect can be treated as a sampling site, and the methods described in Chapter 3 can be applied.

In many situations, visual observation misses some proportion of the population, even in situations where fish are constrained. Because of this, estimates of density for individual sites are imprecise and contribute to the overall imprecision of total density estimates. In order to estimate the proportion observed within a sampling site, additional information needs to be gathered. The most commonly used method is to measure the distance that each animal observed lies off the transect (i.e., the right-angle distance from each animal seen to the transect) or from the center of a fixed point of observation. Depending on the observation technique, this distance can be determined directly, or the distance and angle of departure from the transect can be determined and the right-angle distance calculated by simple geometry. Generally, the proportion of fish present that are

detected (i.e., sightability) declines farther from the point of observation or from the transect surveyed (Figure 8.1). Assuming that fish are randomly distributed with respect to the transect and sightability is 100% at or near the center of the transect, the proportion observed can be estimated as a function of distance from the transect.

Critical assumptions for applying the direct observation approach include (1) fish are randomly and independently distributed, and movement of the observer does not attract or repel fish prior to observation; (2) distances are measured accurately; (3) fish are not counted more than once; (4) fish are detected at their original position with respect to the transect; and (5) sighting of each fish is independent of other fish, meaning that the likelihood of seeing an individual fish
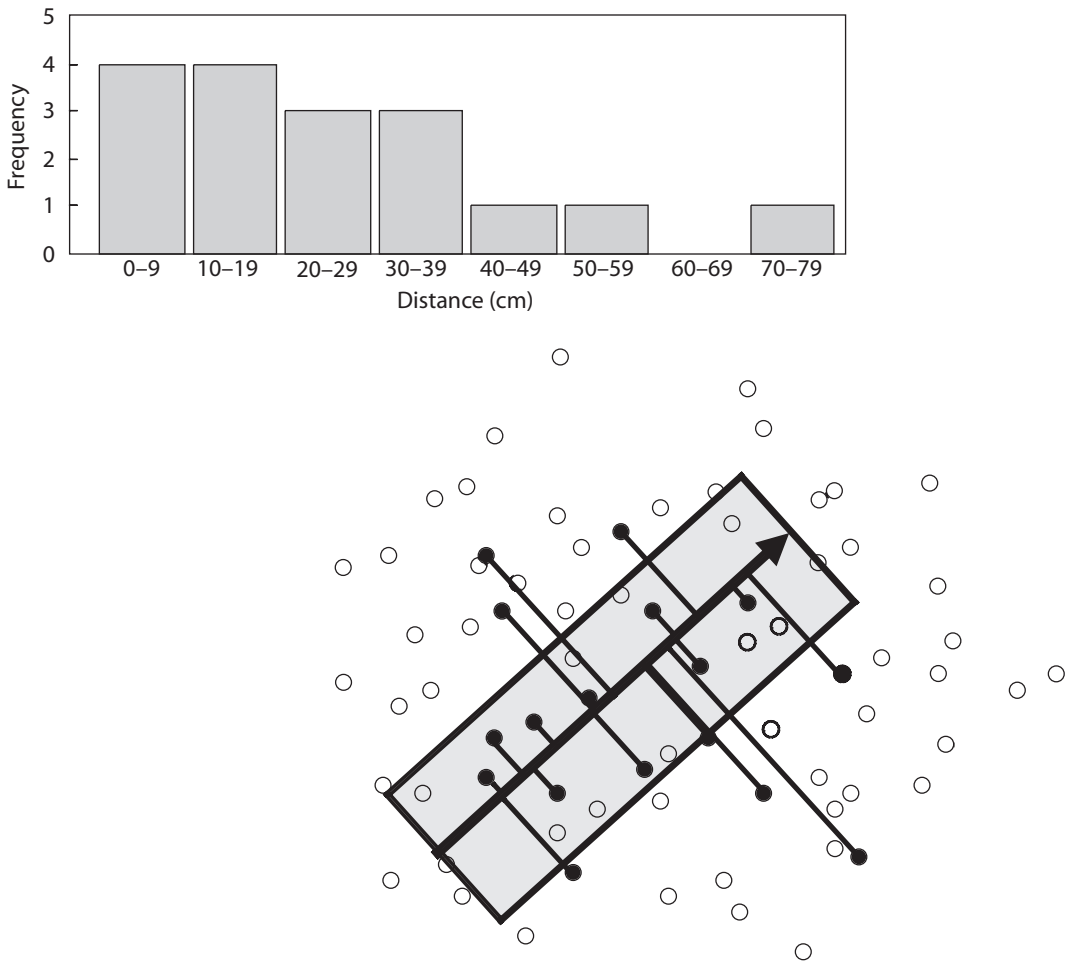
Figure 8.1   Example of animals sighted in a transect survey. The histogram depicts the relative frequency of observations within 0.1-m intervals from the transect. The shaded box depicts the effective width of the transect. Open circles indicate fish that are not sighted and closed circles indicate fish that are sighted. Figure modified from Thompson et al. (1998).

does not depend on the number of other fish in the vicinity (Seber 1982; Buckland et al. 1993; Thompson et al. 1998). Carefully implemented field techniques can help ensure that assumptions 1–4 are met. The assumption of independent sightings, however, depends on the behavior of fish and their schooling behavior and patchiness. When fish are sighted in groups, but the proportion of fish sighted is constant with fish density, the precision of population estimates is generally reduced, but the population estimate is not necessarily biased (Buckland et al. 1993). In cases in which the unit of observation is a school or other aggregation of animals, we refer the reader to Buckland et al. (1993) for methods for appropriately analyzing these data. When sightability varies as a function of density or school size, estimates of fish density are likely to be biased, and the applicability of this approach should be reconsidered.

For a single line-transect survey, the general formula for density is (Buckland et al. 1993)

$$\hat{D} = \frac{n}{2L\hat{w}} \, ,$$ \hfill (8.1)

where $\hat{D}$ = estimated density; n = number of fish observed; $\hat{w}$ = estimated effective width of transect from center; and L = transect length.

When counts are conducted from a single fixed point (point plot survey), the area surrounding the point is observed, resulting in a circular search area. In this situation, the general formula for density is (Buckland et al. 1993)

$$\hat{D} = \frac{n}{2\pi\hat{w}^2} \, ,$$ \hfill (8.2)

where $\hat{w}$ = estimated effective search radius.

In applying these formulae, a critical component is estimating w, the effective width of the transect or search radius from a point. Essentially w corresponds to an equivalent transect for which all fish out to w are detected and all fish beyond w are not. In order to estimate this quantity accurately, it is necessary to select a function describing the pattern of sightability with distance. Many functions can be used to describe the sightability function. We apply two of these functions to illustrate that the choice of sightability function matters, and we provide formulae for estimating total population abundance from density and the total area of the study site in Box 8.1. Buckland et al. (1993) provide a thorough discussion of various sightability functions and methods for selecting among these functions.

The variance for the density estimate (and population size) for a single transect within a site can be estimated approximately based on the binomial distribution describing observed and unobserved fish (Box 8.1), assuming that fish are randomly and independently distributed. When multiple transects or points are observed, the variance among transects should be determined based on the overall sampling design, following methods outlined in Chapter 3.

Specialized software packages are available to estimate population size based on distance sampling (for example, the comprehensive package, DISTANCE; Thomas et al. 2001; available at http://www.ruwpa.st-and.ac.uk/distance/).

Box 8.1   Estimation of Abundance and Density Based on Distance Sampling

An investigator snorkels along a 100-m transect that is randomly located in a stream reach containing 500 m^2. Thirty brook trout are observed at the following right-angle distances (m) from the center of the transect: 0.7, 0.1, 0.6, 0.3, 0.4, 0.1, 3.2, 0.4, 0.6, 1.4, 0.2, 0.1, 2.5, 0.4, 4.6, 2.2, 0.5, 1.6, 0.4, 0.4, 1.5, 0.8, 0.0, 0.2, 2.1, 0.4, 0.4, 0.1, 1.1, and 0.6. The investigator would like to estimate the density of brook trout in the section and the total population in the reach.

We define the following variables:

n	=	number animals observed;
N	=	total population in reach;
A	=	total area of reach (m^2);
D	=	density of fish (number/m^2);
L	=	length of transect (m);
y	=	right angle distance (m) from transect for each animal;
w	=	effective strip width;
$V(\hat{N})$	=	estimated variance of population estimate; and
CI	=	confidence interval.

Based on the assumption that sightability drops off exponentially with distance from the transect, and that fish are independently distributed in the reach, we have the following (Seber 1982):

$$\hat{w} = \frac{\Sigma y}{n-1} = \frac{27.9}{30-1} = 0.962;$$

$$\hat{D} = \frac{n}{2L\hat{w}} = \frac{30}{2 \cdot 100 \cdot 0.962} = 0.156;$$

$$\hat{N} = \frac{nA}{2L\hat{w}} = \frac{30 \cdot 500}{2 \cdot 100 \cdot 0.962} = 78;$$

$$V(\hat{N}) = \frac{n}{\left(\frac{n}{\hat{N}}\right)^2}\left(1 - \frac{n}{\hat{N}} + \frac{n}{n-2}\right) = \frac{30}{\left(\frac{30}{78}\right)^2}\left(1 - \frac{30}{78} + \frac{30}{30-2}\right) = 342;$$

$$CI = \hat{N} \pm Z_{\alpha/2}\sqrt{V(\hat{N})} = 78 \pm 1.96\sqrt{342} = 78 \pm 36 = 42,\ 114.$$

Based on the assumption that the sightability function follows a half-normal distribution, the formula for effective width is (Buckland et al. 1993)

$$\hat{w} = \frac{1}{\sqrt{\dfrac{2}{\pi\Sigma(y^2/n)}}} = \frac{1}{\sqrt{\dfrac{2}{\pi \cdot 1.956}}} = 1.752,$$

and density is calculated as above:

$$\hat{D} = \frac{30}{2 \cdot 100 \cdot 1.752} = 0.086.$$

If sightability drops off exponentially, the estimated population is 78 with an approximate CI of 42 to 114. Note that the density (and hence total abundance) based on a half-normal distribution is approximately half that obtained with an exponential model, highlighting the need to test the assumed sightability function (see Buckland et al. 1993 for these methods).

■ 8.3 POPULATION ESTIMATION: MARK–RECAPTURE METHODS

8.3.1 Closed Population Mark–Recapture Methods

The underlying concepts and assumptions of mark–recapture methods of population estimation have a long history in the fishery literature. Because of the extensive reviews available on this subject (Otis et al. 1978; Seber 1982; Burnham et al. 1987), we will emphasize common applications and methods that provide a base for specialized or particularly complex situations.

8.3.1.1 *Single Marking Period and Single Recapture Period*

In the simplest case, fish are randomly collected from a closed population, and easily recognizable, permanent marks are applied to captured individuals. These individuals are then released and allowed to mix completely with the remainder of the population. A second sampling is undertaken, and the ratio of marked to unmarked fish can be used to estimate the total population. Assumptions in basic mark–recapture studies include (1) the population is geographically closed, with no immigration or emigration, (2) the population is demographically closed, with no birth or deaths, (3) no marks are lost or missed (4) marking does not change fish behavior or vulnerability to capture, (5) marked fish mix at random with unmarked fish, and (6) all animals have an equal probability of capture that does not change over time (Otis et al. 1978; Seber 1982). A number of formulae have been developed for this basic situation. In practical terms, all give similar results when reasonable numbers of marked fish are recaptured (e.g., at least 2–3, but preferably greater than 10; Chapman 1951; Robson and Regier 1964). Because of its widespread use and theoretical basis, we recommend the use of the Chapman estimator (Seber 1982):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \, , \tag{8.3}$$

where n_1 = number caught and marked in first sampling period; n_2 = number caught in second sampling period; and m_2 = number of marked animals in second sampling period.

The variance of this estimator can be approximated as (Seber 1982)

$$V(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)} - 1. \tag{8.4}$$

Numerous approaches are available to develop confidence intervals (CIs) for $\hat{N}$. Unfortunately, a diversity of methods occurs because of different distributional assumptions and different approximations for small and modest sample sizes. As such, a single method has not yet been identified as being generally best. For large sample sizes (e.g., $m_2 > 50$), the normal approximation is generally adequate (Seber 1982), and ($[100 - \alpha]\%$) confidence limits can be calculated as

$$\hat{N} \pm Z_{\alpha/2} \sqrt{V(\hat{N})}. \tag{8.5}$$

For a 95% CI, $\alpha = 0.05$, and $Z_{\alpha/2} = 1.96$. When there are fewer than 50 recaptures, Chapman (1948; reproduced in Seber 1982 and Appendix) provides a table from which CIs can be calculated based on the number of recaptured fish.

8.3.1.2   The Schnabel Method

When multiple marking and recapture samples are collected over a short period (so that the population is closed with no immigration, emigration, recruitment, or mortality), population size can be estimated with the Schnabel method (Schnabel 1938; Seber 1982):

$$\hat{N} = \frac{\sum\limits_{i=2}^{t} n_i M_i}{\sum\limits_{i=2}^{t} m_i + 1}, \tag{8.6}$$

where t = number of sampling occasions; n_i = number of fish caught in ith sample; m_i = number of fish with marks caught in ith sample; and M_i = number of marked fish present in the population for ith sample.

The variance of this estimator can be approximated as (Seber 1982)

$$V(\hat{N}) = \hat{N}^2 \left[\frac{\hat{N}}{\sum n_i M_i} + 2 \cdot \frac{\hat{N}^2}{(\sum n_i M_i)^2} + 6 \cdot \frac{\hat{N}^3}{(\sum n_i M_i)^3} \right]. \tag{8.7}$$

Confidence intervals for $\hat{N}$ with the Schnabel method can be computed following the same recommendations for the Chapman method in a single mark–recapture experiment.

8.3.1.3   Multiple Recapture Events with Uniquely Marked Individuals

In many situations, a simple design using a single marking period and single re-capture period or a Schnabel-type design is sufficient to estimate population abundance. The effectiveness of such designs, however, rests on adequately meeting the assumptions. Unfortunately, it is generally not possible to test these assumptions using the data collected during a single recapture period or when fish are simply marked as being previously caught. To test the assumptions underlying mark–recapture methods of population estimation, it is generally necessary to sample over multiple periods and to have marks that allow for the capture history of individual fish to be determined (e.g., by using individually numbered tags).

For closed populations with uniquely marked fish, Otis et al. (1978) present a hierarchical suite of models intended to cover a range of situations for which particular assumptions hold (Figure 8.2). The simplest, yet most restrictive, model is that for which all assumptions listed earlier apply (M_o). In the next tier of models, three basic mechanisms causing unequal capture probabilities are addressed.
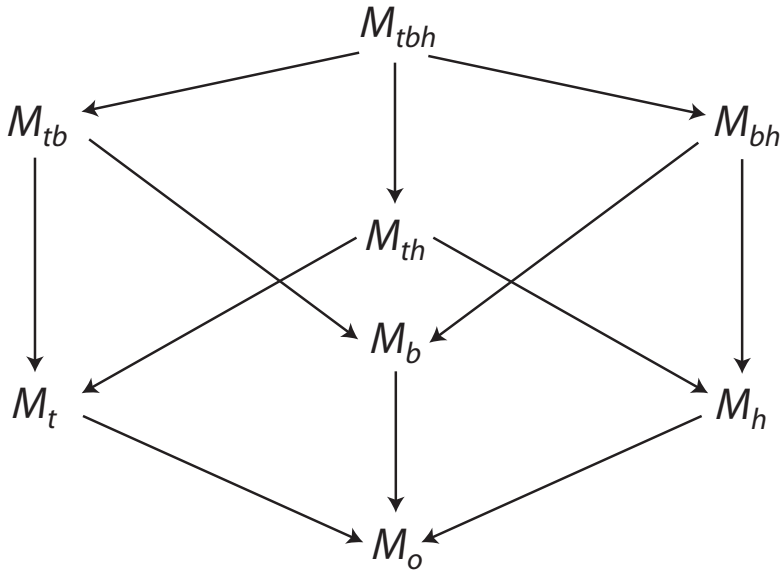
In model M_t, the probability of capture is allowed to vary among different sample periods (time). Variability in capture over time may occur due to factors such as weather or due to changes in the amount or type of fishing gear deployed. In model M_b, the probability of capture is allowed to vary due to behavioral response to prior capture (i.e., fish become more prone or less prone to capture after being caught, handled, and marked). In surveys of small mammals, for example, investigators find that marked animals may become trap happy or trap shy, thus biasing population estimates if such behavior is not considered (Seber 1982). The final model, M_h, allows for heterogeneity in the capture probability of individual fish. This heterogenity may occur for a variety of reasons, including inherent features of each fish, such as its size, or less obvious factors such as variation in the size of home ranges, resulting in different vulnerabilities to passive gears such as trap nets. Methods have been developed to estimate population size for each of these models and are illustrated below. Because of the complexity of the required analyses, we strongly recommend the use of specialized software when applying these models. The program MARK (White and Burnham 1999; available at http://www.cnr.colostate.edu/~gwhite/mark/mark.htm.) is a very flexible software package designed to analyze data from mark–recapture studies.

In the next tier of models, variations in probability of capture occur through combinations of two of the above factors (Figure 8.2). Thus, model M_{tb} represents the case in which capture probability varies over time, as well as with the prior capture history of an animal (behavior). Estimation methods are also available for each of these models; however, we refer the reader to software, such as MARK, specially designed to handle such situations. Unfortunately, no method has yet been developed to estimate population size and account for these three sources of variation simultaneously (i.e., to estimate the parameters for model M_{tbh}).

A central concept to estimating population size by means of these models is the capture history of an animal. Because the population is assumed to be closed, the number of animals in the population (N) remains constant over all sampling periods. As such, during each of the sampling periods (numbered 1 to t), an animal can either be caught or not. For convenience, the capture history of all animals observed can be recorded in a matrix in which a 1 is used to indicate a capture and 0 to indicate no capture during a particular sampling period.

The second concept central to estimating population size based on these models is the likelihood function. Although this is the foundation for many methods of population estimation (in fact, it is the basis for the Chapman and Schnabel estimators), likelihood functions may be unfamiliar to many readers. We provide a brief synopsis of this topic in the context of population estimators in Box 8.2. Readers should consult texts in mathematical statistics (e.g., Bickel and Doksum 1977; Rice 1995) for a more thorough treatment. In some cases, likelihood methods result in a formula for directly estimating population abundance. In most situations, however, there is no direct formula relating the data to the population estimate. Instead, the likelihood function is repeatedly evaluated at trial values of N (or related parameters that determine N) until a value of N is found that produces the maximum value of the likelihood function. This is chosen as the best or

Figure 8.2 Hierarchical organization of models for capture–recapture methods of population estimation as described by Otis et al. (1978). Model M_o allows all assumptions of the mark–recapture model to apply; model M_t allows the probability of capture to vary among sample periods (time); model M_b allows the probability of capture is to vary due to behavioral response to prior capture; model M_h allows for heterogeneity in the capture probability of individual fish; and the remaining models allow variations in probability of capture through combinations of the above factors. Figure modified from Otis et al. (1978).

most likely population estimate, $\hat{N}$. With modern computing power, a "brute force" solution can be found simply by starting with a trial value of N set equal to the total number of distinct individuals caught (i.e., the minimum possible population) and then evaluating the likelihood function for each integer value of N up to an arbitrary maximum. Generally, the logarithm of the likelihood function is evaluated because it is often easier to compute and because it provides a useful basis for comparing between models and for estimating CIs. Further, the likelihood function can often be maximized focusing on one parameter at a time, producing what is called a concentrated likelihood (Seber and Wild 1989). Following precedent in the literature, and for simplicity, we will generally not distinguish between concentrated likelihood functions or likelihood functions that include all parameters.

The log-likelihood function $(\log_e L)$ used to estimate $\hat{N}$ for model M_o (Otis et al. 1978) is

$$\log_e L(N \mid X) = \left\{ \log_e \left(\frac{N!}{(N - M_{t+1})!} \right) + [n_. \log_e(n_.)] + [(tN - n_.)\log_e(tN - n_.)] - [tN\log_e(tN)] \right\}, \quad (8.8)$$

where X = capture history matrix; M_{t+1} = total number of distinct fish caught; $n.$ = total number of fish captured; and t = number of sampling periods.

Once the maximum-likelihood estimate, $\hat{N}$, has been calculated by finding the N that maximizes equation (8.8), the corresponding maximum-likelihood estimate for the probability of capture is

$$\hat{p} = \frac{n.}{t\hat{N}} \cdot \qquad (8.9)$$

An asymptotic estimate of the variance for $\hat{N}$ is (Otis et al. 1978)

$$V(\hat{N}) = \frac{\hat{N}}{\left[(1 - \hat{p})^{-t} - \left(\dfrac{t}{1 - \hat{p}} \right) + (t - 1) \right]} \cdot \qquad (8.10)$$

Confidence intervals for $\hat{N}$ can be obtained in a number of ways. The first method is to estimate variance of $\hat{N}$ by means of equation (8.10) and calculate upper and lower bounds based on equation (8.5). This approach assumes that $\hat{N}$ has a normal distribution, which should be a reasonable approximation when more than 30 animals are recaptured. An alternate method, discussed in Box 8.2, is to use the likelihood function itself to determine CIs. Trial values of N that produce likelihood values that differ from the maximum likelihood by more than 3.841, which is the critical value for a χ^2 distribution with 1 df and an α of 0.05, define the bounds of the CI. The likelihood method for determining CIs is often preferred because it does not require the assumption of normality, thereby allowing for asymmetric CIs for modest sample sizes.

In model M_t, the capture probability for individual animals varies over time. As such, this model has $t + 1$ parameters: N, which is the population abundance, and $p_1, p_2, \ldots, p_t$, which are the time-specific capture probabilities. The log-likelihood function for model M_t is (Otis et al. 1978)

$$\log_e L(N|X) = \log_e \left[\frac{N!}{(N - M_{t+1})!} \right] + \left[\sum_{j=1}^{t} n_j \log_e (n_j) \right]$$
$$+ \left[\sum_{j=1}^{t} (N - n_j) \log_e (N - n_j) \right] - [tN\log_e(N)] . \qquad (8.11)$$

The N that maximizes equation (8.11) is the maximum-likelihood estimate, $\hat{N}$. The corresponding maximum-likelihood estimates for the probability of capture for each time period can be determined by

$$\hat{p}_j = \frac{n_j}{\hat{N}} \cdot \qquad (8.12)$$

Box 8.2   Application of Likelihood Functions in Population Estimation

Here, we illustrate the ideas underlying likelihood functions in the context of estimating population size. For this example, consider the situation in which 60 fish are present in a pool within a stream and we have a 40% chance of catching each fish with one electrofishing pass. In this example, we theoretically could catch between 0 and 60 fish. Assuming that the probability a fish is caught is independent among fish, the probability a specific number of fish will be caught in one pass is given by a binomial probability distribution. For example, the probability of capturing 20 in one pass (i.e., number caught = n =20), assuming catchability is 0.4, is given by the formula

$$P(n = 20 | N = 60, q = 0.4) = \frac{N!}{n!(N-n)!}\, q^n(1-q)^{N-n}$$

$$= \frac{60!}{20!(60-20)!}\, 0.4^{20}(1-0.4)^{60-20} = 0.0616.$$

Applying this formula for each possible outcome, we can see that the outcome with the highest probability (i.e., the most likely outcome) is 24 fish captured (Figure 8.3A). Equations of this type are known as probability functions for discrete distributions or probability density functions for continuous distributions.

When estimating population size by maximum likelihood, we reverse the role of parameters and data. We know our data (or, in this case, datum, i.e., n = 20) and ask what is the most likely population size that would have produced our observation. For simplicity in this example, we assume that q = 0.4 and is known. Now, we can write

$$P(N = 60 | n = 20, q = 0.4) = \frac{N!}{n!(N-n)!}\, q^n(1-q)^{N-n}$$

$$= \frac{60!}{20!(60-20)!}\, 0.4^{20}(1-0.4)^{60-20} = 0.0616.$$

Note that this is mathematically identical to the previous equation. However, we now refer to $P(N = 60 | n = 20, q = 0.4)$ as the likelihood. When using the likelihood, we generally take the view that the parameter we are estimating (N) can be varied to maximize this likelihood. The process of calculating the likelihood for a series of different parameter values over some range is referred to as profiling the likelihood. The fundamental concept of statistical likelihood is that our observations (the data) occur through a stochastic or random process with a defined probability structure. Through this process, we are likely to observe data in proportion to their probabilities as described in the formulae above.

As shown in Figure 8.3B, the likelihood given the data (n = 20) is maximized for N = 50. Our estimate is less than the true value of 60 because we happened to capture somewhat less than one might typically capture. Note that although N = 60 does not maximize the likelihood, it has a likelihood that is reasonably high (Figure 8.3B). Thus, we cannot rule out N = 60, as it could have reasonably generated the observed data. On the other hand, the likelihood is very low for N = 100. If we repeated the process of sampling, sometimes our population estimates would be above and other times they would be below the true value, but our estimates would very rarely be above 100. As such, the likelihood is a measure of how consistent the data are with different population sizes.

(Box continues)

Box 8.2   *(continued)*

In this simple example, we assumed that q was known. If we had not, we could not have computed a unique solution (e.g., our data could have resulted from a combination of smaller q and larger N). As indicated in the introduction to this chapter, we generally need more information than catch per unit effort (C/f) from a single sampling event to estimate true abundance. In our simple example, the additional information we need is the probability of capture with a single pass (i.e., catchability).

To be somewhat more realistic, assume that q is unknown and we apply a depletion sampling experiment (see section 8.4) to the stream and catch 24 fish in the first sampling pass, 17 fish in the second sampling pass, and 8 fish in the third sampling pass. We will also make the usual assumptions that the population is closed and that all fish have equal vulnerability and that this is consistent over time. The details of the likelihood function for the removal method are presented in section 8.4, equation (8.24). Note that the $\log_e$ of the likelihood is often used to make the computations more tractable. Applying the formula to various levels of catchability from 0 to 1.0, we can profile the likelihood for these data as shown in Figure 8.4A.

From Figure 8.4A, it is apparent that it is possible that catchability (q) is equal to 0.6, but it is not very likely relative to other possible values of q. Likewise, q could be 0.01, but that too is not very consistent with our observations. In this example, the value of q that is most consistent with our observations is 0.40. Thus, we term this the maximum-likelihood estimate of q. Because we sampled the population three times, the estimated cumulative proportion of the population removed is $1 - (1 - q)^3 = 1 - (0.6)^3 = 0.784$. Given that we caught a total of 49 fish, the most likely estimate of N is $49/0.784 = 62$ (Figure 8.4B).

There are several ways to estimate variances and CIs associated with maximum-likelihood estimates. One way is to consider how the likelihood changes when the parameters move small distances away from the maximum-likelihood value. The first derivative of the logarithm of the likelihood measures how quickly the likelihood changes relative to a change in the parameter and is equal to zero at the maximum. Variance is estimated by taking the negative of the reciprocal of the second partial derivative of the logarithm of the likelihood with respect to each parameter (Seber 1982). The second partial derivative measures the curvature of the log-likelihood portrayed in Figure 8.4. If the magnitude of the second derivative is large, the likelihood falls off rapidly as we move the parameters away from the maximum-likelihood estimate; the estimated variance would be relatively small because alternative values very far from the estimate are unlikely. Confidence intervals can be constructed from the variance estimated above, assuming a distribution (often normal) for the estimate. The profile likelihood can also be used to construct CIs directly by determining values for the parameters that give a log-likelihood value that is less than the maximum value of the log-likelihood by 3.841. This method is based on the fact that, under the null hypothesis, this difference approximates a χ^2 distribution with 1 df, and 3.841 is the 5% critical value for the χ^2 distribution with 1 df. As shown in Figure 8.4B, the maximum-likelihood estimate of N is 62 with a 95% CI of 51 to approximately 1,650.

Both approaches for computing variances and CIs produce approximations based on asymptotic (i.e., large sample) statistical properties and require relatively large sample sizes to be accurate. The profile likelihood method often performs better because the shape of the likelihood profile is examined and no assumption of normality is made. The better performance of the profile likelihood method comes at the cost of greater computation, however.
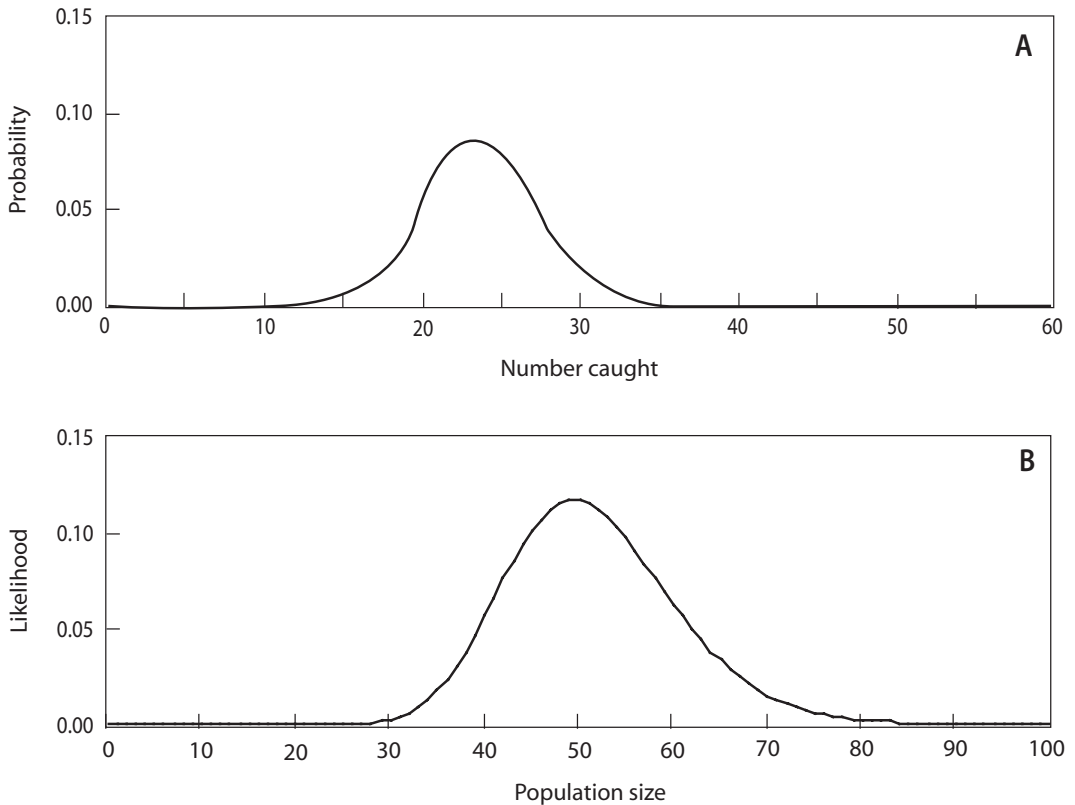
Figure 8.3   (A) Probability of capturing *n* fish from a population with 60 individuals, each with a 40% chance of capture, and (B) log-likelihood of the observation (*n* = 20 fish caught) as a function of population size *(N)*.

The asymptotic variance of $\hat{N}$ under model M_t is (Otis et al. 1978)

$$V(\hat{N}) = \frac{\hat{N}}{\dfrac{1}{\prod\limits_{j=1}^{t}(1 - \hat{p}_j)} + (t - 1) - \sum \dfrac{1}{1 - \hat{p}_j}} .$$

(8.13)

As with model M_o, CIs for $\hat{N}$ under model M_t can be estimated using the variance of $\hat{N}$ and an assumption of normality or through a likelihood-based approach as outlined in Box 8.2.

Model M_b (variability in capture probability due to changes in behavior after capture) has three parameters: N, p, the probability of capturing an unmarked animal, and c, the probability of capturing an animal that was previously captured, marked, and released. The parameter c can be estimated separately from estimation of N and p by (Otis et al. 1978)
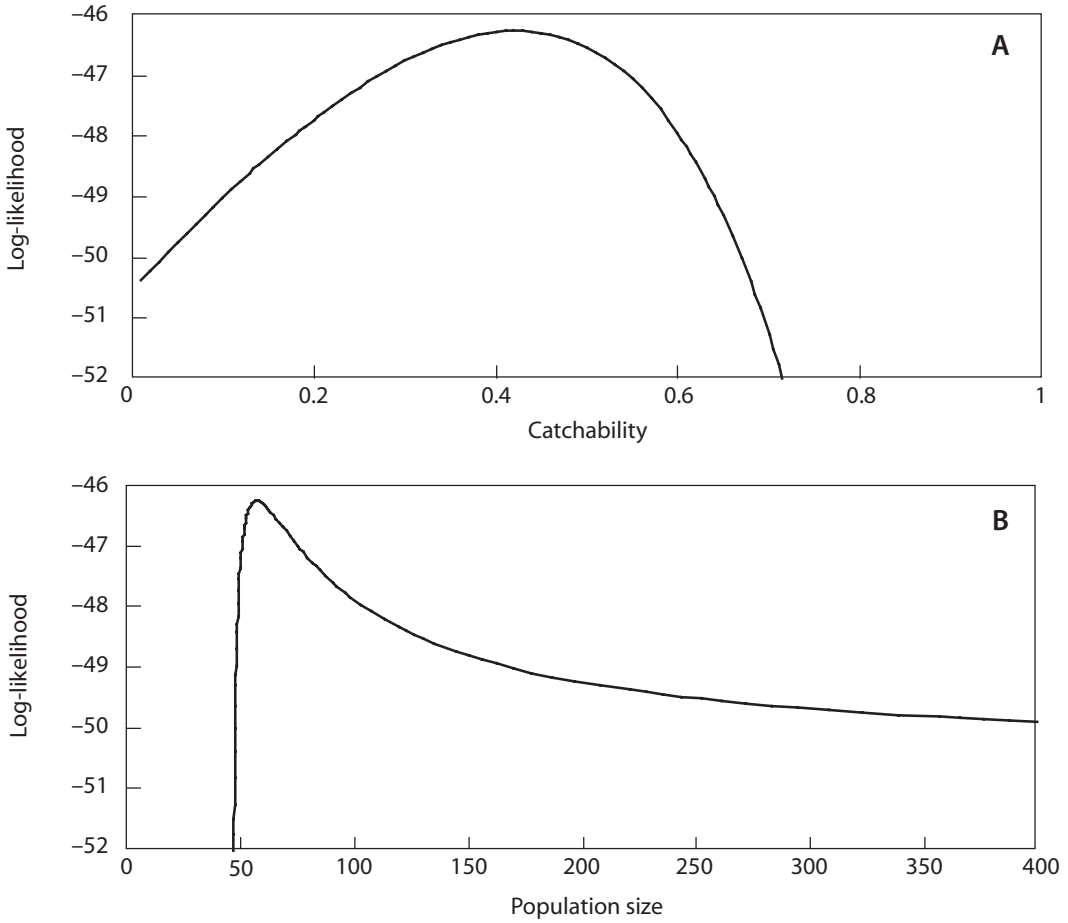
Figure 8.4   Log-likelihood as a function of (A) catchability (q) and (B) population size (N) given depletion sampling experiment described in Box 8.2.

$$\hat{c} = \frac{m_.}{M_.}, \tag{8.14}$$

where $m_. = \Sigma m_j$; m_j = number of marked animals in jth sample; $M_. = \Sigma M_j$; and M_j = number of marked animals in the population for the jth sample.

The likelihood function for model M_b is (Otis et al. 1978)

$$
\begin{aligned}
\log_e L(N) = {} & \log_e\left[\frac{N!}{(N-M_{t+1})!}\right] + \left[M_{t+1}\log_e(M_{t+1})\right] \\
& + \left[(tN - M_. - M_{t+1})\log_e(tN - M_. - M_{t+1})\right] \\
& - \left[(tN - M_.)\log_e(tN - M_.)\right] + m_.\log_e(\hat{c}) + (M_. - m_.)\log_e(1 - \hat{c}).
\end{aligned}
\tag{8.15}
$$

Once $\hat{N}$ has been found by maximizing equation (8.15), the maximum-likelihood estimate of p is calculated as (Otis et al. 1978)

$$\hat{p} = \frac{M_{t+1}}{t\hat{N} - M.} \cdot \qquad (8.16)$$

An asymptotic variance estimate for $\hat{N}$ is (Otis et al. 1978)

$$V(\hat{N}) = \frac{\hat{N}(1 - \hat{p})^t \left[1 - (1 - \hat{p})^t\right]}{\left[1 - (1 - \hat{p})^t\right]^2 - t^2 \hat{p}^2 (1 - \hat{p})^{t-1}} \cdot \qquad (8.17)$$

Estimation of the parameters for model M_h is more problematic than it is for model M_o, M_p, or M_b. The reason for this is that each fish (including unobserved fish) has its own individual catchability. A number of approaches have been taken to solve this problem, generally by making an assumption regarding the statistical distribution of catchabilities. For details of computation for this model, we refer the reader to Otis et al. (1978) and to the program MARK (White and Burnham 1999).

An example applying models M_o, M_p, and M_b is given in Box 8.3. Beyond being able to estimate the parameters for each of these models, an important question is how to choose among them. The most common way of doing this is to compare the maximum-likelihood value for each model and select the model with the highest maximum likelihood. Because the maximum likelihood that can be obtained generally increases as more parameters are added, the likelihood obtained from models with more parameters is typically "penalized" for the additional flexibility offered. The most widely used adjustment to the likelihood function is Akaike's Information Criterion (AIC; Akaike 1973), which is calculated as

$$\text{AIC} = -2 \log_e(\text{likelihood}) + 2 \, (\text{number of parameters}). \qquad (8.18)$$

After computing the AIC, one then selects the model that has the lowest AIC value (Box 8.3).

8.3.2   Open Population Mark–Recapture Methods

Open populations are characterized by having immigration, emigration, mortality, or recruitment occur during the study period. As in closed populations, general models developed to estimate abundance in open populations also make use of the encounter history matrix as the basis for maximum-likelihood estimators and assume that each fish is uniquely marked. Conceptually, the encounter history matrix is important because it defines which animals are observed at particular times. From this, we can also infer which time periods the animal is known to

Box 8.3   Estimation of Population Abundance for a Closed Population Based on Otis et al.'s (1978) Mark–Recapture Models

An investigator conducts a mark–recapture study on a closed population of largemouth bass in a farm pond in order to determine the abundance of adult fish. The sampling consists of four sampling events; fish captured in each event are given a uniquely numbered Floy Tag and released. The capture–recapture data are arranged into a capture matrix in which each cell of the matrix (X_{ij}) is referenced by fish$_i$ in row i and sample period$_j$ in column j. An entry of 1 in the matrix indicates that a fish was caught, and a 0 indicates that the fish was not caught during that sampling period. Fish 1, for example was caught in all four sampling periods, whereas fish 4 was caught in only the first sample period.

Table   Data matrix for mark–recapture study of closed population of largemouth bass.

Fish	Sample 1	Sample 2	Sample 3	Sample 4
1	1	1	1	1
2	1	1	0	0
3	1	0	1	0
4	1	0	0	0
5	1	1	0	1
6	1	0	1	1
7	1	0	0	0
8	0	1	1	0
9	0	1	0	0
10	0	1	0	1
11	0	1	0	0
12	0	1	0	0
13	0	1	1	1
14	0	0	1	0
15	0	0	1	0
16	0	0	1	0
17	0	0	1	1
18	0	0	0	1
19	0	0	1	1
20	0	0	0	1

From these data, the investigator explores which of the Otis et al. (1978) suite of capture–recapture models is most appropriate. For this investigation, we obtain the following basic statistics that are used in the estimation of population abundance, for which t = number of sampling occasions; n_i = number of fish caught in ith sample; m_i = number of fish with marks caught in ith sample; and M_i = number of marked fish present in the population for ith sample.

$t = 4$;
$M_{t+1} = 20$;
$n_1 = 7, n_2 = 9, n_3 = 10, n_4 = 9, n. = 35$;
$m_1 = 0, m_2 = 3, m_3 = 5, m_4 = 7, m. = 15$; and
$M_1 = 0, M_2 = 7, M_3 = 13, M_4 = 18, M. = 38$.

Starting with Model M_o (see Figure 8.2), we compute the log-likelihood for trial values for $\hat{N}$ by applying equation (8.8). Two examples for trial values are 30 and 23. Using these values, we obtain

$$\log_e L(\hat{N}=30|X) = \left\{\log_e\left(\frac{30!}{(30-20)!}\right) + [35\log_e(35)] + [(4\cdot30-35)\log_e(4\cdot30-35)] - [4\cdot30\log_e(4\cdot30)]\right\} = -12.890;\text{ and}$$

$$\log_e L(\hat{N}=23|X) = \left\{\log_e\left(\frac{23!}{(23-20)!}\right) + [35\log_e(35)] + [(4\cdot23-35)\log_e(4\cdot23-35)] - [4\cdot23\log_e(4\cdot23)]\right\} = -11.299.$$

When the log-likelihood is computed and plotted for trial values of $\hat{N}$ ranging from 21 to 100 for model M_t (equation [8.11]), we find that the maximum of the log-likelihood is

$$\log_e L(\hat{N}=30|X) = \log_e\left[\frac{30!}{(30-20)!}\right] + [7\log_e(7) + 9\log_e(9) + 10\log_e(10) + 9\log_e(9)]$$
$$+ \{[(30-7)\log_e(30-7)] + [(30-9)\log_e(30-9)] + [(30-10)\log_e(30-10)]$$
$$+ [(30-9)\log_e(30-9)]\} - [4\cdot30\log_e(30)] = -12.492;\text{ and}$$

$$\log_e L(\hat{N}=23|X) = \log_e\left[\frac{23!}{(23-20)!}\right] + [7\log_e(7) + 9\log_e(9) + 10\log_e(10) + 9\log_e(9)]$$
$$+ \{[(23-7)\log_e(23-7)] + [(23-9)\log_e(23-9)] + [(23-10)\log_e(23-10)]$$
$$+ [(23-9)\log_e(23-9)]\} - [4\cdot23\log_e(23)] = -10.854.$$

The maximum of the log-likelihood for model M_t is -10.854 at $\hat{N}=23$ (Figure 8.5).

When model M_b is employed (equation [8.15]), the log-likelihood for the same trial values is

$$\log_e L(30|X) = \log_e\left[\frac{30!}{(30-20)!}\right] + [20\log_e(20)] + [(4\cdot30-38-20)\log_e(4\cdot30-38-20)]$$
$$- [(4\cdot30-38)\log_e(4\cdot30-38)] + 15\log_e(0.395) + (38-15)\log_e(1-0.395)] = -11.491;\text{ and}$$

$$\log_e L(23|X) = \log_e\left[\frac{23!}{(23-20)!}\right] + [20\log_e(20)] + [(4\cdot23-38-20)\log_e(4\cdot23-38-20)]$$
$$- [(4\cdot23-38)\log_e(4\cdot23-38)] + 15\log_e(0.395) + (38-15)\log_e(1-0.395)] = -11.270.$$

The maximum of the log-likelihood for model M_b is -11.247 at $\hat{N}=24$ (Figure 8.5). The Akaike's Information Criterion (AIC) for each model is

AIC for $M_o = -2(-11.299) + 2(2) = 26.598$;
AIC for $M_t = -2(-10.854) + 2(5) = 31.708$; and
AIC for $M_b = -2(-11.247) + 2(3) = 28.494$.

Based on the AIC, we would choose model M_o as the best model among those considered. The likelihood for this model is not substantially lower than for M_t and M_b, but it requires fewer parameters, resulting in a more parsimonious model.
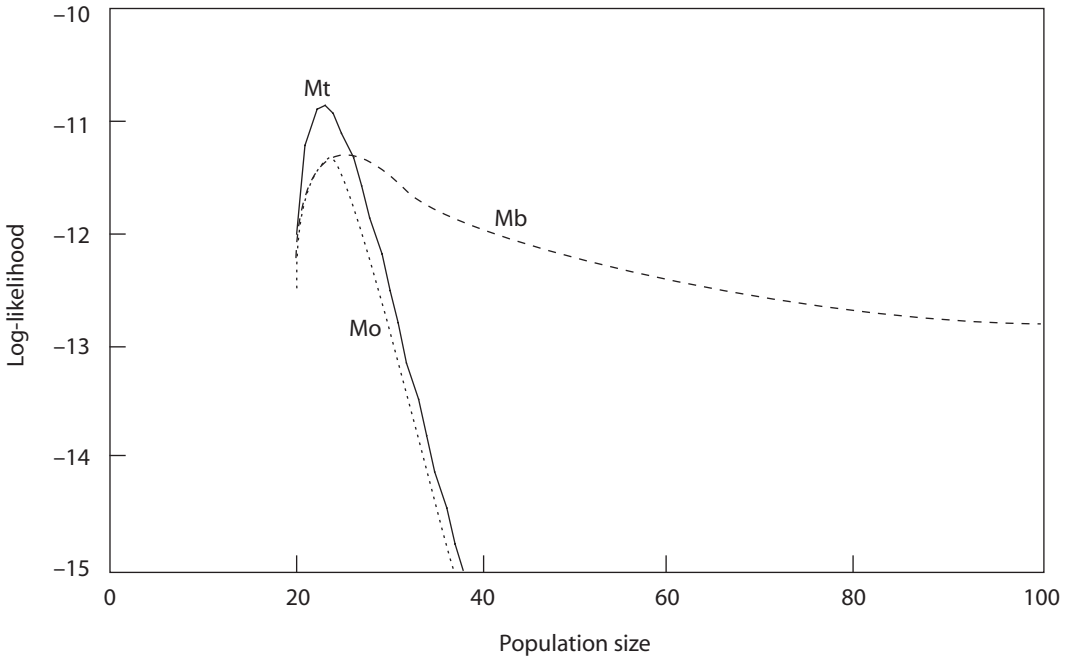
Figure 8.5   Log-likelihood as function of population size *(N)* for Otis et al.'s (1978) hierarchy (see Figure 8.2) based on example in Box 8.3. An approximate confidence interval for *N* under model M_o is where the *x*-axis crosses the log-likelihood curve.

be alive even if it is not observed. For example, a fish marked at the beginning of an experiment, but not observed again until the end, is known to have survived through all intervening sampling events. Open population models are also similar to the Otis et al. (1978) hierarchy of models in that numerous factors and assumptions can be represented in a suite of models applicable to open populations. Compared with closed population models, additional parameters describing losses and additions to the population are necessary for open population models. The additional parameters necessary to describe open populations often lead to a decline in the precision of population estimates. Further, allowing for an open population requires stronger adherence to some of the model assumptions. In particular, heterogenity in capture probability becomes increasingly important and can lead to bias in population estimates.

In Box 8.4, we demonstrate computations for a basic model illustrating the underlying approach applicable to a broader range of possible models for open populations. Lebreton et al. (1992) and Seber (1982) provide in-depth coverage of this broader family of models, commonly referred to as Cormack–Jolly–Seber (CJS) survival models. The software program MARK, referred to earlier, can accommodate CJS models. The program RELEASE (available at http://www.warnercnr.colostate.edu/~gwhite/software.html) was also recommended by Lebreton et al. (1992).

Box 8.4 represents a commonly used open population model in which the abundance of animals changes over time due to births and deaths, survival varies over time, but capture probability is constant over time and across all individuals in the population. As such, this model is analogous to model M_o, with the addition of time-varying population abundance and survival. In the CJS models, four basic sets of parameters are estimated: population abundance (N_i), capture probability (p_i), apparent survival (φ_i), and additions (births and immigrant) to the population (B_i). The term apparent survival is used instead of survival because, in most cases, it is impossible to distinguish any losses due to emigration from mortality. If the population is geographically closed, φ_i is an estimator for actual survival rate. Each of the above parameters are indexed by time, but care must be taken in understanding that φ_i indicates the survival rate from time i to $i + 1$. Further, not all quantities are estimable; for example, abundance at the beginning of the study (N_1) generally cannot be determined. The application of this model is illustrated in Box 8.4. For simple models, closed-form equations exist to estimate population size and other necessary parameters. In more complex situations, an iterative (i.e., starting with an initial guess, and then using a numerical optimization to improve the fit) approach is necessary to solve the likelihood equations.

■ 8.4   POPULATION ESTIMATION: REMOVAL METHODS

8.4.1   Closed Population Removal Methods

Like mark–recapture methods, removal methods rely on sequentially sampling the target population. During each sampling period, the number of fish captured are recorded, and captured fish are temporarily (e.g., during monitoring surveys) or permanently (e.g., in recreational or commercial fisheries) removed from the population. Through the reduction in the population, catch in subsequent sampling periods is reduced. The rate at which catch declines gives a measure of the proportion of the original population that has been removed.

As with mark–recapture methods, removal methods generally rely on the population being closed and individuals in the population having equal vulnerability to the sampling gear. Typically, equal amounts of effort are expended during each sampling period, and it is assumed that the capture probability is equal across all sampling periods. Historically, regressions relating C/f to cumulative catch (Leslie method, Leslie and Davis 1939) or cumulative effort (De Lury method, De Lury 1947) were used to estimate population size in removal experiments. These methods are still commonly used and often result in reasonable population estimates. Currently, there is a shift away from the regression-based methods to likelihood-based methods. The principal advantage of likelihood methods over regression methods is that they provide means for testing some of the assumptions of the removal method and creating models that can accommodate a relaxed set of assumptions. For example, the assumption of equal catchability over all sampling periods can be relaxed if a function can be used to describe how catchability changes over time.

Box 8.4   Estimation of Abundance Based on a Cormack–Jolly–Seber Model for Open Populations

In order to determine the conservation status of desert pupfish, a graduate student performs a 3-year capture–recapture experiment on the population in a desert pool that is closed to immigration and emigration but where recruitment and mortality occur on an annual basis.

Table   Capture matrix from capture–recapture experiment with desert pupfish.

Fish idenfication	Year		
	1998	1999	2000
1	1	1	1
2	1	1	1
3	1	1	0
4	1	1	0
5	1	0	1
6	1	0	1
7	1	0	1
8	1	0	1
9	1	0	0
10	1	0	0
11	1	0	0
12	1	0	0
13	1	0	0
14	0	1	1
15	0	1	1
16	0	1	1
17	0	1	1
18	0	1	0
19	0	1	0
20	0	1	0
21	0	1	0
22	0	0	1
23	0	0	1
24	0	0	1
25	0	0	1
26	0	0	1
27	0	0	1
28	0	0	1
29	0	0	1
30	0	0	1

From these data, we define the following components of the Cormack–Jolly–Seber model for an open population:

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i};$$

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i} = \text{estimated population abundance};$$

$$\hat{p}_i = \frac{m_i}{\hat{M}_i} = \text{estimated capture probability};$$

$$\hat{\varphi}_i = \frac{M_{i+1}}{\hat{M}_i - m_i + R_i} = \text{estimated apparent survival};$$

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\varphi}_i(N_i - n_i + R_i) = \text{estimated additions (births and immigration) to the population},$$

where M_i = number of marked animals in population at start of sample i; m_i = number of marked fish caught in ith sample; n_i = number of fish caught in ith sample; R_i = number of fish caught in ith sample that are marked and released; z_i = number of fish caught before ith sample that are not captured in ith sample but are caught at a later time; and r_i = number of fish released at the ith sample that are later recaptured.

From these components, we can estimate the following quantities:

$m_1 = 0, m_2 = 4, m_3 = 10;$
$n_1 = 13, n_2 = 12, n_3 = 19;$
$r_1 = 0, r_2 = 6, r_3 = 0;$
$z_1 = 0, z_2 = 4, z_3 = 0;$
$\hat{M}_1 = 0$ (by definition), $\hat{M}_2 = 4 + \frac{12 \cdot 4}{6} = 12, \hat{M}_3 = $ not estimable;
$\hat{N}_1 = $ not estimable, $\hat{N}_2 = \frac{12 \cdot 12}{4} = 36, \hat{N}_3 = $ not estimable;
$\hat{p}_1 = $ not estimable, $\hat{p}_2 = \frac{4}{12} = 0.33, \hat{p}_3 = $ not estimable; and
$\hat{\varphi}_1 = \frac{12}{0 - 0 + 13} = 0.92, \hat{\varphi}_2 = $ not estimable.

As this example illustrates, estimating abundance for open populations is much more difficult than for closed populations, with several important population parameters not being estimable.

In the simplest situation, all of the above assumptions hold, and sampling is done during two periods with equal effort. Catch (i.e., the number removed, n_i) is recorded for each sampling period. Zippin (1956, 1958; Seber 1982) showed that the maximum-likelihood estimator in this situation is

$$\hat{N} = \frac{n_1^2}{n_1 - n_2}.$$
(8.19)

Note that n_1 must be greater than n_2 to estimate $\hat{N}$. An estimate of catchability, $\hat{q}$, is given by

$$\hat{q} = \frac{n_2}{n_1}.$$
(8.20)

The variance estimator for $\hat{N}$ is

$$V(\hat{N}) = \frac{n_1^2 n_2^2 (n_1 + n_2)}{(n_1 - n_2)^4}.$$
(8.21)

Because of the dependence on only two data points, the precision of population estimates in this situation is often poor. Moreover, variability in catches can result in higher C/f in the second sampling period, resulting in no estimate of abundance. Heimbuch et al. (1997) present a method for adjusting population estimates in two-pass sampling when many sites are visited. In their method, the catch data are added across sites to allow an estimate of the population for all sites together. By adding data from many sites, variations in the catch at individual sites tend to cancel, resulting in a better estimate of average catchability. Heimbuch et al. (1997) also present extensions to this method by which variability in individual catchability can be accounted for, analogous to model M_h of Otis et al. (1978).

When fish are removed during three sampling periods, the following maximum-likelihood estimators for catchability and population size (Junge and Libosvárský 1965; cited in Seber 1982) may be applied:

$$\hat{q} = \frac{3X - Y - \sqrt{Y^2 + 6XY - 3X^2}}{2X}, \text{ and}$$
(8.22)

$$\hat{N} = \frac{6X^2 - 3XY - Y^2 + Y\sqrt{Y^2 + 6XY - 3X^2}}{18(X - Y)},$$
(8.23)

where $X = 2n_1 + n_2$ and $Y = n_1 + n_2 + n_3$.

Variance estimates and CIs for $\hat{N}$ are covered in the general case (below) of four or more removal passes.

When more than three removal passes are conducted, there is no closed-form equation available for directly estimating population size from the data by means of current maximum-likelihood methods. As in the more complex mark–recapture situations, the relative likelihood of parameter values is calculated, and numerical search methods are used to determine which combination of parameter values is most likely given the observed data. When catchability (q) is assumed to be constant over time, the results of this analysis are easy to portray graphically as a profile likelihood (see Box 8.2). In the maximum-likelihood approach, catchability is generally estimated directly, and $\hat{N}$ is calculated from the cumulative catch and estimated cumulative proportion of the population that this represents, based on the estimated catchability (Box 8.5). The likelihood function (dropping those parts of the function that are constants not affecting estimation) for estimating $\hat{q}$ is (Gould and Pollock 1997)

$$
\begin{aligned}
\log_e(q\,|\,n_1, n_2, n_3, \ldots n_t) &= \log_e\left(\frac{x_{t+1}!}{n_1!, n_2!, n_3!, \ldots n_t!}\right) \\
&+ n_1\log_e\left(\frac{q_1}{1 - q_1 - p_1p_2 - p_1p_2q_3 - \ldots p_1p_2 \ldots q_t}\right) \\
&+ n_2\log_e\left(\frac{q_2p_1}{1 - q_1 - p_1p_2 - p_1p_2q_3 - \ldots p_1p_2 \ldots q_t}\right) \\
&+ n_3\log_e\left(\frac{q_3p_2p_1}{1 - q_1 - p_1p_2 - p_1p_2q_3 - \ldots p_1p_2 \ldots q_t}\right) + \ldots,
\end{aligned}
\tag{8.24}
$$

where t = number of removal passes; n_i = catch in ith sample; x_i = cumulative catch prior to removal pass i; q_i = probability of capture in ith removal pass; and $p_i = 1 - q_i$.

Once q_i has been estimated, $\hat{N}$ is estimated by

$$
\hat{N} = \frac{x_{t+1}}{(1 - \hat{q}^t)}.
\tag{8.25}
$$

When the cumulative removal is relatively large (e.g., greater than 30), the asymptotic variance of $\hat{q}$ and $\hat{N}$ are (Seber 1982)

$$
V(\hat{N}) = \frac{\hat{N}(1 - \hat{q}^t)\hat{q}^t}{(1 - \hat{q}^t)^2 - \{[t(1 - \hat{q})]^2\hat{q}^{t-1}}, \text{ and}
\tag{8.26}
$$

$$
V(\hat{q}) = \frac{[(1 - \hat{q})\hat{q}]^2(1 - \hat{q}^t)}{\hat{N}\langle\hat{q}\,(1 - \hat{q}^t)^2 - \{[t(1 - \hat{q})]^2\hat{q}^t]\rangle}.
\tag{8.27}
$$

Box 8.5   Estimation of Abundance Based on the Removal Method in a Closed Population

In order to estimate the abundance of brown trout in a 50-m section of stream below a culvert, a fishery manager conducts a three-pass removal experiment. Fish cannot move upstream because of the culvert, and the manager places a block net on the lower section of the study reach to insure that the population is geographically closed. All three sampling passes are conducted during the same day by means of a backpack electrofishing unit. During sampling, 24 brown trout are caught in the first sampling pass, 17 in the second sampling pass, and 8 in the third sampling pass.

Although the population size can be estimated applying equation (8.23), we illustrate the application of the more general likelihood equation (8.24). Given a trial value for catchability (q) of 0.2,

$$\log_e(q = 0.2 | n_1 = 24, n_2 = 17, n_3 = 8) = \log_e\left(\frac{49!}{24!17!8!}\right) + 24\log_e\left(\frac{0.2}{1 - 0.2 - (0.8)(0.2) - (0.8)(0.8)(0.2) - (0.8)(0.8)(0.8)(0.2)}\right)$$

$$+ 17\log_e\left(\frac{(0.2)(0.8)}{1 - 0.2 - (0.8)(0.2) - (0.8)(0.8)(0.2) - (0.8)(0.8)(0.8)(0.2)}\right)$$

$$+ 8\log_e\left(\frac{(0.2)(0.8)(0.8)}{1 - 0.2 - (0.8)(0.2) - (0.8)(0.8)(0.2) - (0.8)(0.8)(0.8)(0.2)}\right) = 60.409.$$

A search across a range of $\hat{q}$ from 0.01 to 0.99 in steps of 0.01 indicates that the most likely value of $\hat{q}$ is 0.40, with a log-likelihood value of −49.832. From this, $\hat{N}$ is calculated as

$$\hat{N} = \frac{49}{(1 - 0.4^3)} = 63,$$

with an estimated variance of

$$Var(\hat{N}) = \frac{63(1 - 0.4)^3(0.4^3)}{[(1 - 0.4^3)^2] - \{[3(1 - 0.4)]^2(0.4^2)\}} = 10.55.$$

Confidence intervals are typically obtained from the profile likelihood of $\hat{q}$. From the search across values of $\hat{q}$ ranging from 0.01 to 0.99 (in 0.01 increments), the log-likelihood values for $q = 0.65$ and $q = 0.01$ differed from the log-likelihood at $\hat{q} = 0.4$ by 3.841 or more (which is the critical value for the χ^2 distribution with 1 df). The population sizes corresponding to these values of q are 51 and 1,650 and represent approximate 95% CIs for $\hat{N}$.

Confidence intervals can be obtained by assuming that $\hat{q}$ and $\hat{N}$ are normally distributed (equation [8.5]) or from the profile likelihood of (e.g., Box 8.2). Once $\hat{q}$ and $\hat{N}$ have been estimated, the goodness of fit of the estimates can be assessed by comparing the expected catches with the observed catches. Expected catch for each removal pass is predicted by

$$\tilde{\chi}_1 = \hat{N}\hat{q}; \tag{8.28}$$

$$\tilde{\chi}_2 = \hat{N}\hat{q}(1 - \hat{q}); \tag{8.29}$$

$$\tilde{\chi}_3 = \hat{N} \hat{q} (1 - \hat{q})^2 \ldots; \text{ and} \tag{8.30}$$

$$\tilde{\chi}_t = \hat{N} \hat{q} (1 - \hat{q})^{t-1}. \tag{8.31}$$

Goodness of fit can then be assessed by a χ^2 test by comparing the observed catches with the expected catches. This provides a useful diagnostic test to determine if the assumption of constant catchability over time is reasonable.

$$\chi^2 = \sum \frac{(\chi_i - \tilde{\chi}_i)^2}{\tilde{\chi}_i}, \tag{8.32}$$

where χ_i = observed catch in pass i, and $\tilde{\chi}_i$ = expected catch in pass i.

One of the more common violations of the assumptions in the removal method is that individual fish often differ in their catchability, analogous to model M_h for mark–recapture studies. Two approaches can be used to estimate population size in this situation. The first approach rests on the observation that removal studies can be viewed as a special case of mark–recapture model M_b, where the "response" to capture is removal from the vulnerable population (this is equivalent to setting c in model M_b equal to 1.0). Heterogeneity in individual catchability can then be accounted for by fitting model M_{bh} in the Otis et al. (1978) hierarchy. The calculations for this model are complex, but program MARK includes this option.

The second approach for handling variations in catchability is to fit a time-varying function to $\hat{q}$. Because fish with higher catchability tend to be captured and removed earlier in the sampling process, the average catchability of the remaining population tends to decline as the population is depleted. Thus, additional parameters describing how $\hat{q}$ declines with each sampling pass can be estimated. We refer the reader to Schnute (1983) for more detailed description of this approach.

Several software packages are available to estimate abundance from removal experiments. White and Burnham's (1999) MARK handles removal data well and has the option of fitting alternate models as described above. Van Deventer and Platts' (1989) MicroFish is a software package available through the American Fisheries Society that is designed for removal studies. Its particular strength is that removal experiments from multiple sites and multiple species can be analyzed from a single data file.

8.4.2 Open Population Removal Methods

The application of removal methods to open populations is much more difficult than it is for closed populations because mortality and recruitment need to be estimated in addition to population size. Furthermore, removal methods are generally applied to open populations only when there is a fishery harvesting a substantial portion of the population. As such, the timing and magnitude of removals are often out of the fisheries scientist's control. Further, there is the potential

problem of under (or over) reporting of catch, resulting in biased estimates of population size. This is not to dissuade readers from pursuing removal methods for open populations—this is often the only feasible approach given the data available. Rather, we emphasize that the particular details of the data and the fishery will determine which model is most appropriate. In this chapter, we present a relatively simple formulation requiring minimal data to illustrate the essence of these methods.

Consider a population that is closed to immigration and emigration but is open to natural mortality (M), fishery harvest (C), and recruitment (R). One representation of the dynamics of the population is (Collie and Sissenwine 1983)

$$N_{t+1} = (N_t - C_t + R_t)e^{-M} + E_t. \tag{8.33}$$

In this model, E_t represents random variations in mortality that are not included in either catch or natural mortality (which is assumed to be constant). The parameter E_t reflects what is often called a process error, meaning the unaccounted variation in the underlying dynamical processes. Including this in the population dynamic equation (8.33) is important because process error actually influences system dynamics, and these process errors can accumulate over time. This model implicitly assumes that recruitment and fishery removals occur at the beginning of the year. Natural mortality operates at a constant rate for the remainder of the year, and a proportion (e^{-M}) survive to the beginning of the next year. Alternative formulations can be derived for populations for which the fishery and recruitment occur throughout the year (see Ricker 1977).

For the model described above, information on harvest alone is insufficient to estimate population abundance. Additional information in the form of relative abundance indices (e.g., C/f) for the adult stock (n_t) and recruits (r_t) are also required. Age-structured measures of C/f and population dynamic equations can also be used, leading to methods such as virtual population analysis or statistical catch-at-age. We refer the reader to Ricker (1977), Edwards and Megrey (1989), and Hilborn and Walters (1992) for a detailed discussion of these extensions.

If we assume that the expected C/f for adults and recruits is directly proportional to the true population size (N_t and R_t) and that all members of the population are equally vulnerable to the survey gear, we have

$$n_t = \hat{n}_t \eta_t = qN_t\eta_t, \text{ and} \tag{8.34}$$

$$r_t = \hat{r}_t \delta_t = qR_t\delta_t. \tag{8.35}$$

where q = proportionality constant relating survey C/f to true abundance (i.e., catchability in survey); η_t = measurement error term for adults with a mean of 1.0; and δ_t = measurement error term for recruits with a mean of 1.0.

We have assumed that adults and recruits have equal vulnerability to the survey gear. This assumption or a known ratio of recruit to adult vulnerability is generally required when using these Collie–Sissenwine catch survey models (Mesnil 2003).

A critical concept underlying equations (8.34) and (8.35) is that C/f, which is based on samples from the entire population, is generally estimated with considerable variance. The variance associated with these estimates is often termed measurement error and, in the context of population modeling, implies that C/f should not be treated as an exact measure of relative abundance but rather needs to be treated as being imprecise. Using equations (8.34) and (8.35) leads to the following dynamic equation describing the trajectory of the expected value for adult C/f:

$$\hat{n}_{t+1} = (\hat{n}_t - qC_t + \hat{r}_t)\, e^{-M} + \epsilon_t. \tag{8.36}$$

Here, $\epsilon_t = qE_t$ and is the process error as it influences adult C/f. The estimation procedure attempts to minimize these process errors as well as the measurement errors (see Box 8.6).

Generally, M is assumed to be known and constant over time. Under the additional assumption that the measurement errors are negligible (i.e., all are close to 1.0), equation (8.36) can be rewritten in a form by which standard linear regression can be used to estimate q (and thereby N_t and R_t). However, as Collie and Sissenwine (1983) state, n_t and r_t are generally both measured with substantial imprecision. Because of this, we recommend the methods of Collie and Sissenwine (1983; illustrated in Box 8.6) over a regression approach because the assumption of negligible measurement error is rarely credible.

We are not aware of any software program that handles the broad range of situations that are likely to occur when using removal methods in open populations. As such, practitioners must either use specialized software previously developed for special cases similar to theirs or develop the models and associated estimation routines in a general programming environment (e.g., C++, Visual Basic, or SAS), a spreadsheet environment (e.g., Microsoft Excel), or a specialized programming environment designed for statistical parameter estimation (e.g., AdModel Builder [Otter Research, Sidney, British Columbia]). Schnute et al. (1998) discuss some of the trade-offs faced in choosing software for such modeling.

■ 8.5   BIOMASS AND YIELD ESTIMATION: SURPLUS PRODUCTION METHODS

In situations where a geographically closed population is subjected to a significant fishery (e.g., where the population has been substantially reduced by fishing; Hilborn and Walters 1992), it is sometimes possible to estimate biomass from the pattern of yield (biomass of fish removed) and fishing effort over time. Conceptually, surplus production models (also known as biomass dynamic models, Hilborn and Walters 1992) are based on the idea that the biomass in a given year (B_t) depends on the biomass in the previous year (B_{t-1}) plus recruitment and growth minus yield and natural mortality. It is often convenient to group recruitment and growth into a single term representing processes that contribute to biomass. If this production is in excess of natural mortality, the surplus production will increase the biomass from one year to the next. Alternately, the surplus production

Box 8.6   Estimation of Abundance Based on the Removal Method in an Open Population

A population of lake trout subjected to a commercial fishery was studied from 1985 to 2001 with
the goal of determining trends in abundance over time. The population is sampled each year by a
fishery-independent otter trawl survey. Data collected in the survey provide measures of relative
abundance (C/f) for fish large enough to be vulnerable to capture in the commercial fishery
(adults) and prerecruits that are not vulnerable to the commercial fishery. The number of fish
harvested in the commercial fishery is recorded each year and is assumed to occur at the begin-
ning of the year.

Table   Lake trout catch in annual otter trawl survey.

Year	Catch (number of fish)	Adult C/f	Prerecruit C/f
1985	94,500	43.15	11.24
1986	99,154	38.46	7.99
1987	74,201	29.70	14.17
1988	65,827	32.85	19.15
1989	66,569	35.07	10.37
1990	69,000	34.38	17.56
1991	93,633	34.91	9.52
1992	78,069	31.05	14.06
1993	78,614	23.73	21.20
1994	82,258	37.11	12.41
1995	60,351	22.92	17.05
1996	48,212	23.49	13.23
1997	45,449	27.77	3.50
1998	34,020	28.58	21.12
1999	38,488	38.09	6.60
2000	44,865	32.04	8.75
2001	47,680	34.31	9.01

To proceed, we need initial values for the measurement errors (η_t for the adult C/f index and δ_t for
the prerecruit C/f). A good initial guess would be to set all values to 1.0, but we show the table
below with the final estimates. From these initial guesses of 1.0, we then fill in the columns for the
expected indices by dividing the observed C/f values by these multiplicative errors. The final
column in the table below is a forecast of the adult survey index at time $t+1$ from the expected
index at time t, ignoring process error (see equation [8.33]). To fill in this column, a value for q
(catchability) is required. This is unknown (to be estimated), but an initial guess is needed to get
started for this quantity also. One approach is to use past experience to obtain an initial value for
exploitation rate in recent years, say 25%, and thus approximate N as four times C. Then, the initial
value for q would be N/n, perhaps based on an average of such values over years. We illustrate
calculations, however, with the final estimate for this parameter also. Once a value of q is available,
forecast values are obtained by application of equation (8.36), dropping the process error and
denoting the forecast value as $\bar{n}_t$. For example, the forecasted value for 1986, assuming $q = 0.00011$
and M (natural mortality) = 0.2, is

$$\bar{n}_{1986} = (\hat{n}_{1985} - qC_{1985} + \hat{r}_{1985})e^{-M} = (46.42 - 0.000110 \cdot 94,500 + 11.46)e^{-0.2} = 38.88$$

Note that no prediction is made for the first year of the time series (1985) because survey indices
are not available for the year prior.

Table   Forecasted values for the lake trout fishery. Given are measurement errors (η_t for the adult C/f index and δ_t for the prerecruit C/f); the expected, $\hat{n}_t$, and forecasted, $\tilde{n}_t$, adult survey index; and the expected recruitment survey index, $\hat{r}_t$.

Year	η_t	$\hat{n}_t$	δ_t	$\hat{r}_t$	$\tilde{n}_t$
1985	1.076	46.42	1.020	11.46	
1986	1.032	39.68	1.007	8.04	38.88
1987	1.132	33.63	1.063	15.06	30.14
1988	0.964	31.68	0.979	18.76	33.18
1989	1.111	38.97	1.033	10.71	35.36
1990	0.969	33.32	0.984	17.28	34.68
1991	1.115	38.91	1.031	9.82	35.21
1992	0.810	25.14	0.914	12.85	31.46
1993	1.222	28.99	1.198	25.41	24.07
1994	0.709	26.29	0.902	11.20	37.46
1995	0.879	20.15	0.910	15.52	23.29
1996	1.089	25.59	1.050	13.89	23.76
1997	1.315	36.51	1.040	3.64	27.99
1998	1.017	29.07	1.013	21.39	28.78
1999	0.972	37.01	0.995	6.56	38.25
2000	1.183	37.90	1.050	9.19	32.21
2001	1.000	34.31	1.000	9.01	34.51

Assuming that M is known to be 0.2, the above model has three sets of parameters: q, which applies to both adults and prerecruits; η_t, which encapsulates measurement errors for the adult index; and δ_t, which encapsulates measurement errors in the recruitment index. Parameter estimation is accomplished by minimizing the following sum (representing the sums of squared deviations, or errors [SSE]):

$$\mathrm{SSE} = \sum_t \log_e(\eta_t)^2 + \sum_t \log_e(\delta_t)^2 + \sum_t \epsilon_t^2$$

The first two components are directly calculated from parameter estimates that are also entries in the above table. The values of ϵ_t, the process error, depend jointly on all the estimated parameters and are calculated as $(\hat{n}_t - \tilde{n}_t)$. Thus, q, the ηs, and the δs are adjusted through an iterative search procedure from the initial guesses so as to minimize SSE. Note that underlying this minimization are assumptions that the process errors are normal, the logarithms of the measurement errors are normal (i.e., the original terms are lognormal), and the variances for each of these are equal. The terms in this sum could be weighted to represent different variances for each type of error (Collie and Sissenwine 1983).

Outputs of the model include estimates of the above parameters, as well as the annual population size and number of recruits entering the population. Using an Excel spreadsheet to do the calculations, and the solver function to minimize the SSE by changing the parameters, we obtained the following estimates for population size and recruitment.

(Box continues)

Box 8.6 *(continued)*

Table   Estimate of lake trout fishery population size ($\hat{N}$) and recruitment ($\hat{R}$).

Year	$\hat{N}$	$\hat{R}$
1985	404,106	99,766
1986	345,247	70,078
1987	293,215	130,682
1988	275,807	163,343
1989	339,441	93,111
1990	290,035	150,535
1991	338,783	85,313
1992	220,131	110,506
1993	253,001	220,645
1994	231,912	94,364
1995	175,706	134,730
1996	223,029	120,793
1997	318,281	31,410
1998	253,196	186,325
1999	322,324	57,199
2000	330,591	79,522
2001	299,049	78,541

Collie and Sissenwine (1983) provide details on how to calculate the variance of the parameter estimates.

may be harvested and still maintain the population biomass. Generally, surplus production is related to the standing biomass; at low biomass levels, surplus production is low due to limited recruitment. At high biomass levels, surplus production is also generally low due to density-dependent growth, recruitment, or both. Surplus production typically peaks at intermediate levels of biomass.

Because of the relatively simple representation of population dynamics, surplus production methods do not require age-specific data. As such, these methods are often used in the analysis of difficult-to-age marine fish stocks. Moreover, simulation studies have suggested that management advice based on surplus production methods may be as robust as population estimates based on age-structured analyses using only yield and effort data (Ludwig and Walters 1985). Although surplus production models have not been widely used in freshwater fishery analysis, they are likely to be applicable and beneficial in some situations for which data are limited.

We approach the problem by developing a model of the biomass dynamics, using that model to predict fishery C/f over time, and then fine-tuning the parameters of the model so that the predicted C/f best fits the observed time series. Hilborn and Walters (1992) provide a thorough review of the principal approaches for fitting surplus production models to data in order to estimate biomass, recruitment, and

density dependence. Although not the only approach to estimation, they indicate that the time series approach we follow here appears to be the best. Although there are many variations of surplus production models, a common model is (Hilborn and Walters 1992)

$$B_t = B_{t-1} + rB_{t-1}\left(1 - \frac{B_{t-1}}{K}\right) - C_{t-1} ; \qquad (8.37)$$

$$\text{Observed } C/f_t = \frac{C_t}{E_t} ; \text{ and} \qquad (8.38)$$

$$\text{Predicted } C/f_t = \hat{q}\hat{B}_t , \qquad (8.39)$$

where C_t = yield during year t; E_t = effort during year t; r = intrinsic rate of increase; K = carrying capacity; and $\hat{q}$ = catchability.

This formulation treats the observed yield as an exact measure of removals and C/f as an inexact measure of relative abundance. Although equation (8.37) directly involves only yield information, experience has shown that parameter estimation generally requires additional information on relative abundance over time. Here, we use fishery C/f as this auxiliary information calculated according to equation (8.38) and predicted by equation (8.39). The biomass at the start of the time series is also often estimated as a parameter in the model, allowing the iterative solution of equations (8.37) through (8.39) in order to fit best the observed and predicted time series of C/f. An example of the application of this approach is provided in Box 8.7. A useful software package for surplus production modeling is ASPIC (available at http://sefsc.noaa.gov/mprager/ASPIC.html).

■ 8.6   BIOMASS ESTIMATION

Most of the methods presented in this chapter produce estimates of numerical abundance. In some situations, however, biomass (i.e., weight of the population) may be a better measure of the "size" of a population. Generally, biomass is estimated indirectly by multiplying the numerical abundance by the mean weight or by applying methods such as surplus production models that directly estimate biomass. In this section, we will cover indirect methods for estimating biomass.

In the simplest situation, biomass is estimated as

$$\hat{B} = \hat{N} \cdot \overline{w} , \qquad (8.40)$$

where $\hat{B}$ = estimated biomass (g); $\hat{N}$ = estimated abundance; and $\overline{w}$ = mean weight of fish in the population (g).

In this equation, $\hat{N}$ can be estimated using any of the methods presented earlier, and mean weight is estimated from a random sample representative of the size- or age-groups contained in $\hat{N}$ (Anderson and Neumann 1996).

Box 8.7   Application of Surplus Production Modeling

The commercial fishery for a population of alewife was monitored from 1985 to 2001. Each year, the total weight of the catch (kg) and the total effort (days fished) were recorded, providing C/f as a measure of relative abundance. These data were analyzed using a surplus production model to estimate carrying capacity (K), initial biomass (B_0), catchability (q), and the intrinsic rate of growth (r) for this fishery population.

Table   Catch and effort data for alewife fishery.

Year	Effort (days fished)	Catch (kg)	C/f (kg/d)
1985	825	90,000	109
1986	1,008	113,300	112
1987	1,411	155,860	110
1988	1,828	181,128	99
1989	2,351	198,584	84
1990	2,074	198,395	96
1991	1,877	139,040	74
1992	1,566	109,969	70
1993	1,139	71,896	63
1994	893	59,314	66
1995	1,029	62,300	61
1996	727	65,343	90
1997	658	76,990	117
1998	953	88,606	93
1999	1,012	118,016	117
2000	1,203	108,250	90
2001	1,034	108,674	105

With $B_0 = 800,000$ kg, $K = 4,000,000$, $q = 0.0001$, and $r = 0.17$ as initial guesses for the parameters of equations (8.37) and (8.39), we can predict catch and C/f as follows:

$$\hat{B}_{1986} = \hat{B}_{1985} + r\hat{B}_{1985}\left(1 - \frac{\hat{B}_{1985}}{\hat{K}}\right) - C_{1985}$$

$$= 800,000 + 0.17 \cdot 800,000\left(1 - \frac{800,000}{4,000,000}\right) - 90,000 = 818,800$$

$$\widehat{C/f}_{1986} = q\hat{B}_{1986} = 0.0001 \cdot 818,800 = 81.88 \approx 82$$

Table   Recursive application of equations (8.37) and (8.39) result in time series of predicted values for the alewife fishery.

Year	Predicted biomass (kg)	C/f (kg/d)	Predicted C/f (kg/d)	Squared deviation for C/f
1985	800,000	109	80	841
1986	818,800	112	82	961
1987	816,203	110	82	841
1988	770,784	99	77	484
1989	695,440	84	70	225
1990	594,526	96	59	1369

Year	Predicted biomass (kg)	C/f (kg/d)	Predicted C/f (kg/d)	Squared deviation for C/f
1991	482,178	74	48	676
1992	415,227	70	42	841
1993	368,518	63	37	729
1994	353,498	66	35	961
1995	348,968	61	35	729
1996	340,818	90	34	3,136
1997	328,477	117	33	7,225
1998	302,742	93	30	3,969
1999	261,707	117	26	8,281
2000	185,270	90	19	5,184
2001	107,057	105	11	9,025

Note the discrepancy in the trend between observed C/f and predicted C/f, indicating that our initial guesses for parameter values were not very good. We used the solver function in Excel to perform a nonlinear search across the parameter values (i.e., B_0, K, q, and r were used as the "change cells" in solver) to find the combination of parameters that minimized the sum of squared deviations between predicted and observed C/f. Solver returned estimates of $\hat{B}_0 = 732,506$, $\hat{K} = 1,160,771$, $\hat{q} = 0.0001484$, and $\hat{r} = 0.4049$ with a sum of squared deviations of 1,616.7. (Note that when C/f is rounded to the nearest 1.0, the squared deviations sum to 1,433). Based on these parameter values as the best estimates, the predicted biomass and C/f over time is shown below.

Table Predicted values for the alewife fishery given parameter values that minimize the sum of squared deviations.

Year	Predicted biomass (kg)	C/f (kg/d)	Predicted C/f (kg/d)	Squared deviation for C/f
1985	732,506	109	109	0
1986	751,925	112	112	0
1987	745,852	110	111	1
1988	697,932	99	104	25
1989	629,475	84	93	81
1990	547,540	96	81	25
1991	466,259	74	69	25
1992	440,166	70	65	25
1993	440,828	63	65	4
1994	479,629	66	71	25
1995	534,265	61	79	324
1996	588,713	90	87	9
1997	640,836	117	95	484
1998	680,061	93	101	64
1999	705,480	117	105	144
2000	699,496	90	104	196
2001	703,787	105	104	1

Note that the trend in predicted C/f matches the observed trend in C/f closely after obtaining the best estimates for B_0, K, q, and r.

Assuming that the variance of $\hat{N}$ is estimated through methods described earlier, and the variance of $\bar{w}$ is also estimated, the variance of $\hat{B}$ is approximated as

$$V(\hat{B}) = \bar{w}^2 V(\hat{N}) + \hat{N}^2 V(\bar{w}) - V(\hat{N}) V(\bar{w}). \qquad \text{V(8.41)}$$

This approximation (Goodman 1960) is based on the assumption that $\hat{N}$ and $\bar{w}$ are estimated independently, an assumption that is reasonable in most cases.

Although equations (8.40) and (8.41) provide relatively simple means of obtaining point estimates of biomass and the associated variance, developing CIs for $\hat{B}$ is much more difficult because the distribution of $\hat{B}$ must be known or assumed. We are not aware of any general guidance in the literature suggesting a suitable distribution for $\hat{B}$. Since $\hat{B}$ is computed as the product of two random variables, the lognormal distribution is a reasonable choice (Aitchison and Brown 1976). Assuming a lognormal distribution, approximate 95% CI bounds for $\hat{B}$ are

$$e^{\left(\log_e(\hat{B}) \pm 1.96\sqrt{\text{Var}(\hat{B})}\right)}. \qquad (8.42)$$

In many situations, abundance and mean weight are estimated separately for different age- or size-classes. In such situations, biomass can be estimated as

$$\hat{B} = \sum \hat{N}_i \cdot \bar{w}_i, \qquad (8.43)$$

where $\hat{N}_i$ = estimated abundance for class i, and $\bar{w}_i$ = mean weight of fish in class i.
In this case, the variance of $\hat{B}$ is

$$V(\hat{B}) = \sum \left[\bar{w}_i^2 V(\hat{N}_i) + \hat{N}_i^2 V(\bar{w}_i) \right], \qquad (8.44)$$

and the 95% CI can be computed following equation 8.42.

■ 8.7 PRODUCTION ESTIMATION

8.7.1 Concepts and Definitions

Fish abundance parameters, such as density or biomass, are static measures of a population's status. That is, information on the state of the population is provided only for a single point in time. Conversely, dynamic population measures describe parameters as rate functions over time and may be more descriptive and meaningful for applications in fisheries science. Examples of dynamic population parameters are rates of recruitment, growth, and mortality (Chapters 4–6). Production is the integration of static and dynamic population measures over time, wherein biomass, recruitment, growth, and mortality are synthesized into a single dynamic measure. As such, production is an indicator of ecological success and is

especially responsive to environmental change (Mann and Penczak 1986). Thus, production rate of a fish population can be a useful measure and comparative tool, with many valuable applications for fisheries research and management.

Production is defined as the rate of tissue elaboration over time, regardless of whether it survives to the end of a given period (Waters 1977). It is expressed in units of quantity/space/time, usually kilograms/hectare/year for fish populations. Production rate represents the flow of energy through trophic levels and may also be expressed in units of calories/hectare/year.

The methods and terminology for estimating fish production have evolved to a generally accepted convention, and fish production estimates are routinely found in the literature, especially for fishes of small streams and salmonid species. However, many fisheries scientists rarely consider using this assessment tool, even though they may regularly gather the data required to estimate production. Presumably, this occurs because the computations can be complex and cumbersome and are more so if precision of production estimates and related parameters is estimated. The development of computer software and availability of other technical resources to minimize computation effort and reduce calculation error associated with the process of estimating production may increase the utility of this tool in fisheries science (Railsback et al. 1989; Kwak 1992).

8.7.2   Production Estimation Methods

Five methods to estimate production rate of aquatic animal populations have been developed, refined, and accepted by ecologists (Waters 1977; Bagenal 1978; Chapman 1978). Some of these methods were originally intended for estimating aquatic macroinvertebrate production but were readily adapted for use with fish populations. The five methods include two iterative summation methods, (1) the removal summation and (2) increment summation methods; (3) the instantaneous growth rate method and a graphical representation, (4) the Allen curve; and (5) the size-frequency method. Three of the methods (increment summation, instantaneous growth rate, and size-frequency) have been refined for application to fish populations, and variance estimators for all parameters associated with those methods have been derived. All methods except the size-frequency method are cohort based, meaning that information on the age structure of the fish population is required.

Sampling requirements to estimate fish production are a series of absolute density and biomass estimates (sections 8.3, 8.4, and 8.6) for a population within a 1-year period, with the first and last sampling dates occurring approximately 1 year apart to estimate annual production. Cohort-based methods require stratification and separate estimates by cohort; thus, data must be collected on population age structure. In general, production is estimated by individual cohorts for a single time interval; then, those partial estimates are summed for all cohorts to yield a production estimate for the entire population during the specific interval. The production estimate for a 1-year period (annual production) is the sum of the production estimates for intervals within the annual period. When the size-frequency method is

used, individual losses from one size-group to the next are summed from mean values over the annual period to yield a production estimate.

8.7.2.1   Summation Methods

Summation methods to estimate production stem from the concept that tissue lost from, or accumulated by, a population over a series of time increments is equivalent to an estimate of production. The removal summation method involves estimating the number of individuals lost, by mortality or other removal, from a cohort over a time interval and coupling those data with biomass information, which results in an estimate of production for that cohort during that interval. These are then summed over intervals and cohorts to estimate annual production. Removal summation is not typically applied to fish populations, and algorithms to estimate associated variance are not readily available. As such, we recommend the use of the more commonly used increment summation method in preference to the removal summation method.

Similar to the removal summation method, but quantifying accumulation rather than loss, the increment summation method sums the growth increments of a cohort over time. The growth increment is quantified as the increase in mean individual weight over a time interval for each cohort, and this increment is multiplied by the density of the cohort to obtain a production estimate for the cohort during that interval. Production for each cohort is summed for the population, and production for each interval is summed for an annual estimate.

Explicit formulae for increment summation production estimation and associated variance estimators for fish populations were developed by Newman and Martin (1983) as

$$\hat{P} = \bar{N}\Delta\bar{w}, \tag{8.45}$$

where P = production for a given cohort within a specified interval; $\bar{N}$ = estimated arithmetic mean cohort density from time t to $t+1$; and $\Delta\bar{w}$ = estimated change in mean weight of individuals in the cohort from time t to $t+1$ (i.e., $\bar{w}_{t+1} - \bar{w}_t$).

Sampling variance of the production estimate can be estimated as (Goodman 1960)

$$V(\hat{P}) = \bar{N}^2 V(\Delta\bar{w}) + (\Delta\bar{w})^2 V(\bar{N}) - V(\bar{N})V(\Delta\bar{w}), \tag{8.46}$$

where $V(\Delta\bar{w})$ and $V(\bar{N})$ are the estimated variances of $\Delta\bar{w}$ and $\bar{N}$, respectively.

Algorithms to estimate variance of $\Delta\bar{w}$ and $\bar{N}$ are found in Newman and Martin (1983) and require estimates of variance for each density and mean weight estimate (sections 8.3 and 8.6). The statistical software Pop/Pro (Kwak 1992; available on CDROM) includes a module to estimate fish production by the increment summation method according to cohort and time interval, including related parameters and associated variances.

8.7.2.2   *Instantaneous Growth Rate and Allen Curve Methods*

The instantaneous growth rate method was initially developed to estimate production of fish populations (Ricker 1946; Allen 1949). By this method, production is estimated as simply the product of the estimated instantaneous growth rate and estimated mean biomass as

$$\hat{P} = \hat{G}\bar{B},\qquad(8.47)$$

where $\hat{P}$ = estimated production for a given cohort within a specified interval, $\hat{G}$ = estimated instantaneous growth rate for the cohort from time t to $t+1$ (i.e., $\log_e \bar{w}_{t+1} - \log_e \bar{w}_t$), and $\bar{B}$ = estimated arithmetic mean cohort biomass from time t to $t+1$ (i.e., $\hat{B}_t + \hat{B}_{t+1})/2$).

From Newman and Martin (1983), the variance of the production estimate may be estimated as

$$V(\hat{P}) = V(\bar{B})\,\hat{G}^2 + V(\hat{G})\,\bar{B}^2,\qquad(8.48)$$

where $V(\bar{B})$ and $V(\hat{G})$ are variances of the mean biomass and instantaneous growth rate, respectively. The variance of mean biomass is estimated as

$$V(\bar{B}) = [\,V(\hat{B}_t) + \mathrm{V}(\hat{B}_{t+1})\,]/4,\qquad(8.49)$$

where $V(\hat{B}_t)$ and $\mathrm{V}(\hat{B}_{t+1})$ are the variances of biomass at times t and $t+1$, respectively.

The variance of the instantaneous growth rate may be estimated as

$$V(\hat{G}) = V(\log_e \bar{w}_t) + V(\log_e \bar{w}_{t+1}),\qquad(8.50)$$

where $V(\log_e \bar{w}_t)$ and $V(\log_e \bar{w}_{t+1})$ are variances of the natural logarithms of estimated mean weights of individuals of the cohort at times t and $t+1$, respectively. By using a Taylor series expansion (delta method; Seber 1982; Cone and Krueger 1988), $V(\log_e \bar{w}_t)$ can be approximated as

$$V(\log_e \bar{w}_t) = V(\bar{w}_t)/\bar{w}_t^2.\qquad(8.51)$$

Mean annual density or biomass estimates (and their variances) computed from multiple intervals of different duration must be weighted according to the number of days in each interval (i.e., equations [8.47] and [8.48] must be modified) and should be computed following formulae in Newman and Martin (1983). Fish production, including related parameters and associated variances, can be estimated according to cohort and time interval by the instantaneous growth rate method by means of Pop/Pro statistical software (Kwak 1992). Additional algorithms are available in the software documentation. An example calculation of fish annual production estimated by the instantaneous growth rate method is presented in Box 8.8.

Box 8.8   Production Estimation Based on the Instantaneous Growth Rate Method

Density, mean weight, and biomass (and associated variances) of a brook trout population in Valley Creek, Minnesota, were estimated in a stream reach with an area of 0.181 ha on four dates between March 1974 and March 1975 (Waters 1999). Population statistics for two of these dates are presented below in order to illustrate how to estimate production using the instantaneous growth rate method.

Table   Population statistics for brook trout in Valley Creek, Minnesota.

Age-class and total	Density $(\hat{N})$	$V(\hat{N})$	Mean weight $(\bar{w}, g)$	$V(\bar{w})$	Biomass $(\hat{B}, g)$	$V(\hat{B})$
Sampling date: 8 March 1974						
1	277.85	1,336.05	6.86	0.13	1,905.34	75,455.97
2	157.54	317.71	28.56	0.79	4,499.83	222,126.45
3	36.11	34.00	107.23	19.89	3,872.13	469,764.75
4	11.17	13.16	170.05	42.09	1,898.89	350,364.34
Total	482.67	1,700.92			12,176.19	1,117,711.51
Sampling date: 29 July 1974						
1	276.45	553.56	24.27	0.62	6,709.17	306,074.53
2	68.08	94.58	77.31	2.49	5,262.90	278,582.66
3	9.76	7.64	146.18	100.67	1,427.00	167,558.97
4	8.12	1.11	194.72	1.67	1,582.12	30,259.81
Total	362.41	656.89			14,981.19	782,475.97

To estimate production for the age-1 cohort during this interval, we follow equation (8.47) as

$\hat{P} = G\bar{B}$, or
$\hat{P} = (\log_e 24.27 - \log_e 6.86)[(6,709.17 + 1,905.34)/2] = 5,442.36g.$

where $\hat{P}$ is the estimated production and G is the estimated instantaneous growth rate for a given cohort within a specified interval. To estimate the variance of $\hat{P}$, we begin by estimating the variance $\bar{B}$ of from equation (8.49) as

$V(\bar{B}) = [V(B_t) + V(B_{t+1})]/4$, or
$V(\bar{B}) = (75,455.97 + 306,074.53/4 = 95,383.62g.$

Allen (1951) extended the instantaneous growth rate method to a graphical form to estimate production in what has become known as the Allen curve method. The Allen curve is a growth–survivorship curve for a given cohort, wherein the number of surviving individuals is plotted against the mean weight of those individuals (Figure 8.6). Following this configuration, the biomass of the cohort can be estimated at any point in time on the curve as the corresponding product of number of individuals (or density) and their mean weight. Likewise, the area

Then, we estimate the variance of G from equation (8.50) as

$V(G) = V(\log_e \bar{w}_t) + V(\log_e \bar{w}_{t+1})$, expanded by incorporating equation (8.53) as
$V(G) = V(\bar{w}_t)/\bar{w}_t^2 + V(\bar{w}_{t+1})/(\bar{w}_{t+1})^2$, or
$V(G) = 0.13/6.86^2 + 0.62/24.27^2 = 0.003815$.

Now, we may employ equation (8.48) as

$V(\hat{P}) = V(\bar{B})G^2 + \bar{B}^2 V(G)$, or
$V(\hat{P}) = (95,382.62)(\log_e 24.27 - \log_e 6.86)^2 + [(6,709.17 + 1,905.34)/2]^2(0.003815) = 223,058g$.

The sampling area was 0.181 ha, so to convert our production estimate to a standard area unit (ha), we divide by the area, and to convert to a standard mass unit (kg), we divide by 1,000.

$$\hat{P} = 5,442.36g/0.181 \text{ ha}/1,000 = 30.1 \text{ kg/ha}.$$

Whenever you multiply a statistic by a constant, you multiply the variance of that statistic by the constant squared. Thus, to convert the variance of our production estimate to standard units, we divide by the area (0.181 ha) squared and divide by 1,000 squared as

$$V(\hat{P}) = 223,058/0.181^2/1,000^2 = 6.8 \text{ kg/ha}.$$

Our production estimate ± approximate 95% CIs [$\pm 1.96 V(\hat{P})^{0.5}$] for this cohort during this interval is 30.1 ± 5.1 kg/ha. This procedure is then repeated for the other age-classes to estimate production for the population (rounded to the nearest tenth) during this interval as 62.8 ± 7.4 kg/ha, as below.

Table   Production estimate for population of brook trout during first time interval.

Age-class	Production (kg/ha ± 95% CI)
1	30.068 ± 5.111
2	26.856 ± 4.293
3	4.536 ± 2.664
4	1.303 ± 0.859
Total	62.763 ± 7.240

Note that CIs are not additive, and variances should be summed to compute a CI for a total. The entire procedure is then repeated for the other two intervals within the annual period to estimate annual production and its CI.

under the curve may be calculated in corresponding units as production of the cohort during the specific interval plotted. The Allen curve is rarely presented in recent literature, most likely because explicit variance estimators have not been derived for it and the quantitative form of this concept, the instantaneous growth rate method, is more precise and relatively easy to apply using software applications. Nonetheless, examination of Allen curves can be an instructive means to visualize and elucidate production dynamics of a fish population.
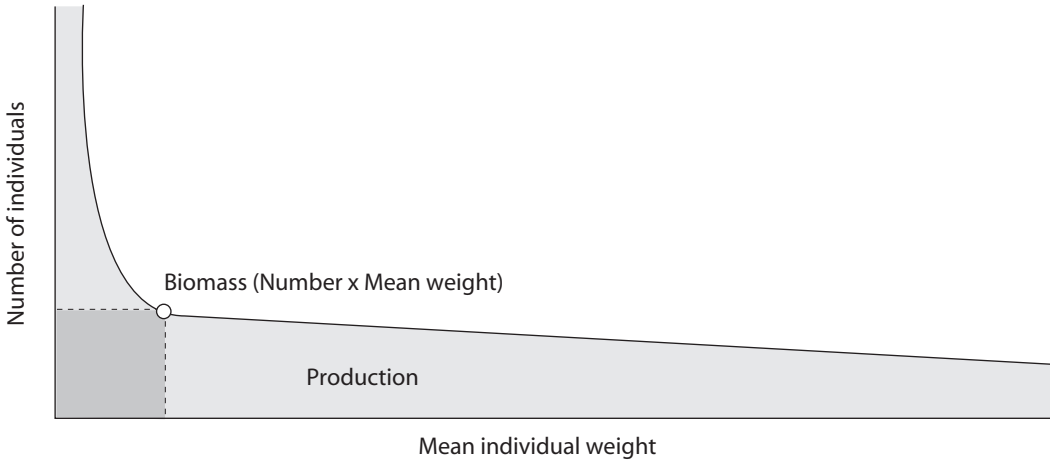
Figure 8.6   A generalized Allen curve depicting growth–survivorship for a fish cohort (after Allen 1951; Waters 1977). Production for the time interval is estimated as the area under the curve (shaded), and biomass at any point in time (dark-shaded area) is the product of the number of individuals (or density) and their mean weight.

8.7.2.3   Size-Frequency Method

The size-frequency method to estimate production was first developed by Hynes (1961) as an alternative means to estimate production when cohort identification was not possible; it was formerly also referred to as the Hynes method. Conceptually, the method is similar to the removal summation method, except that the size-frequency method sums tissue losses between successive size-groups rather than over time intervals. Originally, the method was used to approximate production roughly for multispecies assemblages of aquatic animals, but subsequent criteria and assumptions, established to improve the method, restrict its practical application to single species or closely related species with similar life histories (Waters 1977; Krueger and Martin 1980).

Production is estimated by the size-frequency method for fishes as (Garman and Waters 1983)

$$\hat{P} = 0.5c \left[\overline{w}_1(\overline{N}_1 - \overline{N}_2) + \sum_{k=2}^{c-1} \overline{w}_k(\overline{N}_{k-1} - \overline{N}_{k+1}) + \overline{w}_c(\overline{N}_{c-1} - \overline{N}_c) \right](1/\text{CPI}), \quad (8.52)$$

where P = production for a given population or multispecies group within a specified interval, $\overline{N}$ = estimated mean density (arithmetic mean of estimates) for a specific length-group, $\overline{w}$ = estimated mean weight (arithmetic mean of estimates) of individuals in a specific length-group, k = index for length-groups, c = number of length-groups, and CPI = the cohort production interval (average maximum age of fish in the population or multispecies group in years).

Estimated variance of the production estimate is computed as

$$V(\hat{P}) = (0.5c)^2 \left\{ \begin{array}{l} (\overline{w}_1 + \overline{w}_2)^2 V(\overline{N}_1) + V(\overline{w}_1)(\overline{N}_1 - \overline{N}_2)^2 \\ + \sum_{k=2}^{c-1} [(\overline{w}_{k-1} - \overline{w}_{k+1})^2 V(\overline{N}_k) + V(\overline{w}_k)(\overline{N}_{k-1} - \overline{N}_{k+1})^2] \\ + (\overline{w}_{c-1} - \overline{w}_c)^2 V(\overline{N}_c) + V(\overline{w}_c)(\overline{N}_{c-1} - \overline{N}_c)^2 \end{array} \right\} (1/\text{CPI})^2, \quad (8.53)$$

where $V(\overline{N})$ and $V(\overline{w})$ are variances of mean density and mean weight, respectively, for length-groups. If the production period spans more than a single time interval (more than two samples), then mean density and mean weight estimates (and associated variances) must be weighted by interval length (days) according to algorithms provided by Garman and Waters (1983). An example calculation of fish annual production estimated by the size-frequency method is presented in Box 8.9.

8.7.3   Production to Mean Biomass ($P/\overline{B}$) Ratio

The annual production to annual mean biomass ($P/\overline{B}$) ratio is of special interest as an ecological index (also referred to as the turnover ratio) and as a simple conversion factor to approximate production (Waters 1977). Based on the premise that $P/\overline{B}$ is relatively constant for an organism or related organisms, it has been suggested that production may be approximated from a biomass estimate using the $P/\overline{B}$ ratio as a multiplier. The ratio of $P/\overline{B}$ for most fish species varies from 0.2 to 4.0. However, $P/\overline{B}$ can be quite variable within and among species (Waters 1977, 1999; Mann and Penczak 1986; Elliott 1994) and may vary with the number of cohorts (or life span) of a population (Waters 1992; Kwak and Waters 1997). Thus, this method should be applied carefully and considered an imprecise approximation of production. The exact $P/\overline{B}$ ratio to employ for such estimates should be species specific and may be refined further if the number of cohorts in a population is known (Waters 1992; Kwak and Waters 1997). Estimates of mean annual biomass should be weighted by interval duration if more than a single interval is included. Newman and Martin (1983) present formulae for estimating mean annual biomass and its variance, as well as a variance estimator for the $P/\overline{B}$ ratio.

8.7.4   Production Estimates in Practice

In general, if age data are available, the instantaneous growth rate method is the preferred approach to estimate fish production and associated parameters; otherwise, the size-frequency method may be used. Estimating production using the $P/\overline{B}$ ratio should be used only when data are lacking for application of more precise methods. Computer software is available for using the increment summation or instantaneous growth rate methods (Kwak 1992; available at http://www4.ncsu.edu/~tkwak), and a spreadsheet application can facilitate calculations by other methods. Estimates of variance (precision or sampling error) should be reported for all estimates of production and related population parameters as approximate 95% CIs.

Box 8.9   Production Estimation Based on the Size-Frequency Method

Density and mean weight (and associated variances) of a rainbow trout population in Valley Creek, Minnesota, were estimated in a stream reach on three dates between April 1977 and April 1978 (Garman and Waters 1983). The catch data were broken into 10 size-groups in order to allow investigators to estimate production using the size-frequency method.

Table   Density and weight statistics based on three collection dates for rainbow trout population, Valley Creek, Minnesota.

Length-group	Mean density ($\bar{N}$/ha)	$V(\bar{N})$	Mean weight ($\bar{w}$, g)	$V(\bar{w})$	Mean biomass ($\bar{B}$, g/ha)
1	260.2	2,653.5	3.2	0.2	832.6
2	281.7	1,491.4	6.9	0.1	1,943.7
3	144.9	182.5	12.6	0.1	1,825.7
4	88.8	145.9	27.9	1.4	2,477.5
5	67.7	49.5	49.9	5.1	3,378.2
6	43.1	19.5	75.7	45.0	3,262.7
7	55.9	601.4	109.5	24.8	6,121.0
8	26.9	61.2	158.6	11.8	4,266.3
9	19.8	104.2	196.0	39.9	3,880.8
10	15.0	0.2	260.8	13.1	3,912.0

To estimate annual production for the population, we follow equation (8.52), using 3 years for the cohort production interval (CPI).

$$\hat{P} = 0.5(10)[3.2(260.2 - 281.7) + 6.9(260.2 - 144.9) + \ldots + 260.8(19.8 - 15.0)]/(1/3)$$
$$= 5(-68.80 + 795.57 + 2,430.54 + 2,153.88 + 2,280.43 + 893.26 + 1,773.90$$
$$+ 5,725.46 + 2,332.40 + 1,251.84)(0.333)$$
$$= 32,581.52 \text{ g/ha/year.}$$

Variance of $\hat{P}$ is then estimated according to equation (8.53) as

$$V(P) = [0.5(10)^2] \{(3.2 + 6.9)^2(2,653.5) + 0.2(260.2 - 281.7)^2 + [(3.2 - 12.6)^2(1,491.4) +$$
$$0.1(260.2 - 144.9)^2] + 7 \text{ other summation terms} + [(196.0 - 260.8)^2(0.2) +$$
$$13.1(19.8 - 15.0)^2] \} (1/3)^2$$
$$= 25(270,683.5 + 92.5 + 133,109.5 + 84,203.5 + 211,333.0 + 123,750.9 + 75,532.9$$
$$+ 4,139,575.9 + 473,291.6 + 1,094,002.6 + 1,141.6)0.11$$
$$= 18,168,473.1 \text{ g/ha/year.}$$

To convert our production estimate to a standard mass unit (kg), we divide by 1,000:

$$\hat{P} = 32,581.52/1,000 = 32.582 \text{ kg/ha/year.}$$

The variance is converted as

$$V(P) = 18,168,473.1/1,000^2 = 18.168 \text{ kg/ha/year.}$$

Thus, our annual production estimate ± approximate 95% intervals $[\pm 1.96 V(P)^{0.5}]$ for this population and year is 32.582 ± 8.354 kg/ha/year.

Many assumptions and criteria for applying these methods have been defined and should be considered with application (Waters 1977; Newman and Martin 1983). We suggest that subjective decisions encountered when estimating fish production should be resolved to be conservative, so that the direction of error will be clear, and estimates may be considered minimums. The biomass estimate of age-0 fish, newly recruited into the population, at first sampling should be considered a conservative estimate of production for that cohort during that interval. Negative estimates of production, resulting from negative growth (i.e., weight loss), should be interpreted as no production (zero) for that cohort and interval when using summation methods or the instantaneous growth rate method. However, negative losses (i.e., increase in numbers between size-groups) should be included in the sum when applying the size-frequency method.

Generally, the greater the number of fish population estimates (density and biomass) that are integrated into an annual production estimate, the more accurate that estimate will be. The minimum number of two population estimates will yield a less accurate production estimate than will one based on more estimates within the annual period. A reasonable, general approach to estimating populations over a 1-year period for an annual production estimate is to conduct one estimate prior to spawning (e.g., spring for many temperate fishes), another near the end of the primary growing season (e.g., fall for temperate areas), and a third 1 year after the first estimate (e.g., spring or fall).

Fish production estimates are valuable statistics for understanding population dynamics and elucidating ecological relationships and have great potential for improving fisheries management. Waters (1992) reviewed and proposed the application of annual production, annual $P/\overline{B}$ ratio, and ecotrophic coefficient (annual angler harvest/annual production) to management of stream-dwelling trout fisheries. Incorporating production dynamics into fish assessment and monitoring may provide a broader perspective on the dynamics of harvested fishes. Thus, regulation and assessment of harvest as a proportion of fish tissue produced on an annual basis provides an alternative to the standard approach, based solely on fish density or biomass.

■ 8.8   FUTURE DIRECTIONS

In many studies of fish populations, information is often available beyond that needed to apply the methods outlined in this chapter. In particular, information on the age structure of the population is often collected. When the abundance of a population is estimated on an annual basis, knowledge of the prior age composition is helpful in constraining estimates. As a simple example, the abundance of a cohort cannot be larger than the abundance in the prior year (in a closed population). The constraints imposed by age structure relationships can help improve the precision and accuracy of population estimates. Application of auxiliary information to population estimation opens up a diversity of models. Powerful statistical catch-at-age models (Hilborn and Walters 1992) are an example of a framework that incorporates the extensive information that is often available on

intensively studied fish populations. Because of the complexity of such models and their intensive data needs, such methods are generally applied to marine fish stocks and some stocks in large inland waters (e.g., Great Lakes) where the cost of data collection and analysis is commensurate with the value of the fishery.

Even within the scope of the methods presented in this chapter, there are potential gains to be made by combining data from different sources. In particular, the combination of removal methods with marking fish holds promise for improving population estimates. The methods illustrated here for analyzing mark–recapture data do not make direct use of measures of sampling effort. Removal methods, on the other hand, explicitly assume effort is constant or accommodate changes in effort by standardizing catch to C/f.

The estimation of the variance and CIs for population estimates is an area where substantial improvements need to be made. Although the likelihood methods presented here have a long history of use, and provide a strong statistical basis for estimation, many of the formulae are strictly valid only for large sample sizes or are approximations to the "full" formulae. In many applications, the target population itself may be small (e.g., the number of fish in a 100-m stretch of stream) or the number of marked or recaptured fish is small to moderate (i.e., less than 30). In situations like these, variance estimates and CIs should be interpreted with caution.

A trend we see emerging is the incorporation of a Bayesian approach to data analysis. In many situations, researchers and managers have knowledge from prior experience that is pertinent to the population being studied. Incorporating the experience and beliefs of experts can improve population estimates in many cases (Hilborn and Walters 1992). The Bayesian approach, however, presents several practical concerns regarding how best to represent prior information.

■ 8.9 CONCLUSIONS

In this chapter, we illustrate several approaches for estimating fish abundance, biomass, and production. A foundational concept is that additional information beyond C/f is generally needed to provide accurate population estimates. The incorporation of this information inevitably entails making assumptions about the sampling regime and creating models of this idealized process. Therefore, it is important to test assumptions, where possible, and apply models that best represent the data obtained. Some assumptions can be relaxed by applying alternate models, but some are essential to obtain any valid estimate. The key to meeting critical assumptions is often the judicious planning of the sampling program and the careful application of field methods. Given the wide array of sampling challenges facing fisheries scientists, this chapter should be viewed as an entry into some of the more common and basic methods. Every investigation poses its own set of challenges, but often these problems are not unique. By building on the base developed here, we hope to provide readers with the confidence to face the diversity of situations they are likely to encounter in their professional work.

◾ 8.10   REFERENCES

Aitchison, J., and J. A. C. Brown. 1976. The lognormal distribution with special reference to its uses in economics. Cambridge University Press, Cambridge, UK.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principal. Pages 267–281 *in* B. N. Petran and F. Csaki, editors. International symposium on information theory, 2nd edition. Akademiai Kiadi, Budapest.

Allen, K. R. 1949. Some aspects of the production and cropping of fresh waters. Transactions of the Royal Society of New Zealand 77(5):222–228.

Allen, K. R. 1951. The Horokiwi Stream. New Zealand Marine Department Fishery Bulletin 10.

Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Bagenal, T. 1978. Methods for assessment of fish production in fresh waters. IBP (International Biological Programme) Handbook No. 3, Blackwell Scientific Publications, Oxford, UK.

Bickel, P. J., and K. A. Doksum. 1977. Mathematical statistics: basic ideas and selected topics. Holden-Day, San Francisco.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Monograph 5, Bethesda, Maryland.

Chapman, D. G. 1948. A mathematical study of confidence limits of salmon populations calculated from sample tag ratios. International Pacific Salmon Fisheries Commission Bulletin 2:69–85.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1:131–160.

Chapman, D. W. 1978. Production in fish populations. Pages 5–25 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, UK.

Collie, J. S., and M. P. Sissenwine. 1983. Estimating population size from relative abundance data measured with error. Canadian Journal of Fisheries and Aquatic Sciences 40:1871–1879.

Cone, R. S., and C. C. Krueger. 1988. Comparison of survival, emigration, habitat use, marking mortality, and growth between two strains of brook trout in Adirondack ponds. North American Journal of Fisheries Management 8:497–504.

De Lury, D. B. 1947. On the estimation of biological populations. Biometrics 3:145–167.

Edwards, E. F., and B. A. Megrey. 1989. Mathematical analysis of fish stock dynamics. American Fisheries Society, Symposium 6, Bethesda, Maryland.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.

Foote, K. G., and G. Stefansson. 1993. Definition of the problem of estimating fish abundance over an area from acoustic line-transect measurements of density. ICES Journal of Marine Science 50:369–381.

Garman, G. C., and T. F. Waters. 1983. Use of the size-frequency (Hynes) method to estimate annual production of a stream fish population. Canadian Journal of Fisheries and Aquatic Sciences 40:2030–2034.

Goodman, L. A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708–713.

Gould, W. R., and K. H. Pollock. 1997. Catch-effort maximum likelihood estimation of important population parameters. Canadian Journal of Fisheries and Aquatic Sciences 54:890–897.

Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.

Heimbuch, D. G., H. T. Wilson, S. B. Weisberg, and J. H. Volstad. 1997. Estimating fish abundance in stream surveys by using double-pass removal sampling. Transactions of the American Fisheries Society 126:795–803.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Archiv fur Hydrobiologia 57:344–388.

Junge, C. O., and J. Libosvárský. 1965. Effects of size selectivity on population estimates based on successive removals with electrical fishing gear. Zoological Listy 14:171–178.

Krueger, C. C., and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnology and Oceanography 25:773–777.

Kwak, T. J. 1992. Modular microcomputer software to estimate fish population parameters, production rates and associated variance. Ecology of Freshwater Fish 1:73–75. (Software available at http://www4.ncsu.edu/~tkwak.)

Kwak, T. J., and T. F. Waters. 1997. Trout production dynamics and water quality in Minnesota streams. Transactions of the American Fisheries Society 126:35–48.

Lebreton, J-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. Journal of Animal Ecology 8:94–113.

Ludwig, D., and C. J. Walters. 1985. Are age-structured models appropriate for catch-effort data? Canadian Journal of Fisheries and Aquatic Sciences 42:1066–1072.

Mann, R. H. K., and T. Penczak. 1986. Fish production in rivers: a review. Polskie Archiwum Hydrobiologii 33:233–247.

Mesnil, B. 2003. The catch-survey analysis (CSA) method of fish stock assessment: an evaluation using simulated data. Fisheries Research 63:193–212.

Newman, R. M., and F. B. Martin. 1983. Estimation of fish production rates and associated variances. Canadian Journal of Fisheries and Aquatic Sciences 40:1729–1736.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference for capture data from closed populations. Wildlife Monographs 62.

Railsback, S. F., B. D. Holcomb, and M. G. Ryon. 1989. A computer program for estimating fish population sizes and annual production rates. Oak Ridge National Laboratory, Environmental Sciences Division Publication 3245, Oak Ridge, Tennessee.

Rice, J. A. 1995. Mathematical statistics and data analysis, 2nd edition. Duxbury Press, Belmont, California.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecological Monographs 16:373–391.

Ricker, W. E. 1977. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries and Marine Service, Bulletin 191, Ottawa.

Robson, D. S., and H. A. Regier. 1964. Sample size in Petersen mark–recapture experiments. Transactions of the American Fisheries Society 93:215–226.

Schnabel, Z. E. 1938. The estimation of the total fish population of a lake. American Mathematical Monographs 45:348–352.

Schnute, J. 1983. A new approach to estimating populations by the removal method. Canadian Journal of Fisheries and Aquatic Sciences 40:2153–2169.

Schnute, J. T., L. J. Richards, and N. Olsen. 1998. Statistics, software, and fish stock assessment. Pages 171–184 *in* F. Funk and seven coeditors. Fishery stock assessment models. University of Alaska, Sea Grant College Program AK-SG-98–01, Anchorage.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Edward Arnold, London.

Seber, G. A. F., and C. J. Wild. 1989. Nonlinear regression. Wiley, New York.

Thomas, L., and nine coauthors. 2001. Distance 4.0. Beta 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data—user's guide for MicroFish 3.0. U.S. Forest Service, Intermountain Research Station, General Technical Report INT-254, Ogden, Utah.

Vondracek, B., and D. J. Degan. 1995. Among- and within-transect variability in estimates of shad abundance made with hydroacoustics. North American Journal of Fisheries Management 15:933–939.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91–164.

Waters, T. F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient for management of trout in streams. North American Journal of Fisheries Management 12:34–39.

Waters, T. F. 1999. Long-term trout production dynamics in Valley Creek, Minnesota. Transactions of the American Fisheries Society 128:1151–1162.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–138.

Zippin, C. 1956. An evaluation of the removal method of estimating animal population. Biometrics 12:163–169.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82–90.

Appendix   Shortest 95% confidence interval (CI) for the population estimate N (Reproduced from Chapman 1948).

Confidence intervals for sample sizes of 50 or less are based on the Poisson distribution. The number of recaptures is denoted by m, and estimates of the CI for N are obtained by multiplying the table values by the product of the number of fish caught in the first and second sample (i.e., $n_1 \cdot n_2$).

m	CI Lower limit	CI Upper limit	m	CI Lower limit	CI Upper limit
0	0.0885		26	0.02478	0.0563
1	0.0720	19.489	27	0.02408	0.0539
2	0.0767	2.821	28	0.02342	0.0516
3	0.0736	1.230	29	0.02279	0.0495
4	0.0690	0.738	30	0.02221	0.0475
5	0.0644	0.513	31	0.02165	0.0457
6	0.0600	0.388	32	0.02112	0.0440
7	0.0561	0.309	33	0.02061	0.0425
8	0.0526	0.256	34	0.02014	0.0410
9	0.0495	0.217	35	0.01968	0.0396
10	0.0468	0.188	36	0.01925	0.0384
11	0.0443	0.165	37	0.01883	0.0372
12	0.0420	0.147	38	0.01843	0.0360
13	0.0400	0.133	39	0.01805	0.0350
14	0.0382	0.121	40	0.01769	0.03396
15	0.0365	0.111	41	0.01733	0.03300
16	0.0350	0.1020	42	0.01700	0.03210
17	0.03362	0.0945	43	0.01668	0.03124
18	0.03233	0.0880	44	0.01636	0.03043
19	0.03114	0.0823	45	0.01606	0.02966
20	0.03004	0.0773	46	0.01578	0.02892
21	0.02901	0.0729	47	0.01550	0.02822
22	0.02806	0.0689	48	0.01523	0.02755
23	0.02716	0.0653	49	0.01498	0.02691
24	0.02632	0.0620	50	0.01475	0.02625
25	0.02552	0.0591			