1 Introduction

The final calculation of production is the simplest job that the production biologist has to do; all of the real difficulties are associated with the collection of the data that go into the calculation. However, the literature on secondary production contains such a diversity of equations, some correct and some erroneous, that a newcomer to the field can easily be misled into believing that the calculations are conceptually very difficult. This chapter will attempt to show, as did Gillespie and Benke (1979) that there is only one, simple method of calculating production.

In this chapter, the rate of production by a heterotrophic population will be taken to mean the biomass accumulated by that population per unit time. This definition is generally accepted and is particularly useful because it is conceptually simple and makes it easy to calculate production.

I will illustrate the principle of these calculations by imagining a small, simple population of 10 animals \( N_0 = 10 \) hatching from eggs simultaneously. On hatching, all animals are the same size and each has a dry mass of \( m_0 \). The initial biomass of our imaginary cohort \( B_0 \) is \( N_0 m_0 \). This initial biomass will not be included in the production of our cohort. In other words, the production of eggs or newborns is assigned to that of the parent cohort.

Now, imagine the animals all growing at the same rate until eventually one dies or is eaten by a predator. If this loss occurs when the mass is \( m_1 \), the total production up to that moment is \( 10(m_1 - m_0) \). Figure 2.1a shows that this product of number of animals multiplied by the biomass increment is simply

1. JAD prepared this manuscript from drafts written by FHR. The ideas presented are primarily those of the principal author and 'I' refers to him throughout unless otherwise noted. JAD accepts full responsibility for any errors or omissions.

2. Biomass can be expressed in many ways. During the IBP an attempt was made to impose a uniform method of expressing it as energy equivalent of mass. This attempt failed since biomass can be expressed easily as dry mass, ash-free dry mass, carbon, nitrogen, etc. (see Chapter 7). Since dry mass is usually the first measurement made by most workers, I will express biomass as dry mass. It is not intended to suggest that this is the most generally useful estimator of biomass.
Fig. 2.1 The calculation of production for a cohort with initial population ($N_0$) of 10 organisms and a mass at birth of $m_0$. Panel (A) shows the calculation of production if the mass at death of each individual were known. The area enclosed in the rectangle ABCD is the production up to the death of the first individual, while the area in EFGC is the production between the death of the first animal.
and the second. Other panels show the manner in which the production throughout the life of the cohort is estimated by: (B) the increment summation, (C) the mortality summation, and (D) the Allen curve methods of area integration. The bold points are observations made on the cohort and are means in a size class or during a time period. The shaded areas are errors in estimation.
the area enclosed within the rectangle ABCD on Fig. 2.1a. If the remaining nine animals continue growing at the same rate until a second dies, at a dry mass \( m_2 \), production during the interval between the death of the first and second individual is \( 9(m_2 - m_1) \). This increment of production is given by the area within the rectangle EFGC in Fig. 2.1a. Clearly, if we continue to record deaths and dry mass until the last individual dies with a dry mass of \( m_{10} \), we will have the data necessary to calculate production by the cohort \( P \), which is merely the area under the curve of \( N \) plotted against \( m \) or:

\[
P = N_0(m_1 - m_0) + N_1(m_2 - m_1) + \cdots + N_{i-1}(m_i - m_{i-1})
\]  

where \( N_0 \) is the number of animals living from hatching to the moment the first animal dies, \( N_1 \) is the number living from hatching until the moment the second animal dies, \( m_0 \) is the individual mass at birth, \( m_1 \) is the individual mass at the death of the first animal, and \( i \) is the total number of animals that hatched (\( i = N_0 \) in this case).

This example illustrates the basis of all calculations of secondary production. Considering its simplicity, one might wonder why the literature contains a multitude of different equations for calculating production. The answer is partially that real populations are not as simple as the one in Fig. 2.1a, nor can we always gather data on real populations comparable to data in Fig. 2.1a. For example, not all individuals in a cohort are born at the same time with the same dry mass, and we can rarely measure the mass at death of every individual in the cohort.

In the sections that follow, the 'different' methods of calculating production will be described and the essential similarity of these methods demonstrated. Then the diverse behavior of real populations and the types of data which we can gather about them will be described. Further, the ways in which production calculations have been modified for different types of population behavior or for inadequacies of data will be shown. Finally, we present real examples of the calculation of production for the two major categories of animals.

2 Four Methods of Calculating Production

The hypothetical cohort in Fig. 2.1a will be used again to illustrate the methods that have been used to estimate cohort production. In practice, because it would be virtually impossible to gather the data on the weight at death of every individual, we make do with less information. At best we have samples of the cohort taken at different times during its development or that we divide into different size classes. For each size class or time period we obtain a mean body mass of an individual \( \bar{m}_i \) and an estimate of the number of individuals in that size class \( N_{mi} \). In most cases, \( N_{mi} \) is taken to be an estimate
of the number of individuals that live long enough to attain a body mass of \( m_i \).
This procedure does not give us a complete graph of cohort size against body
mass as was seen in Fig. 2.1a, but (in this example) only four points. From here
on, depending on our whim, we calculate production in one of four ways.

In the first two methods ('growth increment summation' and 'mortality
summation'), we proceed as if we had a complete record and all mortality
occurred at the boundaries between our size classes. The history of the cohort
is reconstructed as a simplified histogram of numbers against individual
mass. In the method of growth increment summation the histogram is divided
into vertical slices, as in Fig. 2.1b, and their total area is calculated. To
calculate production by mortality summation, we merely divide Fig. 2.1a into
horizontal slices (e.g. Fig. 2.1c) and sum the areas of individual slices as in
equation 2.2 (for actual calculations use equation 2.27):

\[
P = (N_0 - N_1)(m_1 - m_0) + (N_1 - N_2)(m_2 - m_0) + \cdots + (N_{i-1} - N_i)(m_i - m_0)
\]

(2.2)

where all variables are as in equation 2.1.

It should be clear from this comparison that the growth increment
summation method and the mortality summation method are really identical.
In particular, it is important to note that they require exactly the same
population statistics and that there are no conditions under which either
method is superior to the other. Example calculations are given in Section 7.

The remaining two methods differ from the first two only in the
interpolation between the observed points. In the Allen curve method (named
after K.R.Allen, 1951, who used it to calculate production of trout in a New
Zealand stream) one merely draws a smooth curve by eye through the points
and extrapolates the curve intuitively to its intercepts with \( m_0 \) and \( N = 0 \)
(Fig. 2.1d). The area under the curve is easily measured by planimeter, square
counting, weighing, or electronic digitizer. As Fig. 2.1d shows, the area under
the smooth curve is similar to the area under the histogram and both give
reasonable approximations of production.

The fourth method merely uses a least squares curve-fitting procedure to
obtain an equation describing the Allen curve (see Chapter 8). The definite
integral from the smallest to largest mass of the individual then gives
production of the cohort. This formal method appears to yield the most
accurate estimate of production, and it does have the advantage of eliminating
subjectivity from the curve-fitting process. Usually, the only way of
significantly improving the estimate of production is by obtaining more and
better estimates of cohort size and body mass.

If natural populations behaved similarly to the hypothetical population in
Fig. 2.1a, the only difficulty would be in obtaining accurate estimates of
population size. However, no real population comprises individuals of all the same size and born at exactly the same time. Some do not even produce recognizable cohorts. Much of the remainder of this chapter will, therefore, deal with the problems posed by the differences between real populations and our hypothetical population.

3 The Simplest Case—A Population with Identifiable Cohorts

A few types of aquatic animals such as fish and lamelli-branch molluscs can be aged and have a reproductive period that is very short relative to their lifespan. Consequently, all members of a cohort can be recognized and analyzed in the same size class. In this case, the techniques in Section 2 can be applied easily. However, the more typical situation for small invertebrates is that of a reproductive period which is long relative to the lifespan, and cohorts, although they exist, are not clearly delineated. In this case individuals from one cohort will be of many sizes. The significant difference for the production biologist is that a sample taken at any point in time will catch members of the same cohort in many different size classes (Fig. 2.2). If animals can be aged there is no problem in determining the number of individuals in a cohort reaching any size, and since Ricker (1971) thoroughly covers this type of population it will be ignored here. Other invertebrates produce only a few cohorts per year and thus can be treated easily by the techniques in Section 2 (see example, Section 8).

In the population illustrated in Fig. 2.2, however, the number of members of a cohort reaching a given size must be estimated indirectly, because at any time during the growth of a cohort individuals will be spread throughout several size classes. One technique for estimating the production of this type of population is outlined below.

Southwood (1966) has developed a method to determine the total population of a cohort, where cohorts are not easily separable (Southwood & Jepson 1962; Southwood 1966). In this method, the abundance of animals in an arbitrary or developmental size class is plotted as a function of time (Fig. 2.3). If there is no mortality of animals as they grow through this size class, the number of animals growing from the lower size limit \(m_{\text{min}}\) to the upper size limit \(m_{\text{max}}\) of the stage can be calculated from the area \(A\) under the curve in Fig. 2.3. This area is equal to the number of animal-days \(m^{-2}\), therefore, if we divide the area by the number of days which it takes an average individual to grow through the size class, we know the number of animals. In the example in Fig. 2.3, the area under the curve is 220 animal-days \(m^{-2}\). If the average time spent in the size class \(D\) is 0.5 days, then the total number of animals that enter and leave the class will be \(A/D = 220/0.5 = 440\).
The standing stock of each instar of *Skistodiaptomus oregonensis* in Teapot Lake during 1966 (from Rigler & Cooley 1974). The figure shows that lack of synchrony in the reproduction of small invertebrates often leads to the members of a cohort being dispersed throughout a variety of instars or size classes. A sample taken at time 't' would contain members of the cohort produced around day 140 that have attained developmental stages N1 to C2. The production of these sorts of organisms can be approximated using equation 2.3.
Fig. 2.3 Plot of hypothetical data for Southwood's technique for determining the number of organisms in a cohort. The data are concentration of organisms in an instar or size class plotted against time. The shaded area is integrated and divided by the average time required for an animal to pass through this stage or class which yields the average number of organisms in the cohort.

It follows that the production of this size class ($P_i$) is given by:

$$P_i = \left( \frac{A_i}{D_i} \right) (m_{\text{max}} - m_{\text{min}})_i$$  \hspace{1cm} (2.3)

If there is mortality within the size category, equation 2.3 may not be strictly correct. The error in the estimate of production that is produced by using equation 2.3 will depend on:

1. The pattern of mortality and growth.
2. The amount of growth.
3. The amount of mortality.

If growth and mortality are both constant with time there will be no error; if all mortality occurs at the beginning or the end of the period spent in the size category there will be no error. However, if growth and mortality are both exponential functions of time, then the application of equation 2.3 will overestimate production. Since exponential growth and mortality probably occur frequently, it is of interest to know the magnitude of the error. Table 2.1 shows that it increases with increased mortality and growth; an error from this source can, therefore, be decreased by increasing the number of size classes. This will decrease not only $m_{\text{max}}/m_{\text{min}}$, but also the percentage
Table 2.1 Percent by which production is overestimated when growth and mortality within a size class are exponential and \( P \) is calculated from equation 2.3.

<table>
<thead>
<tr>
<th>Growth ( [m_{\text{max}}/m_{\text{min}}] )</th>
<th>Mortality (%) ( [100(N_0 - N)/N_0] )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.7 4.1 8.2</td>
</tr>
<tr>
<td>4</td>
<td>3.3 8.2 16.8</td>
</tr>
<tr>
<td>8</td>
<td>4.8 12.2 26.2</td>
</tr>
</tbody>
</table>

mortality within each size class. Alternatively, the error could be estimated from Table 2.1 and an approximate correction applied to the calculated value of production.

Since information on the temporal distribution of mortality within each size category will almost certainly not be available, and will generally be impossible to collect, the recommended procedure is to divide the population into the largest number of size or developmental categories possible.

The methods for estimating the time spent in a size class (\( D \)) will be described in Section 4.4. If cohorts cannot be established with certainty by simple inspection of plots such as Fig. 2.3, probability paper can sometimes be used to determine their boundaries (Harding 1949; Cassie 1950; Southwood 1966). Methods described in Section 4 should be used if cohorts cannot be identified.

4 Populations in a Steady State

4.1 General comments

Not all populations of aquatic animals produce identifiable cohorts. In some populations the instantaneous birth rate (\( b \)) is very similar to the instantaneous death rate (\( d \)). For these populations:

\[ b = d \gg r \quad (2.4) \]

That is to say, the instantaneous rate of change of population size, although not necessarily zero, is very small, and cohorts cannot be recognized from analysis of a temporal series of samples taken from the population. In this situation, a slightly different method is used to calculate the required population statistics.

The method applied to steady-state populations has been called a time-specific analysis by Southwood (1966). In time-specific analysis, because we cannot identify real cohorts, we analyze the population at one point in time, or
determine the average structure during a selected interval of time. Although the method of calculating production of a population in a steady state is essentially identical to the method applied to populations producing cohorts, the method of gathering the data that go into the calculation is different. This difference arises because the time in each size class cannot be inferred from a temporal series of quantitative samples of a population in steady state. In order to convert size classes into age classes one must obtain an independent estimate of growth rate. As will be shown later, this estimate is obtained by measuring the growth of identified individuals held under conditions that simulate natural conditions.

Because the embryo (developing egg) is often the easiest stage to maintain in culture, and because the development rate of the egg is exclusively a function of temperature (e.g. Fig. 2.4) (Eichhorn 1957; Bottrell 1975a, 1975b; Bottrell et al. 1976; Vijverberg 1980) more work has focused on the egg than on other stages. From this work, particularly through the ideas of Elster

![Diagram](image)

**Fig. 2.4** Example of relationship between egg development time and water temperature. The development time of the rotifer *Keratella cochlearis* from Char Lake (Rigler et al. 1974) is compared with those measured by Amrén (1964) and Edmondson (1965).
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(1954; Elster & Schwoerbel 1970) and Edmondson (1960, 1974), the egg ratio method of determining birth rate has become widely used. These birth rates are important in population statistics studies and have been used to examine the effect of various environmental factors and biological relationships on production (Edmondson 1974), and for the calculation of production from turnover in numbers (cf. Section 4.3.3). Because much confusion and dispute has surrounded this method I will describe it in detail and attempt to use it correctly. A later section (4.3) shows that similar population statistics can be used to calculate the productivity of populations for which cohorts are not identifiable.

4.2 The egg-ratio method of calculating birth rate

In the traditional method of estimating birth rate from egg ratio, quantitative samples of the number of eggs in the population \(N_{eggs}\) are taken. The mean temperature to which the developing embryos are naturally exposed is estimated and the average \(D\) under natural conditions is estimated from an equation or graph relating duration of embryonic development \(D\) to temperature (Fig. 2.4). \(N_{eggs}/D\) is then used as an estimator of birth rate. Some important questions remain, however: What is the relation between \(N_{eggs}/D\) and birth rate? Is this a constant relation, and, if so, what is it? The confusion in the literature arose because many different answers have been given to these questions and almost all are both right and wrong. I'll now try to explain this apparent contradiction.

The literature makes a distinction between 'finite birth rate' and 'instantaneous birth rate'. The former is the average birth rate over some finite interval of time and the latter is the birth rate at some point in time. The latter can be thought of as the first derivative of births with respect to time.

Thus, there are two rates that can be calculated from the egg ratio. I will first discuss the calculation of finite birth rate and then the calculation of instantaneous birth rate.

4.2.1 Relation between \(N_{eggs}/D\) and the finite birth rate

Traditionally, the finite birth rate \(\beta\) from \(t\) to \(t+D\) of a population sampled at time \(t\) has been considered to be equal to \(N_{eggs}/D\). Most papers dealing with production or population statistics of invertebrates have made this assumption. However, Paloheimo (1974) has shown that this assumption is valid only under certain conditions. Uncritical acceptance of this assumption can cause large errors in the calculation of birth rates.

The rationale for equating \(N_{eggs}/D\) and \(\beta\) is that the eggs sampled at \(t\) will range in age from 0 to \(D\). By \(t+D\) all of these eggs will have hatched and none...
of the eggs laid after \( t \) will have hatched. Problems arise if there is mortality of females carrying the eggs. If this is the case some eggs will die before they hatch and \( \beta \) from \( t \) to \( t + D \) will be less than \( N_{\text{egg}}/D \). I will return to the calculation of finite birth rate after considering calculation of the instantaneous birth rate.

### 4.2.2 Relation between \( N_{\text{egg}}/D \) and instantaneous birth rate

Although production can be calculated without calculating the instantaneous birth rate (\( b \)), many workers have placed great importance on the calculation of \( b \). This emphasis on \( b \) probably derives from the appeal and the apparent rigour of the exponential equations for population growth.

The point that needs stressing is that the analysis of population parameters by exponential equations is rigorous only when the population under study conforms to the assumptions implicit in these equations, that the birth rate and the death rate are both constant over the time interval between successive samples. Only if they are constant can the growth of the populations be described by:

\[
N_{t_2} = N_{t_1} e^{(b-d)(t_2-t_1)}
\]  

(2.5)

where \( N_{t_1} \) and \( N_{t_2} \) are the numbers of individuals in the population at times \( t_1 \) and \( t_2 \), \( b \) is the instantaneous birth rate, and \( d \) is the instantaneous death rate.

Since the instantaneous constant of population growth \( (r) \) is merely the difference between the instantaneous birth and death rates:

\[
r = b - d
\]  

(2.6)

we can simplify equation (2.5) to:

\[
N_{t_2} = N_{t_1} e^{rt_2-t_1}
\]  

(2.7)

In practice, equations 2.6 and 2.7 are used as follows. First, the population under study is censused on two occasions, \( t_1 \) and \( t_2 \). The estimates of the population size on these dates \( (N_{t_1} \) and \( N_{t_2} \)) are then substituted in equation (2.7) and the equation is solved for \( r \).

This is as far as we can go without an estimate of either \( b \) or \( d \). Since \( d \) is usually impossible to measure (Prepas & Rigler 1978) it is necessary to obtain an estimate of \( b \) to substitute into (2.6).

Practical and conceptual difficulties arise at this stage because \( b \) can be measured directly only under exceptional circumstances. What we normally attempt to measure is the finite birth rate \( (\beta) \) over some specified interval. The finite birth rate is then converted to \( b \).

Depending on the behaviour of the population, one of three equations is used to make this conversion (Table 2.2). These equations only apply when \( b \) and \( d \) are constant over the time interval \( t_2 - t_1 \). If the population is in a steady
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Table 2.2 Equations used to calculate \( b \) from \( \beta \) and the conditions under which each applies.

<table>
<thead>
<tr>
<th>Conditions</th>
<th>Applicable equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>( b ) and ( d ) are both constant</td>
<td>( b = d )</td>
</tr>
<tr>
<td>( b &gt; d &gt; 0 ) from ( t_1 ) to ( t_2 )</td>
<td>( b = \ln(1 + \beta) )</td>
</tr>
<tr>
<td>( \beta ) varies between ( t_1 ) and ( t_2 )</td>
<td>none of the above equations are valid</td>
</tr>
</tbody>
</table>

state because births equal deaths, then the instantaneous birth rate equals the finite birth rate. If there are no deaths from \( t_1 \) to \( t_2 \) then Edmondson's (1960) equation is valid. When \( b \) and \( d \) are not equal and \( d \) is greater than zero, the equation of Leslie (1948) and Caswell (1972) must be used.

The seductive appeal of the exponential growth equation and the rigorous conversion from finite to instantaneous birth rate probably convinces many field ecologists that one or another of the conversions in Table 2.2 must be used. However, real populations rarely conform to the assumptions of the mathematics. Usually \( b \) and \( d \) both vary such that none of the conversions is strictly correct. Therefore, it is not surprising that many field ecologists are confused and unsure about the appropriate conversion.

4.2.3 Usual measurement of finite birth rate

The method usually used to measure finite birth rate is as follows:

1. The relation between the duration of embryonic development (\( D \)) and temperature for the species under study is measured in the laboratory.
2. The mean temperature experienced by embryos in nature is estimated and \( D \) is calculated for the embryo population over finite intervals.
3. From samples of the population, the number of developing eggs (\( N_{eggs} \)) in the population is estimated for the sampling dates.
4. If \( t_i \) is a sampling date then the finite birth rate over the period \( t_i \) to \( t_i + D_i \) is calculated as \( N_{eggs} / D_i \).

Since the absolute birth rate is usually of less interest than the birth rate relative to the number of animals in the population, the results are usually divided by the population size of free-swimming individuals (\( N_i \)) at \( t_i \) to give births over \( t_i \) to \( t_i + D_i \) per animal on \( t_i \).

Thus,

\[
\beta \text{ (from } t_i \text{ to } t_i + D_i \text{)} = \frac{N_{eggs}}{D_i N_i}
\]  

(2.8)
This apparently simple computation is based on a most important, implicit assumption: that all of the developing eggs in the population at $t_j$ will actually survive for the remainder of their development period and hatch. If there is predation on egg-bearing females this assumption is invalid and the real finite birth rate from $t_j$ to $t_j + D_i$ will be lower than that calculated from the egg ratio. A mathematical demonstration of this source of error and an estimate of its magnitude was given by Paloheimo (1974). He showed that $N_{eggs}/D$ and $\beta$ are approximately equal only when $b$, $D$ and $r$ are extremely small.

Again, we are faced with a situation in which the analysis of our data is only valid if the population we are studying conforms to the assumptions of the mathematical treatment. The best way of eliminating the uncertainty is to test our assumptions. Since all of these assumptions concern the age distribution of the embryo population, the simple solution is merely to measure this age distribution if possible (Threlkeld 1979).

Although measurement of the age distribution of embryos is easy, it has been done surprisingly rarely. Several examples show how useful this measurement can be. George & Edwards (1974) studied a population of *Daphnia hyalina* that was approximately in a steady state. Their results clearly showed that the frequency distribution of each morphologically identified group of embryos was indistinguishable from the relative duration of the group. In other words, the age distribution of embryos was uniform. Since the rate of production of eggs was constant, their study showed that embryo mortality was negligible. Consequently, they demonstrated that the egg ratio $= \beta = b$.

Unfortunately, this paper also provides a good example of the confusion that surrounds the calculation of birth rates for, having demonstrated that in their population $\beta = b$, they then made the mistake of applying Edmondson's (1974) formula to convert $\beta$ to $b$.

In a paper strongly advocating the use of age distribution of embryos in population studies, Threlkeld (1979) showed that the age distribution of embryos varied diurnally, and inferred that this showed diurnal changes in mortality of *Daphnia galeata mendotae* females due to predation.

### 4.2.4 Recommended method of measuring birth rate

The method that is suggested here can be applied to any species that carries its eggs or for which an accurate sample of the egg population can be taken, and in which a series of development stages of the embryo can be identified. In principle this method is similar to the use of the Kolmogorov–Smirnov cumulative frequency distribution statistic recommended by Threlkeld (1979; Sokal & Rohlf 1981), but it is intuitively simpler.

First, measure the duration of as many morphologically identifiable stages
of the embryo as is convenient (Obreshkove & Fraser 1940; Green 1956; Lei & Clifford 1974). Select females for observation that have well developed ovaries, maintain them in well-oxygenated water at a constant temperature and record when each lays its eggs. If the eggs can be separated from the female and develop normally one clutch of eggs can be observed repetitively. Otherwise it might be necessary to kill females at intervals to record developmental stages reached by eggs at different times after laying. Total development time (D) is recorded as is the fraction of D spent in each stage.

Although no observations exist to show that development rate of early or late embryonic stages is differently affected by temperature (Cooley 1971; Threlkeld 1979) it would be advisable to test this possibility by making measurements at several temperatures.

When planning the sampling program one must take great care to ensure that samples are representative. Eggs may not be distributed uniformly either horizontally or vertically. Additional care is needed in thermally stratified systems if egg-bearing females do not migrate freely through the temperature range occupied by the species. If this situation occurs, calculation of birth rate should be modified (Prepas & Rigler 1978).

It is also important to establish whether or not there is a diurnal change in age distribution of embryos. Either diurnal predation cycles (Threlkeld 1979) or cycles in egg production could cause temporal changes in age distribution. If such changes are found, it might be necessary to collect day and night samples routinely.

Methods of killing and fixing of specimens are also more important because differential loss of older or younger embryos will bias the results when loose embryos cannot be identified to species. Sometimes the sugar-formalin method of Haney & Hall (1973) is adequate to prevent loss of embryos (Threlkeld 1979) but occasionally this method causes a high loss of older embryos and must be modified. Prepas (1978) found that ice cold sugar-formalin prevented this loss in a population of Daphnia rosea. One must also consider the problems of distortion and weight loss if the same samples are to be used for determining taxon or biomass (see Chapters 3, 4 & 7). It is likely that no one technique will be adequate for all species. Consequently fixation methods should be investigated before sampling is started.

When samples are being counted, the number of embryos in each of the predetermined developmental stages is recorded. More embryos must be counted than in the traditional method. As a rule of thumb, one could increase the number counted by a factor equal to the number of stages identified. For statistical treatments of sampling and counting see Chapters 7 and 8.

If there are no diurnal changes in the age distribution of embryos, the instantaneous rate of egg production and the instantaneous birth rate can be calculated directly as shown in the following hypothetical example.
4.2.5 *Example calculation of instantaneous birth rate*

To illustrate the proposed method of calculating the instantaneous birth rate we will consider a hypothetical population of a species that has six easily identifiable stages of developing embryo. First, we measure in the laboratory the fraction of the total embryonic period spent in each stage (Column 2, Table 2.3). Then on two occasions at $t_1$ and $t_2$ we sample the population of animals ($N$) and the population of developing eggs ($N_{egg}$). The number in each stage on day $t_1$ and day $t_2$ is recorded in Column 4 and Column 5 of Table 2.3.

<table>
<thead>
<tr>
<th>Embryonic stage</th>
<th>Fraction of D in stage</th>
<th>$D_i$ when $D = 2.5$ days</th>
<th>No. of eggs m$^{-2}$ at $t_1$</th>
<th>No. of eggs m$^{-2}$ at $t_2$</th>
<th>Potential finite birth rate at $t_1$</th>
<th>Potential finite birth rate at $t_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.20</td>
<td>0.50</td>
<td>500</td>
<td>750</td>
<td>1000</td>
<td>1500</td>
</tr>
<tr>
<td>2</td>
<td>0.30</td>
<td>0.75</td>
<td>750</td>
<td>925</td>
<td>1000</td>
<td>1233</td>
</tr>
<tr>
<td>3</td>
<td>0.15</td>
<td>0.375</td>
<td>375</td>
<td>325</td>
<td>1000</td>
<td>867</td>
</tr>
<tr>
<td>4</td>
<td>0.15</td>
<td>0.375</td>
<td>375</td>
<td>275</td>
<td>1000</td>
<td>733</td>
</tr>
<tr>
<td>5</td>
<td>0.12</td>
<td>0.30</td>
<td>300</td>
<td>150</td>
<td>1000</td>
<td>500</td>
</tr>
<tr>
<td>6</td>
<td>0.08</td>
<td>0.20</td>
<td>200</td>
<td>75</td>
<td>1000</td>
<td>375</td>
</tr>
</tbody>
</table>

The ratio of the number of eggs in the ith stage ($N_i$) to the time spent in that stage ($D_i$) gives the potential finite birth rate of the individuals in the ith stage (potential $\beta_i$) at the time of sampling, in animals per day, i.e. $N_i/D_i = \text{potential } \beta_i$. Note that $N_i/D_i$ is called the potential finite birth rate. This qualifier is to remind us that the actual finite birth rate of a stage will be lower than $N_i/D_i$ if there is any embryo mortality.

Until now I have considered the potential finite birth rates of embryonic stages. However, we can also think of these rates as applying over finite intervals of time. For example, the stage 6 embryos will hatch over the period from $t$ to $t + 0.2$ days. The stage 5 embryos will hatch over the period from $t + 0.2$ to $t + 0.5$ days. The results from Table 2.3 converted to time periods are shown in Fig. 2.5, where it can be seen that over the 2.5 days following $t_1$, the potential birth rate is constant. This is because the fraction of the population contributed by each stage on sampling date $t_1$ was equal to the fraction of the development time occupied by that stage. If a result such as this were obtained when the population was in steady state, it would tell us that egg
mortality was negligible. Under these conditions, the potential finite birth rate equals the real finite birth rate which in turn equals the instantaneous birth rate.

On sampling date $t_2$, the behavior of the population was quite different. The potential finite birth rate increased steadily over the 2.5 days following $t_2$. Provided the eggs were well sampled and diurnal fluctuations in age distribution did not occur, data such as these indicate one of two situations. Either egg mortality was very high or the population of females was increasing rapidly. Although the two situations are not mutually exclusive it is unlikely that they would coincide.

The situation at $t_2$ illustrates both the error of using $N_{egg}/D$ as an estimator of the finite birth rate, and the value of a careful age analysis of embryos. To simplify the explanation, we will say that the population of adult females at $t_2$ was in a steady state. Consequently, the trend of decreasing potential finite birth rate with increasing age of embryo is due exclusively to mortality of embryos. If we had assumed that $N_{egg}/D$ gave a measure of the finite birth rate from $t_2$ to $t_2 + D$, then we would have concluded that $\beta = 2500/2.5$ or 1000 births m$^{-2}$ day$^{-1}$, whereas we know that the potential finite birth rate of stage 6, which still overestimates the finite birth rate of this stage, is $75/0.2 = 375$
Chapter 2

births m\(^{-2}\) day\(^{-1}\). The shorter the time period following \(t_2\) included in the calculation, the lower and more accurate will be the estimate of finite birth rate at \(t_2\).

This simple calculation merely illustrates what Paloheimo (1974) showed mathematically. All other things being equal, reducing \(D\) reduces the discrepancy between the finite birth rate and the potential finite birth rate.

There are two consequences of this relation. First, the most accurate estimate of \(\beta\) is obtained by choosing late embryonic stages with short duration, provided, of course, that a good estimate of the population in these stages can be made. Second, as the duration of the oldest stage becomes infinitely short, the amount of unmeasured mortality between the sampling and hatching times approaches zero. With an infinitely short duration of the last stage, the potential finite birth rate equals the instantaneous birth rate at \(t_2\). Consequently, to use these data to estimate the instantaneous birth rate we need only assume that the trend of decreasing potential birth rate with increasing age is continuous and extrapolates to \(t_2\). This assumption is much less restrictive than those made by mathematical models. The population is not required to be in a steady state and we do not need to know \(r\).

The simplest method of extrapolating is to apply the potential finite birth rate of a stage at the mid-time of hatching of that stage and fit a curve to the points as shown in Fig. 2.5. In the example given, the results were indistinguishable from a straight line. Therefore, a least squares linear fit was used to give an intercept at \(t_2\) of 325. Other forms of curves could be fitted with other techniques (see Chapter 8). Thus, our estimate of the instantaneous birth rate by the method of embryo stage analysis is 325 births m\(^{-2}\) day\(^{-1}\). The intercept of the line at \(t_2 + D\) can be used as a measure of the instantaneous rate of egg production at \(t_2\). It is important to note that these population statistics are valid only at the time when the population was sampled, unless the age structure of the population remains constant.

4.3 Calculation of the production of populations in steady state

Strictly speaking, this section is not concerned with populations in a steady state because this situation is encountered very rarely in nature. More appropriately, I will be describing the analysis of populations in which cohorts cannot be identified. Since species that produce this type of population are those which reproduce more or less continuously, their populations more closely approximate a steady state than do those that are suitable for cohort analysis. Therefore, it would be more accurate to say that this section will deal with the calculation of production of populations that are in an approximately steady state over discrete time intervals.

Ideally, we need exactly the same information to calculate production of
steady-state populations as we do for those that produce identifiable cohorts. Simply stated, production is calculated as the summation of rates of production for each of a set of identifiable stages or size classes. The production rate of each of the different classes is inferred from measures of number of organisms and rate of growth in each of these classes. However, analysis of steady-state populations is invariably performed with inadequate data, just as cohort analysis is. In fact, we usually have less complete, or less reliable, data for steady-state populations, because growth rates cannot be calculated from samples of the real population but must be measured in the laboratory (e.g. Bottrell 1975b; Bottrell et al. 1976; Vijverberg 1980). Consequently, the methods of calculating production must make more assumptions about the behavior of the population. The different computational methods simply depend on different assumptions.

The two most frequently used methods are 'growth increment summation' and 'instantaneous growth rate'. The former is most accurate when individual growth within size classes is linear and the latter is most accurate when growth is exponential.

4.3.1 Growth increment summation

This calculation is based on the assumption that all individuals within a size class are growing at the same constant rate. Thus, the rate of production is proportional to the number of individuals within the class, and can be calculated from:

\[ P = \frac{N(m_{\text{max}} - m_{\text{min}})}{D} \]  

(2.9)

where \( P \) is the average production in a particular size class per unit time, \( N \) is the average number of individuals in the class at \( t \), and \( m_{\text{max}} \) and \( m_{\text{min}} \) are respectively the maximum and minimum mass of individuals in the size class. \( D \) is the time taken by an average animal to grow from \( m_{\text{min}} \) to \( m_{\text{max}} \). [Note: This technique has been applied to rotifer populations with the added assumption that production due to growth after hatching is negligible. In this case, the production of the population is assumed equal to egg production, \( m_{\text{min}} = 0, m_{\text{max}} = \text{adult mass}, N = N_{\text{eggs}}, \) and \( D \) is equal to the egg development time. The technique is only valid if there is no egg mortality (see Section 4.2, and Fig. 2-7)].

4.3.2 Instantaneous growth method

This method is the one that is most frequently applied to steady-state populations. It assumes that all individuals in the size class are growing
Chapter 2

exponentially. Production will be proportional to the biomass of the size class and can be calculated from:

\[ P = Bg \]  

(2.10)

where \( B \) is the mean biomass of the size class over \( t \), and \( g \) is the constant of instantaneous growth in mass of individuals in the size class.

Since growth is described by \( m_{\text{max}} = m_{\text{min}} e^{Ds} \),

\[ g = \frac{1}{D} \ln \left( \frac{m_{\text{max}}}{m_{\text{min}}} \right) \]  

(2.11)

and we therefore calculate the production of the size class from:

\[ P = \frac{B}{D} \ln \left( \frac{m_{\text{max}}}{m_{\text{min}}} \right) \]  

(2.12)

Provided there is no mortality within the size class, and the population is in an approximately steady-state, equations 2.9 and 2.12 are equally accurate regardless of the shape of the individual growth curve. When mortality is significant, however, it is important to use the equation appropriate to the type of growth characteristic of the size class. Choice of the wrong model can lead to large errors when mortality is high. For this reason, it is important to make growth measurements carefully and to attempt to simulate natural conditions as closely as possible.

4.3.3 A common error: computation of turnover of biomass from turnover of numbers

An apparently simple method of calculating production by steady-state populations has been used by many authors (Stross et al. 1961; Hall 1964; Wright 1965; Heinle 1966; Burgis 1971, 1974; George & Edwards 1974; etc.) and recommended in two reviews of methods of calculating production (G.A. Pecheń in Winberg 1971; Waters 1977). Winberg et al. in Edmondson and Winberg, eds. (1971) were non-committal, but clearly warned the reader that the method was valid only under certain conditions. However, they appear to have missed the critical condition.

I will attempt to clarify the problem with this method by comparing it with the increment summation, and the instantaneous growth methods, but will supplement explanation with a set of example calculations in an attempt to make my point more simply.

The comparison of methods will be made for the simplest case—the case in which there is no mortality of the individuals passing through the size class for which production is being calculated. I will first show that, in this case, the increment summation and instantaneous growth methods are identical. I will then compare the turnover of numbers method and show that only under one unlikely condition is it identical to the other two and thus correct.
To show the identity of the increment summation and instantaneous growth methods one can begin with equation 2.12. Because N is constant in the size class then:

\[ B = N \bar{m} \]  

(2.13)

where \( \bar{m} \) is the average weight of an individual passing through a size class. Therefore, equation 2.12 can be rewritten:

\[ P = \frac{(N \bar{m} / D) \ln (m_{\max} / m_{\min})}{\ln (m_{\max} / m_{\min})} \]  

(2.14)

Riggs (1963) demonstrates that the mean mass of an organism (\( \bar{m} \)) during a time period when its mass is changing exponentially would be calculated as the logarithmic mean:

\[ \bar{m} = \frac{(m_{\max} - m_{\min}) / \ln (m_{\max} / m_{\min})}{\ln (m_{\max} / m_{\min})} \]  

(2.15)

Substituting 2.15 into 2.14 we find that:

\[ P = \frac{N(m_{\max} - m_{\min})}{D} \]  

(2.16)

which is identical to equation 2.9 for the increment summation technique.

The rationale of the turnover method is difficult to explain because its development was intuitive rather than logical. The basis of the method is that, in a steady-state population, the number of new recruits entering a size class per unit time will be constant and exactly balanced by the number leaving the size class by death or by growing through it. Since finite and instantaneous birth rates are equal to each other and death rates the population is easily described by an input or output rate constant (b or d). Then, by analogy with the terminology of radioactive tracer kinetics or compartmental analysis, the reciprocal of this rate constant is called the turnover time in numbers of the size class. This is the time in which a number of individuals equal to the number in the class enters and leaves the class. So far, so good. Difficulties begin when we intuitively see a connection between the numbers passing through the size class (\( T_N \)), the amount of material (biomass) passing through the class (\( T_B \)), and production in the class. In general, it has been assumed that the three are related as in:

\[ \frac{1}{b} = T_N = T_B \]  

(2.17)

If this relation were valid, then daily biomass production (\( P_B \)) would equal biomass divided by the turnover time of biomass (or numbers). Therefore production of a population is often calculated:

\[ P = \bar{m} N / T_N \]  

(2.18)

where \( \bar{m} \) is the mean weight of individuals in the size class, and \( N \) is the number of individuals in the size class. Because the turnover time in numbers of the
population of organisms is the time it takes for the population to be replaced by new recruits, $T_N$ is equal to the development time ($D$) of the population and thus equation 2.18 can be written:

$$P = \frac{mN}{D} \quad (2.19)$$

Although the set of relationships in (2.17) and (2.18) has been accepted uncritically by many experimentalists, several reviews have suggested that they are valid only under certain conditions. There is, however, no agreement about these conditions.

For a class in which there is no mortality the condition can be defined unambiguously as the condition under which equation 2.16 predicts the same production as equation 2.19. That is:

$$\frac{mN}{D} = \frac{N(m_{\text{max}} - m_{\text{min}})}{D} \quad (2.20)$$

and because Riggs (1963) shows that:

$$\dot{m} = \frac{(m_{\text{max}} - m_{\text{min}})}{\ln \left(\frac{m_{\text{max}}}{m_{\text{min}}}\right)} \approx \frac{m_{\text{max}} + m_{\text{min}}}{2} \quad (2.21)$$

the condition under which equation 2.18 yields an appropriate measure of

Fig. 2.6 The percent of true production, calculated by equating turnover of numbers with turnover of biomass, plotted against the ratio of maximum mass to minimum mass of animals in a population or size class. The calculations are simply the ratio of equation 2.19 (assuming equation 2.21) to equation 2.16. The figure shows that if $m_{\text{max}}/m_{\text{min}}$ is low then production is overestimated by the turnover of numbers method, and if $m_{\text{max}}/m_{\text{min}}$ is high then production is underestimated.
production is when:

\[ 3m_{\text{min}} = m_{\text{max}} \]  

(2.22)

that is, when the maximum size of an adult is three times the size at hatching.

The magnitude of errors produced by inappropriate calculations is shown in Figs. 2.6 and 2.7. Figure 2.6 shows that equating turnover of numbers and biomass produces large positive errors when \( m_{\text{max}}/m_{\text{min}} < 3 \) and negative errors when \( m_{\text{max}}/m_{\text{min}} > 3 \). Another factor that leads to errors in this sort of calculation is variability in age structure. This can be brought about not only by expansion and contraction of populations, but also through selective predation or mortality within a size class.

Figure 2.7 shows that when the increment summation method is applied to a size class in which individual growth is exponential the method overestimates

![Graph showing calculated production as a percentage of actual production against mortality rate (k).](image)

**Fig. 2.7** Error of increment summation technique when applied to populations with exponential growth and varying mortality. The data are production, calculated by the increment summation technique, as a percentage of actual production plotted against mortality rate (k), where \( N_t = N_0 e^{-kt} \), for size classes with differing ratios of maximum to initial mass \( (m_t/m_0) \). The rate of exponential growth was determined as in equation 2.11 using \( m_t/m_0 \) ratios and is expressed \( m_t = m_0 e^{kt} \). Actual production from \( t_0 \) to \( t_N \) was determined as the area under a plot of \( N_t \) against \( m_t \). The figure shows that the increment summation technique yields overestimates of production where there is mortality in the size class or where growth is not linear. Higher mortality and larger ratios of \( m_{\text{max}}/m_{\text{min}} \) lead to larger overestimates of production.
production in all cases when mortality is not zero. This error increases with increasing mortality rate and increasing value of $m_D/m_0$.

From the above discussion it is clear that a key to the accurate calculation of production by populations in a steady state is a knowledge, for each age class, of $m_{\text{min}}$, $m_{\text{max}}$, and $m$. Because $m$ will depend on distribution of growth and mortality throughout each age class, these statistics are as important in the analysis of steady-state populations as in cohort analysis. Any method that appears to require less information, such as the turnover method, merely introduces new uncertainties or errors.

5 Two Apparently Simplified Methods

Occasionally a biologist wishes to calculate production from data that were not collected specifically for this purpose. Hence, several methods of approximating production from incomplete data have come into use. Two commonly used methods will be discussed here, although neither is recommended.

5.1 Size-frequency method ('average cohorts')

This method of estimating the production of species that do not produce cohorts, and for which the duration of each size class has not been measured, was first correctly described by Hamilton (1969). It was originally intended for application to a collection of species of stream insects that differ in maximum size and development time but are conveniently treated as one population because they are difficult, or as yet impossible, to separate into species. Those who still recommend using this method generally agree that if it is to be applied to a mixed group of species they should at least have a similar size and development time (Hynes & Coleman 1968; Hamilton 1969; Benke 1979; Waters 1977; Krueger & Martin 1980) and be of the same trophic level (Waters 1979; cf. Peters 1977). Several recent workers have also applied this method to single species (Eckblad 1973; Waters & Crawford 1973; Winterbourne 1974; Martien & Benke 1977; Benke 1979; Waters 1979; Benke & Wallace 1980; Menzie 1980; Waters & Hokenstrom 1980).

Since its first erroneous description by Hynes & Coleman in 1968, this method has generated confusion and conflict. Anyone wishing a history of the debate should consult Zwick (1975), Benke & Waide (1977), Waters (1977), and Menzie (1980). I will not repeat the arguments here, but will merely show that the method is derived from the increment summation method for populations that do not produce identifiable cohorts. Readers who would like a fuller, clear description of the method and its limitations, complete with many numerical examples, should consult Hamilton (1969).
The steps in applying this method are as follows:

1. Collect representative samples of the population or group of populations on a number of occasions evenly spaced over a year. Some of the literature states that the method is only valid if samples are collected at equal intervals. This is not correct; all that is required is a good mean annual value for the number of individuals in each size class.

2. Divide the population into (i) arbitrary size classes and count the number in each class \((N_1 \ldots N_i)\). In the method generally described in the literature, length classes are measured and subsequently converted to volume units. This has the disadvantage of making the method appear more complex than it is. Dry mass or volume could be measured directly. If length is measured, it is wise to remember that the mean of a series of linear measurements is not necessarily equal to the mean of the cubes of those measurements. In addition, see Chapter 7 for a treatment of the important problem of error propagation in length: weight conversion.

3. The total development time \((D_{tot})\) for the population is determined from the voltinism of the animals (e.g. univoltine: \(D_{tot} = 1\) year). The development time of each class \((D_i)\) is then assumed to be an equal fraction of \(D_{tot}\). For example, if \(D_{tot} = 365\) days and there are \(i\) size classes, then each size class is assumed to have a duration of \(365/i\) days.

\[
D_i = D_{tot}/i
\]  

Thus, the rate of production by the \(i\)th size class, instead of being calculated by the normal method of increment summation (equation 2.9), is calculated from:

\[
P_i = N_i(m_{max} - m_{min})/D_i
\]

where \(m_{max}\) and \(m_{min}\) are the maximum and minimum sizes of individuals in each size class. The total annual production is then calculated as the summation of the \(P_i\). Recent work by Benke (1979; and in press) suggests that these production values must be corrected for the actual cohort production interval \((CPI)\) and should therefore be multiplied by \(365/CPI\).

Before deciding to use this simplified method, the production biologist should consider two points. First, this method is no more than a simplification of the increment summation method. It might appear different because, as described in the literature, mortality increment, not growth increment, is summed. However, in Section 2 it was shown that the methods of increment and mortality summation are fundamentally identical (see also Gillespie & Benke 1976). Thus, the average cohort method is subject to the limitations of the increment summation method which, when there is mortality within a size class, gives the correct answer only when the individual growth curve within that size class is linear. It should be noted that this conclusion, which is derived from a consideration of the assumptions of the two mathematical models, and
not from numerical examples, is inconsistent with the conclusion of Benke & Waide (1977; p. 63). The second point to note is that this method substitutes an assumption about $D_i$ for the measurement of $D_i$. Where cohorts cannot be identified, it would be best to use the techniques outlined in Sections 4.3.1 and 4.3.2. See Benke (in press) for a more optimistic treatment.

5.2 The use of production to biomass ratios ($P/B$)

One simplification that has attracted some attention (e.g. Winberg 1971; Gak et al. 1972; Eckblad 1973; Johnson 1974; Kajak & Dusoge 1975; Mikulski et al. 1975; Waters 1977; Hamill et al. 1979; Makarewicz & Likens 1979; Banse & Mosher 1980; Benke & Wallace 1980; Nauwerck et al. 1980; Short & Ward 1980), is the use of production to biomass ratios ($P/B$). The expectation has been that species with similar physiology would have similar $P/B$ ratios. If this were the case, given a knowledge of the production and biomass of one species ($P_1$ and $B_1$), and a knowledge of only the biomass of a second, similar species ($B_2$), we could calculate the production of the second species ($P_2$):

$$P_2 = B_2 P_1 / B_1$$  \hfill (2.25)

Used in this manner, $P/B$ coefficients are anticipated as being a great labour saving device (Winberg 1971), and compilations of measured $P/B$ ratios have been made (Waters 1977) in the hope that empirical rules relating $P/B$ to lifespan or taxonomic group can be derived. Of more interest here is the theoretical work of Waters (1969) and Allen (1971) on the factors affecting $P/B$.

Allen's approach is more useful for the non-mathematical ecologist or for populations whose growth and mortality cannot be expressed in reasonably simple equations. He used families of Allen curves to investigate cohort $P/B$ and produced several useful conclusions:

1. The growth curve (e.g. linear, exponential, or logarithmic) and mortality curve are not very important in affecting $P/B$.
2. $P/B$ increases with increasing ratio of final weight to birth weight. However, this ratio has little effect above a final weight to birth weight ratio of 50, and since most invertebrates have a ratio > 50, this variable is unlikely to have much effect in real populations.
3. The most influential variable is the amount of mortality experienced by a population. The higher the mortality, the higher the $P/B$ ratio.

Allen's conclusions summarized above refer to cohort production; it is generally desirable to perform a simple conversion to annual $P/B$. When individuals are present throughout the year, annual $P/B$ equals cohort $P/B$ regardless of lifespan (Allen 1971) or the number of cohorts maturing in one
year. Since this point was not perceived by Waters (1969, 1977), I will give the simple rules for converting from cohort P/B to annual P/B.

(1) For populations with individuals present all year around, cohort P/B equals annual P/B regardless of voltinism of the population.

(2) For populations with individuals present for only part of the year, cohort P/B can be converted to annual P/B by dividing the former by the fraction of the year in which animals are present.

The reason for this second rule is that production has the dimensions mass/unit area and is unchanged by time span, but mean biomass has dimensions mass/time, thus being averaged over the entire year rather than the time occupied by the population. The result is that the mean annual biomass is reduced.

Allen's (1971) analysis is mathematical, rigorous, and very useful for the production biologist because he provides a table of functions for production, biomass integral, and P/B for populations with a large range of growth and mortality functions. The fundamental problem is the same as that in the analysis of Waters (1969). That is, in order to know what function to use to calculate P/B we must know either the form of the undivided growth curve, or the mortality curve, or both. Allen's conclusion aptly sums up the value of P/B ratios. He says (p. 1576) that 'It is evident, therefore, that to obtain an estimate of the production-biomass ratio for use in estimating production, it is necessary to have as much information as possible regarding the nature of both growth and mortality curves.' But if we need to know the nature of growth and mortality curves in order to use P/B ratios accurately, the P/B ratio method has contributed nothing, since the shape of the growth and mortality curves gives the information required by the other, more rigorous methods of calculation. It was in hope of avoiding the trouble of gathering this information that we turned to the P/B method in the first place.

On the other hand, if we could learn to make accurate predictions of production to biomass ratios (\(P/B\)), then at some point in the future they may save us some effort. A variety of recent research shows that P/B varies significantly as a function of temperature (Schindler 1972, Janicki & DeCosta 1977, Adcock 1979, Nauwerck et al. 1980), body-size (Janicki & DeCosta 1977, Nauwerck et al. 1980), biomass, and food availability (Nauwerck et al. 1980). Other possible variables are considered in Chapter 1. Depending upon the accuracy of these empirical relationships, the production of a population (k) might one day be calculated:

\[
P_k = B_k(P/B) \tag{2.26}
\]

or, because ratios are difficult to handle statistically (see Chapter 8), \(P_k\) may simply be predicted as a non-linear function of biomass and other variables.
6 Concluding Remarks

Simplifications such as the size-frequency technique or the use of production to biomass ratios do not yield 'something for nothing'. They merely substitute assumptions for reliable estimates. In fact, methods such as these are defended (Benke & Waide 1977) on the grounds that they were not intended to give more than rough approximations. The literature yields ample demonstration that this caution is not shared universally.

This might be the time to ask why we want rough approximations. I think the answer is that rough approximations are only useful when the data gatherer is not intending to use the data gathered. They may be gathered because scientific fashion tells us that they might be of interest one day. They are certainly not gathered because the author has undertaken his research to test a specific hypothesis. Because this chapter is written on the assumption that its readers will have a specific purpose in mind before setting out to measure production, I do not recommend the use of 'simplified' methods to replace the effort and ingenuity necessary to gather good population statistics.

7 A Real Example Analyzed by Methods Applicable to Populations with Recognizable Cohorts

Good examples of production calculations for populations with recognizable cohorts are quite common. I (JAD) have chosen to use the data of A.C. Benke (1976) for this example, because they are presented in uncommonly clear manner. Benke (1976) collected dragonfly larvae from an abandoned farm pond (area = 1 ha); mean depth = 1.4 m) near Aiken, South Carolina. Eight replicate Ekman grab samples were taken at less than 1 m depth on each sampling date. Sampling dates were 2–4 weeks apart during warm months, and 1–2 months apart during cold months, and samples were taken over three years. Although Benke presents yearly analyses of data on the production of Ladona deplanata, Celithemis fasciata, and Epitheca spp., only the data on Epitheca during 1970 will be analyzed here.

7.1 Identification of cohorts

Eptiheca was apparently univoltine during each of the years investigated. This can be seen most easily from a plot of mean instar number against time for one of the years (1970) (Fig. 2.8). The continuous decline in instar number (final instar = 0) with time shows that only one cohort was produced. If a second cohort had been produced, Fig. 2.8 would show an increase in instar number. If the situation were less clear-cut, the technique discussed in Section 3 could be used to identify each of the cohorts.
7.2 Required data

Because cohorts can be identified, the data requirements are very simple. We need only collect reliable estimates of mean population density ($\bar{N}_i$) and mean body mass ($\bar{m}_i$) at $i$ points during the year. In the case of *Epitheca* spp., standard errors (see Chapter 8) of population estimates probably ranged between 20% and 50% of mean population density (Downing 1979). We mention this to underscore the necessity of good sampling design; Benke took four times the number of replicate samples that is the median for benthos researchers. Mean body mass data were determined through the use of a length-to-weight regression prepared from freeze dried specimens. There is no reason that $\bar{m}_i$ could not be determined directly by weighing a random sample of *Epitheca* larvae on each date. This would be a more direct technique and would avoid error propagation (see Chapter 7) and possible bias in log:log regressions (Baskerville 1972). The data are reproduced as Columns (1) and (2) in Table 2.4.

7.3 Calculation of production

As explained in Section 2, the calculation of the production of a cohort is only done by calculating the area under a plot of population density against mean weight of individuals. All of the 'different' techniques are simply different...
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Table 2.4 Calculation of the secondary production of Epitheca spp. by the method of growth increment summation. Observations are in Columns 1 & 2 and are estimates of population density ($N_k; m^{-2}$) and mean dry weight (mg) of individual animals ($m_k$). Data are taken from Benke (1976). Calculations use arithmetic means, and calculations using logarithmic means (Riggs 1963) in Columns 3 & 5 are in parentheses. The calculations assume that the population density declines to zero at some point after 28 March and that $m_k$ does not exceed 27.67 mg. Figures in brackets are assumed values.

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<th>(2) $m_k, mg$</th>
<th>(3) $N_k - 11.k$</th>
<th>(4) $m_k - m_{k-1}$</th>
<th>(5) $P_{k-1.k}$</th>
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<td>120-8</td>
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<td>121-2</td>
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<td>53-8</td>
<td>11-989</td>
<td>48-4</td>
<td>7-002</td>
<td>338-9</td>
</tr>
<tr>
<td>25 Oct.</td>
<td>43-0</td>
<td>18-991</td>
<td>51-1</td>
<td>5-841</td>
<td>298-2</td>
</tr>
<tr>
<td>22 Nov.</td>
<td>59-1</td>
<td>24-832</td>
<td>51-1</td>
<td>8-877</td>
<td>44-8</td>
</tr>
<tr>
<td>24 Jan.</td>
<td>43-0</td>
<td>25-709</td>
<td>29-6</td>
<td>1-961</td>
<td>57-9</td>
</tr>
<tr>
<td>28 March</td>
<td>16-1</td>
<td>27-670</td>
<td>8-1</td>
<td>(undef.)</td>
<td>[0]</td>
</tr>
</tbody>
</table>

Total production 1927-6 (1904-0)

means of obtaining this integral. Here we will use only one technique, that of 'growth increment summation', because it is the simplest, both conceptually and mathematically. The equation for calculating the cohort production ($P$) using this technique is:

$$P = \bar{N}_{1,2}(\bar{m}_2 - \bar{m}_1) + \bar{N}_{2,3}(\bar{m}_3 - \bar{m}_2) + \cdots + \bar{N}_{(k-1),k}(\bar{m}_k - \bar{m}_{k-1})$$

(2.27)

where $\bar{N}_{1,2}$ is the average population density over the interval between sampling date 1 and sampling date 2, $\bar{m}_1$ is the average mass of an individual on sampling date 1, and $k$ is the number of sampling dates included in the time period for which production is being calculated. Quite simply, one determines the average number of organisms living during each time period ($\bar{N}_{(k-1),k}$), and then calculates the average change in individual mass during that time period ($\bar{m}_k - \bar{m}_{k-1}$). The product of these two values is the production during each time period. The summation of these throughout a year or the life of a cohort thus yields the annual or cohort production. These computations are carried out in Table 2.4.
7.4 One assumption and its consequences

Both the growth increment summation and mortality summation techniques assume that the relationship between $N$ and $m$ is linear: the data plotted for Epithecra (Fig. 2.9) show that this assumption is not always valid. Where the population density is decreasing at an exponential rate, the logarithmic mean (Riggs 1963; and equation 2.15) would be a better measure of the average population density between $k - 1$ and $k$ than the arithmetic mean. Calculations of the production of Epithecra spp. has also been performed using logarithmic means of population densities and the data are shown in Table 2.4. This does not make a large difference in this calculation (about 1\%) because sampling dates are closely spaced and curvilinearity in Fig. 2.9 is not extreme.

![Epithecra spp.](image)

**Fig. 2.9** Allen-type curve for Epithecra spp. in Dick's Pond (1970 year class). From Benke (1976).

8 A Real Example Analyzed by Methods Applicable to Populations in a Steady State

Good examples of aquatic invertebrate populations in a steady state are rare because birth, death and growth rates of poikilotherms all vary seasonally in response to changing water temperature and other seasonal variables such as food supply. Not surprisingly, the best example we have is a population of Thermocyclops hyalinus in Lake George, a shallow, equatorial African lake with almost constant temperature and primary productivity all year around (Burgis 1970, 1971, 1974). I will use the raw data from these publications and recalculate production correctly. To do this, I will have to make a number of simplifying assumptions or approximations. Since I believe that this is the most difficult part of the analysis, I will emphasize it, and minimize the importance of the final calculation of production.
8.1 Required data

8.1.1 Numbers in each size class and size class duration

Figure 2.10 shows the population of each size class through one year. There are no seasonal trends that suggest cohorts could be identified if all instars had been enumerated separately. This is an obvious example of a population that can be treated as if it were in steady state. Furthermore, there is no reason for analyzing the data in intervals shorter than one year because there are no obvious seasonal trends in numbers. Populations in size classes will be estimated, therefore, as the annual mean population in the following calculations. Also, because the water temperature varies within a range of 1-3 °C throughout the year, there is no basis for suspecting that development rate will vary and we can use a single value for duration of each size class that applies at the mean annual temperature of 26.4 °C. In a system with a significant temperature cycle, it would be necessary to divide the year's data into periods within which temperature is relatively constant even if the numbers of the various size classes remained constant. The length of these periods would be determined by the rate of change of temperature, the periods being of shorter duration with rapid changes of temperature.

8.1.2 Duration of size classes

The second piece of information we need is the average time taken by an animal to grow from the minimum to the maximum size in each size class.
Since Burgis could not infer growth rate from field data, she measured development times of eggs, nauplii and copepodites at various temperatures in the laboratory, and interpolated to obtain the rate at 26.4°C. This is the most unsatisfactory aspect of the analysis of steady-state populations because we have no data to suggest that the development rate of the feeding stages in the natural environment is controlled entirely by temperature. We are, therefore, unsure whether laboratory growth experiments have duplicated the natural food supply. The findings of a number of workers (e.g. Körinek 1966; Węglenśka 1971; Ivanova, in Winberg 1971) have indicated that we could obtain more natural growth rates of zooplankton and benthos by raising animals in cages suspended in the lake water or placed in sediments. If these methods give better estimates of natural growth rates they should be used, despite their added difficulty, because growth rate is as important as N or m in calculation of production and is the measurement most susceptible to error.

### 8.1.3 Weight increment within each size class

As is frequently true in studies of secondary production, the information on weight that we need is not provided by Burgis’ raw data. To extract the data we need, we must make a series of approximations and assumptions.

1. **Egg weight.** Since eggs were not weighed directly we must infer their weight from the difference between the weight of females with eggs (1.61 μg), females without eggs (1.19 μg), and the average clutch size (8). This gives an average egg weight of 0.05 μg.

2. **Initial and final weight of nauplii.** Since no nauplii were weighed, we must derive these figures as best we can. The initial weight of the first nauplius (N1) can be approximated from the egg weight. We will expect it to be less than the egg weight owing to losses by respiration and to the inclusion of egg membranes and egg sac in the egg weight. The data of Rigler & Cooley (1974) suggest that it would be reasonable to assign N1 an initial weight of 20%, less than the average egg weight, or 0.04 μg. To estimate the maximum weight of the sixth nauplius we can extrapolate the regression of logarithm of weight on instar (Fig. 2.11) to obtain the geometric mean between the mean weight of Cl and that of N6. As shown in Fig. 2.11 this is not likely to be the exact value of maximum nauplius weight, but will be a close approximation of it.

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1. Burgis uses a weight of 0.02 μg obtained from measuring egg volume and consequently it is impossible to know what the real egg weight is from the data presented. The real weight is irrelevant here since our concern is with method rather than with production of copepods in Lake George. However, the discrepancy re-emphasizes the importance of obtaining data on the necessary population attributes as accurately as possible.
Fig. 2.11 Relationship of body mass to developmental stage of *Thermocyclops hyalinus* in Lake George, Uganda. Solid dots are observed mean weights, open dot is the estimate of mean body mass between the sixth naupliar and first copepodite stages. The open square indicates the mean body mass of adult males. The broken line indicates expected trends. Data are from Burgis (1970, 1971).

(3) Initial and final weight of copepodites. The value obtained (0.16 μg) can also be used as the minimum weight of C1. Of course, before setting $m_{\text{max}}$ of N6 equal to $m_{\text{min}}$ of C1 we will have made the conscious decision to ignore the contribution of exuviae to total production. If our data were detailed enough to allow analysis of production by each instar we might have decided to include exuviae in our estimate because exuviae can make up almost 15% of total production by a copepod population (Rigler et al. 1974).

(4) Maximum Weight of C5. This can be estimated in several ways using the data given. We can simply take the geometric mean of the weight of females without eggs and of C5s, or we might take the weight of females without eggs to represent the maximum C5 weight. Our decision will be determined by the assumption which we decide to make about the biology of our animal. I will assume that the only weight gained by adult females is in the developing ovary and that the weight of a sample of eggless females is equal to the basic female weight plus one-half of the weight of a complete clutch of eggs. If we further assume that females
carrying eggs are laying down material in their ovaries for another batch of eggs, their average weight will represent the basic weight of a female plus one and one-half clutches of eggs. Consequently, the difference between the mean weight of females with and without eggs is equal to the weight of the clutch being carried \((1\cdot61 - 1\cdot19 = 0\cdot42\ \mu g)\), and the basic female weight (approximately equal to the maximum weight of C5) is equal to the average weight of females without eggs minus half the weight of a clutch of eggs \((1\cdot19 - 0\cdot42/2 = 0\cdot98\ \mu g)\). The maximum weight of C5 obtained in this way is almost identical to that obtained by taking the geometric mean of the weight of females without eggs and the weight of C5 \((0\cdot95)\).

I have laboured through the justification of my choice of maximum weight for C5 *T. hyalinus* not only to direct attention to the importance of the data we use in our calculation of production, but also to direct attention to another problem with our data set. Males weigh less than half as much as females (Fig. 2.11), but we have no data on the abundance of males. Are the copepodite weights applicable only to calculation of the production of females or to an average of female and male production? Simple inspection of Fig. 2.11 suggests that the copepodites weighed were almost all destined to become females. The above comparison of maximum weight of C5 determined by interpolation and that determined from female weights strengthens this conclusion. Therefore, I will assume that males are rare relative to females and that total copepodite production can be calculated from the regression line in Fig. 2.11. Obviously, this is, at best, a temporary expedient. For a more

Table 2.5 Production of *Thermocyclops hyalinus* in Lake George, Uganda, calculated from the data of Burgis (1970, 1971). The technique of growth increment summation is used here because the population has no identifiable cohorts (see Section 4.3.1). The symbol *m* indicates the weight gain by individuals in each class which is calculated \(m_{max} - m_{min}\). The derivations of all other data are explained in Section 8. All masses are expressed as \(\mu g\) dry weight.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Required data</th>
<th>Derived data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>D</td>
</tr>
<tr>
<td>Eggs</td>
<td>220</td>
<td>1.5</td>
</tr>
<tr>
<td>Nauplii</td>
<td>199</td>
<td>6.0</td>
</tr>
<tr>
<td>Copepodites</td>
<td>327</td>
<td>11.0</td>
</tr>
</tbody>
</table>

Total production, all stages: \(35.1 \mu g \text{ day}^{-1}\)
Annual production: \(12.8 \text{ mg l}^{-1} \text{ year}^{-1}\)
accurate estimate of production we would have to recount enough samples to get a measure of the fraction of males in the adult population.

8.1.4 Actual production calculations

With the approximations and assumptions I have described we can generate the data required to calculate production and complete the calculation (Table 2.5). Note that once we have the necessary data, the calculation is extremely simple. The real problem in this example and in any other study of aquatic secondary production is in generating the required data from the raw data. Anyone about to embark on a production study should concentrate on the required data—the mean number in each size class, the average maximum and minimum weight of individuals in each size class and the duration of each size class—and the best methods of obtaining accurate estimates of them.

9 References

The Calculation of Secondary Productivity


The Calculation of Secondary Productivity


