The Enigma of Daphnia Death Rates
Author(s): E. Prepas and F. H. Rigler
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The enigma of *Daphnia* death rates[1]

E. Prepas[2] *and F. H. Rigler*[3]
Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1

Abstract

Birth rates, rates of population change, and mortality rates were computed for *Daphnia pulex* and *Daphnia rosea* collected at three separate stations in 2.5-ha meromictic Crawford Lake. Birth and death rates for the same species at the three separate stations, or at the same station but living at slightly different mean depths were substantially different. A correction for tow net efficiency for young and adult animals increased birth rate values by 40%.

Mean finite birth rate, *B*, for *Daphnia* in a thermally stratified lake is calculated from the relation

$$B' = \frac{\sum_{s=1}^{n} E_s(1/D_s)}{\sum_{s=1}^{n} N_s},$$

where for each stratum, *s*, *E* is number of eggs, *D* is egg development time, *N* is number of animals, and *n* is number of strata. An assumption of this formulation is that all individuals in the population behave similarly, but at Crawford Lake *D. pulex* behaves like two separate populations for at least part of the year.

High death rates were calculated for *D. rosea* in midsummer. A comparison of observed neonates with expected neonates during this period led to the conclusion that most mortality in the population occurs either in late embryos or at hatching.

Ecologists investigating zooplankton communites are interested in factors controlling the number of individual species and interactions between species. The egg-ratio method has been widely used to provide such information about small planktonic species that carry their eggs; it estimates potential daily increases, actual daily increases, and, by subtraction, death rates of a species over a series of short intervals from data that can be collected in the field. The potential daily increase or birth rate is a function of estimated population egg numbers (E), egg development time (D), and animal numbers (N) at some point in time. The actual rate of increase (or decrease) in the population is calculated from the difference between successive estimates of N on two consecutive sampling dates; calculated values for birth and death rates are then used for further analyses. Variations in estimated potential birth rates are related to changes in environmental variables such as temperature, oxygen, and food supply. Where calculations indicate high mortality, predation is suggested as the cause (e.g. Hall 1964; Wright 1965; Allan 1973; de Bernardi 1974).

The two approaches used to calculate birth and death rates stem from different assumptions about the appropriate mathematical formulations to describe the dynamics of natural populations of zooplankton. The first was developed by Elster (1954; Elster and Schwoerbel 1970). It assumes that changes in a population of cladocerans between two sampling dates can adequately be described by linear equations and therefore requires the calculation of finite statistics only. This approach has many inadequacies (Edmondson 1960; Elster and Schwoerbel 1970; Edmondson 1974). One aspect of the linear approach that has not been adequately discussed in the literature is the selection of the appropriate numbers to use; we will show that

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[2] Supported by a fellowship from the National Research Council of Canada.

[3] Present address: Department of Biology, McGill University, 1205 McGregor Avenue, Montreal, Québec H3A 1B1.

the birth and death rates obtained by Elster's method are highly dependent on the estimate of N used in the calculations.

Edmondson (1960) improved on Elster's method by applying nonlinear, exponential equations to approximate the required population statistics, and subsequently (Edmondson 1968, 1974) discussed the assumptions of his improved version thoroughly. This version requires the calcuation of instantaneous rather than finite statistics. Despite extensive descriptions of the exponential model (e.g. Leslie 1948; Andrewartha and Birch 1954) and the mathematical refinements that have been added to it (Edmondson 1968; Caswell 1972; Paloheimo 1974), the occasional worker (Allan 1973) completely ignores these developments and erroneously uses the finite birth rate (B) instead of the instantaneous daily birth rate (b') in the exponential model. We deal here with only one category of problem relevant to population dynamics: the application of Edmonson's egg-ratio method to field data. We do not deal with the mathematical problems raised by Caswell and Paloheimo, although we consider them important.

Since Edmondson's method was developed for use in isothermal lakes, it must be modified slightly for application to plankton in thermally stratified lakes. This is because an important component of b'— egg development time—is a function of temperature (Hall 1964; Elster and Schwoerbel 1970). Only Hall (1964) has modified Edmondson's method for application to a population living in a stratified lake, and we will demonstrate here that his method introduces errors in b'; we present a more accurate method. We further show that while our method can only be applied to a spatially uniform population, a cladoceran population can comprise two spatially separate populations.

Even the appropriate calculations will not give useful results if the population estimates are inaccurate; in most published accounts, the field data simply do not meet the requirements of the model. Egg numbers must also be estimated accurately and because egg development time is sensitive to temperature, the vertical distribution of the egg population in a stratified lake is extremely important. The importance of measuring these parameters accurately has not been generally recognized. Although population estimates fluctuate wildly from day to day, and birth and death rates are both dependent on those population estimates, only Edmondson (1960) and Rigler et al. (1974) smoothed their population data to eliminate spurious fluctuations in birth and death rates that were due to sampling error.

But even the most extreme smoothing cannot overcome the effects of inadequate and biased sampling. For example, Wright (1965) based his calculations on the contents of a single vertical tow at one end of 40-km-long, stratified Canyon Ferry Reservoir. With such samples, corrections for vertical and horizontal distribution cannot be made but will almost certainly be needed; Elster and Schwoerbel (1970) found horizontal variations in animal numbers of more than a factor of 100 on some days in a lake of similar size. de Bernardi (1974) and de Bernardi and Canali (1975), working on the 54-km-long Lago Maggiore, reported data from only one, then two stations in the lake and apparently pooled all the data collected on each date at each station, ignoring the vertical distribution of eggs. Tappa (1965), working on a lake similar in size and shape to Canyon Ferry Reservoir, also took his samples at one end, but did take duplicate vertical distribution series (one on each side of the boat!). He could thus correct b' for vertical distribution of eggs, but presented no data on vertical egg distribution and did not describe his method of calculating an integrated b'. While recognizing the need to correct for horizontal variation in population numbers, Allan (1973) did not take account of the extreme vertical variation in animal numbers which can occur in a bog lake (Haney 1970), and, like Tappa, omitted data on egg distribution and the method of calculating birth rates. This must be interpreted as a failure to recognize the

Table 1. Morphometric data for Crawford Lake and volumes of strata used to calculate *Daphnia pulex* population. Stratum volume in thousands of cubic meters.

Depth (m)	Stratum volume
0.5–1.5	23.2
1.5–2.5	21.9
2.5–3.5	20.5
3.5–4.5	19.1
4.5–5.5	17.8
5.5–6.5	16.4
6.5–7.5	15.0
7.5–8.5	13.7
8.5–9.5	12.3
9.5–10.5	10.8
10.5–11.5	9.3
11.5–12.5	8.0
12.5–13.5	7.0
13.5–14.5	6.3
14.5–15.5	5.5
15.5–16.5	4.9
16.5–17.5	4.3
17.5–18.5	3.7
18.5–bottom	6.6

importance of good data and appropriate calculations. The best sampling was by Hall (1964), but even here, calculations were based on oblique tows at one and sometimes two locations in the lake, taken from three quantitatively undefined strata with a sampler containing no closing device. Once again, the horizontal and vertical data are inadequate for use in the egg-ratio model.

In most published accounts, the investigators also fail to recognize and correct biases introduced by sampling and preservation; an example is the selectivity of a tow net for certain life stages. Hall (1964) and Wright (1965) used tow nets, which are more efficient at capturing young than adult animals, but made no corresponding adjustments to their data. This indicates a failure to recognize the importance of accurate calibration of sampling equipment. Although several workers used 95% alcohol as preservative (Hall 1964; Clark and Carter 1974) to avoid loss of eggs from the brood pouch, others used Formalin which causes considerable egg loss. The loose eggs should obviously be included in the egg counts, but unfortunately in some cases (Tappa 1965) no indication is given that loose eggs were included in the calculations and in others (Wright 1965; Allan 1973) the preservative is not specified. This can only be interpreted as another failure to recognize the importance of complete data.

The lack of essential data makes it impossible to criticize the results of the foregoing studies. We simply do not know if the statistics generated by the model bear any resemblance to what was actually going on in the lakes studied. We will demonstrate the weakness of using data collected by traditional sampling techniques in the egg-ratio model by showing that trends predicted by samples collected at one station in a lake bear no necessary resemblance to those calculated from data collected at other stations on the same lake. The vertical distribution of eggs in stratified lakes and the selectivity of the sampling device for certain life stages must also be considered before the model can be used to make any predictions about factors controlling population numbers.

Field and laboratory assistance was provided by several people, notably M. Ewert, J. Martin, and A. Nakrossius. W. G. Sprules provided lab facilities and equipment during the first year of the study. The Halton Region Conservation Authority permitted the use of Crawford Lake. J. Cornett reviewed the manuscript.

Materials and methods

Crawford Lake (43°28′N, 79°57′W) is a small (2.5 ha), deep (max 23.5 m) meromictic lake in southern Ontario; it is encircled by trees and limestone ridges. It has one inflow and one outflow stream; both are stagnant most of the year. The lake is continuously anoxic below 14 m. The sheltered nature of the lake minimizes the effect of wind on plankton distribution. Dominant Cladocera were *Daphnia pulex* and *Daphnia rosea*. Morphometric data used to calculate the total population are given in Table 1.

Plankton was collected from May 1975

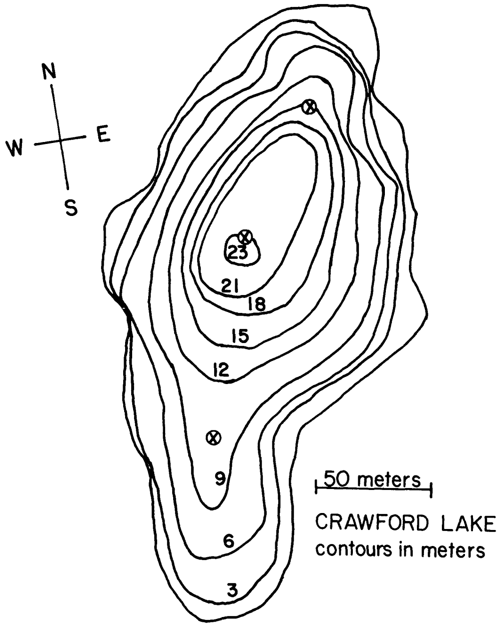

Fig. 1. Contour map of Crawford Lake with three sampling stations indicated.

until June 1976 in a conical 80-μ Nitex tow net, 90 cm long with a 29-cm-diameter aperture. Vertical tows from directly above the bottom to the surface were taken at three fixed stations—north, center, and south—through 15, 22, and 10 m of water (Fig. 1), always by the same person and near midday. The net was towed through the water at a constant speed of 1 $m \cdot s^{-1}$. To reduce the effects of local patchiness three hauls were taken at each station on each sampling date during 1976 and pooled. Ten vertical distribution series were collected at the central station with a 32-liter Schindler-Patalas Plexiglas trap fitted with 73-μ Nitex net: four at 2-m intervals in May and June 1975 and six at 1-m intervals in June and July 1976. Samples were preserved in 4% Formalin and 6% sucrose solution (Haney and Hall 1973) until May 1976, after which the modification of Prepas (1978) was used, to reduce egg loss.

To facilitate counting of *Daphnia* spp., we first skimmed *Chaoborus* and blue-green algae from the surface of the sample. The remaining sample was then poured into a large volume of water in which *Daphnia* and any loose eggs settled rapidly, while the remaining net phytoplankton, rotifers, and copepod nauplii settled slowly. A minimum of 100 young *Daphnia,* 100 adult *Daphnia,* and 100 *Daphnia* eggs were counted, except in the few cases where there were fewer than 100 present. Because 50% of the eggs and embryos were often loose before we began to use chilled preservative, we had to include them in our counts and this required identification of eggs and embryos to species: simple apportioning by number of unreleased eggs was not adequate because a higher percentage of eggs was released by *D. pulex* than by *D. rosea.* Fortunately, eggs of the two species could easily be distinguished: *D. rosea* eggs were ovoid, at least 1.4 times as long as wide; *D. pulex* eggs were more spherical, always with a length:width ratio <1.4. Since embryos were indistinguishable, the number of loose embryos apportioned to each species was based on the percentage of loose eggs for that species in the sample.

Table 2. Tow net efficiency in catching *Daphnia pulex* relative to efficiency of Schindler-Patalas trap at Crawford Lake. Values expressed as percentages.

1976	Young	Adults
23 Jun	82	54
30 Jun	78	58
6 Jul	81	80
13 Jul	56	37
20 Jul	80	56

To convert the raw population data to numbers used in calculations, we first corrected the number of animals per tow for net efficiency. Net efficiency is calculated by comparing the number of animals caught in a vertical distribution series with the number of animals caught in a tow net at the same station, corrected for difference in volume of water filtered by the two devices. The volume of water filtered by the tow net is calculated as a right circular cylinder of radius 14.5 cm and height 16 m. A height of 16 m is chosen because *Daphnia* was not found below 16 m; thus the vertical distribution series went from 1 to 16 m, at 1-m intervals, for the dates when the comparisons were made. If the Schindler-Patalas trap is assumed 100% efficient, an average of 55% of adults and 75% of young were caught in the tow net (Table 2). Then for each station a running average of three was taken to give the number of animals on each date (i.e. for N_{t_2}, the sum of N_{t_1}, N_{t_2}, and N_{t_3} divided by 3). Number of eggs is based on the smoothed number of adults on each date times the actual average number of eggs counted per female. Animal numbers are smoothed, because short term fluctuations are the result of sampling inadequacies and would cause changes in death rate actually due to sampling artifacts. Clark and Carter's (1974) data on *D. rosea* provide a fine example of apparent temporal changes in animal numbers that are obviously artifacts because the largest changes occur when the interval between sampling dates is the shortest. On the other hand, average egg numbers are not smoothed because we know egg numbers can vary dramatically over short periods (Slobodkin 1954). Calculations involving vertical distribution of the animals are based on percentage of animals (young or adult) at each stratum on a particular date times volume of stratum times smoothed N for that date at the central station.

Calculation of population statistics—Elster and Schwoerbel's (1970) linear approach to *Daphnia* population statistics involves calculation of an estimated finite daily birth rate (B), rate of population change (R), and loss rate (L). B is estimated by forming the product of average egg numbers, E, and the inverse of egg development time, $1/D$, for two successive sampling dates, t_1 and t_2, and dividing by the number of animals, N, sampled at time t_1.

$$B = \left(\frac{E_{t_1} + E_{t_2}}{2}\right)\left(\frac{1/D_{t_1} + 1/D_{t_2}}{2}\right)(N_{t_1})^{-1}. \tag{1}$$

R (actual daily per animal change in the population) is estimated by calculating the difference between N in the system at t_1 and t_2, divided by the product of N_{t_1} and the difference between t_2 and t_1.

$$R = \frac{N_{t_2} - N_{t_1}}{N_{t_1}(t_2 - t_1)}. \tag{2}$$

Then from Eq. 1 and 2, estimated L is calculated as

$$L = B - R. \tag{3}$$

Edmondson's (1960) exponential model

$$N_{t_2} = N_{t_1} e^{r'(t_2 - t_1)} \tag{4}$$

uses the symbols b', d', and r' to emphasize that b, d, and r are only crudely estimated in field situations. The estimated instantaneous rate of increase, r', has two components,

$$r' = b' - d', \tag{5}$$

an instantaneous birth rate, b', and death (or loss) rate, d'. Before b' is calculated, a finite daily birth rate, B, where

$$B = \frac{E_{t_1}(1/D_{t_1})}{N_{t_1}}, \tag{6}$$

is calculated for the population. Equation 6 assumes that $d' = 0$, in order to calculate maximum potential B. Then by a fairly simple set of manipulations of Eq. 4–6 (*see* Edmondson 1960), b' can be solved for in terms of B,

$$b' = \ln(1 + B), \tag{7}$$

r' in terms of sampled N at t_1 and t_2,

$$r' = \frac{\ln N_{t_2} - \ln N_{t_1}}{t_2 - t_1}, \tag{8}$$

and d' in terms of the difference between b' and r',

$$d' = b' - r'. \tag{9}$$

Edmondson (1968), Caswell (1972), and Paloheimo (1974) have introduced modifications in the calculation of an estimated birth rate. These changes do not affect the findings reported here.

Hall's (1964) modification of Edmondson's (1960) geometric approach to calculating plankton statistics involves first dividing the lake into three strata. A separate b'_s is calculated for each stratum, as in Eq. 7, and then a weighted estimate of b, b'' is calculated for the entire lake,

$$b'' = \frac{\sum_{s=1}^{3} N_s b'_s}{\sum_{s=1}^{3} N_s}, \tag{10}$$

where N_s is the number of animals estimated to be in stratum s at t_1.

Hall's formulation has two obvious problems. First, a weighted B should be calculated for the entire lake before calculation of b'. To illustrate the mathematical error in Hall's formula, we will show what the formula intends to calculate and what it actually does calculate. The geometric model predicts that the potential number of animals at t_2, $N^*_{t_2}$, is

$$N^*_{t_2} = N_{t_1} e^{b'} \tag{11}$$

when $d' = 0$ and $t_2 - t_1 = 1$ day are substituted into Eq. 4 and 5. Substituting from Eq. 7, $e^{b'} = B + 1$, into Eq. 11 allows for a linear solution of $N^*_{t_2}$, in terms of N_{t_1} and B as follows

$$N^*_{t_2} = N_{t_1}(B + 1). \tag{12}$$

Hall inadvertently calculated $N^*_{t_2}$ by the relation

$$N^*_{t_2} = N_{t_1}(b + 1). \tag{13}$$

For example, his method (Eq. 10) predicts that the integrated birth rate for the data in Table 3 is

$$b'' = \frac{100(0.02) + 100(0.69)}{200} = 0.36.$$

The geometric model can be used to calculate the number of animals that will be in each stratum, after 1 day, assuming no deaths. Once the number of animals present at t_1 and t_2 is known, the correct b,

$$b' = \ln\left(\frac{302}{200}\right) = 0.41,$$

is calculated by solving Eq. 11 for b'. Hall's formula is obviously wrong. In this example, and in general, his formula underestimates the integrated birth rate except when a population birth rate is very small and thus $b \simeq B$.

Table 3. Hypothetical example used to illustrate number of animals calculated to be in a two-strata lake using geometric model (Eq. 12) and Hall's model (Eq. 13).

Stratum	N_{t_1}	B	b	$N^*_{t_2}$ Geometric	 Hall's
1	100	0.02	0.02	102	102
2	100	1.00	0.693	200	169
Total	200			302	271

The second problem with Hall's formula is that the egg and animal numbers used in all the calculations should be weighted for the volume of water in each stratum. In some, but not all, instances for Hall's data, the two errors essentially cancel each other out because of the preference of the animals in this case for the upper strata of the lake; but this cannot be used as a justification for retaining an erroneous computation.

Implicit in the calculation of an integrated birth rate is the assumption that all egg-bearing females wander vertically throughout the entire range occupied by a population and that the fraction of time pent by an individual in each stratum is shown by the fraction of the population in that stratum. If the animals remain in their separate strata, an integrated birth rate cannot theoretically be calculated unless the individual birth rates are equal. This problem can be illustrated by assuming that the animals in our example stay in their separate strata over a 7-day period, where t_1 is day 1 and t_2 is day 8. The equation

$$N_{t_2} = N_{t_1} e^{b'(t_2 - t_1)} \tag{14}$$

predicts that the number of animals in strata 1 and 2 on day 8 would be 115 and 12,787. The birth rate calculated for this 7-day period is

$$b'_7 = [\ln(12{,}902 \div 200)]/7 = 0.60,$$

which is 46% higher than 0.41—the b'—

calculated earlier using the same data, but assuming $dt = 1$ day. Thus the assumption that a constant development time can be used for the entire population is basic to the calculation of an integrated birth rate.

To estimate b for plankton in a thermally stratified lake, we calculate a weighted B, B', for the entire lake. Thus

$$B' = \frac{\sum_{s=1}^{n} \{[N_s \cdot E_s(1/D_s)]/(N_s)\}}{\sum_{s=1}^{n} N_s},$$

which simplifies to

$$B' = \frac{\sum_{s=1}^{n} E_s(1/D_s)}{\sum_{s=1}^{n} N_s}, \tag{15}$$

where n is the number of strata and D_s, E_s, and N_s are the estimated egg development time, and egg and animal numbers in each stratum. In a situation where adult and juvenile instars of the population occupy different parts of the water column, number of adults per stratum should replace N_s as weight. In small lakes the horizontal strata will have quite different volumes. Hence when calculating an integrated birth rate, if we assume that the population has a uniform or random distribution horizontally and is not merely clustered in a small vertical column at the deepest part of the lake, N_s and E_s should be weighted for the volume of stratum, s, before B' is calculated. Weighting each representative sample for volume of water in the corresponding stratum can have a considerable effect on the calculated population statistics. In our example (Table 3), if the volume of stratum 1 were five times that of stratum 2, birth rate would be reduced 59% (to 0.17 from 0.41). Once B' is calculated, estimates for b, r, and d can be calculated by Eq. 7–9, with the additional step of weighting N for the volume of water in each stratum when calculating r'. This series of equations will produce reasonable statistics assuming that Edmondson's mathematical formulations can provide adequate estimates of field population dynamics and that appropriate estimates of E and N can be gathered from field data for cladocerans. It can be verified from the example given in Table 3 that the integrated birth rate calculated by our model is identical to the correct birth rate, 0.41.

The best approach to calculating birth rates in a stratified lake is the integrated method. However, in situations where an integrated birth rate cannot be calculated for each sampling date, mean temperature experienced by egg-bearing females can be estimated and used to calculate birth rates by a simpler method, Eq. 6, 7.

When the population occupies a fairly limited portion of the water column, mean depth of adult females may suffice for calculation of birth rates. However, when egg-bearing females are distributed throughout a portion of the water column where there is a temperature gradient, the nonlinear relationship between egg development time and temperature, as well as necessary volume corrections, must be considered; therefore the depth used to calculate egg development time should be approximated from dates when integrated birth rates can be calculated. Both the simplified and integrated methods are based on the assumption that all egg-bearing females can be treated as having the same temperature experience and hence no new assumptions are introduced by estimating mean depth to calculate egg development time.

Egg development time—The field data give us all the necessary information except egg development time to calculate population statistics from Edmondson's model. However, egg development times reported in the literature for different species of *Daphnia* have been almost identical. Clark and Carter (1974) found development times for *D. rosea* to be indistinguishable from those of Hall (1964) for *Daphnia galeata mendotae*, as are Elster and Schwoerbel's (1970) experimentally derived egg development times for *Daphnia longispina*. Laboratory work on *D. pulex* and similar sized *Daphnia* spp. (Fox et al. 1949; LeSeur 1960) indi-

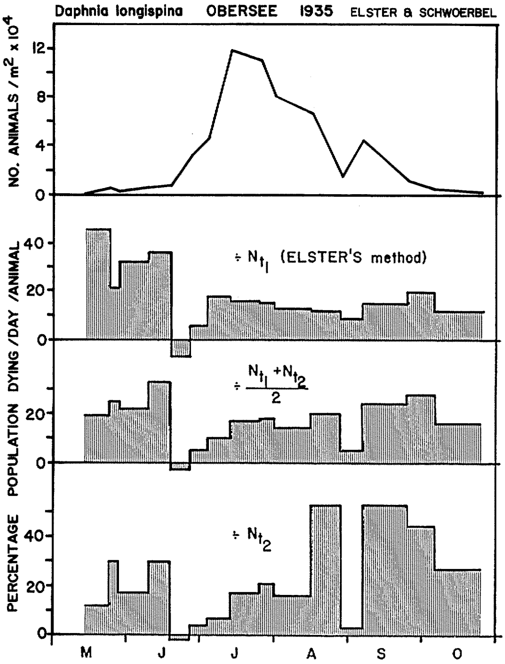

Fig. 2. *Daphnia longispina* in Obersee in 1935. Top panel shows population numbers over year. Following panels show percentage of population lost per day per animal using three different estimates of N in denominator.

cated that egg development time for *D. pulex* is also very close to that for *D. longispina*. The data of Elster and Schwoerbel are used here for calculating egg development time for *D. pulex* and *D. rosea*.

Results

The linear approach to calculating population statistics—Elster and Schwoerbel's (1970) calculations are based on the population of *D. longispina* in upper Bodensee in 1935 (Fig. 2). Their results indicate that the birth and loss rates in this population were highest in spring. (As birth and death rate trends are virtually identical with the Bodensee *Daphnia,* only death rate is shown in Fig. 2.) Birth rate is usually defined as the number of neonates from t_1 to t_2 divided by N_{t_1}. Eggs carried at t_1 can reasonably be used to estimate the number of newborn between t_1 and t_2. However, Elster and Schwoerbel use the average number of eggs sampled on t_1 and t_2 to estimate the number of neonates between t_1 and t_2, whereas their method actually estimates the number of newborn between t_1 and the next sampling date after t_2. The appropriate value of N to use when calculating B (and L) based on average egg numbers on two consecutive sampling dates could be N_{t_1}, N_{t_2}, or some average of the two. For the Bodensee *Daphnia,* the point in time at which N in the denominator of Eq. 1 and 3 is chosen is critical in determining the trends these calculations will show because of overall population trends (Fig. 2) and the time lapse between sampling dates (average 11 days). For example, if the average N on the two sampling dates is used instead of N_{t_1}, the overall trend for B (and L) is

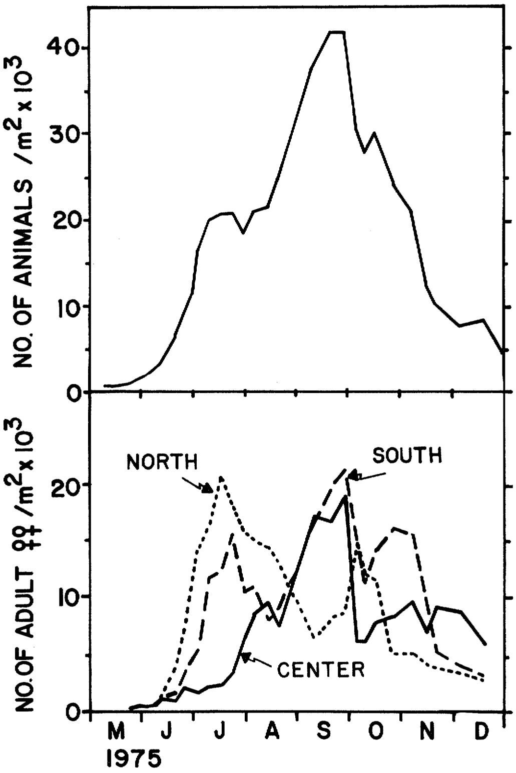

Fig. 3. *Daphnia rosea* population, Crawford Lake 1975. Upper panel: total population over time. Lower panel: number of adult ♀♀ sampled over time at three separate stations.

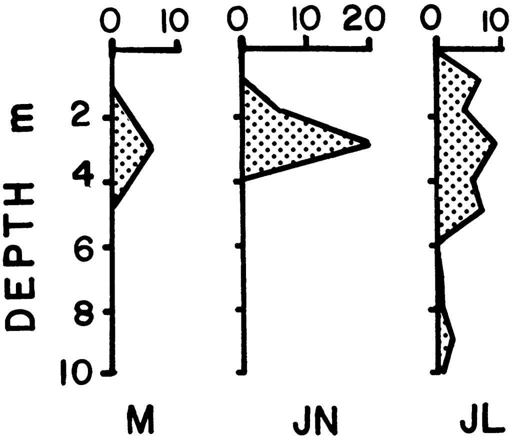

Fig. 4. Vertical distribution of adult female *Daphnia rosea*, Crawford Lake 1975 and 1976. Each series shows combined distribution of all animals sampled in a month.

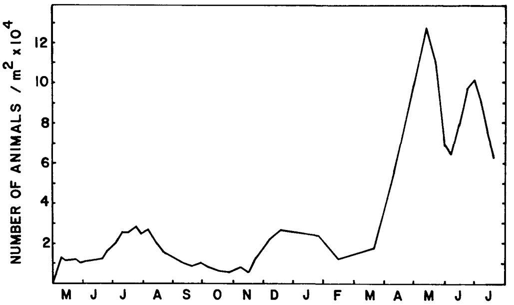

Fig. 5. *Daphnia pulex* at Crawford Lake 1975–1976.

similar for the entire 6-month period. If N_{t_2} is used, Elster and Schwoerbel's findings are reversed, with the highest values of B and L in fall (Fig. 2). The last two estimates of N are just as valid as that used by Elster and Schwoerbel, but give entirely different results. Thus the meaning of the numbers generated is not at all clear. Elster and Schwoerbel have introduced several problems with their method of averaging egg numbers. If the purpose of the averaging was to remove sampling variability, then smoothing N might be more appropriate. Figure 2 shows that all these results would be smoother if the N values were smoothed.

Results from Crawford Lake—We will first present the data relevant to the calculation of population statistics and will then show the results of the calculations.

The population that we call *D. rosea* conforms closely to Brooks' (1957) description of this species, although the females were slightly helmeted from July to October. Another minor taxonomic problem is that although neonates of our *D. rosea* never had a toothed crest on the anterodorsal margin of the head capsule, the young of our *D. pulex* did occasionally have such a crest.

The abundance of *D. rosea* during our study is shown in Fig. 3. The population begins to increase in May when resting eggs hatched and continued to increase to a maximum in September after which it decreased toward a winter minimum. In October, males and ephippia appeared and by January no animals were found in the water. *Daphnia rosea* appeared again the next year, but was too scarce to be studied.

Two features of the temporal and horizontal distribution are relevant to the calculation of population statistics. First, the animals showed a strong tendency to aggregate at the ends of the lake during early summer. Although stations were <100 m apart, the population density of adult ♀♀ at the end stations was often 5 to 10 times as great as at the central station. Although horizontal aggregations of *Daphnia* spp. have frequently been reported (Siebeck 1960; Ruttner 1964; Patalas 1969; Elster and Schwoerbel 1970) such large, consistent differences between stations in the pelagic zone of a small lake were unexpected. Nonhomogeneous distributions such as this will not affect calculations of population statistics provided that all life stages behave similarly, the population does not suddenly shift from one sampling site to another, and other factors influencing population statistics exert the same effect at each station. However in Crawford Lake these conditions were not met. The population density became similar at all three stations in August, but during fall the population shifted around somewhat, although there was a definite tendency

Table 4. *Daphnia rosea* data for three stations, Crawford Lake 1975. Units are numbers of animals per 10 cm^2 of lake surface.

	$\frac{1}{D}$	Young			Adult ♀♀			Eggs/Adult ♀		
		N	C	S	N	C	S	N	C	S
29 May	0.19	0.24	2.36	0.86	0.17	0.39	0.24	2.1	9.6	2.7
4 Jun	0.21	0.61	2.79	1.74	0.32	0.41	0.42	1.2	8.0	2.3
11 Jun	0.23	2.12	3.28	1.71	0.98	1.14	0.61	2.9	3.8	2.2
20 Jun	0.28	6.22	2.10	4.25	3.89	0.89	1.63	3.5	3.2	4.6
25 Jun	0.31	12.08	3.07	6.36	7.33	1.97	3.63	2.7	2.0	6.6
3 Jul	0.36	17.02	3.15	7.86	14.14	1.60	5.46	1.0	1.1	2.4
9 Jul	0.39	17.02	3.62	8.72	16.37	2.06	11.64	1.1	1.6	1.0
16 Jul	0.46	12.63	4.84	9.17	20.74	2.26	12.26	2.4	1.6	1.2
23 Jul	0.46	8.27	5.34	11.38	18.27	3.38	15.75	1.6	2.7	2.3
31 Jul	0.46	5.89	8.18	8.67	15.85	6.37	10.43	2.2	2.4	1.0
6 Aug	0.49	10.99	9.93	7.36	15.11	8.51	10.98	1.7	1.9	1.5
14 Aug	0.49	14.20	10.32	7.98	14.41	9.49	8.11	1.5	1.1	0.91
20 Aug	0.49	17.14	14.44	13.29	13.11	7.55	9.07	0.69	1.1	1.2
10 Sep	0.33	15.15	25.65	31.88	6.49	17.17	16.74	0.25	1.6	1.4
20 Sep	0.28	17.05	31.17	32.99	8.19	16.73	19.47	0.45	1.4	1.0
28 Sep	0.26	18.82	27.48	30.66	8.66	18.79	21.26	1.5	0.90	0.80
5 Oct	0.23	27.71	13.85	13.87	14.79	6.10	14.94	0.46	1.1	0.53
Avg		11.95	10.09	11.69	10.52	6.16	9.57	1.6	2.6	2.0
(excl. 29 May + 4 Jun)								(1.6)	(1.8)	(1.9)

for the animals to aggregate at the south end of the lake (Fig. 3). Furthermore, between-station differences in the average number of eggs per female were usually in the range of 100% (Table 4) but showed no consistent trend with time, and the overall average eggs per female at the three stations (for the dates in Table 4 when population numbers sampled were sufficiently large to be considered reliable, i.e. excluding 29 May and 4 June) were remarkably similar.

Daphnia rosea in Crawford Lake aggregates in spring and early summer, fairly close to the surface (Fig. 4). The mean depth of adult females in May was 3 m, in June 2.8 m, and in July 3.3 m. Consequently, for calculation of egg development times, we have used the temperature recorded to the nearest whole degree at a depth of 3 m on the date the eggs were sampled.

The population size of *D. pulex* throughout 1975–1976 is shown in Fig. 5. This species was present all year, although ephippia were produced in early summer and fall. Ephippial females were abundant only at the north and south stations in June and July of 1975. *Daphnia pulex* showed no consistent pattern of abundance; although it had a summer maximum in both years, that in 1976 was earlier and more than four times as large as that in 1975.

The horizontal distribution of *D. pulex* was much more uniform than that of *D. rosea.* The young were found in almost equal numbers at the three stations throughout the season, and although the adults showed a consistent decrease in numbers from north to south (except for a brief period at the end of May), the average difference was only 65%. The average number of eggs per female was also usually highest at the north end of the lake (Table 5). For calculation of per capita population statistics at individual stations, important artifacts will be introduced by the varying ratio of adult:young from one station to the next (2.2 at the north end to 3.8 at the south), and between-station variation in average number of eggs per female (3.3 at the north end to 2.2 at the south).

An observation crucial to the calculation of population statistics for *D. pulex* was made in June 1976: the animals were distributed throughout the water column from 1–2 m below the surface to the upper few meters of the anaerobic chemo-

Table 5. *Daphnia pulex* data for three stations, Crawford Lake 1976. Units are numbers of animals per $1\ cm^2$ of lake surface.

Date	$\frac{1}{D}$	Young			Adult ♀♀			Avg. Eggs/Adult ♀		
		N	C	S	N	C	S	N	C	S
10 Apr	0.07	3.50	4.17	5.51	1.59	1.16	0.67	2.7	2.8	2.3
30 Apr	0.09	7.85	9.85	7.64	2.07	1.50	0.84	14.1	9.9	7.4
12 May	0.12	10.7	12.0	10.1	2.39	1.66	1.21	5.6	2.9	2.6
21 May	0.14	9.89	9.85	8.52	1.93	1.54	1.45	1.9	0.9	1.1
31 May	0.16	5.63	5.47	5.55	1.41	1.43	1.61	2.0	0.9	3.0
7 Jun	0.19	4.34	4.57	4.48	2.22	1.81	2.02	1.5	1.3	1.8
15 Jun	0.16	5.38	5.91	4.97	3.22	2.24	2.12	4.3	1.7	2.3
23 Jun	0.14	6.70	7.32	6.60	3.87	2.65	2.02	4.0	3.0	2.1
30 Jun	0.16	6.74	8.13	7.52	3.70	2.46	1.73	1.2	2.7	1.7
6 Jul	0.19	6.10	7.06	6.40	3.81	2.33	1.87	1.1	0.8	0.8
13 Jul	0.19	4.22	5.34	5.03	3.56	2.10	2.24	0.8	0.7	0.7
20 Jul	0.19	3.52	4.12	3.78	3.30	2.04	2.45	0.5	0.7	0.5
Avg		6.21	6.98	6.34	2.76	1.91	1.69	3.31	2.36	2.19

cline. This distribution meant that developing eggs experienced temperatures as high as 24°C and as low as 5°C. The animals living at 12 m and deeper, where the oxygen concentration was 1 $mg \cdot liter^{-1}$ or less, were bright red, due to hemoglobin. The development and loss of hemoglobin is a slow process (Fox 1948). Red *D. pulex* from the lake, placed in well aerated water in the laboraoty retained some color for over a week. This suggested that the *D. pulex* might comprise two spatially separate populations.

To test this hypothesis, we counted freshly collected animals before preservation and separated them into those that were pale brown and those that were bright red. The results showed a dramatic vertical separation of the two groups (Fig. 6). Above 8 m there were no red animals. Between 11 and 12 m the red animals suddenly increased from 0–5% to 100% of the total catch. In July the red animals moved up slightly in the water column, so that by 20 July the red animals increased from 0–100% between 9 and 10 m. The night series taken on 20 July 1976 showed that the separation was maintained at night because the red animals failed to migrate upward. The mean depth of both populations, calculated by assigning the animals at 9 m and above to the brown population and 10 m and below to the red population, showed that the brown animals as a group migrated upward slightly at night (from 5.5 to 4.7 m) and the red animals remained at essentially the same mean depth (11.7 m in the daytime and 11.6 m at night). Yet another indication of the separation of these populations is shown on 23 and 30 June when the fecundity of the red animals was 2–3 times as high as that of the brown. From all of these observations we conclude that the *D. pulex* in Crawford Lake comprised two spatially separate populations inhabiting strata of different temperatures. The consequences of this type of behavior for population statistics can also be great and will be considered later.

Table 6. Percentage increase in b', d', and r' when *Daphnia pulex* numbers are corrected for efficiency of tow net in capturing young and adult animals.

1976	r'	% Increase in		
		b'	d'	r'
12 May	−0.02	33	20	0
21 May	−0.05	100	17	0
31 May	−0.01	50	33	0
7 Jun	0.03	40	100	0
15 Jun	0.02	17	25	0
23 Jun	0.01	25	28	0
30 Jun	−0.02	25	20	0
6 Jul	−0.03	33	17	0
13 Jul	−0.03	33	17	0

Calculated population statistics—To demonstrate the importance of correcting

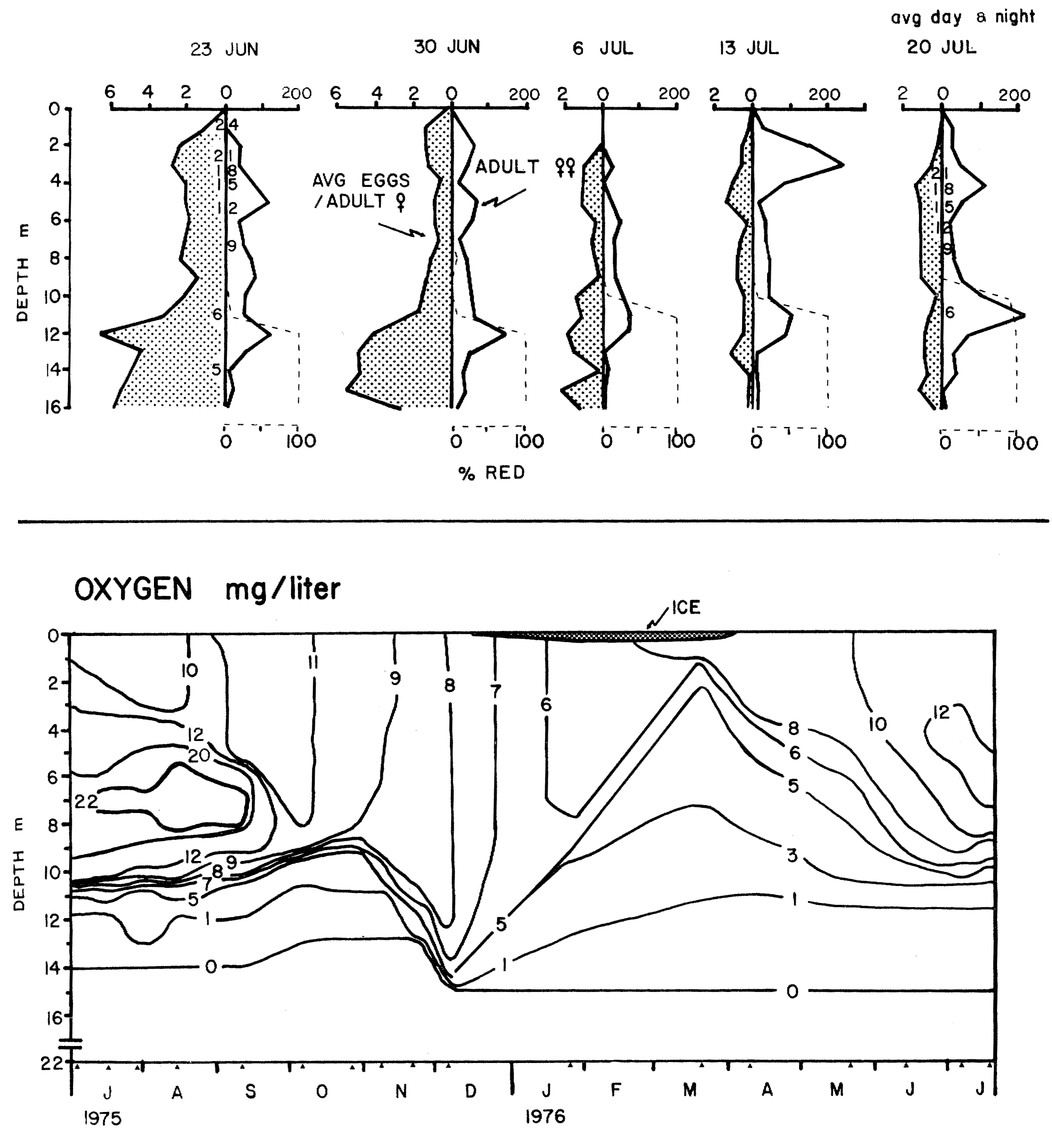

Fig. 6. Upper panel: vertical distribution of adult *Daphnia pulex*, eggs, and red adults, Crawford Lake 1976. Temperature (°C) with depth given in middle of first and last series. Dashed line is percent red adults. Lower panel: isopleths dissolved oxygen in mg·liter^{-1}, Crawford Lake 1975–1976.

for the differential efficiency with which a tow net captures immature and mature *Daphnia*, we recalculated the population parameters of *D. pulex* at the central station for uncorrected data and compared them with corrected data. Table 6 shows that the correction had little effect on r'; this is merely an indication that the ratio of young to adults did not fluctuate much from one sampling date to the next. However, the correction increased calculated b' by an average of 40%. The effect of the correction on d' was variable, and because $d' = b' - r'$ is greater than the effect on b' when r' is positive and less when r' is negative.

When the population under study inhabits a stratified lake, a small change in

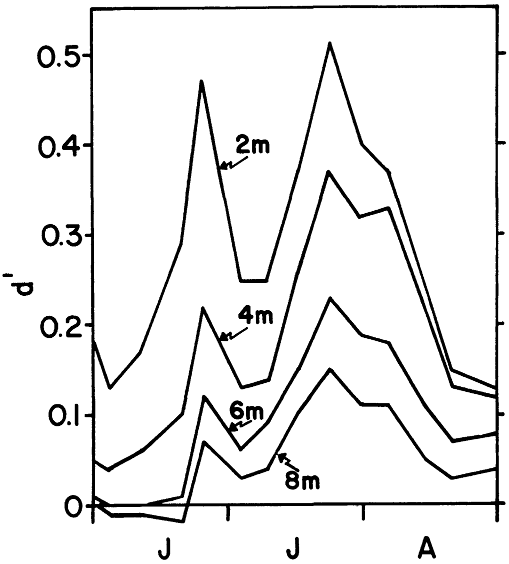

Fig. 7. Calculated d' for *Daphnia rosea* (using average data) assuming population is living at four different depths, Crawford Lake summer 1975.

the estimated mean depth of the egg population can have a large effect on the calculated values of b' and d'. This is because egg development time changes considerably with a change in temperature. To illustrate the effect of mean depth on population statistics, we calculated the death rate of *D. rosea* in 1975 for a series of assumed mean depths of the eggs from 2 to 8 m. Figure 7 shows that in the early part of the summer for every 2-m increase in assumed mean depth, the death rate was halved. This is precisely the time of year for which high death rates for *Daphnia* have been reported based on egg development times that were very crudely estimated. For accurate results it is not sufficient to sample from one, two, or three strata in the lake as de Bernardi (1974), Wright (1965), and Hall (1964) did, or even to measure mean depth of eggs on a few dates through the season as we have done. One should measure the vertical distribution of eggs more frequently than we normally collected samples.

To demonstrate the effects of inadequate horizontal sampling, we calculated

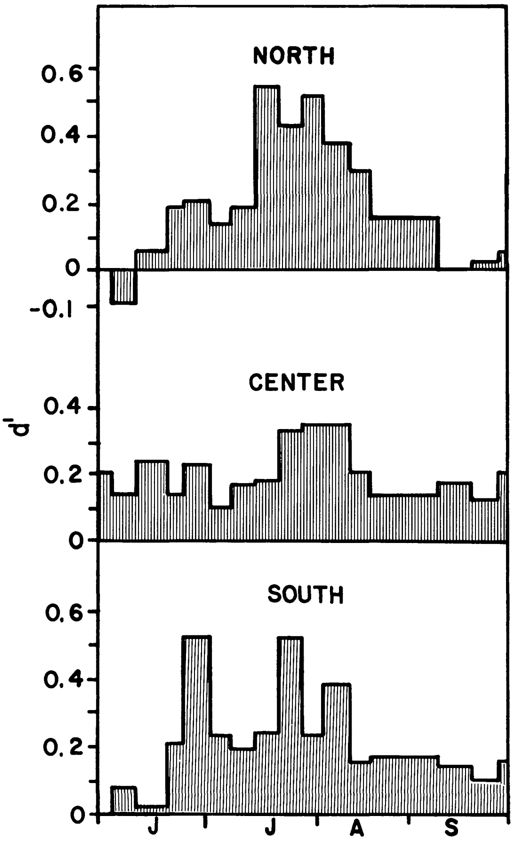

Fig. 8. Calculated d' for *Daphnia rosea* at three separate stations, Crawford Lake June–September 1975.

population statistics from samples collected at each station in Crawford Lake. To calculate *D. rosea* death rates we used Edmondson's original model (Eq. 6-9) and assumed that egg-bearing females all lived at a depth of 3 m. Although our depth distribution series suggested that this would be a good average (Fig. 4), our earlier calculations showed that the absolute values of d' should be accepted with reservations and attention directed mainly to the differences between stations.

The results (Fig. 8) clearly show how our interpretation of the mortality pattern in the lake could be influenced by the station sampled. From samples collected at the north end, we would conclude that mortality was negligible early in June,

Table 7. Estimates of b' for *Daphnia pulex* at central station, Crawford Lake 1975 and 1976. Integrated b' is based on vertical distribution data, whereas simplified b' assumes animals all live, first at 4 m until early June, then move down to 6 m by mid-June.

	Integrated b'	Simplified b'
1975		
9 May	0.08	0.07
23 May	0.14	0.15
29 May	0.05	0.05
4 Jun	0.06	0.06
1976		
23 Jun	0.10	0.10
30 Jun	0.06	0.10
6 Jul	0.02	0.04
13 Jul	0.06	0.04
20 Jul	0.04	0.04

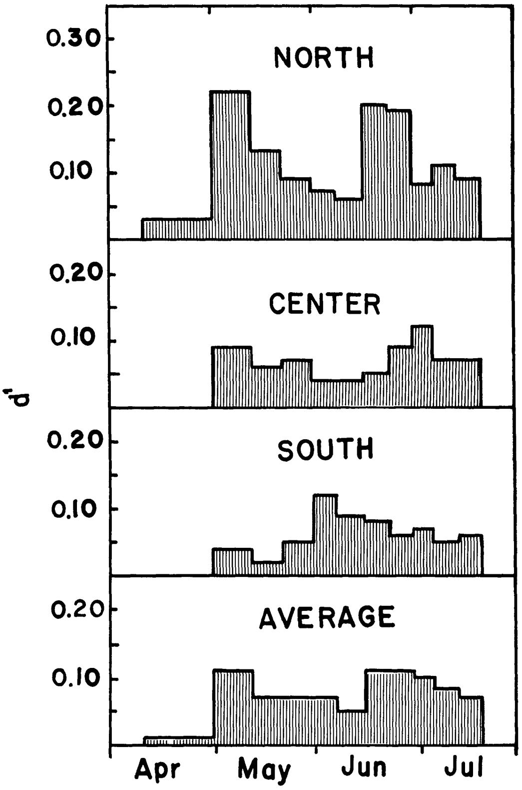

Fig. 9. Calculated d' for *Daphnia pulex* at three separate stations and an average of all three, Crawford Lake April–July 1976.

rose to a maximum of $0.5 \cdot d^{-1}$ in late July and early August and then dropped off to zero again by mid-September; this conclusion would be most satisfying if a predator such as *Leptodora kindtii* appeared in the plankton in midsummer. However, samples taken at the south end would probably be interpreted as showing a maximum mortality rate in late June followed by a slow decline and those from the central station as showing a relatively constant mortality rate of about $0.2 \cdot d^{-1}$ from the beginning of June until the end of September.

Calculation of *D. pulex* population statistics was not straightforward because this species was distributed over a much greater range of temperatures and for at least part of the year comprised two spatially separate populations. Integrated population statistics for *D. pulex* were calculated by using Eq. 15 and then 7 for the dates when vertical distribution data were available. The values generated by this method were very like those obtained by assuming that all the animals lived at 4 m until early June and then moved down to 6 m by mid-June (Table 7). During June and July 1976 *D. pulex* behaved as though it comprised two separate populations; thus, because the egg-ratio model assumes that b' is a constant from one sampling date to the next, two separate sets of population statistics should theoretically be calculated, one for the red population and a second for the brown population. However the red *D. pulex* at Crawford Lake are just an example of a hidden problem: two or more spatially separate groups belonging to one species existing in the same lake. Because Crawford Lake is meromictic we were able to detect two distinct groups of *D. pulex*, but we have no idea of the actual number of spatially separate populations or whether the separate populations are a temporary or permanent phenomenon. In other lakes there may be no visible indication that one species is separated into two or more populations. Since the actual number of populations of *D. pulex* at Crawford Lake remains unknown, and the birth rates of the two identifiable populations were similar, the two populations were treated as

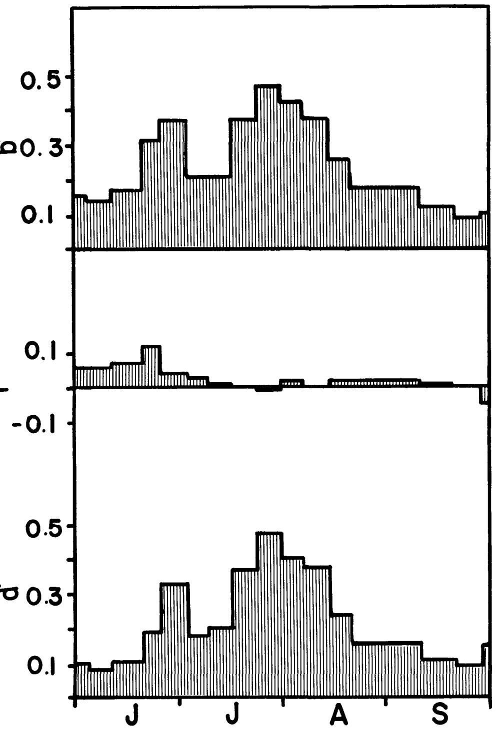

Fig. 10. Average b', r', and d' for *Daphnia rosea*, Crawford Lake June–September 1975.

one so that we could use all the data. We calculated population statistics for *D. pulex* using Edmondson's original model (Eq. 6–9) and assuming that egg-bearing ♀♀ all lived at a depth of 4 m until June and then moved down to 6 m by mid-June.

The results of these calculations from April until July 1976 show once again that mortality rates from individual stations are not representative of those of the population as a whole. There is first a clear trend of decreasing mortality from the north to the south end (Fig. 9). This was produced by the persistent gradient in adult numbers and average eggs per adult female from north to south, combined with the even distribution of immature *D. pulex* throughout the lake (Table 5) which resulted in b' decreasing from north to south. Thus the increased b' at the north end reflects the higher ratio of females to young and eggs to females there, and the d' there reflects the tendency of young to become distributed evenly throughout the lake. This tendency would increase calculated d' at the north end and decrease calculated d' at the center and south end.

Although apparent mortality rates at the north and central stations differed, the seasonal pattern was similar, with maximum mortality at the beginning and end of the period. However, samples at the south station would lead us to conclude that mortality rose slowly to a maximum at the time when it was lowest at the other stations and then decreased when it was rising elsewhere. In fact, the complete sampling showed that mortality rose suddenly at the beginning of May and remained relatively constant around $0.08 \cdot d^{-1}$ until the end of July (Fig. 9).

A prediction tested—Until now we have emphasized the difficulty of obtaining reliable estimates of b' and d' and the inadequacies of our sampling program and that of others. We will now look at a prediction made by our results for *D. rosea* and attempt to test it.

The overall average values of r', b', and d' for *D. rosea* in summer 1975 are shown in Fig. 10. An interesting feature of these results is the high birth and death rates ($\simeq 0.4 \cdot d^{-1}$) for a month in midsummer. Also, because r' is small relative to b', the seasonal patterns of b' and d' are almost identical. Initially one might take these combined results to indicate that b' was grossly overestimated and that this is why d' paralleled it. Why else should b' and d' remain almost identical for 4 months? Perhaps there is a mechanism that could be postulated in the form of an unusual mortality pattern for this species.

To maintain a high b', when r' is low and $d' \simeq b'$, a high ratio of adult females to young must be maintained. That is to say there must be a high mortality rate among the first free-swimming instar (neonates) or late embryos. Thus, in a period such as late July and early August, when $r' \simeq 0$ and d' and b' are high and constant and a steady state distribution of instar abundance is approached, we might expect to find that the number of neonates in the population was much lower than the number of eggs, or that

Table 8. Percentage total juvenile *Daphnia rosea* in each juvenile instar, and actual egg, young, and adult numbers in samples collected, Crawford Lake, 23 and 30 July 1975. Numbers in parentheses are corrected for tow net efficiency in capturing young as opposed to adult animals.

	Percentage total juveniles in sample							
	23 July				30 July			
Juvenile instar	N	C	S	Wt avg	N	C	S	Wt avg
I	9	29	19	20	19	17	12	15
II	13	29	21	22	23	13	23	22
III	24	23	24	26	22	23	30	26
IV	26	10	18	15	22	30	25	24
V	28	9	18	16	14	16	10	12

Sample numbers (N + C + S)	23 July	30 July
eggs	2,504 (3,415)	2,296 (3,131)
young	1,240	1,163
observed neonates	248	175
expected neonates	2,504 (3,415)	2,296 (3,131)
adults	1,327 (1,810)	1,341 (1,829)

the number of second instars was much lower than the number of neonates. This expectation is based on the assumption that the mean temperature experienced by all immature instars and eggs was the same and consequently that duration of these instars is identical. If this is so, then the number in any instar is proportional to the number passing through that instar.

To test this prediction, we recounted six samples from late July and divided (by sight) all of the immatures into five size categories assumed to represent five instars. Although animals could not be assigned to categories by a single measurement such as length, independent observers apportioned the animals similarly. The proportion of animals in a particular instar varied considerably between stations, so for the dates chosen, samples from the three stations were sorted.

The results (Table 8) show that although there is mortality throughout the juvenile life it is small and $\simeq 1\% \cdot d^{-1}$, assuming that equal time is spent in each immature instar—an assumption consistent with Peters' (1972) data on juvenile *D. rosea.* This mortality increases to only $3\% \cdot d^{-1}$ if the animal is assumed to spend 2.5 times as long in the last as in the first immature instar, as reported by Anderson and Jenkins (1942) for *Daphnia magna.*

Similarly, adult mortality is low. Adult duration can be estimated by assuming a steady state system where juvenile mortality is zero and duration of all instars is equal; then

$$\frac{\text{No. juveniles}}{\text{No. adults}} = \frac{\text{duration juveniles}}{\text{duration adults}}.$$

Solving for average adult duration with the data in Tables 4 and 8,

$$\frac{1{,}200}{1{,}300} = \frac{11 \text{ days}}{\text{duration adults}},$$

gives an estimate of 12 days for adult duration time. Twelve days is likely an underestimate for two reasons: first, not all young survive to the fifth instar; second, the numbers have not been corrected for the relative efficiency of the tow net in capturing young and adult animals. Assuming survival of 70% of the animals to the fifth instar, or a net efficiency ratio of 1.36 for young as compared to adult animals, increases adult duration to 17 days, and, combining the two corrections, to 24 days. Thus estimated adult mortality is in the range of 4–8% per day.

The greatest mortality, up to 90%, occurs between the eggs and neonates, either very late in egg development or very early in the life of the neonate. This conclusion is consistent with the prediction from our population statistics and inconsistent with the general pessimism of our earlier work.

Discussion

Although our ability to predict the fluctuations in abundance of any given species requires a detailed knowledge of the controls on birth rate, the causes of mortality, and the life stages on which mortality acts, a good starting point is simply the birth and death rates of the population in time. The planktonic community has appealed to ecologists as one in which these rates should be easily obtained for a number of species, yet despite our early optimism we have almost no reliable estimates of the population statistics of zooplankton populations. There are many reasons for this failure and our purpose here was merely to demonstrate a few of these.

The first problem arises from the need to choose a model on which to base calculations. The linear model used by Elster and Schwoerbel (1970) has much promise but has not been exploited, possibly because it was initially applied incorrectly. Elster and Schwoerbel's method of using the average number of eggs from t_1 and t_2 to calculate the number of neonates between t_1 and t_2 is inappropriate for several reasons. It biases the estimate of B so that B is too high when the population is increasing and too low when the population is decreasing, it assumes that the age distribution of eggs is always uniform, and it averages egg ratio and egg development time over the interval between successive samples. Although methods might be developed to overcome all of these problems, neither the original work of Elster and Schwoerbel nor the subsequent paper by Rey and Capblancq (1975) attempted to justify the procedures used or to suggest ways of improving them. This may account for the greater use that has been made of the exponential model.

Edmondson's (1960) exponential model assumes that the most apt description of the potential rate of population growth is given by the positive exponential equation. It assumes a rate of potential increase over the sampling interval that is proportional to population size and consequently circumvents the problem of deciding what is the appropriate population size to use as denominator. Although some sophisticated attempts (Paloheimo 1974; Argentesi et al. 1974) have been made to elaborate this model, most workers to date have used Edmondson's original model.

Perhaps more significant than the need to elaborate the original model is the need to modify it so that it can be applied to populations of Cladocera living in thermally stratified lakes. In a classic paper, Hall (1964) made a first attempt to do this, but we have now shown his computation to be erroneous. Furthermore, we have shown that the appropriate method of calculating an integrated b' depends on the assumption made about the behavior of egg-bearing females. If they behave as a single population, in which each individual migrates throughout the temperature range spanned by the population, spending an amount of time in each temperature stratum proportional to the fraction of the total population in that stratum, then our Eq. 15 is the appropriate method. However, the data from Crawford Lake showed that *Daphnia* populations do not necessarily behave in this way. For a species behaving like *D. pulex* in Crawford Lake separate calculations should be made for each spatially separate population. This poses the most serious problem of all because the opportunity of detecting the different groups of females by their color is rarely presented. Similarly separated populations may exist in many lakes without being recognized.

The final difficulty—that of collecting adequate samples—although probably the greatest, has received the least attention. The sampling methods in all studies including ours were clearly inadequate to produce accurate statistics. Samples taken at one site at the end of a long lake simply cannot yield statistics representative of the population. Enough sites should be sampled to account for the horizontal dispersion that is characteristic of zooplankton. In a small simple lake such as Crawford, three sites were barely enough. Had we used only one collecting site, the existing horizontal differences in animal and egg numbers were sufficient that the seasonal patterns of mortality and the average mortality rate found would have depended on which sampling site was chosen. When more than one spatially separate subpopulation is present the number of samples required to calculate population dynamics for each group would be prohibitively large.

Even data collected from the best sampling program will require smoothing, because our field techniques are refined only to the point of being able to detect long term (and not short term) fluctuations in animal numbers. Smoothing animal numbers over time makes a considerable difference in the week-to-week variation in r'. Because $b' = r' - d'$, a negative r' means a higher d', and in a number of cases in the literature (Clark and Carter 1972; Wright 1965) the high death rates are clearly sampling artifacts.

Perhaps even more important and difficult to obtain is an accurate estimate of the vertical distribution of eggs in stratified lakes. Without this information the egg duration cannot be estimated, because calculated b' is more sensitive to variation in temperature than any other variable. That the importance of temperature has been neglected is shown by the fact that previous workers have failed to emphasize the method by which they calculated mean depth of the egg population (Wright 1965; Tappa 1965; de Bernardi 1974).

Finally, it is essential to collect all life stages with equal efficiency. Tow nets are frequently used in studies of population statistics because they collect large samples, but as we have shown for *D. pulex* they may be avoided by the larger individuals. This is not an error confined to tow nets; during the day, copepodites of *Diaptomus oregonensis* escape a Juday trap much more than do nauplii (Rigler and Cooley 1974). If the relative efficiency of the collecting device for different life stages is not known, considerable errors (up to 100%) can be introduced into estimates of mortality rates.

Until now our emphasis has been on the difficulty of obtaining good population statistics and the inadequacies of most published attempts. We do not mean that there is nothing to be gained from examination of the results obtained to date or from attempts to develop improved methods. The potential value of these data makes both attempts worthwhile. As an example, the high sustained birth rate of *D. rosea* when population remained constant suggested a high mortality of eggs or neonates. This observation prompted us to examine the original samples and to attempt to segregate the immatures into instars. The results of this exercise were consistent with the original hypothesis in suggesting that most mortality occurs either in late embryos or at hatching. This is interesting in suggesting a startling difference between calanoids and cladocerans. The populations of freshwater calanoids for which instar mortality has been measured show insignificant mortality of eggs (Rigler and Cooley 1974; Rigler et al. 1974) and almost no mortality over the first few naupliar instars. The juvenile mortality pattern for *D. rosea* is also very different from that reported by Hall (1964) for *D. galeata mendotae* in Base Line Lake, where the highest mortality (26% per day) was reportedly experienced by all juvenile instars, and shows that survival of *D. rosea* in Crawford Lake is largely a matter of being successfully born. After birth, survival is very high and there is no indication that young or adults suffer seriously from selective predation. Although we cannot say yet whether this generalization applies over the whole productive season in Crawford Lake, or to any other populations, it does appear that a careful study of the ratio of eggs to neonates might help dispel the enigma of high *Daphnia* death rates.

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