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## HOW WELL DOES THE EDMONDSON-PALOHEIMO MODEL APPROXIMATE INSTANTANEOUS BIRTH RATES?<sup>1</sup>

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**Abstract.** An equation independently derived by Edmondson and Paloheimo for estimating instantaneous birth rates without a knowledge of mortality rates has been extensively employed by zooplankton ecologists. This expression is exactly true only under the unlikely conditions that the age distribution is stable and that egg mortality is equal to that averaged across the entire population. Here I compare estimates of instantaneous birth rates ( $b$ ) using the Edmondson-Paloheimo equation to those determined with a general model which accounts for age structure instability and egg mortality in two *Daphnia pulex* populations. Despite the fact that the assumptions of the Edmondson-Paloheimo model are rarely met, it mimics the seasonal pattern of  $b$  quite well, with few exceptions. An analysis of variance suggests that the model will provide an adequate approximation of the true population birth rate when a variance in  $b$  of 0.003 can be tolerated. A much more critical factor in the analysis of instantaneous rates in plankton populations is the development of accurate sampling techniques.

**Key words:** birth rates; Cladocera; *Daphnia pulex*; demography; egg ratio; rotifers; zooplankton.

A great deal can often be inferred about the factors regulating population densities from measures of two population parameters, the instantaneous birth and mortality rates,  $b$  and  $m$ . The estimation of  $b$  has been thought to be particularly simple for planktonic cladocerans and rotifers whose adults bear live young which are easily enumerated in preserved samples and whose egg development rates are simple functions of temperature. Edmondson (1960) first introduced the egg ratio technique as a means of estimating instantaneous birth rates with preserved samples of planktonic rotifers. In theory the method can be extended to any population characterized by continuous growth.

Under the special conditions of zero population growth, zero egg mortality and a stable age distribution, the age distribution of eggs will be even, and the finite birth rate of the population is

$$\beta = E/D$$

where  $E = C_t/N_t$  is the average number of eggs per individual in the population (the egg ratio),  $C_t$  and  $N_t$  being the total number of eggs and individuals in the population at time  $t$ , and  $D$  is the duration of egg development (days). Under these constraints,  $\beta$  is related to the instantaneous birth rate by

$$\begin{aligned} b &= \ln\left(N_t + \frac{C_t}{D}\right) - \ln(N_t) \\ &= \ln(1 + \beta). \end{aligned} \quad (1)$$

An alternate expression for  $b$  which makes no assumptions about the age distribution of eggs, but which still assumes zero population growth and zero egg mortality, is

$$\begin{aligned} b_{EP} &= \frac{\ln(N_t + C_t) - \ln(N_t)}{D} \\ &= \frac{\ln(1 + E)}{D} \end{aligned} \quad (2)$$

(Edmondson 1968). The attractiveness of both of these expressions lies in their independence from  $m$  which is often the final product of interest. Given an additional estimate of the actual rate of population growth,  $r$ , the population mortality rate can then be determined by difference using the relation

$$m = b - r. \quad (3)$$

Since few populations are either free from egg mortality or stable in size or age distribution, Eqs. 1 and 2 would seem to be inappropriate. However, the use of Eq. 2 has been further encouraged by a derivation by Paloheimo (1974) which, despite its incorporation of egg mortality, turns out to be independent of mortality and identical to Eq. 2. This convenient absence of egg mortality from Eq. 2 occurs only when the mortality rate of eggs is exactly equal to that averaged across the entire population ( $m$ ). Furthermore, the independence of Eq. 2 from  $r$  is still a consequence of assuming a stable population age distribution.

Threlkeld (1979) has suggested that the accuracy of birth rate estimates could be improved by examining the age distribution of eggs. Although this approach would seem to be an advance over the Edmondson-Paloheimo model, it is not yet clear whether the additional work is warranted.

A large part of the problem is that, with few exceptions (DeMott 1980, Keen and Nassar 1981), previous investigations involving the egg ratio method have not attempted to estimate the variance of the rates in Eq. 3. In the absence of such information it is not only impossible to compare the adequacy of different tech-

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niques, but a comparison of instantaneous rates between dates or sites is risky at best. An analysis of variance for  $b$  and  $r$  becomes particularly critical when  $m$  is estimated by difference. Many studies show dramatic fluctuations in  $m$  over very short time intervals (Clark and Carter 1974, Kwik and Carter 1975, Goldman et al. 1979), and without variance estimates these cannot be identified as real or artifactual. Negative estimates of  $m$ , which often arise from Eq. 3, are usually attributed to the hatching of uncensused resting eggs, although they are just as likely to be a consequence of poor estimates of  $r$  resulting from inadequate sampling or biased determinations of  $b$  resulting from faulty assumptions of the Edmondson-Paloheimo model.

Despite these problems, zooplankton ecologists continue to rely heavily on Eq. 2 (see Bottrell et al. 1976, Goldman et al. 1979, Kerfoot and Peterson 1979, Lynch 1979 for several recent applications), and it seems likely that many will continue to do so in the interest of time. Thus, it is of interest to know the extent to which deviations from the assumptions inherent in the Edmondson-Paloheimo equation are reflected in poor estimates of birth rates in field studies. Such an analysis has not been possible in the past because the magnitude by which the assumptions have been violated has been difficult to quantify. Computer simulations are of only limited value in examining this problem (Seitz 1979) because the choice of input parameters is necessarily subjective. The application of a sequential sampling technique for estimating size-specific mortality rates in cladoceran populations (M. Lynch, *personal observation*) now allows the collection of the necessary information. This paper provides an empirical test of the efficacy of the Edmondson-Paloheimo model by comparing estimates of  $b$  by Eq. 2 with those obtained for two *Daphnia pulex* populations for which instabilities in age structure and differential egg mortality are accounted for.

#### THE GENERAL MODEL

Since a generalized model for estimating instantaneous birth rates from egg ratio data has not been previously published I will start by deriving such an expression. Throughout this paper I will assume a homogeneous population, i.e., one in which all individuals are exposed to the same physical and biological factors. I also assume that egg development times and size-specific rates of growth, egg laying, and mortality are constant over the interval  $(t - D, t)$ . (Since the structure of the population may change over  $[t - D, t]$ , this does not imply constancy of these rates as population parameters.) For populations for which  $D$  is on the order of a few days, as it is in most of the planktonic organisms to which the egg ratio model has been applied, such approximations do not seem unreasonable. However, where these assumptions are significantly violated, no simple expression for esti-

imating  $b$  by an egg ratio method can be derived, and alternate empirical approaches must be sought.

The ideal egg ratio model makes no assumptions about the internal structure of the population, but considers the individual contribution of each class of individuals to the total population birth rate. Although the classification scheme is arbitrary, I will derive the model in the context of a population of an arbitrary number of size classes ( $w$ ) since most organisms may be more easily classified by size than by age.

The total number of eggs derived from size class  $x$  which hatch during time  $(t, t + dt)$  is equal to the total number of eggs laid during time  $(t - D, t - D + dt)$  by individuals of that size class which survive to hatching (most planktonic organisms, especially cladocerans, do not change size classes while carrying a clutch),

$$b_x N_{x,t} dt = l_x N_{x,t} e^{-r_x D} e^{-m_x D} dt, \quad (4)$$

where  $b_x$  = the instantaneous birth rate of size class  $x$  ( $\text{day}^{-1}$ ),

$N_{x,t}$  = the number of individuals in size class  $x$  at time  $t$  (number per square metre),

$r_x = (\ln N_{x,t} - \ln N_{x,t-\tau})/\tau$  is the growth rate of size class  $x$  ( $\text{day}^{-1}$ )

$l_x$  = the instantaneous rate of egg laying by size class  $x$  ( $\text{day}^{-1}$ ), and

$m_x$  = the instantaneous mortality rate of size class  $x$  ( $\text{day}^{-1}$ ).

The size-specific rate of egg laying,  $l_x$ , can be re-expressed in terms of the mean size-specific clutch size  $E_x$ , as follows. The total number of eggs carried by size class  $x$  at time  $t$  is

$$C_{x,t} = \int_{t-D}^t l_x N_{x,\tau} e^{-m_x(t-\tau)} d\tau. \quad (5)$$

Noting that

$$N_{x,t} = N_{x,t} e^{-r_x(t-\tau)}$$

and

$$E_x = C_{x,t}/N_{x,t}$$

and integrating Eq. 5,

$$l_x = \frac{E_x(r_x + m_x)}{1 - e^{-D(r_x + m_x)}}. \quad (6)$$

Substituting Eq. 6 into Eq. 4 gives the size class specific birth rate

$$b_x = \frac{E_x(r_x + m_x)}{e^{D(r_x + m_x)} - 1}.$$

The instantaneous birth rate for the entire population is

$$\hat{b} = \sum_{x=k}^w \frac{P_x E_x(r_x + m_x)}{e^{D(r_x + m_x)} - 1}, \quad (7)$$

where  $P_x$  is the proportion of the total population

in size class  $x$ , and  $k$  is the size class at first reproduction.

Noting that Eq. 2 may be rewritten as

$$b_{EP} = \sum_{x=k}^w \frac{P_x E_x b_{EP}}{e^{D b_{EP}} - 1},$$

and rewriting Eq. 7 as

$$\hat{b} = \sum_{x=k}^w \frac{P_x E_x [\hat{b} + (r_x - r) + (m_x - m)]}{e^{D[\hat{b} + (r_x - r) + (m_x - m)]} - 1} \quad (8)$$

it becomes clear that the deviation between  $\hat{b}$  and  $b_{EP}$  is a function of the size-specific patterns of mortality, growth, and clutch size, as well as the size distribution of the population. All previously derived expressions for  $b$  (Edmondson 1960, 1968, Caswell 1972, Paloheimo 1974, Seitz 1979) are special cases of Eq. 7 and can be derived from it by restricting the appropriate conditions. Only when the age distribution is stable ( $r_x = r$  for all  $x$ ) and mortality is independent of size ( $m_x = m$  for all  $x$ ) does Eq. 7 reduce to the Edmondson-Paloheimo model.

If we are to determine the adequacy of Eq. 2, then it is important that we establish the variance in our estimates of  $\hat{b}$ . Assuming that  $D$  and the  $E_x$  values can be determined to a high degree of accuracy and precision, then the variance of  $\hat{b}$  is a function of only the variance of the  $(r_x + m_x)$  terms. For all  $x$ , the variance of  $r_x$  is equivalent to the variance of  $r$ ,

$$r = \frac{\ln N_t - \ln N_{t-\tau}}{\tau},$$

where  $N_t$  and  $N_{t-\tau}$  are the total population sizes at time  $t$  and  $t - \tau$ . By Taylor expansion (Kendall and Stuart 1977:246-247),

$$\text{Var } r_x = \text{Var } r = (\tau)^{-2} \left[ \frac{\text{Var } N_t}{N_t^2} + \frac{\text{Var } N_{t-\tau}}{N_{t-\tau}^2} \right]. \quad (9)$$

Further, assuming independence between  $r$  and  $m_x$ ,

$$\text{Var}(r_x + m_x) = \text{Var } r + \text{Var } m_x,$$

and

$$\text{Var } \hat{b} = \sum_{x=k}^w (P_x E_x)^2 \left\{ \frac{[1 - D(r_x + m_x)] e^{D(r_x + m_x)} - 1}{(e^{D(r_x + m_x)} - 1)^2} \right\}^2 \cdot \text{Var}(r_x + m_x). \quad (10)$$

Complete expressions for the variances of  $m_x$  are available from the author on request.

#### SENSITIVITY OF $\hat{b}$ TO PATTERNS OF MORTALITY AND AGE STRUCTURE INSTABILITY

The adequacy of the Edmondson-Paloheimo equation clearly depends upon the sensitivity of the general equation to false assumptions about class-specific growth and mortality rates. Letting

$$\theta_x = r_x + m_x$$

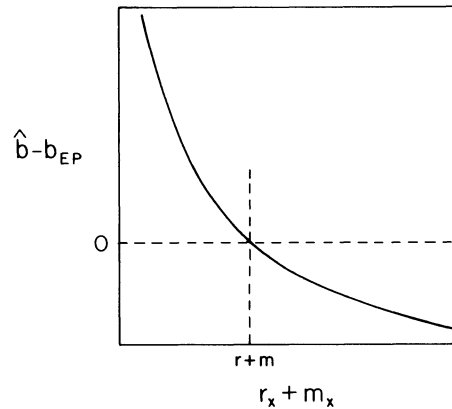


FIG. 1. The relative effect of  $(r_x + m_x)$  for any adult size class on the deviation of birth rate estimates by the Edmondson-Paloheimo equation ( $b_{EP}$ ) from those of the general model ( $\hat{b}$ ), assuming all other size classes have  $\theta_x = r + m$ .

and

$$\Delta = \hat{b} - b,$$

then

$$\frac{\partial \Delta}{\partial \theta_x} = \frac{P_x E_x [(1 - D)e^{D\theta_x} - 1]}{[e^{D\theta_x} - 1]^2},$$

and

$$\frac{\partial^2 \Delta}{\partial \theta_x^2} = \frac{P_x E_x D e^{D\theta_x} \{(D - 1)[e^{2D\theta_x} + 1] + 2e^{D\theta_x}\}}{[e^{D\theta_x} - 1]^4}.$$

Since  $D$  is invariably  $> 1$ ,

$$\frac{\partial \Delta}{\partial \theta_x} < 0 \quad \text{and} \quad \frac{\partial^2 \Delta}{\partial \theta_x^2} > 0,$$

and the effect of  $\theta_x$  on  $\Delta$  appears as in Fig. 1. Thus in order for the Edmondson-Paloheimo equation to overestimate  $\hat{b}$ , something in excess of half of the eggs in the population must reside in size classes for which  $\theta > r + m$ , the actual amount depending upon the size-specific pattern of mortality,  $D$ , and the distribution of the eggs.

An examination of the relation between  $r + m$  and  $\theta_x$  reveals the conditions under which Eq. 2 will tend to misrepresent  $b$ . Consider a population consisting of just two classes: adults (indexed by  $a$ ) and juveniles (indexed by  $j$ ). Then, for short intervals,

$$r + m \approx P_a(r_a + m_a) + (1 - P_a)(r_j + m_j),$$

where  $P_a$  is the proportion of the population in the adult class. Now, while  $r_a + m_a \neq r + m$  is a necessary condition for  $b_{EP} \neq \hat{b}$ , the deviation becomes negligible as adults increase in relative abundance. That is,

$$\lim_{P_a \rightarrow 1} (r + m) = r_a + m_a.$$

Thus, the Edmondson-Paloheimo equation is more

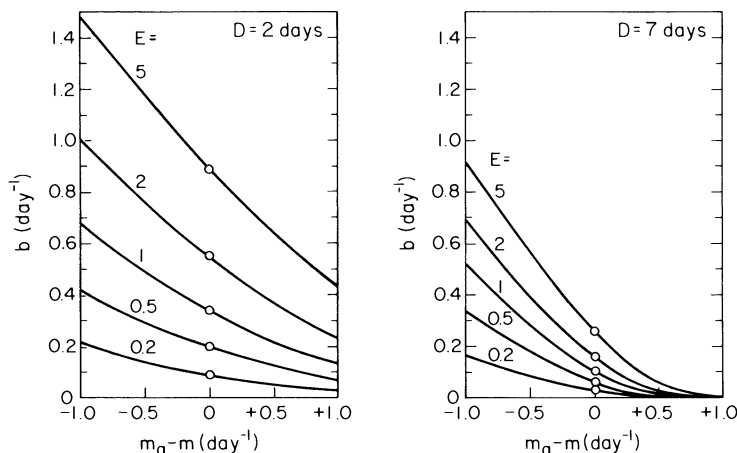


FIG. 2. Instantaneous birth rates estimated by Eq. 11 as a function of the difference between adult and population mortality rates ( $m_a - m$ ), egg ratio ( $E$ ), and duration of egg development ( $D$ ). Open points are estimates of  $b$  by the Edmondson-Paloheimo equation which are independent of ( $m_a - m$ ).

likely to give inaccurate estimates of  $\hat{b}$  when adults comprise a small fraction of the population.

Fig. 2 illustrates the problem for the simplified case in which the population has only two classes (adults and juveniles) and a stable age distribution. Under these conditions Eq. 7 reduces to

$$b = \frac{E(b + m_a - m)}{e^{D(b + m_a - m)} - 1} \quad (11)$$

When  $m_a < m$ , Eq. 2 underestimates  $\hat{b}$  because it overestimates egg mortality; the reverse results when  $m_a > m$ . The absolute difference between  $b_{EP}$  and  $\hat{b}$  increases with increasing egg ratios, while proportional differences are most significant at low egg ratios. For instance, when  $m_a - m = -0.2$ ,  $D = 2$  d, and  $E = 0.2$ ,  $b_{EP}$  underestimates  $\hat{b}$  by  $0.02 \text{ d}^{-1}$  (20%), compared to  $0.08 \text{ d}^{-1}$  (15%) when  $E = 2.0$ . Discrepancies between estimates by Eqs. 2 and 11 become much more significant at higher egg development times because the effects of differential mortality on adults accumulate over longer periods.

#### A TEST OF THE EDMONDSON-PALOHEIMO MODEL

An exact test of the efficacy of the Edmondson-Paloheimo model requires an accurate knowledge of the size-specific parameters in Eq. 7. While most of these can be determined relatively easily in well-censused populations, the size-specific mortality patterns are more elusive. However, as can be seen in Eq. 8, relative estimates of size-specific mortality are sufficient for solving Eq. 7 so long as they are all biased to the same extent.

Using a sequential sampling technique, I have assembled the necessary data on  $P_x$ ,  $E_x$ ,  $r_x$ ,  $m_x$  and  $\text{Var } m_x$  for two populations of the planktonic cladoceran *Daphnia pulex* which allow an examination of

the relation between birth rates predicted by the Edmondson-Paloheimo model and by Eq. 7. These data should provide a rigorous test of the Edmondson-Paloheimo equation. There is considerable variation in the combinations of size-specific characteristics among the different experiments (condensed in Table 1). Furthermore, the age structure of these populations is conducive to setting up the differences between

TABLE 1. Data for *Daphnia pulex* used to estimate instantaneous birth rates in Fig. 3.  $P_a$ , ( $r_a + m_a$ ) and  $E$  actually condense more detailed size-specific information;  $P_a = \sum_{x=k}^w P_x$ ;  $r_a = [\ln N_{a,t+\tau} - \ln N_{a,t}]/\tau$ ;  $m_a = \ln N_{a,t} - \ln[(N_{a,t}/P_a) \sum_{x=k}^w P_x e^{-m_x}]$ ;  $E = \sum_{x=k}^w P_x E_x$ .

Date	$E$	$D$	$P_a$	$r_a + m_a$	$r + m$
<b>Busey Pond</b>					
5-9 May 1978	0.14	6.65	0.114	0.094	0.016
18-23 May 1978	0.51	4.19	0.610	0.076	0.103
13-15 Jun 1978	1.72	3.14	0.400	-0.080	0.555
11-13 Jul 1978	0.16	2.92	0.196	0.419	0.024
25-27 Jul 1978	0.53	2.50	0.439	0.074	0.181
20-23 Apr 1979	0.97	5.54	0.205	0.186	0.180
4-7 May 1979	0.67	6.25	0.169	0.027	0.074
21-23 May 1979	0.05	4.19	0.043	-0.346	0.024
4-6 Jun 1979	0.07	3.50	0.295	0.383	0.019
18-20 Jun 1979	0.33	2.95	0.314	-0.142	0.104
20-23 Aug 1979	0.19	2.81	0.208	0.124	0.063
31 Aug-3 Sep 1979	0.01	2.91	0.042	0.170	0.003
14-17 Sep 1979	0.02	4.19	0.200	0.000	0.005
<b>Little Lake</b>					
26 Apr-1 May 1978	0.03	4.30	0.023	0.017	0.006
11-15 May 1978	0.07	4.69	0.124	0.003	0.018
25-30 May 1978	0.08	3.33	0.262	0.070	0.021
18-20 Jul 1978	0.24	2.69	0.207	0.579	0.068
1-3 Aug 1978	0.10	2.46	0.136	0.105	0.034
28-30 May 1979	0.86	2.16	0.370	0.033	0.400
11-13 Jun 1979	0.20	2.20	0.374	0.347	0.060

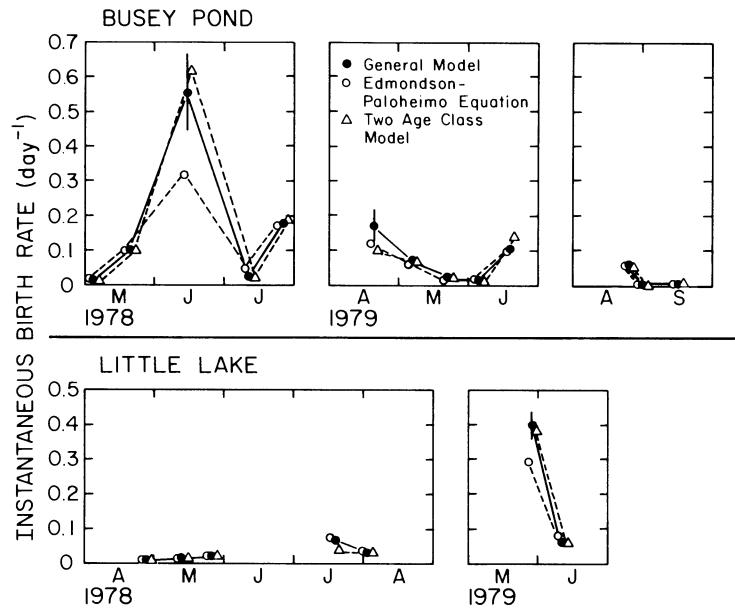


FIG. 3. Instantaneous birth rates for two *Daphnia pulex* populations estimated by the Edmondson-Paloheimo equation, by the general model, and by the two-age-class model. 95% confidence limits are included for the general model.

$(r_a + m_a)$  and  $(r + m)$  which cause divergences between  $b_{EP}$  and  $\hat{b}$ . Only on one occasion does  $P_a$  exceed 0.5, and on a majority of dates it is  $<0.25$ .

Given the large amount of effort required to estimate the size-specific parameters in Eq. 7, it is also worth examining whether a model with a minimum number of classes (i.e., juveniles and adults) is a reasonable compromise between Eqs. 2 and 7. Under these conditions the general model simplifies to

$$b = \frac{E(r_a + m_a)}{e^{D(r_a + m_a)} - 1} \quad (12)$$

where  $r_a$  is the rate of increase of adults.

The birth rate estimates by Eqs. 2, 7, and 12 are plotted in Fig. 3. Eleven of the 20 estimates by the Edmondson-Paloheimo model are contained within the 95% confidence limits of their associated  $\hat{b}$  values (calculated under the assumptions of normality, Keen and Nassar 1981). The average absolute deviation between  $b_{EP}$  and  $\hat{b}$  is  $0.026 \text{ d}^{-1}$ , only 2 of the 20 deviations exceeding  $0.05 \text{ d}^{-1}$ . Furthermore, there are no differences in the temporal patterns of instantaneous birth rates predicted by the two models.

On the average, the two-age-class model provides a better estimate of  $\hat{b}$  than  $b_{EP}$  does, the mean absolute deviation being equal to 0.012, and the largest discrepancy being  $0.069 \text{ d}^{-1}$ . However, it is important to note that Eq. 12 sometimes actually produces birth rate estimates which are farther from  $\hat{b}$  than  $b_{EP}$ . This is because the two-class model can conceal important linkages between characteristics within more restricted size classes (i.e.,  $E_x$ ,  $P_x$ ,  $r_x$ , and  $m_x$ ) at times

when the Edmondson-Paloheimo equation fortuitously compensates for them.

#### DISCUSSION

This analysis supports the continued use of the Edmondson-Paloheimo equation within certain limits. Since the mean deviation between  $b_{EP}$  and  $\hat{b}$  in this study was  $0.026 \text{ d}^{-1}$ , the 95% confidence limits for  $b_{EP}$  with respect to  $\hat{b}$  must be in excess of that. Based on the exact deviations for the 20 experiments, 90% of the  $b_{EP}$  were within 0.047 of their associated  $\hat{b}$ , while 95% were within 0.112. Given the extreme divergence between  $(r_a + m_a)$  and  $(r + m)$  during some of these experiments (Table 1), it seems unlikely that deviations between  $b_{EP}$  and  $\hat{b}$  for other species and/or environments would greatly exceed those here. Thus, as a rough approximation, if a variance in  $b$  of about  $(0.112/1.96)^2 = 0.003$  can be tolerated, then the Edmondson-Paloheimo model provides an adequate estimate of  $\hat{b}$ , and one need not resort to the additional work of ageing embryos by Threlkeld's (1979) technique, or to the analysis of age classes as suggested by Seitz (1979), or to the analysis of multiple samples (Keen and Nassar 1981). Furthermore, under the assumption of equal variances in different samples, we can estimate the absolute difference between any two estimates of  $b$  necessary for statistical significance. Using the standard normal deviate (Keen and Nassar 1981) a critical difference of  $0.15 \text{ d}^{-1}$  is found to be required for significance at the 0.05 level. These results might be useful in assessing the validity of pre-

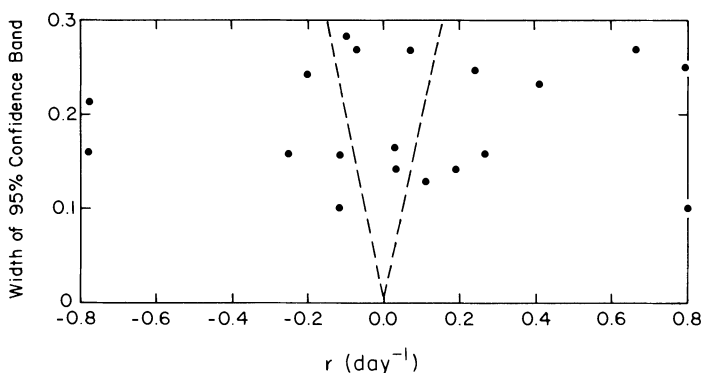


FIG. 4. Distribution of estimated rates of increase and their associated 95% confidence limits for *Daphnia pulex* in Busey Pond and Little Lake. Points between the dashed lines have confidence limits which contain  $r = 0$ , and which cannot be discriminated as positive or negative at the .05 level of significance.

viously published interpretations which have been based on the Edmondson-Paloheimo model.

An equally important problem in zooplankton demography is the general lack of attention to the sources and magnitude of the variance in the other instantaneous rates in Eq. 3. The importance of sampling variability as a source of variance for  $r$  has only recently been investigated theoretically by Keen and Nassar (1981). Their results are empirically underscored by this study.

The sampling scheme I employed was unusually thorough, involving sampling by 15 vertical hauls and counting at least 5 subsamples. The coefficients of sampling (0.051) and subsampling (0.066) variation are roughly three times lower than any that have been previously reported. Yet the 95% confidence limits for the estimated rates of population increase (from Eq. 9, assuming normality) averaged  $\pm 0.098 \text{ d}^{-1}$ , and as can be seen in Fig. 4, 25% of the estimates cannot be characterized as positive or negative at the 0.05 level. For coefficients of variation three times as large, only 30% of the  $r$  estimates would be distinguishable from zero.

The problem becomes particularly serious when attempting to estimate  $m$  by difference. By the additivity of variances,

$$\text{Var } m = \text{Var } r + \text{Var } b.$$

Assuming the variance of  $b_{EP}$  to be 0.003, and taking the average variance of  $r$  estimated here (0.0025), a rough estimate for the 95% confidence limits of  $m$  for this study using Eqs. 2 and 3 is a rather substantial  $\pm 0.145 \text{ d}^{-1}$ . For coefficients of sampling and subsampling variation three times as large, the 95% confidence limits would increase to  $\pm 0.313 \text{ d}^{-1}$ . These results echo the caveat of Prepas and Rigler (1978) and Keen and Nassar (1981) that the development of more accurate methods for estimating population densities, and not the exact structure of the birth rate equation,

is the most critical factor in the struggle to predict demographic parameters of planktonic populations.

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#### LITERATURE CITED

- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419-456.
- Caswell, H. 1972. On instantaneous and finite birth rates. *Limnology and Oceanography* 17:787-791.
- Clark, A. S., and J. C. Carter. 1974. Population dynamics of cladocerans in Sunfish Lake, Ontario. *Canadian Journal of Zoology* 52:1235-1242.
- DeMott, W. R. 1980. An analysis of the precision of birth and death rate estimates for egg-bearing zooplankters. In W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. American Society of Limnology and Oceanography, Special Symposium 3:337-345.
- Edmondson, W. T. 1960. Reproductive rates of rotifers in natural populations. *Memorie dell'Istituto Italiano di Idrobiologia* 12:21-77.
- . 1968. A graphical model for evaluating the use of the egg ratio for measuring birth and death rates. *Oecologia* 1:1-37.
- Goldman, C. R., M. D. Morgan, S. T. Threlkeld, and N. Angeli. 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. *Limnology and Oceanography* 24:289-297.
- Keen, R., and R. Nassar. 1981. Confidence intervals for birth and death rates estimated with the egg-ratio technique for natural populations of zooplankton. *Limnology and Oceanography* 26:131-142.
- Kendall, M., and A. Stuart. 1977. *The advanced theory of statistics*. Volume 1. Distribution theory. Fourth Edition. Macmillan, New York, New York, USA.
- Kerfoot, W. C., and C. Peterson. 1979. Ecological interactions and evolutionary arguments: investigations with predatory copepods and *Bosmina*. *Fortschritte der Zoologie* 25:159-196.

- Kwik, J. K., and J. C. H. Carter. 1975. Population dynamics of limnetic Cladocera in a beaver pond. *Journal of the Fisheries Research Board of Canada* **32**:341–346.
- Lynch, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. *Limnology and Oceanography* **24**:253–272.
- Paloheimo, J. E. 1974. Calculation of instantaneous birth rate. *Limnology and Oceanography* **19**:692–694.
- Prepas, E., and F. H. Rigler. 1978. The enigma of *Daphnia* death rates. *Limnology and Oceanography* **23**:970–988.
- Seitz, A. 1979. On the calculation of birth rates and death rates in fluctuating populations with continuous recruitment. *Oecologia* **41**:343–360.
- Threlkeld, S. T. 1979. Estimating cladoceran birth rates: the importance of egg mortality and the egg age distribution. *Limnology and Oceanography* **24**:601–612.

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