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## Estimation of size-specific mortality rates in zooplankton populations by periodic sampling<sup>1</sup>

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### *Abstract*

Many populations of small, mobile organisms cannot be analyzed with standard demographic techniques. A method is introduced for estimating patterns of size-specific mortality for such species from periodic samples. The technique does not require that individuals be marked or recaptured and may be extended to age and other quantitative characters so long as the class distribution of the population and the rate of flux of individuals between classes can be accurately determined. The most serious difficulty in applying the technique seems to be the ability to sample adequately populations that are patchy in space. However, even if the problem of patchiness cannot be eliminated, so long as the size-frequency distribution can be accurately described, the technique generates the correct pattern of size-specific mortality and will provide minimum estimates of mortality for the different classes. Preliminary results presented for four species of planktonic cladocerans suggest that more widespread application of the technique may allow an empirical test of the assumptions on which zooplankton community theory is based.

Existing theory of zooplankton community structure critically rests on assumptions relating the mortality patterns of natural zooplankton populations with body size. It is well known that vertebrate predators (fish and salamanders) selectively prey on large zooplankton and that invertebrate predators preferentially remove small species and instars (Hall et al. 1976). Since vertebrate predators are thought to effectively remove the large invertebrate predators, it is frequently suggested, either explicitly or implicitly, that herbivorous zooplankton living in the presence of vertebrates will be subject to more intense mortality as they become larger; the opposite pattern is expected in vertebrate-free environments (Allan 1974; Dodson 1974; Kerfoot 1975; Hall et al. 1976; Lynch 1977, 1979, 1980). These arguments are often invoked to explain species distributions, morphologies, and life histories, even though the size-specificity of mortality in natural zooplankton

populations has never actually been measured.

Actual size-dependent mortality patterns in zooplankton communities could be very different from theoretical expectations. In many environments vertebrate and invertebrate predators coexist. Non-predatory sources of mortality, such as starvation, disease, and physiological stress may also be important. Unless the relative importance of all of these sources of mortality is known, measuring the size-specificity of individual mortality sources, although valuable in itself, provides no information on the pattern of size-specific mortality from a zooplankton's perspective.

Standard mark and recapture techniques cannot be easily applied to the zooplankton since most of them molt at regular intervals. Even were marking possible, zooplankton generally live in such large populations that enormous numbers of individuals would have to be labeled before an appreciable probability of recapture was attained. Furthermore, marking of small individuals may often alter their appearance or impair their behavior in ways that could magnify their vulnerability.

Some models do exist that allow a par-

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tioning of the mortality incurred by zooplankton populations without marking or recovering individuals, but these are extremely restrictive either with respect to the number of classes dealt with (Argentesi et al. 1974; Seitz 1979; Taylor and Slatkin 1981) or to the population characteristics assumed (e.g. stationary size distribution, constant recruitment, absence of prerecruitment mortality, uniform distribution of individuals within classes) (Smith *cited in* Cooper 1965; Fager 1973; Van Sickle 1977). I have developed a more general technique that may be applied to any population for which the size structure and size-specific growth and reproductive rates can be periodically and accurately assessed. Although it is expressed here primarily in the context of size-specific mortality, the model may be rederived in terms of any other characters (including age) so long as the flux rates of individuals into and out of classes can be predicted.

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### The theory

A knowledge of the size-abundance distribution and the size-specific growth and reproductive rates of a population allows one to predict the number of individuals in a specific size class at some future date under the assumptions of no mortality in that size class,

$$N_{x,t} = N_{x,0} + \sum_{i=1}^{x-1} G_{i,x} P_{i,x} - \sum_{i=x+1}^w G_{x,i} + \sum_{i=1}^w R_{i,x} \quad (1)$$

[where  $N_{x,0}$ ,  $N_{x,t}$  are densities ( $\text{No.} \cdot \text{m}^{-2}$ ) of individuals in size class  $x$  at times 0 and  $t$ ,  $G_{i,x}$  the expected number of individuals in size class  $i$  at time 0 that would

grow into and remain in size class  $x$  over time period  $(0,t)$ ,  $P_{i,x}$  the probability of individuals in  $G_{i,x}$  surviving to enter size class  $x$ ,  $G_{x,i}$  the expected number of individuals in size class  $x$  at time 0 growing into size class  $i$  over time period  $(0,t)$ ,  $R_{i,x}$  the expected number of newborns derived from size class  $i$  and accumulating in size class  $x$  over time period  $(0,t)$  (weighted by their probability of survival before entering size class  $x$ ), and  $w$  the index for the last size class].

Let the expected size of an individual at time  $t$  ( $B_t$ ) be described by the general growth function

$$B_t = g(B_0)$$

and designate the lower bound of size class  $x$  as  $L_x$ . Then the minimum size at time 0 necessary to enter size class  $x$  by time  $t$  is

$$M_x = g^{-1}(L_x).$$

If we assume that all individuals of equal size behave homogeneously with respect to growth, all individuals with  $M_x \leq B_0 < L_x$  will reside in a size class  $\geq x$  at time  $t$ . The potential number of size classes which individuals may grow through during time  $(0,t)$  depends on the magnitude of  $t$  as well as on the width of the designated size classes. Since the object is to estimate size-class-specific mortality rates, it is important that these parameters be set so that over  $(0,t)$  individuals go through a minimum number of size classes. For completeness in the following derivation, I allow for the possibility that some individuals may pass through one entire size class over  $(0,t)$ . The following boundary conditions then apply:

$$\begin{aligned} G_{i,x} &= 0 & \text{for } i \leq x - 3, \\ G_{x,i} &= 0 & \text{for } i \geq x + 3, \\ G_{w,w+2}, G_{w,w+1}, G_{w-1,w+1}, G_{0,1}, G_{0,2} &= 0, \end{aligned}$$

and

$$\sum_{i=1}^w R_{i,x} = 0 \quad \text{for } x \geq 3.$$

The growth of individuals into and out of the size classes is estimated as follows. If  $M_x \geq L_{x-1}$ , then

$$\begin{aligned} G_{x-2,x} &= 0, \\ G_{x-1,x} &= N_{x-1,0} \cdot I_{x-1,x} \end{aligned}$$

(where  $I_{x-1,x}$  is the proportion of individuals in size class  $x - 1$  for which  $M_x \leq B_0 < M_{x+1}$ ). If  $M_x < L_{x-1}$ , then size class  $x$  receives recruits from the two smaller size classes:

$$G_{x-2,x} = N_{x-2,0} \cdot I_{x-2,x}$$

and

$$G_{x-1,x} = N_{x-1,0} \cdot (1 - I_{x-1,x+1}).$$

Depending on the degree of precision acceptable for determining the size-abundance distribution of the population, one can use different methods of estimating the  $I$  values. If individuals are assigned to size classes without recording their precise sizes, one must assume a uniform distribution of individuals within each class. However, when precise measurements of individuals are recorded, the distribution of individuals within size classes can be determined, and more accurate estimates of the flux rates are possible.

The predicted flux of individuals between size classes by growth provides a sufficient base for estimating instantaneous size-specific mortality rates ( $m_x$ ) for  $x > 2$ .  $m_x$  (day<sup>-1</sup>) is determined by comparing the actual density of individuals in a size class at time  $t$  with that predicted in the absence of mortality. ( $G_{x-2,x} + G_{x-1,x}$ ) is actually the maximum expected influx of individuals into size class  $x$  when there is no mortality in size classes  $x - 2$  and  $x - 1$ . Thus, so as not to inflate the mortality rate estimate for size class  $x$ , its potential recruits should be weighted by their probability of surviving to enter size class  $x$  as in Eq. 1; for instance,  $G_{x-1,x}$  should be reduced by an appropriate function involving  $m_{x-1}$ . Unfortunately, this exact approach is not possible; the mortality rates of the first two size classes cannot be determined until their expected influx of newborns is known, which in turn requires a knowledge of the mortality rates of adults. Thus, prerecruitment mortality between size classes has been ignored in previous attempts to partition

the death rate among classes (cf. a derivation by F. E. Smith *cited in* Cooper 1965).

This problem can be partially avoided by assuming that the recruits to any size class  $x$  are at time 0 sufficiently close to  $L_x$  that their mortality rate is about equal to that of size class  $x$ . The validity of this assumption can be maximized by making the size class widths considerably greater than the expected growth increments, i.e.  $L_x - M_x \ll L_x - L_{x-1}$ . The instantaneous mortality rates for  $x \geq 3$  are then approximated by

$$\begin{aligned} m_x &= \{ \ln [N_{x,0} + (G_{x-1,x} + G_{x-2,x}) \\ &\quad \times \exp(-m_x t/2) \\ &\quad - (G_{x,x+1} + G_{x,x+2})] \\ &\quad - \ln [N_{x,t}] \} / t, \end{aligned} \tag{2}$$

which can be solved by Newton's method or other suitable numerical techniques.

Once the mortality rates of adults have been determined, the rate of production of offspring can be derived. The total number of eggs from adults of size class  $x$  hatching during time  $(0, dt)$  is equal to the total number of eggs laid during time  $(-D, -D + dt)$  that survive to hatching, where  $D$  is the egg development time. For live bearers, such as cladocerans and rotifers,

$$b_x N_{x,0} dt = 1_x [N_{x,0} \times \exp(-r_x D)] \times \exp(-m_x D) dt \tag{3}$$

[where  $b_x$  is the instantaneous birth rate for size class  $x$  (day<sup>-1</sup>),  $1_x$  the instantaneous rate of egg laying by size class  $x$  (day<sup>-1</sup>), and  $r_x = (\ln N_{x,t} - \ln N_{x,0})/t$  the size-class-specific growth rate (day<sup>-1</sup>)].

Integrating Eq. 3 and assuming the parameters defined above to be constant over  $(0, t)$ , we find the expected production of newborns by size class  $x$  over  $(0, t)$  is

$$\begin{aligned} R_x &= 1_x \times \exp(-m_x D) \\ &\quad \times N_{x,0} \int_0^t \times \exp[-r_x(D - \tau)] d\tau, \end{aligned}$$

which simplifies to

$$\begin{aligned} R_x &= 1_x N_{x,0} \times \exp[-(m_x + r_x)D] \\ &\quad \times [\exp(r_x t) - 1] / r_x. \end{aligned} \tag{4}$$

The instantaneous rate of egg laying,  $l_x$ , can be expressed in terms of a more easily measured parameter, the mean clutch size for the size class, as follows. The total number of eggs and embryos attributable to size class  $x$  at time 0 is

$$E_{x,0} = l_x \int_{-D}^0 N_{x,\tau} \times \exp(m_x \tau) d\tau.$$

Noting that  $N_{x,\tau} = N_{x,0} \exp(r_x \tau)$  and integrating, we find the egg ratio for size class  $x$  to be

$$\begin{aligned} C_{x,0} &= \frac{E_{x,0}}{N_{x,0}} \\ &= \frac{l_x \times \{1 - \exp[-(m_x + r_x)D]\}}{m_x + r_x}. \end{aligned} \tag{5}$$

Rearranging Eq. 5 and substituting for  $l_x$  in Eq. 4 gives

$$R_x = \frac{C_{x,0} N_{x,0} (m_x + r_x) [\exp(r_x t) - 1]}{r_x \{ \exp[(m_x + r_x)D] - 1 \}}.$$

Finally, when the sampling interval  $(0, t)$  is long enough for some individuals born during  $(0, t)$  to grow through the first size class, it is necessary to partition  $R_x$  into  $R_{x,1}$  and  $R_{x,2}$ . This requires an estimate of the time,  $s$ , it takes a newborn of size  $B^*$  to grow to size  $L_2$ . The instantaneous rate of growth for an individual of size  $B_0$  is

$$q(B_0) = \{ \ln[g(B_0)] - \ln B_0 \} / t$$

so that

$$\left. \frac{dB}{dt} \right|_{B^*} = q(B^*) \times B^*.$$

Then

$$s = t \int_{B^*}^{L_2} \frac{1}{B \{ \ln[g(B^*)] - \ln B^* \}} dB,$$

most forms of which can be solved by numerical integration techniques.

If  $s \geq t$ , then

$$R_{x,2} = 0,$$

and

$$R_{x,1} = R_x;$$

if  $s < t$ , all juveniles born over the interval  $(0, t - s)$  will be in size class 2, so that

$$R_{x,2} = \frac{C_{x,0} N_{x,0} (m_x + r_x) \cdot \{ \exp[r_x(t - s)] - 1 \}}{r_x \{ \exp[(m_x + r_x)D] - 1 \}},$$

and

$$R_{x,1} = R_x - R_{x,2}.$$

Note that  $R_{x,2}$  is not yet weighted by mortality incurred in the first size class.

Equations for the mortality rates of the first two size classes can now be derived, assuming that size classes 1 and 2 do not reproduce. For size class 1,

$$\begin{aligned} m_1 &= \{ \ln[N_{1,0} + \sum_{x=3}^w R_{x,1} - (G_{1,2} + G_{1,3})] \\ &\quad - \ln[N_{1,t}] \} / t. \end{aligned}$$

For the second size class, if  $s \geq t$ ,

$$\begin{aligned} m_2 &= \{ \ln[N_{2,0} + G_{1,2} \times \exp(-m_1 t / 2) \\ &\quad - (G_{2,3} + G_{2,4})] - \ln[N_{2,t}] \} / t; \end{aligned}$$

if  $s < t$ ,

$$\begin{aligned} m_2 &= \{ \ln \{ N_{2,0} + [N_{1,0}(1 - I_{1,3}) \\ &\quad \times \exp(-m_1 s / 2)] \\ &\quad + [\exp(-m_1 s) \sum_{x=3}^w R_{x,2}] \\ &\quad - (G_{2,3} + G_{2,4}) \} - \ln[N_{2,t}] \} / t. \end{aligned}$$

### Applications with planktonic cladocerans

Size-specific mortality rates were estimated on several occasions for a population of *Daphnia pulex* in a temporary environment, Busey Pond, Illinois, an old oxbow with a maximum width of 5 m and a maximum depth of 1.5 m. The patterns of size-specific mortality simultaneously falling on three smaller Cladocera (*Bosmina longirostris*, *Ceriodaphnia lacustris*, and *Diaphanosoma leuchtenbergianum*) were examined in Dynamite Lake, Illinois. This shallow (2-m max depth), dilute lake has a surface area of about 0.6 ha.

The application of the periodic sampling technique requires that the size-abundance distribution of a population be accurately determined. Routine sampling was by 16 evenly spaced vertical hauls from a 10- × 10-m sampling grid with a 63- $\mu$ m Wisconsin net with a 13-cm mouth

Table 1. Within- and between-sites comparisons of density estimates and coefficients of sampling and subsampling variation for four species of cladocerans ( $N$ —number of sampling sites).

	$N$	$F$ -test ( $P$ )		C.V.	
		Within-site	Between-site	Sample	Subsample
Dynamite Lake, 27 Jun 79					
<i>Bosmina longirostris</i>	6	NS	—	0.108	0.208
<i>Ceriodaphnia lacustris</i>	6	NS	—	0.196	0.215
<i>Diaphanosoma leuchtenbergianum</i>	6	0.01	—	0.308	0.155
Dynamite Lake, 11 Jun 80					
<i>B. longirostris</i>	3, 5	NS	<0.01	0.220	0.136
<i>C. lacustris</i>	3, 5	NS	NS	0.053	0.234
<i>D. leuchtenbergianum</i>	3, 5	NS	<0.01	0.146	0.089
Little Lake, 30 Nov 78					
<i>Daphnia ambigua</i>	6	NS	—	0.051	0.066

opening. For counting animals, 5–10 1-ml subsamples were scored from each pooled sample (normally 5–10% of the total volume). Size-frequency distributions were estimated by measuring with an ocular micrometer to the nearest 0.01 mm a minimum of 200 individuals from the top of the head to the base of the tail spine (for cyclomorphotic species carapace length is the preferred measure). This detailed information allowed the  $I$  values to be estimated from information on the size distribution of individuals within size classes.

Simultaneous sampling with a clear 3.5-liter Kemmerer and the Wisconsin net provided no evidence that the net preferentially excluded or collected any sizes of the species in Table 1. Had this been a problem, correction factors based on net selectivity could have been used to improve the accuracy of the size-abundance distributions.

Horizontal variation in the size-frequency distribution of populations can be another problem, particularly if patches change location during an experiment. On 11 June 1980 five adjacent grids were sampled in Dynamite Lake and the size-frequency distributions of the three cladocerans were determined for each by the standard technique; the central station was sampled three times to determine the within-site variation. A  $\chi^2$  heterogeneity test with both 0.10- and

0.05-mm size classes indicated that the size-frequency distributions of all three species were homogeneous within and between sites. Thus, for this lake it appears that our sampling procedure adequately portrays the size-frequency distribution of populations over a scale of at least 30 m.

If the size-frequency distribution of a population can be accurately determined, the estimated pattern of size-specific mortality is independent of the total population size estimates. This can be seen most easily by considering all terms in Eq. 2 to be functions of  $N_0$  or  $N_t$ ; the estimated  $m_x$  values all deviate from their true values by the same absolute amount determined by the error in  $N_0$  and  $N_t$ . Only the absolute values of the mortality estimates depend on the density estimates.

The adequacy of this sampling scheme for density estimates has been examined on three occasions (Table 1). With only one exception, replicate density estimates within sites were homogeneous. Only the 1980 experiment allowed an examination of between-sites variation; for two of the three species there were significant density differences between sites. The amount of error in the absolute values of the mortality rate estimates caused by this horizontal variation in population size will depend on the degree of horizontal migration; in the absence of hori-

Table 2. Variance estimates for  $m_x$  assuming the estimates of population densities to be the dominant source of variance.

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Variance expressions for mortality rate estimates

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For  $x > 2$ , and for  $x = 2$  if  $s > t$ ,

$$\text{Var}(m_x) = \frac{(1/tN_0)^2\text{Var}(N_0) + (1/tN_t)^2\text{Var}(N_t)}{1 + \frac{k_2}{2[k_1\exp(m_x t/2) + k_2]}}$$

where  $N_0, N_t$  = the estimated total population sizes at time 0 and  $t$ ,

$$k_1 = (N_{x,0} - G_{x,x+1} - G_{x,x+2})/N_0,$$

$$k_2 = (G_{x-1,x} + G_{x-2,x})/N_0.$$

For  $x = 1$ ,

$$\text{Var}(m_1) = (1/tN_0)^2\text{Var}(N_0) + (1/tN_t)^2\text{Var}(N_t) + \sum_{x=2}^w \text{Var}(m_x) \{E_x N_{x,0} [\exp(r_x t) - 1]\}^2 \left\{ \frac{[1 - (m_x + r_x)D] \times \exp[(m_x + r_x)D] - 1}{r_x t \{ \exp[(m_x + r_x)D] - 1 \}^2 [k_3 + \sum_{x=2}^w R_{x,1}]} \right\}^2$$

where  $k_3 = N_{1,0} - G_{1,2} - G_{1,3}$ .

For  $x = 2$ , if  $s \leq t$ ,

$$\text{Var}(m_2) = (1/tN_0)^2\text{Var}(N_0) + (1/tN_t)^2\text{Var}(N_t) + \text{Var}(m_1) \left\{ \frac{s[(N_{1,0}/2) \times \exp(-m_1 s/2) + \exp(-m_1 s) \sum_{x=2}^w R_{x,2}]}{sk_4} \right\}^2 + \sum_{x=2}^w \text{Var}(m_x) \times \{ \exp(-m_1 s) E_x N_{x,0} [\exp(r_x t) - 1] \}^2 \left\{ \frac{[1 - (m_x + r_x)D] \times \exp[(m_x + r_x)D] - 1}{r_x t \{ \exp[(m_x + r_x)D] - 1 \}^2 k_4} \right\}^2$$

where  $k_4 = N_{2,0} + N_{1,0} \times \exp(-m_1 s/2) + \sum_{x=2}^w R_{x,2} - (G_{2,3} + G_{2,4})$ .

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zontal migration, the problem will be eliminated. The problem can be minimized by sampling a larger grid.

The usefulness of the periodic sampling technique depends on the sensitivity of the mortality estimates to sampling variance. On the assumption that extensive analyses of collected samples can provide accurate descriptions of the size-frequency distributions, the size-class-specific clutch sizes, and the growth rate function, then the variance of  $m_x$  is simply a function of the sampling and subsampling variance for the total population density estimates. Expressions for the variance of  $m_x$  derived following Kendall and Stuart (1977, p. 246-247) are given in Table 2; other potential components of variance could be accounted for by further Taylor expansion. In the following analyses I have used these expressions to estimate confidence limits for the mortality rates by calculating the variances of population size from the mean species-

specific coefficients of variation in Table 1; normality of the mortality estimates seems likely (Keen and Nassar 1981). Ideally one should use direct estimates of variance in the variance equations but this would require extra fieldwork. When multiple samples are available for both dates, dependence on these variance expressions can be avoided entirely by randomly pairing samples and making multiple estimates of  $m_x$  (Keen and Nassar 1981).

Size-class-specific clutch sizes,  $C_{x,0}$ , were almost always averages of 20-50 measures in this study. The size at birth,  $B^*$ , was approximated by averaging the two smallest individuals measured on both the initial and final sampling of an experiment. The egg development time,  $D$ , a function of temperature, was taken from Bottrell et al. (1976) for *D. pulex*, Kerfoot and Peterson (1979) for *Bosmina*, and Kwik and Carter (1975) for *Ceriodaphnia*. In the absence of published egg

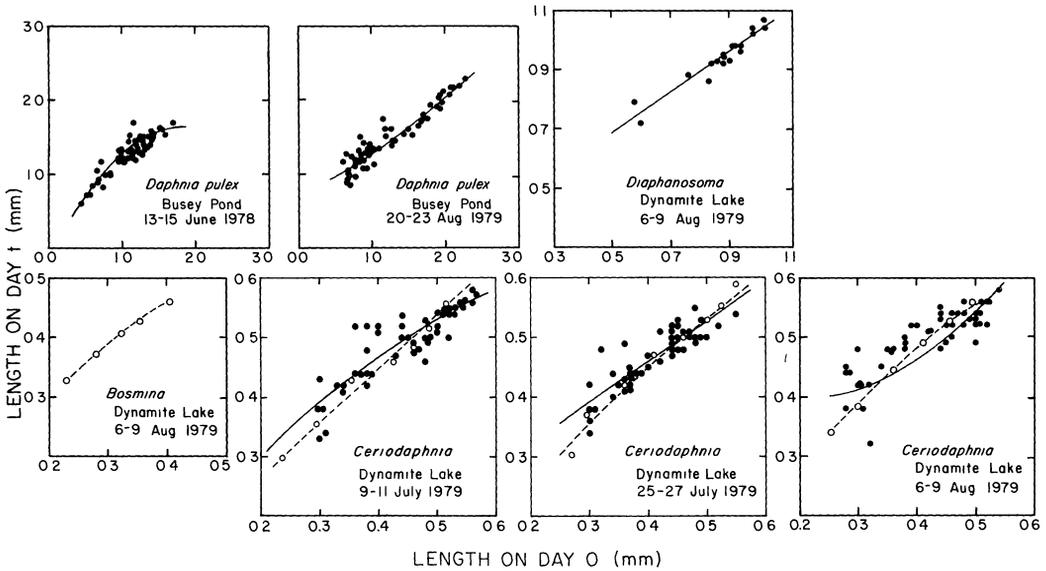


Fig. 1. Some representative samples of growth determinations for cladocerans. Solid circles and lines are for laboratory experiments; open circles and dashed lines for *Bosmina* and *Ceriodaphnia* are for instar analyses.

development times for *Diaphanosoma*, the average of *D* for *Bosmina* and *Ceriodaphnia* was used as an estimate for the egg development time of this species; as indicated by Bottrell et al. (1976) and Herbert (1978) there is little variation in *D* between species.

Busey Pond and Dynamite Lake do not stratify. Therefore, I could determine the size-specific growth rates in a laboratory incubator set for pond temperature and light conditions. For each experiment, 50–100 random individuals were removed from the field, measured to the nearest 0.01 mm, and individually maintained in 40 ml of fresh pond water that had previously been strained through 60- $\mu$ m Nitex netting, a procedure that removes other zooplankton but leaves the available food particles intact. The duration of each experiment and the width of size classes used in the analyses were set so that individuals could not grow through more than one size class. For experimental periods about equal to the duration of an instar, this procedure probably adequately portrays the growth function since the molt cycle is likely to be physiologically set before individuals are returned to the

laboratory (Passano 1960). First- or second-order regressions of size at the final measure on initial size were used to express the growth functions. Some representative fits are provided in Fig. 1.

The size-specific growth rates of *Bosmina* could not be determined by this procedure because individuals tended to become caught at the air–water interface. However, when individuals from preserved samples are separated into narrow size classes, it is generally possible to estimate average instar sizes and growth functions for *Bosmina* as well as *Ceriodaphnia* (Figs. 1, 2). A regression of size at instar  $x + 1$  on size at instar  $x$  can be converted to the standard regression of size on day  $t$  vs. size on day 0 as follows. The mean daily rate of growth for individuals of size  $B_0$  is  $(B_D - B_0)/D$ , and the mean increment in size over time  $(0, t)$  is  $(B_D - B_0)t/D$ . Thus,

$$B_t = B_0 + [t(B_D - B_0)/D]. \quad (6)$$

If we let the binomial regression of instar sizes be

$$B_D = a_1 B_0^2 + a_2 B_0 + a_3,$$

substituting in Eq. 6 then yields

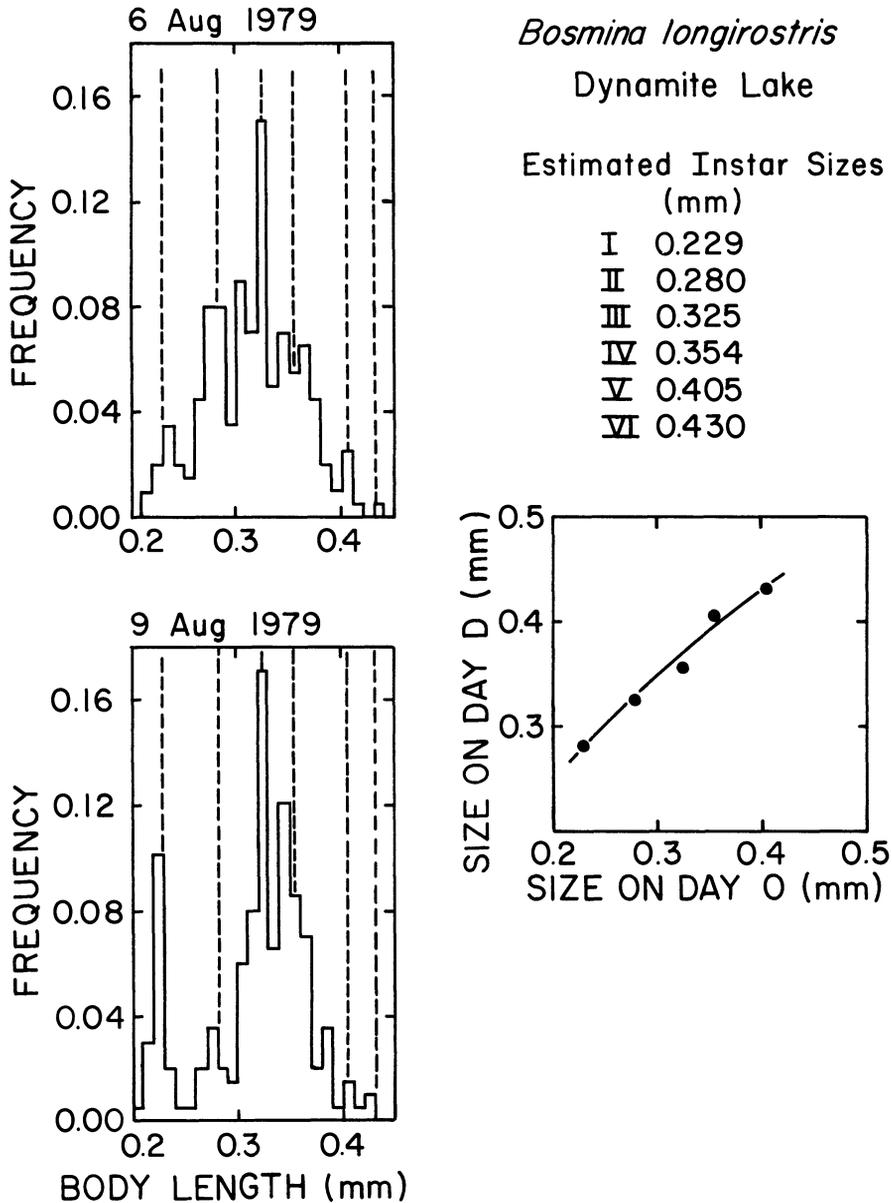


Fig. 2. Example of an analysis of instar sizes to provide an estimate of growth function for *Bosmina*. Average instar sizes were determined as weighted means of discrete clumps of size measures that appeared on both sampling dates of an experiment. A regression of size on day  $D$  on size on day 0, i.e. between adjacent instar sizes, was then converted to the growth rate function (Fig. 1) as described in text.

$$B_t = [a_1 t B_0^2 + (D + a_2 t - t) B_0 + a_3 t] / D.$$

The fact that both the instar analysis with preserved samples and the laboratory growth experiments yield similar growth

curves for *Ceriodaphnia* provides support for this method of analysis (Fig. 1).

Estimated patterns of size-specific mortality are given for several dates for *D. pulex* in Fig. 3. The 95% C.L. for the

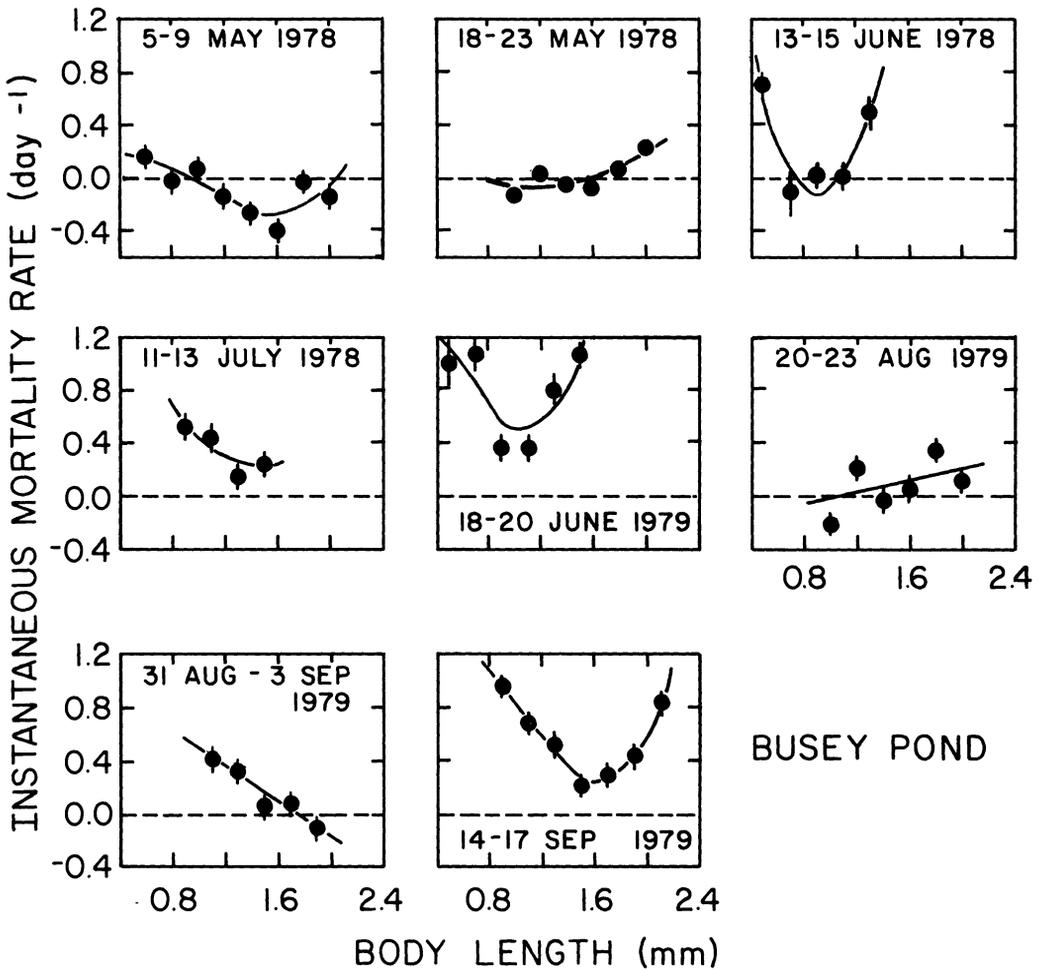
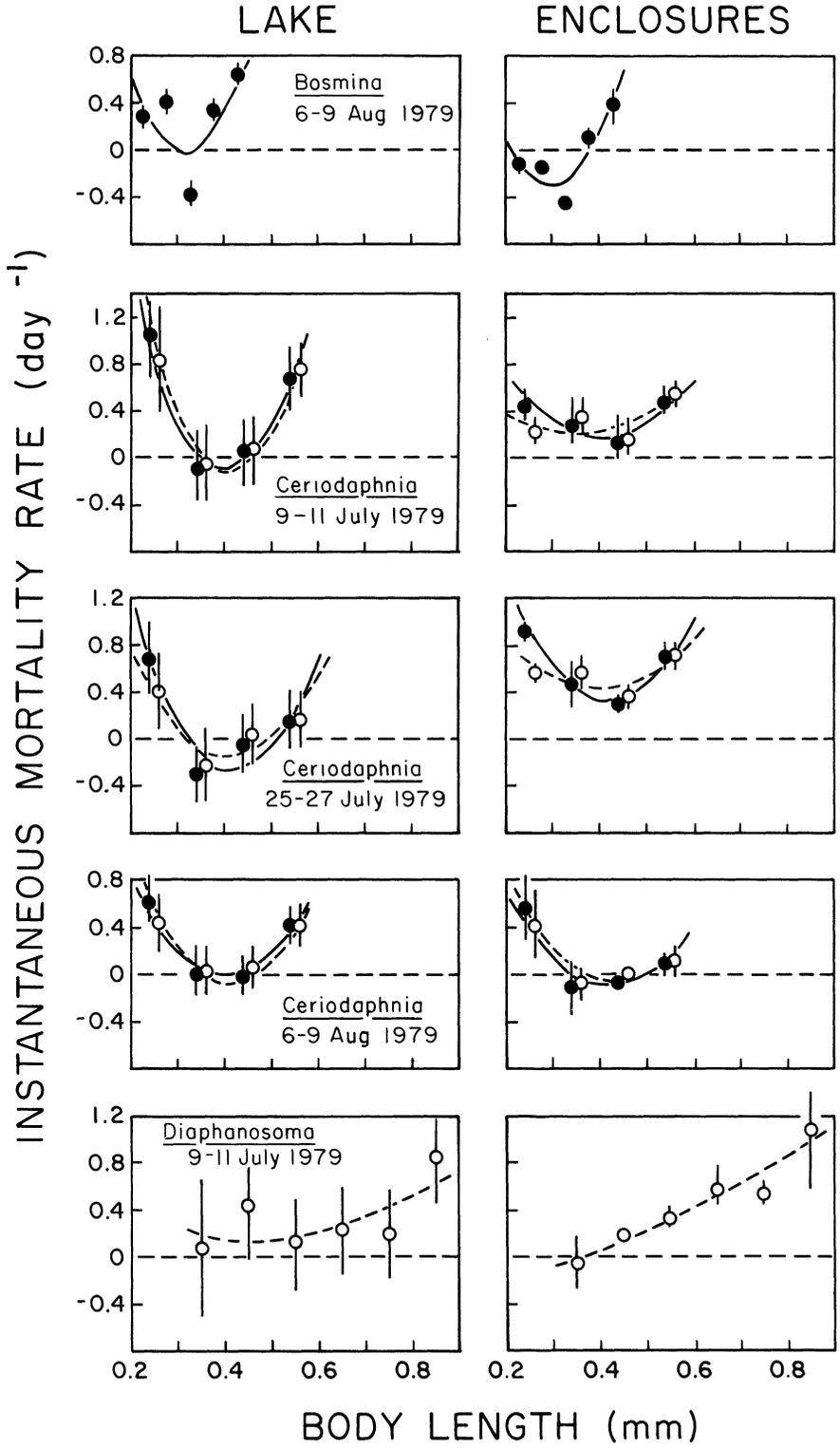


Fig. 3. Estimates of size-specific instantaneous mortality rates and 95% C.L. for *Daphnia pulex* in Busey Pond fitted with polynomial regressions.

mortality estimates of this species are narrow relative to the difference between size classes so that size variation in mortality can indeed be detected. Negative mortality rate estimates were not unexpected for the one or two smallest size classes; when recruitment from resting eggs occurs, as it does in this population, the periodic sampling technique will underestimate the production of offspring during an experiment. For that reason, those size classes that could receive newborns during the experiment have been excluded from Fig. 3 except on dates when their estimated mortality was con-

spicuously high relative to that of the larger size classes. Conspicuous negative mortality estimates for adult size classes only arose on 5-9 May 1978, and it is of interest that this was the only occasion on which sampling was at a single point in the pond rather than over a grid. In future applications, the use of Keen and Nassar's (1981) multiple sampling technique should further minimize problems with negative mortality estimates.

Figure 4 contains the direct estimates of size-specific mortality determined for the three species of cladocerans in Dynamite Lake. As in Busey Pond, the con-



fidence limits for the  $m_x$  values were generally small enough that size-specificity of mortality could be discerned. With the exception of *Bosmina*, significantly negative mortality estimates were rare.

Parallel experiments were run on each date in Dynamite Lake in triplicate 1.0-m-diameter polyethylene enclosures extending from the lake surface to the sediments. The bottoms of these chambers consisted of a rigid hoop across which was stretched 0.5-cm netting, the purpose being to separate fish predation from the other components of mortality (potential physiological problems and invertebrate predation) operating on the cladoceran populations (Lynch et al. 1981). The enclosure results further implicate horizontal heterogeneity as a potential factor contributing to negative mortality rate estimates. Stirring the enclosures before sampling effectively eliminated any possibility of spatial heterogeneity and gave rise to negative mortality rates much less frequently than did the lake. In a total of four experiments the proportion of size-specific mortality rates significantly  $<0$  at the 0.05 level in the lake and bags were: *Bosmina*—0.57 ( $N = 21$ ) and 0.27 ( $N = 30$ ), *Ceriodaphnia* (using laboratory growth functions)—0.06 ( $N = 17$ ) and 0.00 ( $N = 37$ ), and *Diaphanosoma*—0.28 ( $N = 25$ ) and 0.05 ( $N = 74$ ).

The higher incidence of negative mortality estimates in *Bosmina* is troubling, particularly because it is consistent between enclosures and lake on a given date (Fig. 4). The most likely explanation is that the growth rate expressions for this species are erroneous, perhaps because Kerfoot and Peterson's (1979) instar duration times do not apply to this population. Some laboratories have been highly successful in handling *Bosmina* (C. Goulden pers. comm.), and the use of

more delicate and sensitive techniques may permit direct estimates of *Bosmina* growth rates in the future.

Actually the mortality model can tolerate a fair amount of error in the growth rate function, as can be seen by comparing the patterns of size-specific mortality for *Ceriodaphnia* generated by using the growth functions from direct observations and from instar analyses given in Fig. 1. In all six cases illustrated in Fig. 4 the two patterns of mortality are nearly identical.

Finally, a comparison of estimated mortality rates between enclosures places some confidence in the replicability of the technique. As can be seen by the ranges of size-specific mortality rates plotted in Fig. 4, the differences between enclosures tend to be quite small, generally less than the width of the 95% C.L. in the lake.

#### Discussion

In light of the potential complications that could have arisen in the estimation of  $m_x$  by periodic sampling but did not, these preliminary results suggest that the insights into size-specific mortality generated by the model may be well worth the large amount of work necessary for its application. Extension of this kind of analysis to a variety of populations and environments should allow critical evaluation of several of the assumptions implicit in the theoretical foundations of zooplankton community ecology. For example, application of the technique to the cladocerans of Dynamite Lake, a lake with an extremely dense planktivorous fish population, cast serious doubt on the widely accepted assumption that direct size-selective predation by fish is the dominant selective force operating on such communities (Lynch et al. 1981);

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←  
 Fig. 4. Estimates of size-specific instantaneous mortality rates for three species of planktonic cladocerans in Dynamite Lake. 95% C.L. are provided for lake values, means and ranges for enclosures. Solid circles and curves are for estimates derived using instar analyses; open circles and dashed curves are for values derived from laboratory experiments.

these results have recently been corroborated by experimental manipulations of fish densities (M. Vanni in prep.).

Clearly the estimation of size-specific mortality rates by periodic sampling is not satisfactory in all respects. For organisms living in homogeneous environments like unstratified lakes and ponds, the determination of size-specific flux rates may be accomplished under controlled laboratory conditions, by enclosing individuals in the field (Threlkeld 1979), or by instar analysis. However, these techniques will often be inappropriate when individuals encounter an unpredictable array of environmental conditions during an experiment, as in the case of vertically migrating zooplankton in stratified waters. It might be possible to resort to instar analysis to estimate the growth function in such cases, provided that the duration of the different instars (which may be a function of vertical distribution) can be ascertained.

As with any demographic technique applied to the plankton, the periodic sampling technique is sensitive to the horizontal distribution of populations. An accurate estimate of the size-frequency distribution of the population is particularly critical for determining the correct pattern of size-specific mortality. There is no evidence that this is a problem for the populations described here, but that does not imply that a different or more elaborate sampling procedure might not be preferable in other settings. A more serious problem may be estimating population size. As is true of population mortality rates (Keen and Nassar 1981; Polishchuk and Ghilarov 1981; Lynch 1982), negative size-specific mortality rates may arise when, because of sampling error, an abnormally large population size is estimated on the second date or an abnormally small value on the first date. The multiple sampling approach suggested by Keen and Nassar (1981) is the most judicious method of minimizing this problem.

It is worth emphasizing that even if population densities cannot be estimated

with absolute certainty, the model still provides the correct pattern of size-specific mortality so long as the size-frequency distributions and flux rates of individuals between classes are accurately known. A simple knowledge of the shape of the mortality functions for natural zooplankton populations would substantially improve our understanding of the evolutionary ecology of zooplankton communities, since most speculations on these functions have been concerned more with their shape than with their absolute value. This is with good reason. The evolution of many life history traits depends not so much on the absolute value of mortality as on its age-specific pattern (Charnov and Schaffer 1973).

If we assume that the sampling scheme is sufficiently accurate to describe the size-frequency distribution of the population, it is possible to estimate the minimal mortality rates for the size classes. Under these conditions, the true mortality rate

$$\hat{m}_x = m_x + \theta$$

for all  $x$ . Estimating the constant  $\theta$  requires that  $\hat{m}_x$  be known for at least one size class which, of course, is impossible to determine with absolute certainty. However, noting that  $\hat{m}_x \geq 0$  for all  $x$ , and letting the minimum estimated mortality rate be  $\min(m_x)$ , we find that a minimal estimate of  $\theta$  is  $-\min(m_x)$ .

Ultimately, the efficacy of the periodic sampling technique, as with all demographic techniques, would be much more firmly established if the mortality estimates that it generates could be compared with those independently derived by other methods. Yet the technique was developed for use with those organisms that are not amenable to analysis by existing demographic techniques. These initial results from the replicate bag experiments provide a good, but internal, test of the model, and the refinement of techniques to minimize the variance of the parameter estimates will further enhance the level of confidence that can be placed on any single mortality function.

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