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Estimating population birth rates of zooplankton when rates of egg deposition and hatching are periodic

R.M. Dorazio
Division of Biological Sciences and Department of Atmospheric and Oceanic Science, The University of Michigan, Ann Arbor, MI 48109, USA

Summary. I present a general method of computing finite birth and death rates of natural zooplankton populations from changes in the age distribution of eggs and changes in population size. The method is applicable to cases in which eggs hatch periodically owing to variable rates of oviposition. When morphological criteria are used to determine the age distribution of eggs at the beginning and end of a sampling interval, egg mortality can be incorporated in estimates of population birth rate. I raised laboratory populations of *Asplanchna priodonta*, a common planktonic rotifer, in semicontinuous culture to evaluate my method of computing finite birth rate. The *Asplanchna* population became synchronized to a daily addition of food but grew by the same amount each day once steady state was achieved. The steady-state rate of growth, which can be computed from the volume-specific dilution rate of the culture, was consistent with the finite birth rate predicted from the population's egg ratio and egg age distribution.

Environmental variability is a fact of life for zooplankton. The time scale of variation may be measured in hours for animals that migrate vertically through the water column experiencing different temperatures and food concentrations, or in days or weeks for populations that persist through seasonal changes in these properties. Because rates of metabolism, individual growth, and egg development rely primarily on temperature and food concentration (Edmondson 1974), variation in these two properties is expected to alter the age structure and birth rate of zooplankton populations. Diel cycles in egg deposition and hatching, for example, are common in natural zooplankton populations (Harding et al. 1951; Green 1956; Mullin 1968; Brubaker 1972; Gophen 1978; Saunders 1980; Magnien and Gilbert 1983; Tessier 1984) and may be consequences of exposure to diel changes in temperature or food concentration.

Despite the early recognition of diel periodicity in egg laying and hatching, models formulated to estimate birth rates of natural zooplankton populations (Elster 1954; Edmondson 1960; Caswell 1972; Argentesi et al. 1974; Paloheimo 1974; Seitz 1979; Taylor and Slatkin 1981; Lynch 1982; Dorazio and Lehman 1983) do not incorporate periodic recruitment owing to diel cycles. Instead the general approach is to make simplifying assumptions about the age distributions of eggs and animals in the population, to assume that population size changes exponentially during the interval between samples, and to sample populations at logistically convenient time intervals. This approach, however, leads to serious errors in estimates of population birth and death rates when the pattern of population growth and age structure is inconsistent with model assumptions (Taylor and Slatkin 1981).

In this paper I present a general method of computing birth and death rates of natural zooplankton populations that includes cases in which egg laying and hatching are periodic. The method uses the age distribution of eggs and changes in population size to compute *finite* rates of birth and death. I will show that finite rates have advantages over instantaneous measures of population growth as long as restrictions about the length of time between samples are observed. I will also discuss methods of estimating measurement error of these rates so that rates determined over different time intervals may be compared statistically.

To evaluate the model's ability to predict finite birth rate accurately, I raised laboratory populations of *Asplanchna priodonta*, a common planktonic rotifer, in semicontinuous culture. The *Asplanchna* population became synchronized to the daily addition of food causing eggs to hatch during restricted periods of each day. When the culture achieved steady-state growth, population numbers increased by the same amount each day. I was therefore able to compare finite birth rates predicted from the age distribution of eggs and egg ratio with the actual rate of birth known by virtue of culture design.

Theory

Ignoring immigration and emigration,

$$\frac{N_{t+\Delta t}-N_t}{N_t \Delta t}=B-M \tag{1}$$

expresses the per capita rate of change in population size N during the time interval Δt. B is the per capita

increment in population numbers owing to births that occur over Δt. Similarly M is the per capita death rate of the population. B and M are *finite* rates of change and have units of births or deaths per individual present at time t per unit time. This approach was originally formulated by Leslie (1948). In this case, however, the sampling interval Δt is chosen to make the assumption of exponential population growth unnecessary. Specifically, Δt is short enough so that animals born during the period between samples cannot produce offspring of their own.

The terms in Eq. 1 that can be evaluated are limited by information that is commonly available from plankton samples. Some investigators have tried to estimate mortality rates directly from temporal changes in the size distribution of animals (Tonolli 1961; Polischuk and Ghilarov 1981; Lynch 1983). These size differences, however, are generally measurable only for crustaceans and are not always good indicators of age because many zooplankton species discontinue growth upon reaching adulthood (Lynch 1980) and because individual growth rate, being dependent on food concentration and temperature, may vary with time. A routine census of the plankton usually yields the following information for each species: the total number of animals, the total number of eggs, and, if eggs are incubated until hatching or if egg ages are determined morphologically, the age distribution of the eggs (Edmondson 1965; Threlkeld 1979). Therefore, taking the approach of most egg ratio models (Edmondson 1979), the finite death rate M is computed indirectly by using census data to estimate B and the net rate of increase or decline in population numbers.

The problem of calculating finite recruitment over an interval separating two samples (i.e. population birth rate) reduces to determining the fraction of eggs present initially that hatch during Δt. Thus the finite birth rate may be computed from

$$B=\frac{E_t H}{N_t \Delta t}. \tag{2}$$

E_t = the total number of eggs in the population at time t, N_t = the total number of animals in the population at time t, and H = the fraction of eggs that hatch into newborn during the interval t to $t+\Delta t$. E_t/N_t is simply the ratio of eggs to animals or egg ratio (Edmondson 1960). H is the most difficult quantity to estimate in Eq. 2.

Rather than calculate H by assuming that the age distribution of eggs is uniform (Elster 1954; Edmondson 1960; Caswell 1972; Argentesi et al. 1974) or stable (Paloheimo 1974; Seitz 1979; Taylor and Slatkin 1981; Lynch 1982; Dorazio and Lehman 1983), H may be estimated directly if the age distribution of eggs is known. There are two ways of obtaining this distribution from zooplankton samples, and, as Threlkeld (1979) points out, they both have limitations. Originally proposed by Edmondson (1965), one way is to incubate a randomly collected sample of eggs under conditions that simulate those encountered in nature and monitor them at frequent intervals noting the times required for all eggs to hatch. The egg that takes the longest time to hatch is the youngest, and the ages of all other eggs are calculated by subtracting the lengths of time they require to hatch from the development time of the youngest egg. This procedure assumes that the incubated eggs develop similar to those in the plankton and that the sample contains representatives of eggs in all stages of development. The second assumption is not generally true because periodicity in rates of oogenesis or egg development can produce cohorts of even-aged eggs. Magnien and Gilbert (1983), for example, observed diel periodicity in hatching rates of *Keratella crassa* eggs. Regardless of when eggs were collected during a 24-h interval, all eggs hatched during the same time of day. Therefore, incubations generally do not yield the entire age distribution of eggs. They can still be used to predict H, however, when precautions are taken with respect to the interval of time between successive samples. If the interval between samples, Δt, does not exceed the length of time required for all the incubated eggs to hatch, then

$$H=\frac{1}{N_e}\sum_{i=1}^{m} N_i. \tag{3}$$

N_e = the total number of eggs that are incubated, N_i = the number of incubated eggs that hatch during the ith interval of observation, and m = the number of observation intervals of length Δx days required to make up Δt days of time (i.e. $m\Delta x=\Delta t$). Put simply, Eq. 3 yields the fraction of incubated eggs that hatch after Δt days. Notice that substituting H from Eq. 3 into the finite birth rate formula (Eq. 2) overestimates the true finite birth rate when eggs in the plankton do not hatch during the interval Δt owing to predation or other sources of egg mortality. This source of bias is inherent in hatching rates computed from incubations of eggs.

An alternative method of calculating H is to measure the age distribution of eggs directly using morphological criteria to assign eggs to developmental stages (Threlkeld 1979). Egg morphology can be used to predict age because the relative duration of each morphological stage is constant. Thus, although the absolute time spent in each stage of development varies with the total duration of egg development, the proportion of time per stage is invariant. This property is true for several zooplankton species (Cummins et al. 1969; Threlkeld 1979; Venkataraman and Job 1980) and may be a general characteristic of these animals. Johnsen (1983) provided equations for computing the fraction of eggs expected to hatch in one day given the frequency distribution of egg stages and the total duration of egg development. His approach can be extended to include sampling intervals of arbitrary length Δt as follows. Let A_i = the proportion of egg development time associated with egg stage i ($i=1, 2, \ldots, n$) and D_e = the total duration of egg development. Then $D_i = D_e A_i$ = the duration of egg stage i. Define P_i as the proportion of eggs in stage i that are expected to hatch during the next Δt days. For computational purposes P_i may be thought of as the fraction of an egg stage's duration D_i included in the egg age interval $D_e-\Delta t$ to D_e. If all eggs in egg stage i can potentially hatch during the next Δt days, then

$$\Delta t \geqq \sum_{k=i}^{n} D_k \quad \text{and} \quad P_i=1. \tag{4}$$

If egg stage i comprises eggs that are less than $D_e - \Delta t$ days old, then none of the eggs in this stage are expected to hatch during Δt:

$$\Delta t \leqq \sum_{k=i+1}^{n} D_k \quad \text{and} \quad P_i = 0$$
$$i = 1, \ldots, n-1. \tag{5}$$

A third case arises when only a fraction of the eggs in stage i are developed enough to hatch during Δt:

$$\sum_{k=i+1}^{n} D_k < \Delta t < \sum_{k=i}^{n} D_k$$

and

$$P_i = \left(\Delta t - \sum_{k=i+1}^{n} D_k\right) \Big/ D_i \qquad i = 1, \ldots, n-1$$

$$\Delta t < D_i \quad \text{and} \quad P_i = \Delta t / D_i \qquad i = n \tag{6}$$

Eq. 6 assumes that the age distribution of eggs within stage i is uniform. Using these expressions for P_i, the fraction of eggs expected to hatch during the next Δt days equals

$$H_t = \sum_{i=1}^{n} P_i F_{i,t} \tag{7}$$

in which $F_{i,t}$ = the observed relative frequency of eggs in stage i at time t.

So far no provision has been made for egg mortality that occurs during Δt. The hatching rate predicted by Eq. 7 therefore suffers from the same bias associated with the hatching rate predicted by incubating eggs (Eq. 3). One possible solution to this problem is to use the age distribution of eggs at the end of the sampling interval (i.e. at time $t + \Delta t$) to estimate egg survivorship over Δt. Let G_t = the proportion of eggs present at time t that are expected to develop into eggs aged $D_e - \Delta t$ to D_e during the interval t to $t + \Delta t$ (Fig. 1). Let $H_{t+\Delta t}$ = the fraction of eggs present at time $t + \Delta t$ that are included in the egg age interval $D_e - \Delta t$ to D_e. (Equations for computing G_t and $H_{t+\Delta t}$ are provided in the appendix.) If all $E_t G_t$ eggs survive the interval t to $t + \Delta t$, then $E_t G_t$ should equal $E_{t+\Delta t} H_{t+\Delta t}$; otherwise the probability that eggs survive the interval equals $(E_{t+\Delta t} H_{t+\Delta t})/(E_t G_t)$. Thus, the best estimate of the proportion of eggs present at time t that will hatch during Δt equals

$$H = \frac{E_{t+\Delta t} H_{t+\Delta t}}{E_t G_t} \times H_t. \tag{8}$$

For $(E_{t+\Delta t} H_{t+\Delta t})/(E_t G_t)$ to be a legitimate estimator of egg survivorship, Δt must be less than or equal to $D_e/2$. Therefore, using morphological criteria to census the age distribution of eggs and estimate a finite birth rate (Eq. 2 and 8) confines the interval between samples to be less than or equal to one half the total egg development time. This method of estimating B also assumes that the duration of egg development is constant during the interval between samples. If rates of egg development change enough to produce variable hatching rates during Δt, this method may yield biased birth rates. On the other hand, if the variability in hatching rates owes to periodicity in rates of oviposition (e.g. Harding et al. 1951; Mullin 1968; Magnien and Gilbert 1983), then Eqs. 2 and 8 provide accurate estimates of finite birth rate.

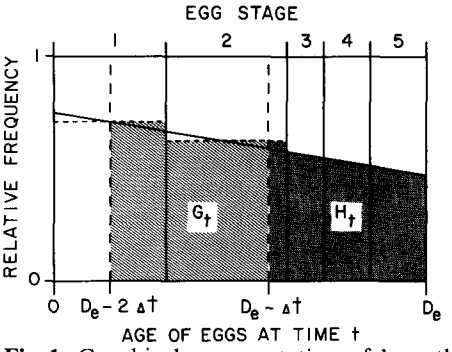

Fig. 1. Graphical representation of how the frequency distribution of egg stages is used to compute egg survivorship and hatching rates. For those stages in which only a fraction of eggs are included in G_t or H_t (stages 1 and 2), a uniform age distribution is used to compute P_i and R_i. Eggs aged $D_e - \Delta t$ to D_e (H_t) can potentially hatch during Δt. Eggs that may develop into the egg age interval $D_e - \Delta t$ to D_e during Δt (G_t) are between $D_e - 2\Delta t$ to $D_e - \Delta t$ days old at time t

Materials and methods

Stock culturing procedures

Stock cultures of *Cryptomonas erosa* v. *reflexa* and *Asplanchna priodonta* were obtained from R.S. Stemberger, who isolated the organisms from Lake Michigan. *Cryptomonas erosa* is a nutritionally adequate food source for *Asplanchna*, and I have maintained successful cultures for over 18 mo. Both *Cryptomonas* and *Asplanchna* were raised in Stemberger's (1981) modification of WC medium except that Fe was decreased by half to reduce formation of precipitates after autoclaving. Culture medium was prepared from distilled water passed through Barnstead ion-exchange and organic-removal columns.

Batch cultures of *Cryptomonas* and *Asplanchna* were maintained at 14° C in 2- and 1-liter Erlenmeyer flasks, respectively. Lighting on a 14:10 LD cycle was provided by cool-white fluorescent bulbs at approximately 100 μEinst $m^{-2} s^{-1}$. Every 5 to 8 d the rotifer culture medium was changed by pouring half the contents of the flask into a Nalgene bottle with a side opening covered with 155-μm Nitex screen. The rotifers were concentrated and rinsed with fresh, sterile medium and then poured into a clean, sterile flask containing 1/4 sterile medium and 3/4 *Cryptomonas* culture. The volume removed from the *Cryptomonas* culture was then replaced with fresh, sterile medium.

Semicontinuous cultures

While others have used continuous culture techniques to raise populations of algae and rotifers under steady-state conditions (Droop 1975; Scott 1980; Boraas 1983; Walz 1983; Rothhaupt 1985), I used semicontinuous culture methods to achieve steady states. Dilutions are done manually at precisely the same time each day in semicontinuous cultures. Consequently, unlike a con-

tinuous culture, the number of organisms in a semicontinuous culture vessel does not remain constant over 24 h. What *is* constant at steady state is the number of organisms harvested every 24 h because the population grows by the same amount each day. The population's growth rate is therefore limited by the rate at which food resources are supplied through dilution. If F equals the volume of culture replaced each day and V equals the culture volume, then $D = F/V$ is the volume-specific dilution rate of the culture.

To obtain populations of *Asplanchna* with steady-state growth, I raised *Cryptomonas* and *Asplanchna* in separate semicontinuous cultures. The *Cryptomonas* were cultured in a 2,800-ml polycarbonate Erlenmeyer flask at 14°C. Full-strength medium was used so that *Cryptomonas* growth rates were limited by light, not nutrients. Incident light ranged from 82.5 μEinst $m^{-2} s^{-1}$ at the bottom of the flask to 115 μEinst $m^{-2} s^{-1}$ at the top and was provided on a 14:10 LD cycle. At the end of the experiment light within the culture was measured to be 50 μEinst $m^{-2} s^{-1}$. Each day at noon the *Cryptomonas* culture was swirled back and forth to obtain a uniform distribution of cells and exactly 400 ml were removed by pouring into a sterile graduated cylinder. Of this total volume 350 ml were used for the *Asplanchna* semicontinuous culture influent. The absorbance (500 nm wavelength, 10 cm path) of the remaining 50 ml was measured to estimate cell concentration from a previously established calibration curve. The *Cryptomonas* culture was brought back up to its original volume (2484 ml) by adding 400 ml of medium with a sterile graduated cylinder.

The *Asplanchna* were cultured semicontinuously in a 2,000-ml glass Erlenmeyer flask in the same incubator as the algae but in dim, indirect light (1.40–2.35 μEinst $m^{-2} s^{-1}$). Each day at noon the *Asplanchna* culture was swirled back and forth to obtain a uniform distribution of animals and exactly 350 ml were removed by pouring into a graduated cylinder. The effluent was concentrated on a 155-μm Nitex screen and preserved with cold, carbonated, 5% formalin solution to determine *Asplanchna*'s concentration. Every animal in the 350-ml effluent was enumerated to eliminate counting error in estimates of *Asplanchna* concentration. The 350 ml removed from the *Cryptomonas* culture were then used to replace the volume removed from the *Asplanchna* culture. Every 2 d the entire rotifer culture was poured into a clean, sterile flask before being diluted with algae. *Asplanchna* have blind guts and therefore regurgitate indigestible parts of *Cryptomonas* cells. These detrital fragments were aggregated, sank readily, and stuck to the flask's bottom so that transfer of the culture to a clean flask effectively precluded any accumulation of detritus. The objective was to raise a healthy *Asplanchna* population whose growth rate was limited by the rate at which food was supplied through dilution. All culture dilutions were performed under a hood equipped with a UV germicidal lamp.

Incubation of eggs

Unlike most other rotifers, *Asplanchna* is ovoviviparous. Eggs are laid one at a time, and embryos develop in the mother's oviduct, which expands to form a uterus. At the end of embryonic development live offspring are extruded from the cloaca. *Asplanchna*'s embryos are analogous to eggs of oviparous zooplankton species. Despite the obvious inaccuracy, I will continue to use terms such as egg ratio and hatching rate when referring to *Asplanchna* because oviparity is far more common among zooplankton than ovoviviparity. *Asplanchna*'s "egg ratio" therefore corresponds to the ratio of embryos to animals in the population, and "hatching" refers to birth of live offspring.

To estimate hatching rates of eggs from the semicontinuous culture, gravid *Asplanchna* were randomly picked out of the daily effluent and incubated with food in wells of sterile, transparent tissue culture plates (Linbro 76-033-05). Four gravid females were incubated in each well with enough volume of *Cryptomonas* suspension to make the concentration of *Asplanchna* equal that present in the culture after dilution. The concentration of *Cryptomonas* matched that which animals in the semicontinuous culture received at the beginning of each 24-h period of semicontinuous dilution. In this way the daily ration of cells provided to each animal in the semicontinuous culture was also given to the incubated females. Preliminary incubations established that this rationing scheme was necessary to avoid acceleration of hatching rates caused by higher average food concentrations. The incubated animals were observed every 6 h for hatching of eggs and were transferred to new wells containing fresh food every 24 h. *Asplanchna*'s total duration of egg development was greater than the interval of time between ovipositions. Consequently some gravid females contained two or three eggs, all in different stages of embryonic development. To avoid inclusion of eggs laid during the period of incubation, each female was incubated until the number of eggs she contained initially hatched into newborn; then she was discarded.

Two days after eggs were collected for incubation, I began to sample the semicontinuous culture of *Asplanchna* every 5 h to census the concentrations of *Asplanchna* and *Cryptomonas* and the frequency distribution of eggs per female. During each day five 70-ml samples were collected equalling the total volume usually removed every 24 h. *Cryptomonas* cells were collected for enumeration by passing the sample through a 155-μm Nitex screen to remove *Asplanchna*, preserving the filtrate with Lugol's iodine solution, and then concentrating the filtrate by settling approximately 60 ml for at least 48 h. Subsamples of the resulting 10-ml concentrate were placed in a Sedgwick-Rafter counting chamber where cells in transects were enumerated to estimate *Cryptomonas* concentration in the semicontinuous culture.

Results

Semicontinuous cultures

The *Cryptomonas* culture was diluted at a low rate (F = 400 ml d^{-1}, V = 2,484 ml, D = 0.161 d^{-1}) so that cell concentration would be high enough to sustain positive net growth of the *Asplanchna* population. Initially the population of *Cryptomonas* decreased so that more

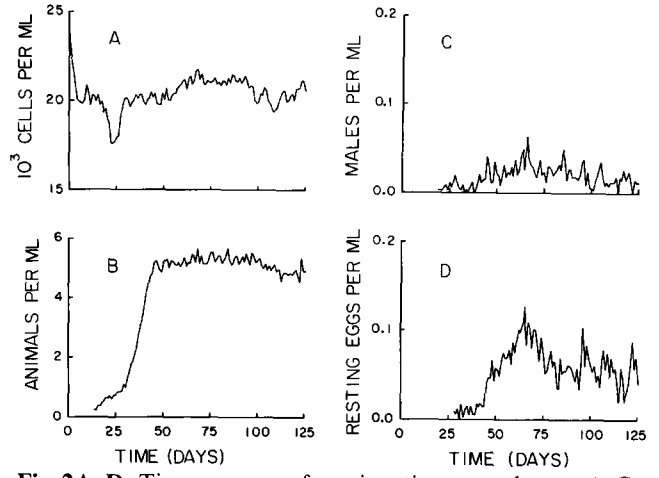

Fig. 2A–D. Time courses of semicontinuous cultures. **A** Concentration of cells in the *Cryptomonas* culture effluent. **B** Concentration of parthenogenetic females in the *Asplanchna* culture effluent. **C** Concentration of males in the *Asplanchna* culture effluent. **D** Concentration of females with resting eggs in the *Asplanchna* culture effluent

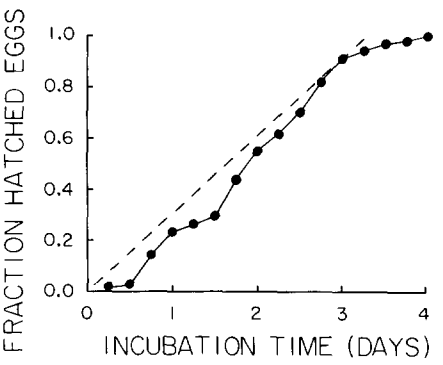

Fig. 3. Cumulative distribution of egg hatching times obtained from incubation of gravid *Asplanchna* taken from the semicontinuous culture effluent. Incubation times that are integer multiples of a day correspond to observations made at 1500 h; other observations were made at 0300, 0900, and 2100 h. The dashed line indicates the cumulative distribution of hatching times expected when the age distribution is uniform and egg development time equals 3.25 d

light would be provided to each cell (Fig. 2A). After about 12 d, cell division rates balanced the rate of dilution, and cell concentration at harvesting remained constant at approximately 20,300 cells ml^{-1}. For some unknown reason the population of *Cryptomonas* abruptly declined in size on day 18 of the experiment. Within a short time, however, the concentration of cells returned to its original steady-state level. Perhaps some component was accidentally omitted from a batch of culture medium. In any event the concentration of *Cryptomonas* at harvesting did not vary appreciably during the remainder of the experiment. The average over the last 95 d was 20,581 cells ml^{-1} (SD = 552 cells ml^{-1}). Constancy in cell numbers was important because it guaranteed that the *Asplanchna* culture was supplied with a fixed quantity of food each day.

The semicontinuous culture of *Asplanchna* was started 14 d after the *Cryptomonas* culture. The total culture volume was 1,880 ml, and 350 ml were replaced each day; therefore $D = 0.186\ d^{-1}$. The population of animals initially grew rapidly but eventually became food limited and achieved an average maximum concentration of 5.18 animals ml^{-1} (Fig. 2B). Although the semicontinuous culture of *Asplanchna* contained mostly healthy parthenogenetic females, a few males and females with resting eggs were present in most samples. However, the number of males never exceeded 2.33% of the amictic females, and the number of females with resting eggs never exceeded 2.30% (Fig. 2C and D). Also, to check whether new genotypes were ever recruited into the population over the course of the experiment, I incubated females carrying resting eggs individually in wells of tissue culture plates containing abundant food. Not one resting egg ever hatched after 10 d of observation. Since the fraction of total culture volume that remained each day equals 0.814 (i.e. $1-D$), the probability that any animal remained in the culture after 10 d equals 0.128. If resting eggs were able to hatch under the conditions of semicontinuous culture, it is therefore unlikely that they hatched before being washed out by dilution.

Estimation of Asplanchna birth rate

To assess whether the egg ratio model described earlier (Eq. 1 and 2) accurately predicts the *Asplanchna* population's finite birth rate, I incubated a random sample of the population's eggs to determine the proportion of eggs that hatched in 24 h, *H*. Gravid females were obtained from the semicontinuous culture effluent on day 119 of the experiment, well after the *Asplanchna* population had attained steady-state growth. Of the total 402 eggs that were incubated, 89.6% hatched as viable amictic females; the remaining eggs were either stillborn or hatched as males. Of the eggs that hatched as viable amictic females, 94.4% did so by 3.25 d (Fig. 3). The cumulative distribution of hatching times shows obvious departures from uniformity ($\chi^2 = 112$, $df = 12$, $P \ll 0.0005$) and resembles a stair-step pattern with more eggs hatching at the end of 1, 2, and 3 d of incubation than during intermediate times. The distribution implies that hatching rates were synchronized over 24 h. Data obtained from a 48-h time course of samples collected from the semicontinuous culture support this proposal (Fig. 4). Each day at noon fresh *Cryptomonas* cells were added to the *Asplanchna* culture. The animals consumed these cells rapidly, reducing their concentration by approximately 52% in 5 h. From 10 to 20 h after semicontinuous dilution, the *Asplanchna* population's brood size and egg ratio increased markedly while numbers increased only gradually. During the last 4 h before semicontinuous dilution, brood size and egg ratio sharply declined and there was a pulsed increase in animal concentration. Both laying and hatching rates of eggs were therefore strongly synchronized to the daily addition of food, and this periodicity was mirrored in the distribution of hatching times.

The *Asplanchna* population's true finite birth rate can be calculated from the semicontinuous dilution rate *D* as follows. Let N_t and N_{t+1} equal the concentration

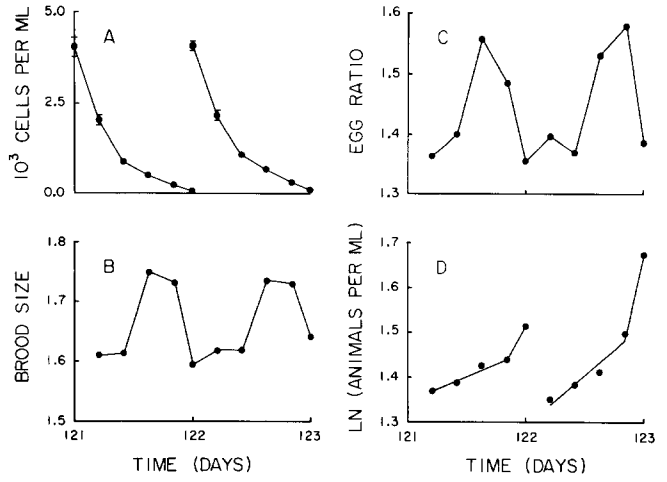

Fig. 4A–D. Time course of samples collected from the semicontinuous *Asplanchna* culture over 48 h. Times that are integer multiples of a day correspond to observations made at 1200 h; other observations were made at 0300, 0815, 1700, and 2200 h. **A** *Cryptomonas* mean concentration ± 2 SE. **B** Ratio of eggs to gravid females. **C** Ratio of eggs to animals. **D** Natural logarithm of *Asplanchna* concentration. Lines drawn by eye

of *Asplanchna* in the semicontinuous culture effluent at time t and one day later at time $t+1$. N_{t+1} must equal the sum of the number of animals that remain after dilution, $N_t(1-D)$, and the number of births that occur during the day, β:

$$N_{t+1} = N_t(1-D)+\beta \tag{9}$$

Eq. 9 assumes that deaths are absent in the population of *Asplanchna*. This assumption is probably valid because animals examined in the daily collections seldom exhibited any visible signs of death (the body cavity becomes opaque and feeding ceases as animals approach their end of life) and because estimates of survivorship obtained in life-table experiments (Dorazio 1986) at the appropriate food concentrations indicate that few animals should die before being washed out of the culture by dilution (mean residence time within culture = 5.4 d). Although another possible source of mortality, cannibalism, is well known among some species of *Asplanchna* (Gilbert 1980), cannibalistic behavior was never observed among individuals of the stock cultures and animal remains were never found in the guts of animals collected from the semicontinuous culture.

The size of the *Asplanchna* population at harvesting was constant at steady state. Thus, $N_{t+1} = N_t = N$, and the number of births that occurred each day must have equalled DN. Expressed as a fraction of population size after dilution,

$$\frac{DN}{N(1-D)} = \frac{D}{(1-D)} \tag{10}$$

is the fraction by which the semicontinuously cultured population increased each day. Equation 10 predicts that the finite birth rate of the *Asplanchna* population was 0.229 d^{-1}.

The finite birth rate can also be estimated from the model I described earlier (Eq. 2). To estimate average concentrations of eggs and animals in the semicontinuous culture of *Asplanchna* at the time of harvesting, I arbitrarily chose samples collected 5 days prior to the day that eggs were isolated for incubation. Because egg and animal abundances were constant at steady state, any set of samples should yield similar estimates of E and N. I enumerated 1/3 of the eggs and animals in each of the 5 successive samples. The mean number of eggs was 752.8 ($SD = 70.2$), and the mean number of animals was 563.2 ($SD = 30.3$). Thus, the average egg ratio of the population was 1.337 eggs $animal^{-1}$. Of the 402 eggs that were incubated, 21.9% hatched as viable amictic females during the first 24 h of incubation. Thus, Eq. 2 predicts an average finite birth of (1.337 eggs $animal^{-1}$) $\times$ (0.219)/(1 d) = 0.293 births $animal^{-1}$ d^{-1}, or simply 0.293 d^{-1}. Although this average is 28% higher than the rate of birth predicted by the culture dilution rate, errors in E, N, and H must be considered to place a confidence interval around the estimate of B.

Estimating errors for E and N is straightforward because sample estimates of their variances may be computed directly. Estimating the variance of H, however, is more complicated because H is computed from the distribution of hatching times (Eq. 3). One way of proceeding is to simulate the sampling distribution of H by drawing random samples from the observed distribution of hatching times. A mean and variance can then be computed from the simulated distribution of H values. This method of parameter estimation, called Monte Carlo simulation (Meyer 1975), is illustrated for H as follows. Recall that N_i = the number of incubated eggs that hatch in the ith interval of observation and N_e = the total number of incubated eggs (Eq. 3). During each incubation time interval the number of eggs that hatch is assumed to be the outcome of a binomial process that depends on the probability of hatching during the interval and the number of eggs that remain unhatched at the beginning of the interval. Let

$$p_i = N_i \Big/ \left(N_e - \sum_{j=1}^{i-1} N_j\right) \tag{11}$$

be the probability that an egg hatches during the ith observation interval. Define S_k such that $S_k = 1$ if an egg hatches during the interval and $S_k = 0$ if it doesn't; thus $\Pr(S_k = 1) = p_i$. At each ith incubation interval p_i is compared to the value of a uniformly distributed random variable U_k with range [0, 1]. If $U_k \leq p_i$, then $S_k = 1$; otherwise $S_k = 0$. Thus, a realized distribution of egg hatching times can be calculated from

$$M_1 = \sum_{k=1}^{N_e} S_k$$

$$M_i = \sum_{k=1}^{n} S_k \quad \text{where } n = N_e - \sum_{j=1}^{i-1} M_j$$

$$i = 2, 3, \ldots, m \tag{12}$$

Notice that Eq. 12 is recursive. The number of comparisons between U_k and p_i depends on the number of eggs that remain unhatched at the end of the previous observation interval. The realized distribution of egg

Table 1. Results of simulated distributions of the proportion of *Asplanchna*'s eggs that hatch after one day. H was computed using Eq. 13

Number of simulated H values	Mean H	Variance of H
100	0.2208	4.558×10^{-4}
500	0.2186	4.307×10^{-4}
1,000	0.2192	4.111×10^{-4}

hatching times is therefore said to follow a chain-binomial distribution (Chiang 1968; Pielou 1977). For each realized distribution of hatching times a value of H is computed from

$$H = \frac{1}{\bar{N}_e} \sum_{i=1}^{m} M_i. \tag{13}$$

This process is repeated enough times to approximate the sampling distribution of H.

Using the egg incubation data, I simulated distributions of H (Table 1). A distribution composed of 1,000 values of H had a mean of 0.2192 and a variance of 4.111×10^{-4}. The mean is only slightly larger than 0.219, the expected value based on the observed distribution of hatching times.

Estimates of the means and variances of E, N, and H make it possible to establish a confidence interval for the finite birth rate. However, there are two ways to proceed. A confidence interval may be determined either by approximating the variance of B with first-order error analysis (Meyer 1975) and assuming that B is normally distributed or by simulating the distribution of B using Monte Carlo procedures. I will demonstrate both methods and show that first-order error analysis, which is easier to use, approximates the variance of B determined from Monte Carlo simulation very well.

To simulate the distribution of B, I drew random samples from the distributions of E, N, and H. The sampling process for H has already been described. Random values of E and N were drawn from normal distributions parameterized by the sample means and variances of these variables. Approximating the distribution of B by drawing 1,000 random samples yielded a mean value of 0.293 d^{-1} and a variance of 1.695×10^{-3} (Table 2). I obtained the 95% confidence interval for B by counting 25 values (2.5%) from each tail of the distribution of B. The 95% confidence interval was 0.218–0.380 d^{-1}.

First-order error analysis (Meyer 1975) can also be used to estimate the variance of B. Assuming that errors in E, N, and H are uncorrelated and independent (i.e. their covariances equal zero), the variance of B is approximated by

$$\mathrm{var}(B) = \frac{(\bar{H}/\bar{N})^2 \mathrm{var}(E) + (\bar{E}\bar{H}/(\bar{N}^2))^2 \mathrm{var}(N) + (\bar{E}/\bar{N})^2 \mathrm{var}(H)}{\Delta t^2} \tag{14}$$

$\bar{E}$, $\bar{N}$, and $\bar{H}$ equal the sample means of these variables. Using $\bar{H}$ and var(H) based on 1,000 random values of H (Table 1), Eq. 14 predicts that var(B) equals 1.73×10^{-3}, which is only 2.1% higher than the variance calculated from Monte Carlo simulation (Table 2). First-order error analysis yields a 95% confidence interval for B of 0.209–0.377 d^{-1}, assuming a normal distribution for B.

Table 2. Results of simulated distributions of the finite birth rate of the *Asplanchna* population. B was computed using Eq. 2 and 13 and has units of d^{-1}

Number of simulated B values	Mean B	Variance of B	95% Confidence interval
100	0.296	1.664×10^{-3}	(0.206, 0.373)
500	0.293	1.629×10^{-3}	(0.218, 0.378)
1,000	0.293	1.695×10^{-3}	(0.218, 0.380)

The rationale for propagating errors in E, N, and H through calculations of B was to make a statistically valid comparison between the finite birth rate predicted by the egg ratio model (Eq. 2) and the rate of birth predicted from the culture dilution rate (Eq. 10). The value of B calculated from Eq. 10 (0.229 d^{-1}) lies within the confidence intervals established both by simulation (Table 2) and by first-order error analysis.

When eggs hatch during restricted portions of the day as those of *Asplanchna* did, calculating H directly from the distribution of hatching times is superior to assuming that the age distribution of eggs is uniform. Edmondson's (1960) model, for example, assumes uniformity and computes a daily hatching rate from the average rate of egg development, $1/D_e$. This rate may be estimated by regressing the cumulative fraction of hatched eggs against incubation time. The slope is an estimate of $1/D_e$ and equals 0.296 d^{-1} (SE = 0.012 d^{-1}) for the incubated eggs of *Asplanchna*. This daily hatching rate must be reduced slightly, however, to account for stillborn and male offspring that never get recruited into the growing population of amictic females. During each day 97.4% of the eggs hatched as viable amictic females. Using this correction factor, Edmondson's method predicts an average finite birth rate of (1.337 eggs animal^{-1}) × (0.974) × (0.296 d^{-1}) = 0.385 d^{-1} for *Asplanchna*. Using first-order error analysis to approximate the variance of Edmondson's estimate of B produces a 95% confidence interval of 0.297–0.473 d^{-1}. The birth rate predicted from the culture dilution rate (Eq. 10) lies well below the lower bound of this interval. Thus, Edmondson's method of computing B overestimates the *Asplanchna* population's actual birth rate.

Discussion

The basic idea of using finite rates of birth and death to analyze the dynamics of zooplankton populations is not new. Elster (1954) predicted births during a sampling interval Δt by multiplying the initial abundance of eggs by $\Delta t/D_e$. The model's shortcomings include its assumptions of uniformity in the egg age distribution and absence of egg mortality. Elster's approach was originally criticized, however, because the sampling interval usually exceeded the duration of egg develop-

ment, thereby making it possible for animals born during Δt to produce offspring of their own. In that event Elster's forecast would underestimate the actual population birth rate. Edmondson (1960) attempted to improve on Elster's model by estimating births that occur during one day and then assuming an exponential pattern of population growth to account for sampling intervals that exceed D_e. However, the exponential extrapolation of births implicit in Edmondson's model may be inaccurate when environmentally determined changes in population age structure and fecundity occur during Δt.

The general method of calculating finite rates of birth and death that I have presented (Eq. 1 and 2) involves frequent sampling of the plankton to eliminate exponential extrapolations that can bias estimates of birth and death rates. My procedure for computing B and M requires an estimate of each species' egg development time to select appropriate sampling intervals. However, D_e is determined primarily by water temperature (Hall 1964; Weglenska 1971), and functional relationships between D_e and temperature have been determined for many zooplankton species (Bottrell et al. 1976). To account for egg mortality in an estimate of finite population birth rate, I have shown that Δt must not exceed $D_e/2$ (Eq. 8). This may constrain sampling to very short intervals when the dynamics of rotifer populations are under investigation because D_e can be less than 24 h in some species. On the other hand, egg development times of most crustacean zooplankton range from about 2 to 18 days over the range of commonly encountered water temperatures (Bottrell et al. 1976); this allows greater freedom in choosing Δt.

Periodic exposure to different water temperatures is common for zooplankton that display daily, vertical migrations across thermal density gradients. In these animals either rates of oviposition or rates of egg development could vary as they encounter strata of different temperatures. When rates of oviposition vary during the interval between samples, I have shown that using egg morphology to estimate population birth rate automatically accounts for variability in oviposition rates. However, the method I have presented for estimating B may not be accurate when rates of egg development vary during Δt because the duration of each egg stage does not remain constant. Meyers (1984) has shown that egg development times based on average temperatures do not yield accurate hatching rates and suggests that the vertical distribution of temperature and animals be monitored continuously. Determining a correction for biases that owe to variable rates of egg development challenges zooplankton ecologists to derive even more accurate estimators of population birth rate.

Using the model that I have presented, the finite death rate of a population is obtained by solving for M in Eq. 1 and substituting the expression for B in Eq. 2:

$$M=\frac{1}{\Delta t}+\frac{E_t H}{N_t \Delta t}-\frac{N_{t+\Delta t}}{N_t \Delta t}. \tag{15}$$

If the distribution of egg developmental stages (Threlkeld 1979) is measured at the beginning and end of a sampling interval, H is computed from Eq. 8, which contains a correction for egg mortality. Let $P=$ the probability that eggs survive the interval t to $t+\Delta t$; thus $P=(E_{t+\Delta t}H_{t+\Delta t})/(E_t G_t)$. If all egg mortality is associated with predation on gravid females, then $(1-P)$ is the probability that these females will die during Δt. Under these circumstances the finite mortality rate of the adult segment of the population can be calculated from

$$M_A=\frac{A_t(1-P)}{N_t \Delta t} \tag{16}$$

in which $A_t=$ the number of adults in the population at time t. A_t cannot be measured in all zooplankton species because of the morphological similarity of juveniles and adults. However, if animals do not lose their eggs during a sample's preservation (Haney and Hall 1973; Prepas 1978), adults may be identified by the presence of eggs. Also, Edmondson and Litt (1982) have shown how to distinguish juvenile and adult *Daphnia* using differences in the relative lengths of this animal's postabdominal processes. Once A_t is measured, M_A can be calculated and used to determine juvenile mortality from the difference of M and M_A. The ability to assess age-specific mortality provides insight into potential regulatory mechanisms of population growth. For example, if juveniles are more susceptible than adults to death by starvation (Goulden and Hornig 1980; Goulden et al. 1980; Tessier et al. 1983) or predation (Swift and Fedorenko 1975; Pastorok 1980), correlations should exist between rates of juvenile mortality and the abundances of food or predators.

The general model that I've described in this paper estimates finite rates of birth and death from data commonly available in samples of the plankton. The data are not measured without error, and some attempt must be made to propagate that error through calculations of birth and death rate so that rates determined over different time intervals can be compared with statistical security. I used Monte Carlo simulation and first-order error analysis to obtain confidence intervals for estimates of B when eggs of *Asplanchna* were incubated. Similar methods can be applied to data from field samples that include the total number of animals, the total number of eggs, and the distribution of egg stages. DeMott (1980) and Keen and Nassar (1981), for example, examined the effects of measurement error on Paloheimo's (1974) estimator of instantaneous birth rate. Analyzing data from zooplankton populations in Lake Erie, DeMott (1980) concluded that intensive sampling is required to achieve even modest precision in estimates of birth and death rates. Further investigation is therefore required to determine the extent to which variability in measurements of the distribution of egg stages affects estimates of population birth rate.

Conclusions

When zooplankton are sampled frequently enough to eliminate the assumption of exponential population growth, finite rates of birth and death can be used to analyze the population dynamics of these animals. These rates may be calculated from data that are commonly available in plankton samples, and the rates are

applicable to situations in which eggs hatch periodically because rates of oviposition are variable. Hatching rates calculated from egg incubations will generally overestimate population recruitment when egg mortality is important. However, when the age distribution of eggs, determined from morphological criteria, is compared at the beginning and end of a sampling interval, hatching rates can be calculated to include egg mortality. Measurement errors profoundly affect our ability to compare population rates of birth and death statistically and therefore cannot be ignored.

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Appendix

The proportion of eggs present at time t that are expected to develop into eggs aged $D_e-\Delta t$ to D_e during the time interval t to $t+\Delta t$ equals

$$G_t=\sum_{i=1}^{n} R_i F_{i,t} \tag{A1}$$

in which $F_{i,t}$ = the observed relative frequency of eggs in stage i at time t (Fig. 1). R_i is the proportion of eggs in stage i at time t that are expected to develop into the egg age interval $D_e-\Delta t$ to D_e during the time interval t to $t+\Delta t$ and is calculated as follows:

$$\text{if } \Delta t \geqq \sum_{k=i}^{n} D_k \text{ then } R_i=0 \quad i=1,\ldots,n \tag{A2}$$

$$\text{if } \sum_{k=i+1}^{n} D_k < \Delta t < \sum_{k=i}^{n} D_k$$

$$\text{then } R_i=\left(D_i-\Delta t+\sum_{k=i+1}^{n} D_k\right)\Big/ D_i$$

$$i=1,\ldots,n-1 \tag{A3}$$

$$\text{if } \Delta t \leqq \sum_{k=i+1}^{n} D_k \text{ and } 2\Delta t \geqq \sum_{k=i}^{n} D_k$$

$$\text{then } R_i=1 \quad i=1,\ldots,n-1 \tag{A4}$$

$$\text{if } \sum_{k=i+1}^{n} D_k < 2\Delta t < \sum_{k=i}^{n} D_k$$

$$\text{then } R_i=\left(2\Delta t-\sum_{k=i+1}^{n} D_k\right)\Big/ D_i$$

$$i=1,\ldots,n-1$$

$$\text{if } 2\Delta t < D_i \text{ then } R_i=\Delta t/D_i \quad i=n \tag{A5}$$

$$\text{if } 2\Delta t \leqq \sum_{k=i+1}^{n} D_k \text{ then } R_i=0 \quad i=1,\ldots,n-1. \tag{A6}$$

The fraction of eggs present at time $t+\Delta t$ that include eggs of ages $D_e-\Delta t$ to D_e equals

$$H_{t+\Delta t}=\sum_{i=1}^{n} P_i F_{i,t+\Delta t} \tag{A7}$$

in which $F_{i,t+\Delta t}$ = the observed relative frequency of eggs in stage i at time $t+\Delta t$ and P_i is defined by Eq. 4 to 6.

Values of P_i and R_i depend on the length of the sampling interval Δt, temperature (which determines the duration of egg development D_e), and the proportion of development associated with each egg stage A_i. As an example, the following values of P_i and R_i are calculated for *Daphnia* eggs at different temperatures using Bottrell et al. (1976) to compute D_e, using Threlkeld's (1979) suggestions for A_i, and assuming $\Delta t = 1$ d.

Temp. (°C)	D_e (day)	P_1 R_1	P_2 R_2	P_3 R_3	P_4 R_4	P_5 R_5
4	21.00	0	0	0	0	0.2979
		0	0	0	0	0.2979
6	14.77	0	0	0	0	0.4232
		0	0	0	0	0.4232
8	10.76	0	0	0	0	0.5811
		0	0	0	0.1997	0.4189
10	8.09	0	0	0	0	0.7727
		0	0	0	0.6712	0.2273
12	6.25	0	0	0	0.0001	1
		0	0	0.3452	0.9999	0
14	4.94	0	0	0	0.3275	1
		0	0.0880	1	0.6725	0
16	3.97	0	0	0	0.7060	1
		0	0.3955	1	0.2940	0
18	3.25	0	0	0.2081	1	1
		0	0.7475	0.7919	0	0
20	2.69	0	0	0.9432	1	1
		0.1560	1	0.0568	0	0

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