

## Obtaining life table data from stage-frequency distributional statistics

In a commendable critique of current methods for the analysis of zooplankton cohort data, Hairston and Twombly (1985) presented a detailed argument for why the popular method of Rigler and Cooley (1974) is correct only under limited and ecologically unrealistic conditions. As a general conclusion, Hairston and Twombly stated that it is impossible, by the approach of Rigler and Cooley, to estimate both the development times and survivorships solely from the information available in a single data set.

In their derivation of a more general form of the central equation in the Rigler-Cooley method, instead of deriving the relationship between the mean of an abundance curve on the one hand and survival and development time on the other, Hairston and Twombly (1985) derived the relationship between the median and the two population parameters. Thus their equation 11 is not a direct generalization of the equation presented by Rigler and Cooley (1974). Below we derive the corresponding expression incorporating the mean and point out some of the consequences of using the median instead of the mean.

The Rigler-Cooley approach utilizes the areas and temporal means of the stage-frequency curves in estimating stage recruitment, development time, and survival. This approach has also been advocated by Manly (1977). Using his results, we show that it is indeed possible to estimate both survival and development time from a single data set. We also show that the assumption that survival rate be constant over all stages, often cited as a prerequisite for methods based on this approach, can be omitted.

As pointed out by Hairston and Twombly, the Rigler-Cooley method is based on two fundamental assertions (the notation of Manly 1977 is used throughout):

$$M_i = A_i/a_i \quad (1)$$

and

$$B_{i+1} - B_i = 1/2(a_{i+1} + a_i) \quad (2)$$

where  $M_i$  is total number of individuals that enter stage  $i$  ( $N_i$  in Hairston and Twombly's notation),  $A_i$  is the area of the abundance curve of instar  $i$  ( $A_i$ ),  $a_i$  is the development time of instar  $i$  ( $T_i$ ), and  $B_i$  is the temporal position of the mean of the abundance curve for instar  $i$  ( $M_i$ ).

By deriving the general forms of Eq. 1 and 2, Hairston and Twombly intended to show the errors associated with the above equations. In their derivation, however, Hairston and Twombly stated that the temporal mean,  $m_i$ , of a stage-frequency distribution is the point on the time axis for which the areas on both sides under the abundance curve are equal, or where

$$\int_0^{m_i} M_i \exp(-\theta_i t) dt = \int_{m_i}^{a_i} M_i \exp(-\theta_i t) dt \quad (3)$$

where all individuals are recruited at  $t = 0$ , and  $\theta_i$  is the mortality coefficient. The point  $m_i$  is the temporal median, however, not the temporal mean. The temporal mean (or "center of gravity": Rigler and Cooley 1974) is defined by

$$B_i = \frac{\int_{-\infty}^{\infty} t N_i(t) dt}{\int_{-\infty}^{\infty} N_i(t) dt} \quad (4)$$

If we assume that all individuals,  $M_i$ , recruit to instar  $i$  at time 0, and that all survivors at time  $a_i$  (which is still the duration of instar  $i$ ) enter stage  $i + 1$  simultaneously, Eq. 4 becomes (with these assumptions, the temporal mean is denoted  $G_i$ )

$$G_i = \frac{\int_0^{a_i} tM_i \exp(-\theta_i t) dt}{\int_0^{a_i} M_i \exp(-\theta_i t) dt} = \frac{1}{\theta_i} - \frac{a_i \exp(\theta_i a_i)}{1 - \exp(-\theta_i a_i)}, \quad (5)$$

while use of the median gives (Hairston and Twombly 1985)

$$m_i = -\ln \left[ \frac{\exp(-\theta_i a_i) + 1}{2} \right] / \theta_i. \quad (6)$$

The temporal mean and median are equal only when the stage frequencies are distributed symmetrically around the temporal mean. Under the above assumptions, this will only occur when the mortality term is zero.

Equation 11 in the paper of Hairston and Twombly is thus not a general form of the equation of Rigler and Cooley (1974). Insertion of known stage-specific survival rates and estimates of temporal means (or temporal medians, *see below*) in their equation 11 will therefore lead to biased estimates of development time. With the formula for the temporal mean (Eq. 5), the general form of the equation of Rigler and Cooley becomes

$$G_{i+1} - G_i = \frac{1}{\theta_{i+1}} - \frac{1}{\theta_i} - \frac{a_{i+1} \exp(-\theta_{i+1} a_{i+1}) / [1 - \exp(-\theta_{i+1} a_{i+1})] + a_i \exp(-\theta_i a_i) / [1 - \exp(\theta_i a_i)] + a_i. \quad (7)$$

The term  $a_i$  appears in the equation since the recruitment to stage  $i + 1$  takes place at  $t = a_i$  (which is identical to the duration of stage  $i$ ). Following the approach of Hairston and Twombly, we find the actual error associated with the equation of Rigler and Cooley by using the above equation instead of equation 11 of Hairston and Twombly.

Although the errors introduced by the Hairston and Twombly median in most cases are minor compared to other sources

of error, the errors associated with parameter estimates of later stages will not generally be small. The adult stage represents a special case because the only way individuals leave this stage is by dying. The "development" time is thus infinite and Eq. 5 and 6 reduce to

$$G_6 = 1/\theta_6$$

and

$$m_6 = -\ln 0.5/\theta_6, \quad (8)$$

which give (the index, 6, denotes the adult stage)

$$G_6 - m_6 = \frac{1}{\theta_6} (1 + \ln 0.5) = \frac{0.3068}{\theta_6}. \quad (9)$$

Thus the smaller the adult mortality rate, the larger the differences between the Hairston and Twombly median and the mean. When  $\theta_6$  is 0.05 or smaller, the difference is more than 6 d. This means that serious bias is introduced, since the difference may be of the same magnitude as the entire development time of stage V.

Rearranging Eq. 9 gives

$$\theta_6 = \frac{0.3068}{G_6 - m_6}, \quad (10)$$

which means that adult mortality, in theory, can be estimated from the expressions for the Hairston and Twombly median and the temporal mean of the adult stage-frequency curve, together with independent estimates of both the mean and the median.

It is important to note, however, that the above discussion is restricted to the case where all individuals are recruited simultaneously. Hairston and Twombly present a detailed argument for why the area under the instar abundance curve is the same whether all individuals enter the instar simultaneously or not. A corresponding argument can be shown to apply also for the temporal mean of such an abundance curve. Unlike the area and the temporal mean, the temporal median of a stage-frequency curve,

Table 1. Differences (in days) between the true median and the Hairston and Twombly median for various combinations of  $\sigma$  and  $\theta$  for adult stages.

$\sigma$	$\theta$		
	0.1	0.2	0.3
5	1.00	0.92	0.76
10	1.88	1.26	0.93

however, is not independent of the way the individuals are recruited to an instar. This means that, in the general case with recruitment distributed over a considerable time period (which is the realistic situation that Rigler and Cooley had in mind), the estimated, temporal median of a stage-frequency curve will be a biased estimate of the parameter denoted  $M_i$  by Hairston and Twombly in their equation 9. In this situation, the area under the abundance curve to the left of their parameter (here denoted  $m_i$ ) is smaller than the corresponding area to the right. In the simple case of the adult stage, the difference between the left and right areas ( $D_6$ ) can be shown to be

$$D_6 = 2 \sum_{t=-\infty}^{\mu_6-1} f_6(t) M_6 \cdot \exp[-\theta_6(m_6 - t)] / \theta_6 \quad (11)$$

where  $f_6(t)$  denotes the rate of recruitment at day  $t$ . This recruitment function is assumed to be symmetrically distributed around a mean time of recruitment ( $\mu_6$ ).

Obviously this bias implies that the true median of the stage-frequency curve will lie to the right of the  $m_i$  of Hairston and Twombly to an extent depending on the quantity  $D_i$ . The actual size of this bias can thus not be assessed unless the recruitment function,  $f(t)$ , is known. An illustrative example is presented in Table 1, however, for various cases in which recruitment to the adult stage is assumed to be normally distributed with a temporal standard deviation of  $\sigma$ . Equation 7 above is, on the other hand, based on the temporal means, and should therefore be valid independent of the form of the recruitment function.

Hairston and Twombly (1985) concluded that development times and survivorships

cannot, using the approach of Rigler and Cooley (1974), both be calculated from the information available in a single cohort analysis. This is correct if the equations involving the area and the temporal mean are considered alone:

$$A_i = M_i [1 - \exp(-\theta_i a_i)] / \theta_i \quad (12)$$

$$B_i = G_i + \mu_i = \frac{1}{\theta_i} + \mu_i - a_i \exp(-\theta_i a_i) / [1 - \exp(-\theta_i a_i)] \quad (13)$$

where  $\mu_i$  is the mean time of recruitment to stage  $i$ . Two simple relationships connecting corresponding parameters in successive instars may also be used, however,

$$M_{i+1} = M_i \exp(-\theta_i a_i) \quad (14)$$

and

$$\mu_{i+1} = \mu_i + a_i \quad (15)$$

Equations 12–15 were also used by Manly (1977).

The three parameters,  $M$ ,  $\theta$ , and  $\mu$ , are to be estimated for the adult stage, while for other stages the development time ( $a$ ) must be estimated as well. With six stages (including the adult one) we have 23 parameters to be estimated and only 22 equations, since Eq. 14 and 15 are not defined when  $i = 6$ . If one stage duration is known (as assumed by the Rigler-Cooley method), the set of equations becomes solvable (by first solving a nonlinear equation by iteration). If no stage durations are known, it is possible to reduce the number of parameters by assuming some of them to be equal. It is not necessary, however, to assume equal survivorship for all stages.

Going one step further, Manly (1977) also utilized the relationship between the variance,  $C$ , of the stage-frequency curve and the population parameters

$$C_i = \frac{1}{\theta_i^2} + \sigma_i^2 - a_i^2 \exp(-\theta_i a_i) / [1 - \exp(-\theta_i a_i)]^2 \quad (16)$$

The parameter  $\sigma$  denotes the temporal standard deviation of the recruitment distribution. Parslow et al. (1979) assumed equal  $\sigma$  for all stages in their lag-Manly model. With this assumption (which seems reasonable) we obtain 23 parameters to be estimated and 27 equations. All parameters can therefore be estimated without assuming constant survival rates over stages.

We therefore conclude that it is possible to obtain both survivorship and development times in a single cohort analysis by stage-frequency distributional statistics. Furthermore, it is not necessary to introduce the limiting assumptions that Hairston and Twombly have shown the Rigler-Cooley method to be based upon. Finally, rather than the equations suggested by Rigler and Cooley or the generalizations suggested by Hairston and Twombly, Eq. 12–16 should be used for estimation purposes: They require less external information, they are less restrictive, and in addition they make it possible to estimate parameters of the recruitment distribution. Furthermore, indepen-

dent estimates of some of the parameters (such as known development times) can easily be incorporated in the estimation procedure.

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