

COMMENT

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A perspective on the use of cohort analysis to obtain demographic data for copepods¹

Plankton ecologists have devised several methods for extracting demographic information on copepod populations from abundance data. The most widely used of these methods was developed by Rigler and Cooley (1974), who noted the failure of earlier methods to take full advantage of the information in instar-specific abundance data. The Rigler-Cooley method provides estimates of development times and survivorship from the mean pulse times of instar abundances. The Rigler-Cooley method is most often used in estimating development times that are to be used in estimating secondary production (Boers and Carter 1978; Burns 1980; Lewis 1979).

Hairston and Twombly (1985) recently undertook a critical appraisal of the Rigler-Cooley method, among others, and concluded that underlying assumptions impose serious limitations on its utility. Hairston and Twombly show that the Rigler-Cooley method is strictly correct only under the unlikely condition that survival is perfect. We believe that this is correct. In addition, however, Hairston and Twombly present a very pessimistic view of the general usefulness of the Rigler-Cooley method. We believe that the Rigler-Cooley method is of much broader usefulness than one might conclude from the work of Hairston and Twombly.

In view of the virtual certainty that assumptions of the Rigler-Cooley method will be violated, we have studied the robustness of the method for the estimation of development times of copepods. If the method is robust, violations of its underlying assumptions within certain limits may not be of great practical importance. For example,

assumptions of parametric statistical tests are frequently violated, yet, because of the general robustness of these tests, the violations often do not invalidate their use.

Hairston and Twombly use a simple two-instar cohort ($i, i + 1$) to model development and to examine the influence of changes in development time (T) and in the proportion surviving through the instar (S) on the accuracy of the Rigler-Cooley model. Hairston and Twombly also present examples of the error inherent in the use of the Rigler-Cooley method. We take a somewhat different approach to the assessment of error. Our aim is to identify those combinations of T and S that result in relatively small errors (absolute value $< 10\%$) for estimates of development time by the Rigler-Cooley method. We define error as the Rigler and Cooley estimate minus the true value over the true value, expressed as percent.

In theory, any combination of survivals is possible for the two instars in the model. In order to study combinations of S_i and S_{i+1} , we constrain T_{i+1} relative to T_i . We use three values for the ratio of T_{i+1} to T_i : 1.5, 1.0, 0.67. Under the condition $T_{i+1} = T_i$, many combinations of S_{i+1} and S_i will yield acceptable estimates of development time (Fig. 1). For example, when S_i is 0.60, the Rigler-Cooley method works well as long as S_{i+1} is > 0.24 . When we allow T_{i+1} to exceed T_i by a factor of 1.5, the boundaries within which the absolute value of the error is $< 10\%$ shift upward with respect to S_{i+1} . As S_i becomes small (< 0.5), the likelihood increases that S_{i+1} will be too low for the Rigler-Cooley method to provide correct results. At the other extreme, when T_{i+1} is short relative to T_i , the region defining $\pm 10\%$ error shifts downward with respect to S_{i+1} . The asymmetry of the envelope shows that the Rigler-Cooley method gives

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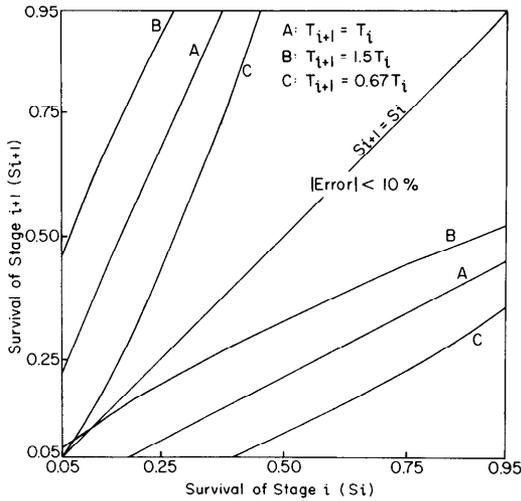


Fig. 1. Analysis of error due to use of the Rigler-Cooley method to estimate development times. S_{i+1} varies with respect to S_i at three fixed conditions for T_{i+1}/T_i . The diagonal line corresponds to $S_{i+1} = S_i$; other lines indicate $\pm 10\%$ error. See text for definition of error.

acceptable estimates of development time for more combinations of S_{i+1} and S_i when instar-specific survivorship is increasing with age than when it is decreasing with age. The Rigler-Cooley method performs quite well when instar-specific survivorship exceeds 0.5.

The accuracy of the Rigler-Cooley method is also affected by the relationship between the true development times of the two instars. In order to examine this aspect of the model, we constrain S_{i+1} relative to S_i . Again we use three ratios: 1.5, 1.0, 0.67. For each of the three conditions of fixed survivorship, we examine the effect of varying T_{i+1}/T_i on the accuracy of predictions by the Rigler-Cooley model (Fig. 2). When survival is constant ($S_{i+1} = S_i$) and $S_i > 0.30$, estimates will be good if T_{i+1} is between 0.5 and 2 times T_i . Even when S_i is < 0.30 , T_{i+1} can vary widely with respect to T_i and estimated development time will remain within 10% of the actual. Performance of the Rigler-Cooley method improves when $S_{i+1} > S_i$ at most values of T_{i+1}/T_i (Fig. 2). When $S_{i+1} < S_i$, upper limits are more stringent for T_{i+1}/T_i . Nevertheless, performance of the Rigler-Cooley method is good, especially when $S_i > 0.50$.

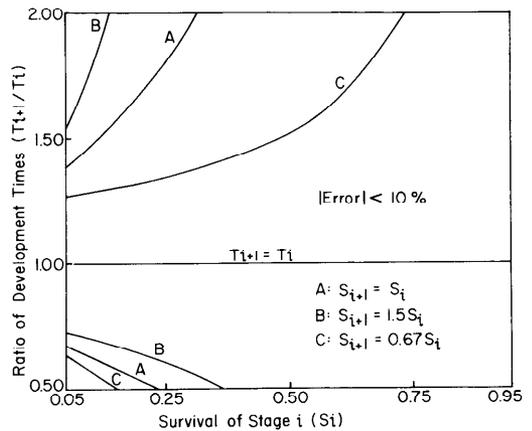


Fig. 2. Analysis of error due to use of the Rigler-Cooley method to estimate development times. The proportion T_{i+1}/T_i varies with respect to S_i at three fixed conditions for S_{i+1}/S_i . See text for definition of error.

An ecologically realistic view is possible if we consider what is known about copepod demography. In marine calanoid copepods, development times of adjacent stages tend to be so similar that a "rule" of isochronal development has been proposed (Miller et al. 1977; but see Landry 1983). Thus T_{i+1} is typically close to T_i , albeit usually somewhat longer (Geiling and Campbell 1972). Similar data exist for freshwater copepods, for which T_{i+1}/T_i typically falls in the range $2/3$ – $3/2$ (Elmore 1982).

It is more difficult to establish ranges for S_{i+1} and S_i . Because we are dealing with immature instars, we would expect survival to be high for all stages in the absence of control by starvation or predators (Hairston et al. 1983; Lonsdale 1981; Wyngaard 1983). Optimal growth conditions and no predation would result in S_{i+1} approximately equal to S_i , and the Rigler-Cooley method would work well. Any change in survivorship from instar i to instar $i + 1$ will increase the departure of the Rigler-Cooley estimate from the true development time, but the error will be small unless the change in S is large and abrupt. It is conceivable, for example, that ontogenetic shifts in food types could result in the release of individuals from a bottleneck caused by poor food for a certain stage. Size-selective predation could also cause a relatively sharp change in S with

maturation into a vulnerable stage. Thus major changes in S over the life cycle of the copepod are possible, but would almost certainly be evident in temporal patterns of abundance; the investigator would not be without clues.

The final item to consider is the absolute magnitude of S . Ignoring for the moment those cases in which S changes abruptly for two adjacent instars, we can identify a range of common values for S . We assume that time from hatching to maturation is about 21 d and that the average instar requires about 2 d to develop (cf. Landry 1983). If the mortality rate, α , is 0.10 d^{-1} and the development time, t , is 2 d, $S = 0.8$ where $S = \exp(-\alpha t)$. If we apply the same mortality rate over all instars, 12% of individuals will reach maturity, and this should be ample to sustain the population. For $\alpha = 0.3$, $S = 0.55$ for one instar, but $S = 0.002$ over all instars. The reproductive output of a female copepod is very unlikely to offset such low survival.

In summary, we expect the following for most copepod populations: $T_{i+1} > T_i$, but not by more than 50%; S_{i+1} sometimes variable with respect to S_i ; and S_{i+1} and $S_i > 0.5$. Within these limits, the Rigler-Cooley method will typically estimate development times within 10% of the true value. Abrupt changes in S outside these limits should be apparent from field population data and will be the most likely reason to mistrust development times derived from the Rigler-Cooley method. We concur with Hairston and Twombly that appropriate use of the Rigler-Cooley method requires judgment on the part of the investigator, but we believe that the method will often be applicable to natural populations.

A very attractive feature of the Rigler-Cooley method is that it requires only accurate measurements of density for each instar as a basis for estimating development times. The Hairston-Twombly method requires, in addition, knowledge of instar-specific survivorship. In practice, survivorship is difficult to measure. For obtaining development times to use in production estimates, the Rigler-Cooley method is robust

to violations of assumptions over a broad range of conditions that are ecologically realistic for copepods, and the method can be applied without precise knowledge of survivorship.

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References

- BOERS, J. J., AND J. C. H. CARTER. 1978. Instar development rates of *Diaptomus minutus* (Copepoda: Calanoida) in a small lake in Quebec. *Can. J. Zool.* **56**: 1710-1714.
- BURNS, C. W. 1980. Instar development rates and production of three generations of *Boeckella dilatata* (Copepoda: Calanoida) in a warm monomictic lake. *Int. Ver. Limnol. Theor. Angew. Verh.* **21**: 1578-1583.
- ELMORE, J. L. 1982. The influence of food concentration and container volume on life history parameters of *Diaptomus dorsalis* Marsh from subtropical Florida. *Hydrobiologia* **89**: 215-223.
- GEILING, W. T., AND R. S. CAMPBELL. 1972. The effect of temperature on the development rate of the major life stages of *Diaptomus pallidus* Herrick. *Limnol. Oceanogr.* **17**: 304-307.
- HAIRSTON, N. G., JR., AND S. TWOMBLY. 1985. Obtaining life table data from cohort analyses: A critique of current methods. *Limnol. Oceanogr.* **30**: 886-893.
- , W. E. WALTON, AND K. T. LI. 1983. The causes and consequences of sex-specific mortality in a freshwater copepod. *Limnol. Oceanogr.* **28**: 935-942.
- LANDRY, M. R. 1983. The development of marine calanoid copepods with comment on the isochronal rule. *Limnol. Oceanogr.* **28**: 614-624.
- LEWIS, W. M., JR. 1979. Zooplankton community analysis. Springer.
- LONSDALE, D. J. 1981. Influence of age-specific mortality on the life history traits of two estuarine copepods. *Mar. Ecol. Prog. Ser.* **5**: 333-340.
- MILLER, C. B., J. K. JOHNSON, AND D. R. HEINLE. 1977. Growth rules in the marine copepod *Acartia*. *Limnol. Oceanogr.* **22**: 326-334.
- RIGLER, F. H., AND J. M. COOLEY. 1974. The use of field data to derive population statistics of multivoltine copepods. *Limnol. Oceanogr.* **19**: 636-655.
- WYNGAARD, G. A. 1983. In situ life table of a subtropical copepod. *Freshwater Biol.* **13**: 275-281.