COMMENTARY


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Lehman and Branstrator (1995) characterize our (Yurista and Schulz 1995) bioenergetic prediction of Bythotrephes predation rates as an overestimate. They contend that two parameters (assimilation efficiency and development times) make our estimate high; they use an assimilation efficiency (AE) which they claim is high but appropriate and they use modeled development times that are longer than the development times we used. These values result in a difference of 40-50% in model results. We believe their parameter estimates and results are in error, and the difference in model results is significant for understanding the Great Lakes food webs and ecosystems.

We first address the contention by Lehman and Branstrator (1995) that the assimilation value (AE) should be high (0.85, Lehman 1993) compared to our AE of 0.60. We based our AE on 33P tracer studies (Schulz 1996); P has no important gaseous phase and all pools were measured to construct a complete 33P budget for the analyses. Corrections were made for excreted P (Schulz 1996) contrary to the statement by Lehman and Branstrator (1995). We conducted sensitivity analyses (Yurista and Schulz 1995) to investigate how errors in parameter estimates affect the model and concluded that our bioenergetic model for Bythotrephes is most sensitive to multiplicative factors such as ingestion efficiency and assimilation efficiency. Thus high estimates for AE will result in large changes in the model output.

In contrast, the AE used by Lehman and Branstrator (1995) was determined using 14C as a tracer (Lehman 1993). Lehman was unable to construct a complete carbon budget when determining AE because he did not measure the respired 14CO2 (see Lampert 1975, 1977). Animals were destructively sampled during the time course of the assimilation experiment to determine retention efficiency (sensu Peters 1984) and egestion, but the input from ingestion (ING) and loss to respiration were unknown. Lehman attempted to correct for an incomplete budget by estimating respiration as the apparent decrease in total counts of his experimental animals and egested material (C*chase + C*pred; notation from Lehman 1993). This method requires that the initial activity ingested is either known or is a constant value that could be determined by regression with time (Respiration = Loss = ING - (C*chase + C*pred)). The ING was not known and the activity ingested was not constant; Lehman tried to reconstruct ingestion by estimating unknown respiratory losses (C*ing = (C*chase + C*pred) x 1.05time; eq. (5) Lehman 1V93). Although the Daphnia were “uniformly” labeled, the amount of label ingested would vary between measurements because the Daphnia did not contain the same absolute amount of 14C due to differences in their mass. Even with equivalent masses, activity ingested would not be constant due to the variability (range -30-80%) observed within ingestion measurements (see Lehman 1993, Fig. 1). The estimated amount of ingestion and unmeasured 14CO2 respiration for each animal results in errors that decrease the precision of AE.

Second, Lehman used a power function (1.05time) to correct for respiration loss, which has no biological basis or empirical relationship to measurements for zooplankton. The pattern of 14CO2 respiration loss from discrete prey consumption by Bythotrephes should approximate the pattern of loss from pulse-fed (10 min) Daphnia (Lampert 1975).

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Tracer studies have shown that Daphnia have both a large structural and a much smaller metabolic pool and therefore a two compartment model is appropriate for zooplankton tracer kinetics (Lampert 1975, Lampert and Gabriel 1984). Lehman's exponential correction results in 52% of assimilated 14C being lost to respiration after 12 hours, whereas the value predicted from Lampert's two compartment model would be on the order of 32% (Fig. 1). This exponential model also implies that all of the 14C assimilated will be respired within a day after ingestion, ignoring the fact that according to Lampert (1975) much of the assimilated material is shunted to the structural pool. Thus the exponential correction used by Lehman for estimating respiration loss is not biologically sound (Fig. 1) and is an overestimate of respiration from a radiolabelled prey item that had been ingested up to 12 hours before, biasing the assimilation estimates high, and contributing to our doubts about the use of an AE of 0.85.

Our second major concern is the difference in development times proposed by Lehman and Branstrator (1995). They claim that longer times should be used for 2- and 3-barb instar development (D2 and D3) at 16°C based on additional measurements that supplement Yurista (1992). They have three new measurements for these instars, one for D2 at 21°C and two for D3 at 15.3°C and 21°C. We believe actual development times are less than what Lehman and Branstrator claim based on their (1) selective use of published data, (2) lack of acclimation control for adult instar measurements, and (3) use of a statistically-biased development model.

First, Lehman and Branstrator (1995) use a D2 measurement at 12.7°C from Yurista (1992) but omit a D3 measurement at 12.7°C, selectively biasing high their D3 development time. The D3 data point in Yurista (1992) was fully controlled for acclimation and development at 12.7°C and should have been included as was the D2 value to estimate instar times (Lehman and Branstrator 1995).

Second, prior developmental history has a large impact on current developmental processes through temperature acclimation and through the availability or lack of resources. The D3 measurements of Lehman and Branstrator (1995) were conducted with 2-barb animals of unknown developmental history that had been collected from Lake Michigan and placed in an environment and temperature different from their previous history. Measurements were begun as animals molted to the 3-barb instar. The stress resulting from temperature changes, sometimes indicated by increased mortality, is often accompanied by slower development times (Landry 1975, and see below). We have included Lehman
and Branstrator’s D3 data for calculations in the present response, which skews the time estimate slightly high at 16°C. However, we see no evidence that substantially longer development times are appropriate.

Because it is evident that prior developmental history is important in determining development times, we modify our 12.7°C development times (not suggested by Lehman and Branstrator) by estimating development time as time spent within each instar rather than accumulated time from birth (Yurista 1992). Some difference exists between the accumulated time estimate and the instar difference estimate because animals that completed the first or second instar, but died before having offspring, had significantly longer D1 development than did animals completing full development (Kruskal-Wallis n = 34,10; P = 0.013). Stress that leads to a premature death is observed to increase development time of the first instar upwards, and by subtraction from accumulated times, biases the later instar development times downward (Landry 1975). This observation of stress effects in early development times leads to additional concerns about the development times for first and second instars (Lehman and Branstrator 1995) which were not reported as living to primaparity. The reanalyzed instar development times for animals at 12.7°C that live through primaparity are 4.60 d (0.70 sd, n = 10) for D1, 3.80 d (0.63 sd, n = 10) for D2 and 5.60 d (0.84 sd, n = 10) for D3.

Third, the development times at 16°C used by Lehman and Branstrator (1995) were estimated using a reciprocal relationship rather than the IBP Zooplankton Ecology Group recommended and less statistically biased log-transformed model for development (Bottrell 1975, Bottrell et al. 1977, Yurista 1992). We refit the log-transformed model to the embryo development times (all data from Yurista 1992 and one new point from Lehman and Branstrator 1995) and adjusted it to all data points for D1, D2, and D3 development stages, assuming a constant relationship between instar durations (Landry 1975, Corkett 1984, and as in Yurista (1992) and Lehman and Branstrator (1995)) (Table 1). First instar development time at 16°C did not change significantly with reanalysis (D1 = 3.63 compared to the previous D1 = 3.76). The log-transformed model for both D2 and D3 predicted lower development times at 16°C (D2 = 3.1 d, D3 = 4.6 d) than did the reciprocal model used by Lehman and Branstrator (D2 = 3.5 d, and D3 = 5.1 d). Also, the log-transformed model fit the data better than did the reciprocal model; the sum of squared errors (SSE) are lower for the log-transformed model than the reciprocal model with a percent difference for SSE of 67% for D2 and 23% for D3. The log-transformed model is therefore better for both statistical and empirical reasons.

### TABLE 1. Parameters for the recommended log-transformed model (Bottrell et al. 1977) of instar development (D in hours) at a temperature T [Log(Di) = a + b*Log(T) + c*(Log(T)²)] fit to the data of Lehman and Branstrator (1995) and Yurista (1992) (A). The development stages are assumed to maintain a constant proportion of development time throughout the temperature range (Landry 1975, Corkett 1984). Bioenergetic estimates of prey consumption rate (Yurista and Schulz 1995) are compared to prey consumption rate estimates using the longer development times as calculated with the revised log-transformed development model from the data of Lehman and Branstrator (1995) combined with Yurista (1992) (B).

#### A) Development stage | Model parameter | a | b | c
--- | --- | --- | --- | ---
embryo | 6.167 | -6.096 | 1.950
D1 | 6.454 | -6.096 | 1.950
D2 | 6.381 | -6.096 | 1.950
D3 | 6.559 | -6.096 | 1.950

#### B) Development stage | Yurista and Schulz (1995) (µg C d⁻¹) SE | This comment (µg C d⁻¹) SE
--- | --- | ---
D1 | 48 (0.68) | 48 (1.3)
D2 | 122 (2.1) | 111 (3.0)
D3 | 187 (2.74) | 152 (4.9)
Lifetime | 1,132 (16.9) | 1,214 (35.6)
We re-ran our bioenergetic model at 16°C with the longer development times, D1 (3.63 d), D2 (3.1 d), and D3 (4.6 d), determined using the reanalyzed log-transformed model of instar development (Table 1). The results of the re-run model differ from the original estimate by a small percentage on a daily basis (Table 1). The D3 decrease, however, is due largely to the inclusion of data from Lehman and Branstrator (1995) we consider biased. The overall lifetime consumption increased to meet additional respiratory losses that occur as a result of the longer growth period. The total predation of Bythotrephes is larger with an increased development period, but spread out over a small increase in time. The juvenile stages still have a significant impact and the adults eat a large percentage of their weight each day as found by Yurista and Schulz (1995).

Finally, we point out an apparent error in the reported parameters in Lehman and Branstrator's (1995) equation for relative growth (eq. 10). We found that the fit parameters were $c = 4.034$ and $d = -0.837$ ($r^2 = 0.993$) a difference of 24 and 44% from the values reported by Lehman and Branstrator (1995); relative dry weights during growth are better predicted with the new values (Table 2). All results of Lehman and Branstrator (1995) for growth and respiration are dependent on these parameters.

We conclude that Lehman and Branstrator (1995) have underestimated the predation rate of Bythotrephes. First, there is evidence that (a) Lehman's (1993) AE estimate is unsound given the accepted methodology for tracer studies and the biological basis for their interpretation; (b) their report of longer development times derived from selective use of published data, an inappropriate model, and an inconsistent methodology for determining development stages, contributes to the lower daily consumption rate; and (c) their computations use poorly determined parameters (Table 2). Second, we have experimental data (Schulz 1996, Schulz and Yurista in review) that support the predation estimates from our model, and recommend that the model parameters and results in Table 1 or in Yurista and Schulz (1995) be used at present for estimation of food web effects from Bythotrephes.

### TABLE 2. Reanalysis of parameters to equation 10 (Lehman and Branstrator 1995); $W_{rel(trel)} = \exp[c \times (1 - \exp(d \times trel))]$ for relative weights at age data in their Table 4. The data were fit using nonlinear techniques (SYSTAT and SAS). Included are the predicted values using the parameters of Lehman and Branstrator ($c = 3.052$, $d = -1.486$), and those of the reanalysis ($c = 4.034$, $d = -0.837$).

<table>
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<th>Stage</th>
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<th>Relative Age</th>
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REFERENCES


