

Appendix A: Estimating bioenergetic model parameters from synthesized literature data.

In this appendix, we explain in detail the sources of data and the methods used to estimate the parameters in our molt-by-molt Dynamic Energy Budget model of *Daphnia magna*. We standardized all the data to units of ‘mgC’ for mass and energy, ‘mm’ for length and ‘days’ for time. We use the conversion factor of 0.42 to convert from mg dry weight to mgC for *D. magna* and a respiratory coefficient of 0.89 as an average of the values seen by Lampert and Bohrer (1984) for starving and well-fed animals. All the confidence intervals reported here are at the 95% level.

Weight-length relationship

The existence of a reliable relationship between weight and length of *D. magna* is well documented in the literature. The choice of literature data was restricted to weight measurements of individuals with no eggs or embryos in the brood pouch (either before allocation to reproduction, soon after reproduction, or after the eggs were removed), but including the carapace. It was harder to strictly control for the definition of length between length defined as the distance between the top of the head and the base of spine, but given the consistency in the relationships obtained from the data, we chose to ignore this source of inconsistency. The data were fit using a linear regression on a log-log plot ensuring normality of the residuals using a Shapiro-Wilk test. We fit general log-log weight-length relationship $W = \left(\frac{L}{L_w}\right)^{\mu_w}$. The relationship reported by Porter et al. (1982) is $W = \left(\frac{L}{6.3822}\right)^{2.3907}$, which agrees closely in exponent with our cumulative estimate. The larger scale factor is most likely due to the conflation of egg-bearing and egg-bearing individuals in the Porter et al. (1982) data.

TABLE A1. Weight length relationship: The estimates obtained from three sources and the corresponding confidence intervals in the estimates. The estimates are fairly consistent and mostly fall within the confidence intervals in the remaining estimates.

Source	L_w	C. I. (L_w)	μ_w	C.I. (μ_w)
Sophia Solter (Plön)	10.78	[9.464, 12.379]	2.37	[2.271, 2.468]
Kersting and Leeuw-Leegwater (1976)	6.423	[5.198, 8.248]	2.269	[2.073, 2.465]

Schindler (1968)	9.023	[5.97, 15.819]	2.026	[1.71, 2.343]
<i>Cumulative estimate</i>	10.857	[9.327, 12.85]	2.306	[2.193, 2.42]

Dependence of respiration on the weight of individuals

The respiration costs of individuals are composed of the basal metabolic rate, specific dynamic action (SDA) and activity costs. The respiration rate measured for starved or fasting individuals represents the basal metabolic rate with minimal activity costs of swimming and gas exchange. Schindler (1968) found no significant effect of respiration on motion, crowding, light intensity, or reproductive state. However, there is an almost linear increase in respiration rate with assimilation rate (Fig. 8, Lampert 1986; Fig. 5, Bohrer & Lampert 1988), while similar increasing trends have been observed with feeding rate and filtering rates. In our model, this assimilation rate-related respiration can be directly incorporated as a decrease in the effective assimilation efficiency of individuals in our net production formulation (recall, net production = assimilation – maintenance (= respiration + carapace costs)).

While we would ideally want a dynamic representation of respiration to account for the rapid changes in rates observed in step-up and step-down food experiments (Lampert 1986), these changes in respiration occur at time scales significantly faster than the molt durations and feeding intervals for batch cultures considered here, and hence, we ignore these effects in our model. We use data from five sources (Schindler 1968; Kersting & Leeuw-Leegwater 1976; Bohrer & Lampert 1988; Glazier 1991; Glazier & Calow 1992) to fit the power-law relationship

$$R = R_{20}W^{\mu_R}, \text{ where } R \text{ is in mgC/mgC Daphnia/d and } W \text{ is in mgC,}$$

and our fits are summarized in Table A2; we use a linear regression on log-log data and ensure normality of the residuals using the Shapiro-Wilk test. Data was separated between adults and juveniles when specified in the data, while 42 ugC was used as the threshold for maturity when maturity of the individuals was unavailable and for the cumulative data fitting.

Our cumulative fits suggest that respiration is nearly isometric with weight and agrees with the regression performed by Glazier and Calow (1992). In fact, by separating apart the respiration rates of eggs, embryos and adults, Glazier (1991) concludes that the respiration rate is nearly isometric and the sublinear estimates produced from other data is due to the presence of eggs in the brood chamber that have only ~40% of respiration rate as adult somatic tissue. Given this finding and that we have attempted to strictly use weight as the mass of adults without eggs, the simplest solution is to use

$$R = R_{20}W,$$

where $R_{20} = 0.11$.

TABLE A2. Synthesis of data on juvenile and adult *D. magna* respiration rates against individual mass

Source	Juveniles	Adults	Complete data
Bohrer and Lampert (1988)	$R = 0.0873W^{0.8237}$ $R_{20} \in [0.0655, 0.1162]$ $\mu_R = [0.7567, 0.8906]$	$R = 0.1162W^{1.013}$ $R_{20} \in [0.0973, 0.1387]$ $\mu_R = [0.938, 1.087]$	$R = 0.0707W^{0.7887}$ $R_{20} \in [0.064, 0.078]$ $\mu_R = [0.7567, 0.821]$
Schindler (1968)	$R = 0.0837W^{0.925}$ $R_{20} \in [0.0756, 0.0928]$ $\mu_R = [0.9006, 0.9494]$	$R = 0.0711W^{0.858}$ $R_{20} \in [0.0384, 0.1316]$ $\mu_R = [0.644, 1.071]$	$R = 0.0872W^{0.9335}$ $R_{20} \in [0.0811, 0.0937]$ $\mu_R = [0.915, 0.952]$
Kersting and Leeuw-Leegwater (1976)			$R = 0.085W^{0.7812}$ $R_{20} \in [0.0476, 0.1518]$ $\mu_R = [0.6326, 0.93]$
Glazier (1991)	$R = 0.1129W^{1.0226}$ $R_{20} \in [0.1129, 0.3065]$ $\mu_R = [0.9153, 1.13]$	$R = 0.0489W^{0.5181}$ $R_{20} \in [0.0372, 0.0642]$ $\mu_R = [0.3752, 0.6611]$	$R = 0.112W^{0.9089}$ $R_{20} \in [0.1009, 0.1242]$ $\mu_R = [0.8752, 0.9427]$
<i>Cumulative estimate</i>	$R = 0.1009 W^{0.9014}$ $R_{20} \in [0.0749, 0.136]$ $\mu_R = [0.8323, 0.9705]$	$R = 0.1207 W^{0.9968}$ $R_{20} \in [0.1024, 0.1422]$ $\mu_R = [0.926, 1.068]$	$R = 0.0972 W^{0.896}$ $R_{20} \in [0.0892, 0.1059]$ $\mu_R = [0.8704, 0.9215]$
Glazier and Calow (1992)			$R = 0.113 W^{0.951}$

Carbon content of carapace in *Daphnia* individuals

Glazier and Calow (1992) measured the relationship between dry weight and the weight of cast skin for 2 clones at two different food levels. Three of the relationships are not significantly different, and the fourth relationship that is significantly different yields bizarre results (i.e., large adults having carapaces representing approximately 30% of their body weight, as opposed to the more typical value of 12-15 % observed in other cladocerans). The following relationship represents the correct average of the three relationships reported in Glazier and Calow in carbon units

$$C = \left(\frac{W}{W_C} \right)^{\mu_C} = \left(\frac{W}{2.8962} \right)^{1.259},$$

with confidence intervals $W_C \in [2.343, 3.531]$ and $\mu_C = [1.2, 1.3167]$.

Life-history and molt duration in juveniles and adult *Daphnia*

Neonates: Ebert (1993) measured the offspring size at different food levels for two different clones and at the first and second clutch. Except for the highest food levels at first clutch, the size at birth for neonates $\sim 0.9 - 1.05\text{mm}$.

Using the weight-length relationship in Table A1, the weight of neonates at birth is $7.6 - 10\text{ ug}$ dry weight ($3.2 - 4.5\text{ ugC}$), which agrees well with the dry weight ($7.5 - 9.75\text{ ug}$) of third brood neonates reported in Glazier (1992) for two different clones; the experimental method for standardized tests typically use cultured third brood neonates to initiate each run.

Eggs: The weight of eggs depends on the food level, brood number (through maternal body mass) and clone, and range from $6 - 11\text{ ug}$ dry weight ($2.5 - 4.5\text{ ugC}$) according to Glazier (1992). This range is also supported by Trubetskova and Lampert (1995). Assuming the maintenance requirements of brooding eggs is identical to somatic biomass of individuals during the brooding instar, we can estimate depending on the environment and life-history, the size of the eggs required to produce neonates between $0.9 - 1.05\text{mm}$ in length.

Maturity: The age and time to maturity of juveniles is food-dependent. However, a simple size-threshold for maturity (McCauley et al. (1990)) can capture this food-dependence. Ebert (1992) finds evidence for the size of juveniles, two instars before laying eggs, staying consistent across food levels at 1.71mm for the clone used in that study; note, *D. magna* takes two instars of commitment to reproduction before eggs are first laid. Thus, the variability in age at maturity and size at maturity is determined by the variability in duration of the instar preceding the eggs being laid in the brood pouch. This is in line with Porter et al.'s (1983) determination that the size at the onset of reproduction was higher (1.93mm) than at a food level one order of magnitude smaller (1.8mm). We choose the size threshold for maturity as $\sim 1.7\text{mm}$.

Molt durations: Noguiera *et al.* (2009) report that an exponential relationship between instar duration and length of individuals. For adults (with size $> L_{Th}$), the instar duration varies between $1.5 - 3.5$ days and for juveniles the molt duration is $1-1.5$ days. Since, instar duration depends both on carapace construction in juveniles and adults and brood development in adults, explicit length- (size-) dependence of the molt duration is reasonable. The best exponential fit of the molt duration is $0.8188e^{0.4912L}$. Considering the 90% confidence envelope of this fit on the data yields

exponential bounds for the minimum and maximum molt duration as $0.7307e^{0.3746L}$ and $0.9174e^{0.4692L}$ respectively.

Porter *et al.* (1983) report average adult molt/brood durations as ranging between 5 days at the lowest food level and 3 days at the highest food levels. For juveniles, they report age and number of instars to onset of reproduction that produces juvenile molt durations between 1.5 and 3 days.

Glazier (1992) presents the age of different broods for two clones at a low and high food level. The average adult brood duration from this dataset is 1.5-3 days, with the larger duration for the higher food level (which incidentally contradicts our model formulation). Ebert (1991) reports the development time of the first clutch (1st brood) to be 5.2 days across multiple clones and states that the brood duration did not differ across clones. The data of Porter *et al.*, Glazier and Ebert fall mostly within the exponential bounds constructed from the Noguiera *et al.* (2009).

TABLE A3. Summary life-history parameter estimates for *D. magna*.

Parameter	Estimated value
Size at birth of neonates (L_0)	0.9 -- 1.05 mm
Length threshold for maturity (L_{Th})	1.7 mm
Minimum molt duration of 1mm <i>Daphnia</i> at 20°C (t_{min}^{20})	0.6965 d
Maximum molt duration of 1mm <i>Daphnia</i> at 20°C (t_{max}^{20})	0.9625 d
Minimum molt duration length exponent at 20°C (μ_{min})	0.3546 mm^{-1}
Maximum molt duration length exponent at 20°C (μ_{max})	0.4891 mm^{-1}

Food- and size- dependence of ingestion rate

Evers and Kooijman (1989) present the only data we are aware of relating the maximum ingestion rate to the length of the individual *D. magna* at a food concentration of 4.295 mgC/l (0.5E6 cells/cc) of *S. subspicatus* (the algal carbon content per unit cell volume was obtained from (Rocha & Duncan 1985) and cell volume is provided by Evers and Kooijman). Digitizing their data and converting to carbon units, we get the maximum ingestion rate in mgC/individual/d is

$$I_{max}(T = 20) = I_{max20}L^{\mu_1} = 0.0111 L^{1.8159}$$

The type II functional response for ingestion allows the estimation of the maximum rate and the half-saturation constant of the response to be decoupled. We use data from (Kersting & Leeuw-

Leegwater 1976; Porter *et al.* 1982; Bohrer & Lampert 1988) to estimate the half-saturation constant in mgC/l and summarized in Table A4. Concentrations of algal food were expressed in carbon units using Rocha and Duncan (1985), when not provided with the data (It must be noted that expressing algal food concentrations in cells/ml or mgC/l is likely to produce similar results as Rocha and Duncan (1985) find almost constant carbon to volume ratios and *Daphnia* feed on algal cells in a fairly restricted size range). While Evers and Kooijman (1989) present data on the functional response of *D. magna* with food concentration, their data is scaled to 4 mm length individuals that appears to skew the half-saturation constant to a much higher value than the other data.

TABLE A4. Estimation of the type II feeding response of *D. magna*.

Source	f_h estimate	I_{\max} estimate	Evers & Kooijman I_{\max} prediction
Kersting and Leeuw-Leegwater (1976)	0.0098 [0.0281, 0.3767]	89.82 [59.755, 176.019]	89.55
Porter <i>et al.</i> (1982)	0.0545 [0.0142, 0.1635]	11.52 [9.5086, 13.604]	67.396
Bohrer and Lampert (1988)	0.1394 [0.0943, 0.2022]	61.8332 [56.44, 67.806]	154.61

As seen above the predictions from Evers and Kooijman of the maximum rate of ingestion is in the general range of the estimates produced from fitting of the functional response. We therefore use the average of the half-saturation constant estimates as $f_h = 0.1$ and use an ingestion rate function of the form

$$I_{\max 20} \frac{F}{F + 0.1} = 0.0111 L^{1.8159} \frac{F}{F + 0.1}.$$

Temperature dependence of metabolic processes

The temperature dependence of physiological processes is well known, but the relationship is not so well characterized in the literature. Typically, the metabolic processes are observed to peak at some optimal temperature and are modeled using the Arrhenius function for chemical reaction kinetics. Instead, here we use available data in the literature to fit a polynomial function to the processes in our bioenergetic model.

Ingestion: Kersting and Leeuw (1976) measure the temperature profile for ingestion over a range of temperatures for *D. magna*. We reproduce the fourth-order polynomial fit of Kersting and Leeuw and rescale the maximum ingestion rate at 20°C as

$$I_{\max}(T) = I_{\max,20}(-15.239 + 3.80589T - 0.33877T^2 + 0.013192T^3 - 0.000187T^4)$$

Respiration: McFeeters and Frost (2011) study the variation in respiration of *D. magna* with temperature and phosphorus content of the algal food. Since they find almost identical temperature dependence of respiration rates for both phosphorus levels and the low-phosphorus measurements at 20°C are more compatible with other measurements at that temperature, we construct a temperature profile of the form

$$R(T) = R_{20}\lambda(T) = R_{20}(0.055T - 0.1), \text{ with temperature } T \text{ in Celsius}$$

The increase in metabolic rates with temperature is the main contributor to increased respiration and hence, we assume that molt development rates also have the same scaling,

$$t_{\min}^X(T) = t_{\min,20}^X\lambda(T).$$

Allocation of net production to reproduction

A positive net production is allocated to growth and reproduction in a ratio that is dependent on the maturity and size (length) of the *Daphnia*. Note that there is a subtle difference between a weight and length measure as weight is continuously varying in our model whereas length changes discretely at the molts. Any positive net production in a juvenile *Daphnia* is allocated all to growth. Glazier and Calow (1992) measure the partitioning of energy to growth, reproduction, respiration and carapace formation in two clones of *D. magna* at two different food levels. They present data on the weight specific rates of energy allocation at different instars to growth and reproduction. We assume all the net production in these experimental *Daphnia* is split only between growth and reproduction. We match the instar where allocation to reproduction begins to the first brooding instar in Glazier (1992) for each of the *Daphnia* clones at the two food levels to obtain the carbon body mass at each instar. We then use the weight-length relationship from Table A1 to obtain the length of *Daphnia* at each instar and fit the fraction allocated to reproduction as a function of length for adult *Daphnia* ($L > L_{Th}$) according to

$$\kappa = 1 - \frac{1}{1 + \gamma\mu_A(L - L_{Th})_+^{\mu_A}}.$$

Dropping data points where $\kappa = 0$ for $L > L_{Th}$ as outliers, we get parameter estimates of $\gamma = 0.2666 \text{ mm}^{-1}$ and $\mu_A = 2.4533$.

LITERATURE CITED

- Bohrer, R.N. & Lampert, W. (1988) Simultaneous Measurement of the Effect of Food Concentration on Assimilation and Respiration in *Daphnia magna* Straus. *Functional Ecology*, 2:463-471.
- E. G. Evers & S. A. L. M. Kooijman. (1989) Feeding, Digestion and Oxygen Consumption in *Daphnia Magna* a Study in Energy Budgets. *Netherlands Journal of Zoology*, 39:56-78.
- Ebert, D. (1992) A Food-Independent Maturation Threshold and Size at Maturity in *Daphnia magna*. *Limnology and Oceanography*, 37:878-881.
- Ebert, D. (1993) The Trade-Off Between Offspring Size and Number in *Daphnia-Magna* - the Influence of Genetic, Environmental and Maternal Effects. *Archiv fuer Hydrobiologie*, 453-473.
- Glazier, D.S. (1991) Separating the Respiration Rates of Embryos and Brooding Females of *Daphnia magna*: Implications for the Cost of Brooding and the Allometry of Metabolic Rate. *Limnology and Oceanography*, 36:354-362.
- Glazier, D.S. (1992) Effects of Food, Genotype, and Maternal Size and Age on Offspring Investment in *Daphnia Magna*. *Ecology*, 73:910-926.
- Glazier, D.S. & Calow, P. (1992) Energy Allocation Rules in *Daphnia magna*: Clonal and Age Differences in the Effects of Food Limitation. *Oecologia*, 90:540-549.
- Kersting, K. & Leeuw, W. (1976) The use of the Coulter Counter for measuring the feeding rates of *daphnia magna*. *Hydrobiologia*, 49:233-237.
- Kersting, K. & Leeuw-Leegwater, C. (1976) Effect of food concentration on the respiration of *Daphnia magna*. *Hydrobiologia*, 49:137-142.
- Lampert, W. (1986) Response of the respiratory rate of *Daphnia magna* to changing food conditions. *Oecologia*, 70:495-501.
- Lampert, W. & Bohrer, R. (1984) Effect of food availability on the respiratory quotient of *Daphnia magna*. *Comparative Biochemistry and Physiology Part A: Physiology*, 78:221-223.
- McFeeters, B.J. & Frost, P.C. (2011) Temperature and the effects of elemental food quality on *Daphnia*. *Freshwater Biology*, 56:1447-1455.

- Nogueira, A.J.A., Baird, D.J. & Soares, A.M.V.M. (2009) Testing physiologically-based resource allocation rules in laboratory experiments with *Daphnia magna* Straus. *Annales de Limnologie - International Journal of Limnology*, 40:257-267.
- Porter, K.G., Gerritsen, J. & Orcutt, J.D. (1982) The Effect of Food Concentration on Swimming Patterns, Feeding Behavior, Ingestion, Assimilation, and Respiration by *Daphnia*. *Limnology and Oceanography*, 27:935-949.
- Porter, K.G., Orcutt, J.D. & Gerritsen, J. (1983) Functional Response and Fitness in a Generalist Filter Feeder, *Daphnia Magna* (Cladocera: Crustacea). *Ecology*, 64:735-742.
- Rocha, O. & Duncan, A. (1985) The relationship between cell carbon and cell volume in freshwater algal species used in zooplanktonic studies. *Journal of Plankton Research*, 7:279 -294.
- Schindler, D.W. (1968) Feeding, Assimilation and Respiration Rates of *Daphnia magna* Under Various Environmental Conditions and their Relation to Production Estimates. *Journal of Animal Ecology*, 37:369-385.
- Trubetskova, I. & Lampert, W. (1995) Egg size and egg mass of *Daphnia magna*: response to food availability. *Hydrobiologia*, 307:139-145.