

CONSERVED ONTOGENY AND ALLOMETRIC SCALING OF RESOURCE ACQUISITION AND ALLOCATION IN THE DAPHNIIDAE

JEFFRY L. DUDYCHA¹ AND MICHAEL LYNCH

Department of Biology, Indiana University, Bloomington, Indiana 47405

¹E-mail: jdudycha@bio.indiana.edu

Abstract.—Life histories vary widely among taxa, but within phylogenetic groups there may be a fundamental framework around which trait variation is organized, perhaps as a consequence of lineage-specific developmental constraints. In organisms with indeterminate growth, there is an ongoing problem of optimally allocating resources between growth and reproduction, and that allocation decision may manifest itself through allometric scaling. Previous work on freshwater zooplankton has shown that the ontogenetic pattern of resource allocation can be described by simple mathematical functions. An important component of understanding how such functions can explain life-history variation is to discover which parameters in these functions are robust, with respect to both resource availability and evolutionary diversification, and which parameters exhibit interspecific allometry. To shed light on these issues, detailed life table experiments were conducted on eight species in the family Daphniidae (Crustacea) at high and low levels of resources. Using data on growth, reproduction, and instar duration, the ontogeny of resource allocation to growth and reproduction could be described as functions that plateau at or shortly after the onset of maturity. To be sure that the results were not an artifact of phylogenetic structure, the parameters were tested in a phylogenetically controlled fashion. The results suggest a simple set of resource allocation rules for daphniids, whereby all species exhibit a similar form of ontogenetic change in allocation, and reach a plateau where approximately 94% of available resources are allocated to reproduction. The asymptotically maximal rate of net resources incorporated in growth and reproduction was positively related to size at maturity, whereas the rates of approach to plateaus (for both net resource assimilation and proportional allocation to reproduction) were negatively related to body size. Per-offspring investment was positively related to the square root of size at maturity. Using this approach, a wide range of interspecific variation in life-history features can be related to a single underlying trait, the size at first reproductive investment.

Key words.—Body size, *Ceriodaphnia*, correlated evolution, *Daphnia*, indeterminate growth, life-history resource assimilation.

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The allocation of resources to competing functions is the central problem of life-history evolution because allocation decisions directly affect fitness. Much effort has therefore been directed toward modeling and measuring resource allocation, initially focusing on the determination of an optimal balance among life-history traits (Schaffer 1974; Cohen 1976; van Noordwijk and de Jong 1986; Engen and Saether 1994; Worley et al. 2003) and later incorporating ecological influences on that balance (Taylor and Gabriel 1992; Heino and Kaitala 1996; Fiksen 1997; Shertzer and Ellner 2002; Lardner and Loman 2003). One trait that has justifiably received special attention for its influence on resource acquisition and allocation is body size (Peters 1983; West et al. 2001; Zhang and Jiang 2002; Hurst and Conover 2003). Size matters to virtually all of an organism's functions and interactions. In particular, it is often a key determinant of both survival and fecundity, the two aspects of life history that demarcate the essential resource allocation problem.

For organisms with indeterminate growth, the problem of how best to allocate resources is one that individuals must confront continuously throughout their adult life (Kozłowski 1996; Heino and Kaitala 1999). Resources can be allocated to basic maintenance functions, growth, or reproduction. Models have often assumed that basic maintenance needs are met in full first, and only the remaining resources can be applied to growth and reproduction. However, there is no reason to expect that the resources available for allocation to growth and reproduction, or the proportion of that allocated to reproduction, will remain constant throughout life. Benefits of allocating resources to growth may include increased

survival probability, increased future reproductive capacity, or increased ability to acquire and assimilate additional resources. As an individual grows, both the marginal gains from further growth and the associated maintenance costs may change, in turn altering the optimal allocation strategy. Allowing the allocation decision to vary ontogenetically represents a significant modeling challenge, and thus many attempts to explain indeterminate growth theoretically have assumed simple, fixed allocation rules in which the division of resources does not vary ontogenetically (Heino and Kaitala 1999). A number of authors have explored dynamic optimization models to allow the division of resources to change with each age or stage class (reviewed in Perrin and Sibly 1993). In these models, sophisticated mathematical techniques are used to recast the dynamic problem into a series of static problems for each time point.

An alternate approach that has recently been developed begins by considering ontogenetically changing characters to be manifestations of an underlying function-valued trait, rather than a series of age-specific traits (Pletcher and Geyer 1999; Jaffrezic and Pletcher 2000; Jaffrezic et al. 2004). This approach has been successfully applied to life-history traits, particularly with respect to senescence, in which the ontogenetic change of a trait has been summarized by empirically determined equations. This approach simplifies comparative problems because it allows comparison of a function's parameters, rather than relying on separate comparison of each age class. The initial challenge of employing this approach is to identify suitable functions that provide a good ontogenetic description of the trait of interest.

Daphnia are ideal organisms for the study of life-history evolution and resource allocation. They are widespread freshwater microcrustaceans with a cyclically parthenogenetic life cycle including variable periods of asexual reproduction punctuated by sex under appropriate environmental triggers (Lynch 1980a). Like all crustaceans, they have indeterminate growth that occurs at the time of molting between successive instars. In the laboratory, clonal lines can be maintained indefinitely so that many genetically identical individuals can be included in phenotypic assays. In addition, estimates of reproductive investment are not complicated by the need for mating. *Daphnia* are also of general importance in aquatic ecosystems as the dominant grazers in many lakes and ponds (Hutchinson 1967; Sterner 1989; Leibold 1989). They have been the focus of substantial research on the ecology of consumer-resource interactions, and therefore have allowed linking life-history variation to community ecology (McCauley et al. 1988; Diehl et al. 1993; Tessier et al. 2000; Tessier and Woodruff 2002a,b; Steiner 2003). A recurring theme in the ecology of zooplankton trophic interactions has been the importance of body size, both with respect to predator avoidance (Brooks and Dodson 1965) and exploiting phytoplankton (Gliwicz 1990), and thus relationships between size and life history are often thought to be driven by selection on size (Hall et al. 1976; Lynch 1980a,b; Gabriel 1982; Dorazio and Lehman 1983).

There have been several studies of resource allocation in *Daphnia* (e.g., Taylor and Gabriel 1992, 1993; Glazier and Calow 1992; Stibor 2002), and two previous reports on the ontogeny of resource allocation in *Daphnia* (Lynch 1989, 1992) revealed that important components of life histories could be characterized by a few essential features. In particular, simple asymptotic functions gave good fits to the ontogenetic change in quantity of resources allocated to growth + reproduction, the proportion of that sum allocated to reproduction, and instar duration for *Daphnia pulex*. The general form of these functions also applied to *D. ambigua* and *Ceriodaphnia quadrangula*, two species that mature at a much smaller size than *D. pulex*. Moreover, instar-specific durations and the size-specific allocation patterns of reproductive investment were found to be independent of food level. Important differences found among the taxa included longer residence of the two small species in young instars and shorter residence time in older instars (Lynch 1992), and the two species that are small at maturity invested a greater proportion of available resources in reproduction on a size-specific basis (Lynch 1992). That is, an individual *D. ambigua* invests a greater proportion of available resources to reproduction than does a same-sized individual *D. pulex*. This led to the idea that body size may be associated with resource allocation patterns independent of size-specific mortality (Lynch 1992). If such an association exists, parameters describing the ontogeny of life-history allocation patterns should exhibit strong interspecific allometry.

In this study, we report a comparative analysis of the resource allocation of eight species of *Daphnia* and *Ceriodaphnia* under abundant and scarce resource conditions. Our primary objective is to determine which aspects of the previously identified resource allocation patterns are robust across taxa. To accomplish this, we sample broadly across

the size range of species and place our results in the context of a robust phylogenetic hypothesis. Thus, we are able to evaluate whether the interspecific patterns are the result of allometric scaling or evolutionary history, providing insight into the scope of developmental constraints on size-specific resource allocation patterns in indeterminately growing animals.

MATERIALS AND METHODS

Experimental Protocol

The empirical methods used in this study have been previously described in detail (Lynch et al. 1986; Lynch 1989, 1992). A single clone of each of eight species, all in the genera *Daphnia* or *Ceriodaphnia* and isolated from a central Illinois lake or pond, were assayed in life tables. Body length, reproduction, and survivorship data were gathered daily for two sets of approximately 50 individuals of each clone, one set acclimated and grown on a low food concentration, and the other set on a high concentration. Clones were acclimated to experimental conditions for at least two generations prior to analysis, and experimental animals were taken from the second clutch or later. Animals were cultured individually in 40 ml of zooplankton medium (Lynch et al. 1986). The food consisted of a standard mixture of two green algae (*Chlamydomonas* and *Scenedesmus*, quantified via hemocytometer counts), replenished every day along with fresh culture medium. The high concentration, equivalent to approximately 1.54 μg carbon/ml, is near or above the saturation level for most species (Lynch et al. 1986; Lynch 1989, 1992). The low concentration, 0.154 μg carbon/ml, supported growth of all species, but was below the saturation level. All animals were maintained at 20°C on a 12:12 light:dark photoperiod. Due to the large amount of work involved and the periodic availability of some species, the assays were staggered over a two-year period. The data for *D. pulex*, *D. ambigua*, and *C. quadrangula* have been previously published (Lynch 1989, 1992).

To determine rates of investment in growth, species-specific length-mass relationships were obtained from approximately 40 individuals for each clone of a wide range of sizes at each food concentration. To ensure that the estimated size-specific changes in mass were associated primarily with somatic tissues, these masses were obtained only from females with recently depleted ovaries, after the recently laid eggs were removed from the carapace (Lynch et al. 1986). As previously reported (Lynch 1989, 1992), the logarithmic regressions of dry masses on length were very similar under both food concentrations (with neither a main effect nor interaction with food level; analysis not shown), except in one case (*C. quadrangula*). Except in the latter case, the data were pooled to yield the fits reported in Table 1. Table 1 also shows that the standard errors on the pooled regression parameters are very small, illustrating the lack of resource level effects.

Dry masses of newly laid eggs were obtained from all species by weighing four to five batches of 10–35 eggs from mothers of random ages as in Lynch (1989, 1992). For *D. mendotae*, *C. reticulata*, and *C. lacustris*, egg masses were measured only at the high food level. Since the egg masses

TABLE 1. Dry weight per egg and least-squares estimates of the parameters of the logarithmic length-weight regression, $\ln W = \alpha_1 + \alpha_2 \ln L$, with standard errors in parentheses. Units of W and L are μg and mm (from the base of the tailspine to the top of the eyespot). The data for *Daphnia pulex* are from Lynch 1989, and those for *Ceriodaphnia quadrangula* and *D. ambigua* are from Lynch 1992. Instances where values differed between the resource environments are indicated as high (H) or low (L). B_m gives the average mass in the instar prior to the first clutch (estimated from data in Fig. 2) used in the allometric analyses as an estimate of species-specific body size.

Species	B_m (μg)	Egg weight (μg)	Length-weight regression	
			α_1	α_2
<i>Daphnia pulex</i>	18.385	2.39 (0.03) (H) 1.93 (0.03) (L)	1.98 (0.01)	2.34 (0.06)
<i>D. obtusa</i>	12.241	1.81 (0.08)	1.94 (0.14)	2.28 (0.07)
<i>D. mendotae</i>	6.094	1.41 (0.13)	1.73 (0.19)	2.19 (0.14)
<i>Ceriodaphnia quadrangula</i>	3.447	0.62 (0.07)	2.05 (0.14)	1.92 (0.18) (H) 2.28 (0.09) (L)
<i>D. ambigua</i>	2.954	0.85 (0.05)	1.70 (0.14)	2.44 (0.08)
<i>D. parvula</i>	2.135	0.95 (0.06)	1.56 (0.12)	2.20 (0.09)
<i>C. reticulata</i>	2.028	0.64 (0.05)	1.93 (0.12)	2.28 (0.10)
<i>C. lacustris</i>	1.630	0.49 (0.06)	1.83 (0.17)	2.14 (0.20)

of all other species, with the exception of *D. pulex* (Lynch 1989) did not differ significantly across food concentrations, the egg masses for all species but *D. pulex* were assumed to be independent of food level (Table 1).

Data Analysis

Combined with the daily observations on length and clutch size, the data in Table 1 permit the computation of instar-specific net investments in growth plus reproduction (μg dry mass/day). Empirically, this investment in growth and reproduction is the net assimilation of mass. By *net assimilation of mass*, we emphasize that this is the quantity of assimilated resources that are not allocated to other functions, such as respiration, locomotion, or elements of baseline maintenance. As will be seen below, in all cases, the relationship between the total quantity of resources allocated to growth plus reproduction (F , net assimilation of mass) and body size (B , dry mass) is asymptotic, following the function:

$$F = F_{\max}[1 - e^{-k_F(B-B_{F,\min})}], \quad (1)$$

where F_{\max} is the maximum rate of net assimilation of mass, k_F is a coefficient that determines the rate of approach to the maximum, and $B_{F,\min}$ is the implied body size below which net assimilation of mass is negative. F_{\max} can be thought of as the maximum rate at which an individual *Daphnia* can convert resources into biomass, and in that sense is a measure of maximum net production rate, whereas k_F reflects how rapidly neonates progress from their initial resource exploitation capacity to the maximum. For each species, the constants in equation (1) were first estimated at both food concentrations by applying least-squares analysis to the average estimates of F and B for each instar. These analyses excluded data on the last four instars of all individuals, to avoid biases associated with senescence-related asynchrony of molting, growth, and reproduction. Because the estimates of $B_{F,\min}$ are dependent on the relatively few datapoints at small B , where F also changes rapidly with B , they are highly sensitive to individual measurements. Therefore, the preliminary estimates of $B_{F,\min}$ obtained for both the high- and low-food datasets were averaged, and then subject to this constraint,

estimates for F_{\max} and k_F for the two food levels were then re-evaluated.

The proportion of F that is allocated to reproduction can also be represented by an asymptotic function with respect to size,

$$R = R_{\max}[1 - e^{-k_R(B-B_{R,\min})}] \quad (2)$$

where R_{\max} is the asymptotic proportional allocation to reproduction at large size, k_R is the rate of approach to the asymptote, and $B_{R,\min}$ is the size below which all net assimilation is allocated to growth. As in the case of F , this function was fit to data exclusive of the last four instars using least-squares criteria.

The function:

$$D_x = D_{\max}/[be^{-k_Dx} + 1] \quad (3)$$

was used to fit the average instar-specific durations (in days) to instars (x), again excluding individuals in their last four instars. Although the precise structure of these formulae is somewhat arbitrary, the fits to the data are uniformly good, and the parameters have relatively easily interpretable biological meanings.

Phylogenetic Comparison

We performed a phylogenetic comparison to evaluate whether any allometric relationships of resource allocation and body size were an artifact of evolutionary history. Our comparison used the phylogenetic generalized least-squares method (PGLS) of Martins and Hansen (1997). In this approach, traits are evaluated in a linear model with phylogenetic information, including both topology and distance, incorporated in the error term (Hansen and Martins 1996; Martins and Hansen 1997). We ran our analyses using COMPARE version 4.5 (Martins 2003), which offers a straightforward implementation of PGLS. Because COMPARE assumes linear relationships for comparisons among traits analyzed, data were log-transformed for analysis.

Our comparison was based on the available 12s ribosomal phylogeny of North American *Daphnia*, augmented with data from sequencing the 12s region in *C. quadrangula* and *C.*

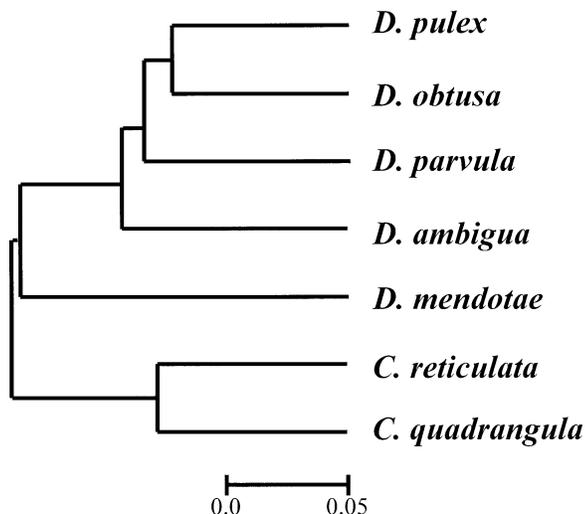


FIG. 1. Linearized phylogenetic relationships of species in this study, based on 12S ribosomal DNA.

reticulata (suitable tissue of *C. lacustris* was unavailable for analysis). To obtain the new sequences, we used the same primers as reported for the 12s *Daphnia* phylogeny (Colbourne and Hebert 1996) and a standard polymerase chain reaction protocol, with sequencing performed on an ABI 3700 automated DNA sequencer at the Indiana Molecular Biology Institute (Applied Biosystems, Foster City, CA). These *Ceriodaphnia* sequences have been deposited into GenBank under the accession numbers AY822006 and AY822007. We then estimated phylogenetic topology and distances via neighbor-joining in MEGA 2.1 (Kumar et al. 2001), which yielded the same relationships for *Daphnia* as previously published (Colbourne and Hebert 1996). Phylogenetic analyses were performed with the tree topology illustrated in Figure 1, using two alternate assumptions about branch lengths. First, we assumed that the rate of phenotypic evolution was proportional to molecular divergence as given by branch lengths in Colbourne and Hebert (1996). Alternatively, we assumed that the rate of phenotypic evolution was constant, and therefore linearized branch lengths to reflect time (Takedaki et al. 1995; see Fig. 1). These alternate assumptions did not qualitatively change our results.

RESULTS

Size at Maturity

Given that much of this study is devoted to identifying the allometric scaling of life-history determinants, an obvious priority is a measure of adult size that is relatively stable to environmental effects. Body size in the instar prior to the appearance of the first clutch appears to provide such a measure, as this character is remarkably constant across food levels, whereas there is a tendency for the size of the instar carrying the first clutch to be reduced at low food levels, particularly in the case of the larger species (Fig. 2). This prefirst clutch instar marks the point in life at which energy is first sequestered for reproduction, with this investment being reflected in the clutch deposited into the brood chamber at the start of the next instar. In the allometric relationships

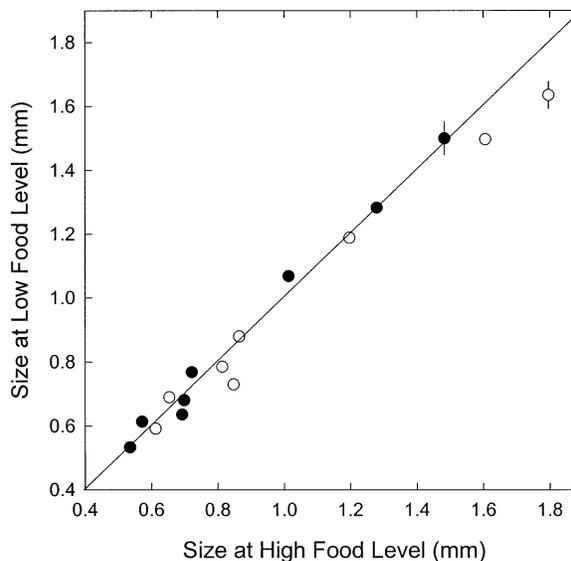


FIG. 2. Relationship between measures of average size at maturity under high and low food conditions. The solid line gives the line of perfect correspondence. Filled circles represent size in the instar prior to the first clutch; open circles represent the instar carrying the first clutch. For size in the instar prior to the first clutch, the correlation coefficient is 0.995, the slope is not significantly different from one (slope = 1.015, SE = 0.043) and the intercept is not significantly different from zero (slope = 0.0018, SE = 0.0399). Except where visible, the standard errors of the species-specific measures are less than the diameters of the plotted points.

described below, the average size in the instar prior to the first clutch is denoted B_m . Using this criterion as a measure of species-specific body size, there is an order of magnitude range between the largest of the study species, *D. pulex* (18.4 μg dry mass), and the smallest, *C. lacustris* (1.63 μg dry mass; Table 1).

Net Assimilation of Mass

The fits to equation (1) demonstrated that there was a reduction in instar-specific investment in (growth + reproduction) at the low food concentration, although the hyperbolic relationship between F and B was maintained (Fig. 3, Table 2). A strong positive allometric scaling exists for the minimum size for positive net energy intake, with $B_{F,\min} \approx 0.27B_m^{0.68}$ (Table 3). At the high food level, there is an almost perfect and linear scaling for the maximum rate of net energy intake, with $F_{\max} \approx 1.52B_m^{1.04}$, and an almost perfect inverse scaling for the rate of approach to the maximum, $k_F \approx 1.00B_m^{-0.88}$ (Table 3). Although directional scaling of these latter two parameters with body size is weaker under low food conditions, in neither case is it significantly different from the high food condition.

Investment in Reproduction

The average dry weight of individual eggs (B_0) scaled with approximately the square root of adult size, with $B_0 \approx 0.44B_m^{0.56}$ (Table 3). Although there was some tendency for offspring size (size in the first instar, in mm) to increase with adult instar number in a few species, the overall range of variation within a species was generally less than 10%, with

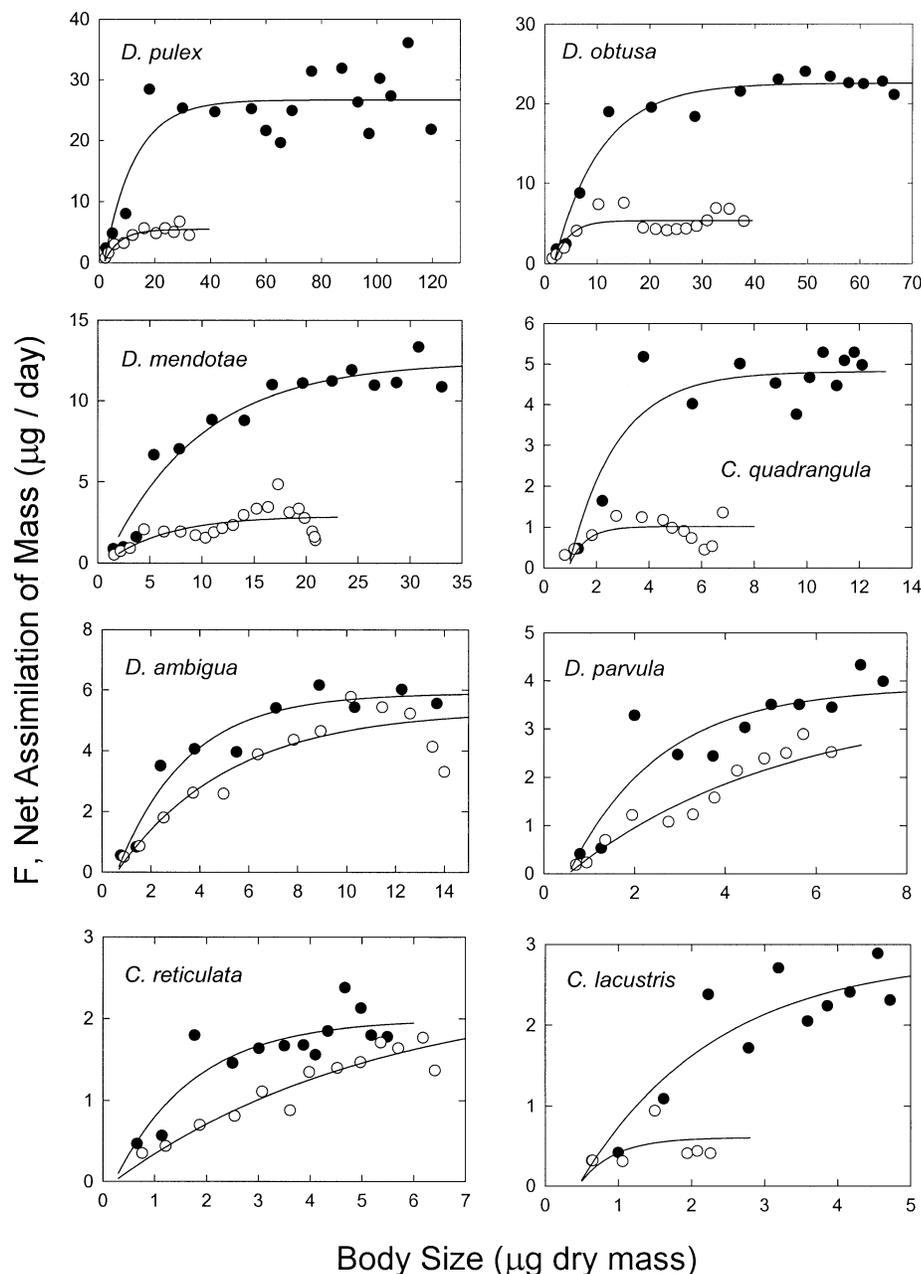


FIG. 3. Relationship of net investment in growth + reproduction to instar-specific body size at high (filled circles) and low (open circles) resource levels. Solid lines are the least-squares fits to equation (1). Note that the panel axes have substantially different scales. Panels are arranged from the largest species in the upper left corner in the smallest species in the lower right corner.

most of the variation being due to reduced offspring size in the first clutch (data not shown, but see Lynch 1989, 1992). In addition, there was no tendency for offspring size to change directionally with food concentration. The regression of species-specific offspring size at low versus high food concentration is highly significant ($r = 0.990$, $df = 6$), with an intercept (-0.005 ± 0.018 SE) not significantly different from zero and a slope (0.996 ± 0.058 SE) not significantly different from one. Averaging offspring weights over both food conditions, virtually the same scaling with adult size was obtained as for egg weight (Table 3). Thus, at birth,

smaller species are proportionately much closer to their sizes of maturity than large species.

The relative investment of energy into reproduction versus growth follows a very similar pattern with body size under both high and low food conditions for all species, with the exception of *C. reticulata* (Fig. 4). Earlier work (Lynch 1989, 1992) has shown that the R parameters are unassociated with food concentration in *C. quadrangula*, *D. ambigua*, and *D. pulex* over a broad range of food conditions, providing further justification for pooling the data sets from both high and low food conditions to obtain species-specific estimates of the R

TABLE 2. Estimates of the parameters of the net resource assimilation function (eq. 1). r^2 denotes the fraction of the variation in observed F explained by the model.

	$B_{F,\min}$	High food			Low food		
		F_{\max}	k_F	r^2	F_{\max}	k_F	r^2
<i>Daphnia pulex</i>	1.720	26.671	0.091	0.788	5.459	0.178	0.901
<i>D. obtusa</i>	1.728	22.559	0.111	0.952	5.357	0.346	0.674
<i>D. mendotae</i>	0.733	12.429	0.111	0.945	2.893	0.173	0.569
<i>Ceriodaphnia quadrangula</i>	0.928	4.821	0.543	0.821	1.011	1.564	0.233
<i>D. ambigua</i>	0.609	5.895	0.352	0.937	5.334	0.218	0.887
<i>D. parvula</i>	0.546	3.864	0.496	0.810	3.563	0.215	0.974
<i>C. reticulata</i>	0.220	1.993	0.655	0.776	2.370	0.200	0.986
<i>C. lacustris</i>	0.449	2.850	0.542	0.870	0.609	2.089	0.134

parameters (Table 4). For all species, the maximum amount of reproductive effort (R_{\max}) is asymptotically approached at large body size and falls in the range of 0.91 to 1.00 (Table 4). The average value for this trait is 0.94 (0.01 SE), and there is no notable allometric scaling. On the other hand, there is a nearly perfect inverse scaling between the coefficient k_R and species-specific body size, with $k_R \approx 1.90B_m^{-1.10}$ (Table 3). In addition, the intercept scales very strongly and nearly linearly with B_m , with $B_{R,\min} \approx 0.46B_m^{0.92}$ (Table 3). It should be noted, however, that the model parameter $B_{R,\min}$ is not, strictly speaking, a measure of size at first reproductive investment. As can be seen in Figure 4, for the first instar in which reproductive investment exceeds zero, R is often greater than 0.4; that is, there is a rather discontinuous jump from zero to nonzero R .

There is a high degree of parallelism with respect to the species-specific F and R functions. This can be seen by inspection of Figure 4, where the F functions are scaled to maximize at values of 1.0 (by dividing by F_{\max}) and drawn as dashed lines. Within each species, the F and R functions reach their asymptotes at approximately the same size. The parallel nature of the two curves can also be shown more formally by comparing the parameters fitted to the two hyperbolic functions (Fig. 5). For the slope parameters k_R and k_F , the correlation is significant ($r = 0.783$, $df = 6$, $P = 0.022$), the intercept (0.053 ± 0.189 SE) is not significantly

different from zero, and the slope (1.381 ± 0.448 SE) is not significantly different from one. Similarly, for the species-specific body sizes at which R and F have attained 95% of their fitted maxima, the correlation is also significant ($r = 0.872$, $df = 6$, $P = 0.004$), the intercept (-2.136 ± 4.620 SE) is not significantly different from zero and the slope (1.066 ± 0.237 SE) is not significantly different from one.

Instar Duration

The species-specific relationships between instar duration and instar number are essentially invariant with respect to food level (Fig. 6, Table 5), so joint fits to equation (3) for data from both high and low food levels were obtained. The species-specific estimates for all three parameters of the D function exhibited significant, but fairly weak allometric scaling: $D_{\max} \approx 2.2B_m^{0.08}$, $k_D \approx 0.5B_m^{-0.24}$ and $b \approx 0.8B_m^{0.38}$. Thus, there is a tendency for larger species to have shorter instars than smaller species early in life, while smaller species have shorter instars than larger species late in life.

Phylogenetic Comparison

In virtually all cases, estimates of allometric parameters under the phylogenetic generalized least-squares method were within one standard error of the estimate given in Table 3. In fact, for all traits in Table 3 denoted as significant, the

TABLE 3. Fitted coefficients of allometric relationships (standard errors in parentheses), where the dependent variable, y , is fitted to the linearized version of $y = aB_m^b$. Double asterisk denotes statistical significance at the 0.01 level.

Character	Food	$\ln(a)$	b	r
Net energy intake:				
$B_{F,\min}$	high, low	-0.570 (0.158)	0.678 (0.155)	0.873**
F_{\max}	high	0.183 (0.113)	1.042 (0.111)	0.968**
k_F	high	-0.005 (0.149)	-0.879 (0.147)	0.926**
F_{\max}	low	0.074 (0.307)	0.557 (0.301)	0.603
k_F	low	-0.167 (0.439)	-0.429 (0.431)	0.376
Reproductive effort:				
$B_{R,\min}$	high, low	-0.341 (0.079)	0.916 (0.078)	0.979**
R_{\max}	high, low	-0.011 (0.015)	-0.025 (0.015)	0.577
k_R	high, low	0.280 (0.084)	-1.098 (0.082)	0.984**
Egg weight	high, low	-0.358 (0.097)	0.560 (0.095)	0.924**
Offspring weight	high, low	-0.316 (0.064)	0.567 (0.062)	0.965**
Instar duration:				
D_{\max}	high, low	0.348 (0.260)	0.080 (0.034)	0.694**
k_D	high, low	-0.257 (0.040)	-0.241 (0.072)	0.819**
b	high, low	-0.037 (0.091)	0.347 (0.108)	0.800**

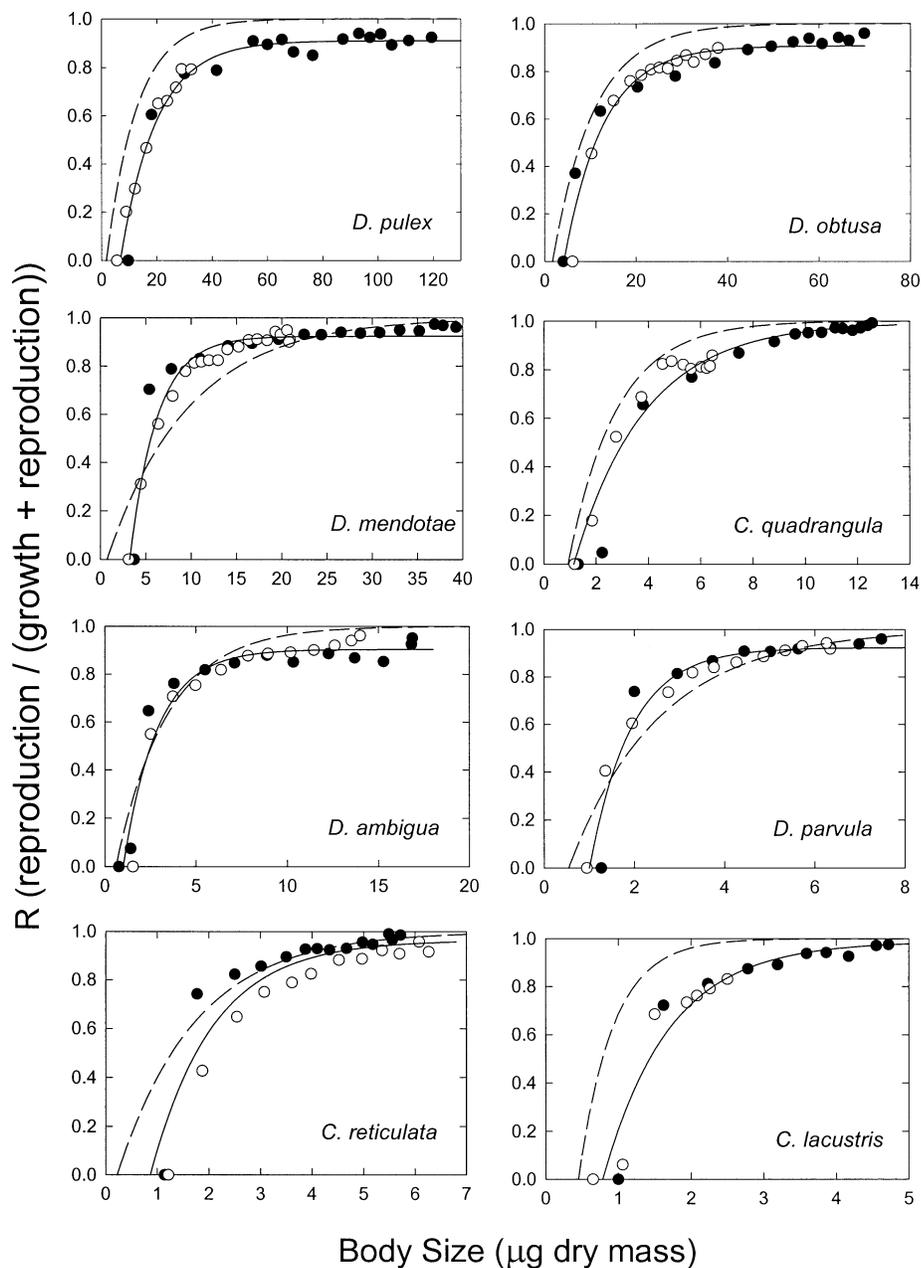


FIG. 4. Relationship of proportional reproductive effort to body size at high (filled circles) and low (open circles) resource levels. Solid lines denote the least-squares fits to equation (2). Dashed lines are the fits (from Fig. 2) of F scaled so that the maximum equals 1.0. Panels are arranged as in Figure 3.

PGLS estimates deviated from the nonphylogenetic estimates by less than one-half of one standard error, and all allometric features described above remained. Furthermore, the correlation coefficient for these traits never differed from that in Table 3 by more than 0.01, regardless of whether branch lengths had been linearized or not. The sole difference in the phylogenetic analysis was the slope parameter for k_F at low food ($b = -0.1049$, $SE = 0.4028$ under PGLS when phenotypic evolution was assumed proportional to molecular divergence), which in any case was not significantly different from zero.

DISCUSSION

This study revealed that, although the quantitative details of daphniid life-history components may be both evolutionarily divergent and strongly influenced by the environment, the resulting variability can be placed in a simple framework and described by a relatively few parameters. Much as morphological variation within a group of related taxa is limited by basic features of a body plan, it appears that life-history variation can be limited by basic structural relationships. Several life-history ‘‘assembly rules’’ for daphniids are apparent from our data. First, the size at which most species first invest

TABLE 4. Estimates of the parameters of the reproductive effort function, equation (2). r^2 denotes the fraction of the variation in observed R explained by the model.

Species	R_{\max}	k_R	$B_{R,\min}$	r^2
<i>Daphnia pulex</i>	0.912	0.077	6.548	0.995
<i>D. obtusa</i>	0.907	0.117	4.207	0.995
<i>D. mendotae</i>	0.924	0.333	3.220	0.996
<i>Ceriodaphnia quadrangula</i>	0.995	0.368	1.144	0.991
<i>D. ambigua</i>	0.904	0.531	1.005	0.992
<i>D. parvula</i>	0.923	1.082	1.005	0.993
<i>C. reticulata</i>	0.964	0.827	0.862	0.991
<i>C. lacustris</i>	0.988	1.094	0.784	0.948

resources in reproduction is largely invariant with respect to resource level, although this size does vary among species. Second, the functions for size-specific net assimilation of mass (F), proportional allocation of resources to reproduction (R), and instar duration (D) provide an effective description of these traits in all species. Third, despite indeterminate growth, all species appear to reach a maximum rate of net resource assimilation (i.e., that available for growth and reproduction, F_{\max}), and this maximum is positively related to size at maturity. Fourth, the proportional allocation of resources to reproduction (R) is largely independent of resource level, with all species having a maximum allocation to reproduction of approximately 94% of available resources. And finally, the rates at which species approach their plateaus in these functions show a tight negative relationship to size at maturity.

The work presented in this paper is conceptually allied to the life-history invariant approach of Charnov (1993) and others. The life-history invariants associated with indeterminate growth proposed earlier (Charnov 1993) involve body length, mortality rate, and maximum longevity (Beverton 1992). Our results suggest that there may be comparable ratios associated with resource allocation, but data on a far greater number of species would be necessary to characterize anything as invariant. Leaving aside the question of whether such invariants are indeed invariant (Kozłowski 1996), both the invariant approach and our concept of a life-history framework attempt to discern general patterns of life-history structure. By identifying general patterns, we hope to provide targets that are amenable to future quantitative-genetic and ecological experimentation and to reduce the dimensionality of the problems of understanding life-history variation in daphniids, a globally ubiquitous group of organisms.

Absolute Allocation to Growth plus Reproduction

The net assimilation of mass, F , is a measure of the absolute allocation to growth + reproduction since it excludes resources that were acquired but applied to maintenance costs. An important result is that the maximum rate of mass increase (F_{\max}) scales approximately linearly with mass at maturity (B_m) when resources are abundant, with $F_{\max} \approx 1.5B_m$. In contrast, the rate of approach to the maximum (k_F) scales inversely with mass at maturity, such that $k_F \approx 1/B_m$. Thus, large species reach a substantially higher F_{\max} than do small species, and small species approach their asymptotic limit much more rapidly. These allometric relationships are

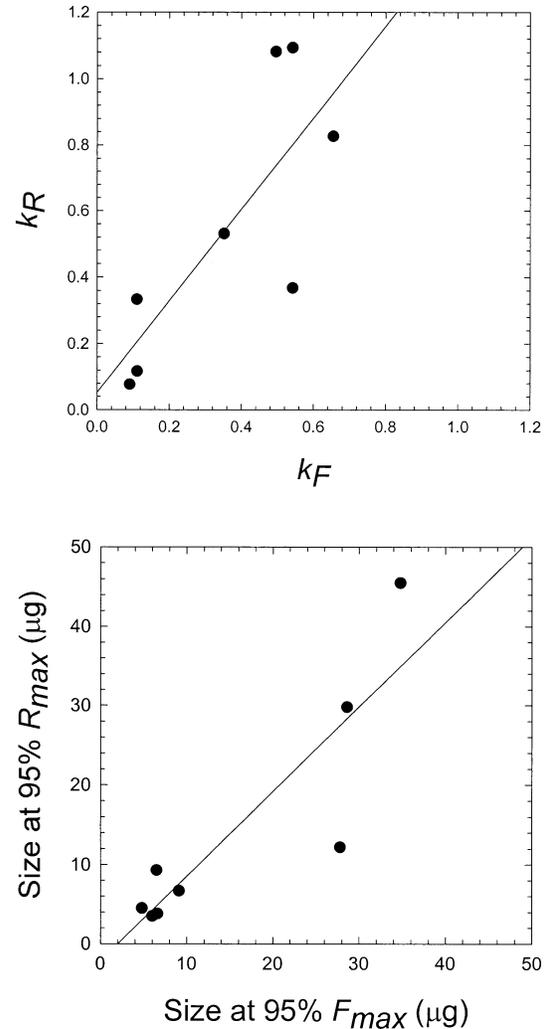


FIG. 5. Regressions of features of the F (net resource assimilation) and R (proportion of F allocated to reproduction) functions. Top: rate of approach to the functions' maxima. Bottom: approximate body size where the functions' maxima are reached.

qualitatively similar at low resources (allometric coefficients and exponents are of the same sign), but are muted in degree and present a poorer fit to the data. The sensitivity of the strength of the relationships to resources suggests that body size is an important determinant of the ability to assimilate abundant resources, but that other factors (for example, digestion efficiency) may rise in importance when resources are scarce.

All species reach a plateau in the net assimilation of mass at the time of maturation, or shortly thereafter. Why should this be the case? The majority of the approach to the plateau occurs in the first four instars, which is the typical juvenile period in *Daphnia*. One possibility is that important developmental changes in the apparatus of resource acquisition occur throughout juvenile ontogeny. For example, there is evidence that filtering meshes expand during maturation in a number of species (Brendelberger and Geller 1985). Additionally, the digestive system or musculature required to control water filtration may continue to develop in juveniles.

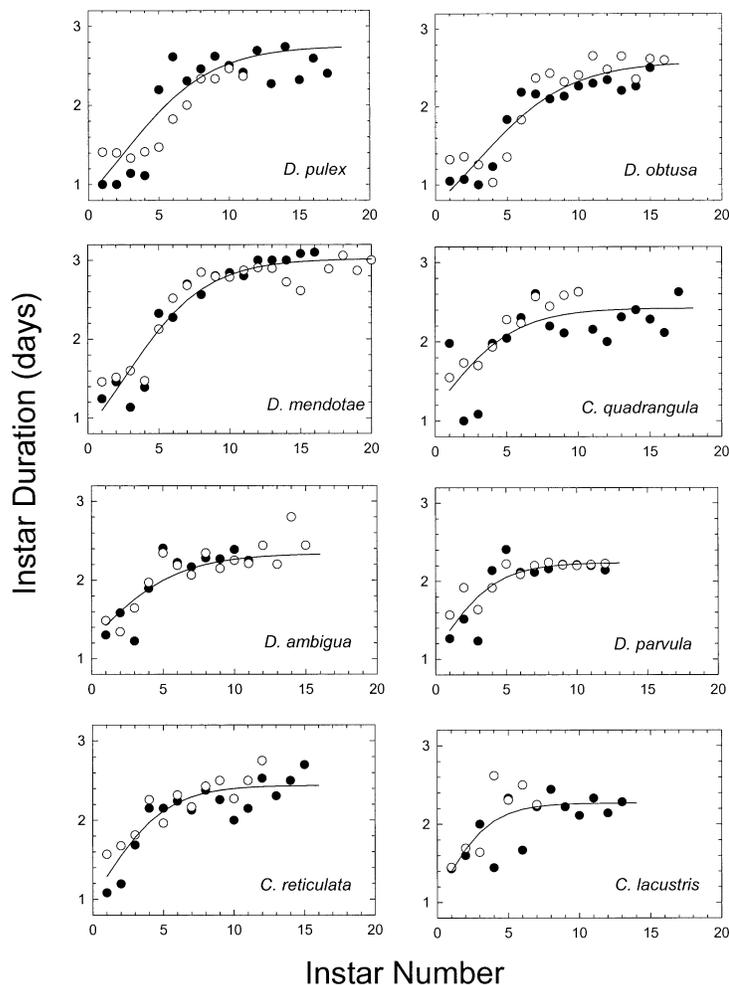


FIG. 6. Relationship of average instar duration to instar number at high (filled circles) and low (open circles) food conditions. Solid lines denote the least-square fits of the joint data from high and low foods to equation (3). Panels are arranged as in Figure 3.

In other words, juvenile *Daphnia*, despite outward appearances, may not simply be small versions of their adult selves. Once the animal is fully mature, any size-based gains in absolute resource gathering abilities may then be offset by size-based costs of molting, such that no further gains in net resource assimilation are made. Another possibility is that as an animal grows, its gut, which is essentially a simple tube, may widen such that a greater portion of the collected particles pass through undigested, although this may be coun-

TABLE 5. Estimates of the parameters of the instar-duration function, equation (3). r^2 denotes the fraction of the variation in observed D explained by the model.

Species	D_{\max}	k_D	b	r^2
<i>Daphnia pulex</i>	2.750	0.320	2.170	0.884
<i>D. obtusa</i>	2.581	0.312	2.444	0.924
<i>D. mendotae</i>	3.019	0.352	2.487	0.946
<i>Ceriodaphnia quadrangula</i>	2.422	0.382	1.090	0.747
<i>D. ambigua</i>	2.340	0.330	0.890	0.867
<i>D. parvula</i>	2.239	0.486	1.026	0.846
<i>C. reticulata</i>	2.440	0.443	1.392	0.888
<i>C. lacustris</i>	2.270	0.573	1.106	0.751

tered by longer gut passage times. Finally, we point out that it is unlikely that these plateaus reflect constraints of the method by which resources were supplied in the experiment. Were that the case, all species would have plateaued at the same level, whereas the results show this clearly not to be the case (Fig. 5, bottom).

Even though all species reach a net resource assimilation plateau, they do so at strikingly different levels (spanning an order of magnitude) and approach their plateau at different rates. This variation is clearly linked to body size at maturation: positively for the plateau level, inversely for the rate. The end result is that, for a given size, large-bodied (at maturity) species are able to allocate substantially more resources to growth and reproduction than small-bodied species. It is difficult to attribute this variation to species' differences in the structure and size of filtering apparatus. Although a number of studies have documented variation among species in filter mesh size, filter area, filtering rate, and the ontogenetic allometry of these traits, none of these aspects of filtration appear to be associated with species body size (Geller and Muller 1981; Porter et al. 1983; Gophen and Geller 1984; Brendelberger and Geller 1985). For example,

Geller and Muller (1981) showed that *C. quadrangula* and *D. magna* (a species considerably larger than any in our study) both had fine meshes, whereas *D. pulicaria* and *D. galeata* (medium sized, similar to *D. mendotae*) had relatively coarse meshes. However, the retention efficiency of small particles by filtering combs is higher in small-bodied than large-bodied species (Gophen and Geller 1984; Brendelberger 1985; Hessen 1985), suggesting that they may have an advantage in exploiting natural bacterioplankton. Conversely, for larger particles, larger species have a feeding advantage (DeMott 1985). In any event, the food we provided is large enough for all of our species to harvest efficiently. Taken together, the available evidence on the ontogeny of feeding structures in daphniids suggests that though it may play a role in the existence of the net assimilation plateau, it offers little insight into the interspecific variation in the level of or approach to the plateau.

Another possible source of interspecific variation in maximum net resource assimilation is the cost of molting. Although we did not explicitly quantify the costs of molt replacement, a previous study showed that the molt replacement cost of *D. ambigua* and *C. quadrangula* was more than twice that of a same-sized individual *D. pulex* (Lynch 1992). Small-bodied species, therefore, appear to have greater size-specific molt-replacement costs and this may restrict the resources that can be applied to growth and reproduction. This is consistent with the hypothesis that adaptation for optimal performance at small sizes may also involve selection for a heavy, thick carapace that offers advantages against invertebrate predators or provides additional protection to the dormant eggs produced in the sexual phase of their life cycle.

We are left with a puzzle as to why small-bodied species have not evolved better abilities to sequester resources for growth or reproduction, such that on a size-specific basis they are equal to large-bodied species. This may be tied to the size-specific basis of the balance between resource acquisition (filter structures, digestion efficiency) and maintenance costs (metabolism, molting), but though there is a large body of data on these topics in daphniids, careful size-specific comparisons have yet to be done. Given that allometry offers such a clear organizing principle for describing interspecific variation in net resource assimilation, an important future goal is to evaluate the ontogeny and allometry of both resource acquisition capabilities and maintenance costs.

Proportional Allocation to Reproduction

We did not find evidence of an allometric relationship for the maximum proportion of available resources allocated to reproduction (R_{\max}). However, there were allometric relationships for aspects of how that reproductive effort was achieved. First, k_R showed a strong inverse relationship with body size, indicating that larger species need to grow more to progress from their initial level of reproductive effort to their maximum level. This is a critical period of life history, since the first few clutches produced largely define an individual's fitness. Second, two related estimates of reproductive effort partitioning, egg mass and neonate mass, scaled approximately with the square root of body size. This shows that per-offspring investment increases with adult body size,

but not as a direct proportion of body size, consistent with the overall pattern in Cladocera (Lynch 1980a). In sum, although all species appear capable of eventually allocating virtually all available resources to reproduction, the time it takes to manifest that capability, and how that allocation is partitioned is clearly related to body size. Thus, if reproductive strategies differ in how much they emphasize rapidly reaching maximum reproductive output versus the actual maximum level of reproduction, they may contribute to the evolution of adult body size. Similarly, different selection regimes may target neonate size, and adult body size may evolve in concert.

Consequences of Resource Level

The allometry of net resource assimilation (F) varies with resource level somewhat, suggesting that the relationship between body size and net resource assimilation is dependent on resources. This may reflect phenotypic plasticity in the development of resource acquisition structures. However, none of the reproductive investment parameters had allometric relationships that differed between the two resource levels. This suggests that the allometric relationships of reproductive allocation decisions are robust to food level, and consequently can be regarded as structural constraints with respect to resources.

Conclusion

The zooplankton literature has long been dominated by the idea that size-selective predation has driven evolutionary diversification of body size. We are not challenging the importance of direct selection on size, but rather suggest that resource allocation constraints may have important indirect effects. Evolutionary changes in body size are apparently associated with coordinated changes in the ontogeny of life-history components. These changes are in the parameters describing the ontogeny of both net resource assimilation and the proportion of those resources that are allocated to reproduction, which suggests that it will be productive in future work to reconsider daphniid life history in terms of function-valued traits. One possibility is that size-selective predation defines a range of sizes at which a species can be successful, whereas resource allocation determines the ontogeny of life history. Our data show that there is a fixed core structure of life history in daphniids, and that quantitative variation of life history diverges in association with body size. Future efforts at modeling resource allocation can take advantage of the functions herein, allowing explicit incorporation of ontogenetic change in resource allocation. Since multiple components of resource allocation appear to be coordinated through ontogenetic development, it is possible that a small number of master regulatory genes are responsible for the patterns we found.

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Corresponding Editor: T. Day