



**The Life History Consequences of Resource Depression in Ceriodaphnia
Quadrangula and Daphnia Ambigua**

Michael Lynch

Ecology, Vol. 73, No. 5. (Oct., 1992), pp. 1620-1629.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199210%2973%3A5%3C1620%3ATLHCOR%3E2.0.CO%3B2-X>

Ecology is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

THE LIFE HISTORY CONSEQUENCES OF RESOURCE DEPRESSION IN *CERIODAPHNIA QUADRANGULA* AND *DAPHNIA AMBIGUA*¹

MICHAEL LYNCH

Department of Biology, University of Oregon, Eugene, Oregon 97403 USA

Abstract. An analysis of the life history and energetics responses of two small planktonic cladocerans, *Daphnia ambigua* and *Ceriodaphnia quadrangula*, to food limitation is presented. The results are consistent with an earlier study of *D. pulex* in that the size-specific instar durations and proportional investments in reproduction are independent of the food level. Compared to *D. pulex*, these smaller species spend more time in early instars but less time in adult instars. Of the energy available for (growth + reproduction), a much greater fraction is allocated to reproduction than in the case of similar-sized *D. pulex*, and it quickly reaches an asymptote of 94–97%. As in the case of *D. pulex*, the net rate of energy intake reaches a plateau shortly after maturity. This, combined with the increased cost of molting as the animal grows, causes age-specific reproduction to level off and eventually decline. The maximum rate of net energy intake is much lower and the cost of molting much higher for *D. ambigua* and *C. quadrangula* than for the larger *D. pulex*. This puts an upper limit on body size for the two smaller species that is much lower than that attainable in *D. pulex*. The data suggest the possibility that the sizes of planktonic cladocerans may be less a direct consequence of size-selective mortality than a correlated response to selection operating on energy-related traits.

Key words: Ceriodaphnia; Cladocera; cost of molting; Daphnia; energetics; life history evolution; reproductive effort; resource depression.

INTRODUCTION

Despite the central role of cladocerans in freshwater planktonic communities, as consumers of suspended particulate matter and as prey of both vertebrate and invertebrate predators, we still know relatively little about the response of their life histories to food limitation. Certainly, we can expect resource depression to result in a reduction in age-specific survival and reproduction. However, the quantitative responses of these two types of traits may vary substantially between species with different evolutionary histories. Moreover, the response of the growth trajectory to resource depression merits special attention in the Cladocera, since members of this group have dietary breadths and feeding rates that depend on body size (Burns 1968, 1969) and are almost always exposed to size-selective predators (Lynch 1980a). Due to the latter factor, food limitation and predation cannot be viewed as independent evolutionary forces in cladoceran communities.

Recently, I reported on the life history consequences of resource depression for the large planktonic cladoceran, *Daphnia pulex* (Lynch 1988, 1989). In that study, it was possible to distill the essential features of the life history down to a small number of determinants: (1) a hyperbolic function for size-specific net energy intake, (2) the mass per egg, (3) the instar-specific du-

urations, (4) the size-specific pattern of the allocation of net energy intake into growth vs. reproduction, and (5) the investment in molts. Only the first two of these properties were influenced by the food level, and these responses could be described in a rather simple manner. It was therefore possible to model the *D. pulex* life history fairly accurately with only a small number of parameters. In order to test the generality of the conclusions of that study, I now extend this type of work to two smaller species of planktonic cladocerans, *Ceriodaphnia quadrangula* and *Daphnia ambigua*.

METHODS

Since all of the empirical and computational methods employed in this study have been described previously (Lynch et al. 1986, Lynch 1988, 1989), their discussion will be kept to a minimum. Complete life table data were gathered for ≈ 50 acclimated individuals of each species at six food levels (20°C, 12:12 light: dark diel cycle), the lowest of which did not support the growth of *Ceriodaphnia*. The food consisted of a standard mixture of *Scenedesmus* and *Chlamydomonas* provided in a 40-mL volume, which was replaced every other day. Both cladoceran species were represented by single clones (from central Illinois ponds), so although the work extended over a year, the genetic background of the study species must have been essentially constant throughout (Lynch 1985).

Conversion of the daily measures of growth and reproduction into an energy budget requires information

¹ Manuscript received 18 September 1989; revised 1 August 1991; accepted 2 August 1991.

on the relationship between length and dry mass, between length and the molt mass, and on the mass of individual eggs. Our protocol for estimating adult dry mass follows exactly that in Lynch et al. (1986:21). As in the case of *Daphnia pulex* (Lynch 1989), the length-mass regression was found to be independent of the food carbon concentration in *D. ambigua*. Approximately 50 (range of 37–73) individuals of various sizes were weighed at four food carbon concentrations ranging from 0.154 to 3.61 $\mu\text{g}/\text{mL}$. A linear analysis of the log-transformed data revealed no significant food effect ($P = .99$) or food \times $\ln(\text{length})$ ($P = .71$) interaction. Therefore, the data for *D. ambigua* were pooled to estimate the parameters of the relation $B = \alpha_1 L^{\alpha_2}$ where B is the dry mass (in micrograms) of an individual and L is its length from the base of the tailspine to the top of the eyespot (in millimetres). Using least squares linear regression on the log-transformed data, the parameter estimates (with 1 SE) are $\ln(\alpha_1) = 1.83 \pm 0.09$ and $\alpha_2 = 2.44 \pm 0.07$ ($r^2 = 0.88$, $n = 184$). A similar analysis for *C. quadrangula* at food carbon levels of 0.154, 0.54, and 1.54 $\mu\text{g}/\text{mL}$ (respective sample sizes = 40, 35, and 25) revealed a different situation. The direct effect of food was nonsignificant ($P = .81$), but there was a significant food \times $\ln(\text{length})$ interaction ($P = .01$). The regression equation for this species can be expressed as $\ln B = \alpha_1 + \alpha_2 \ln L + \alpha_3 C \ln L$, where C denotes the food carbon concentration in micrograms per millilitre. $\alpha_1 = 2.05 \pm 0.06$, $\alpha_2 = 2.32 \pm 0.11$, and $\alpha_3 = -0.26 \pm 0.10$. Since the growth and reproduction of this species appeared to be saturated at $C \geq 1.54 \mu\text{g}/\text{mL}$ (below), the $\ln B$ equation for the one *C. quadrangula* life table above that level was taken to be the same as that for 1.54 $\mu\text{g}/\text{mL}$.

Dry masses of eggs from mothers of random ages, obtained as in Lynch et al. (1986:21), were 0.84 ± 0.05 , 0.92 ± 0.05 , and $0.79 \pm 0.04 \mu\text{g}$ at food carbon concentrations of 1.54, 0.54, and 0.154 $\mu\text{g}/\text{mL}$ for *D. ambigua* and 0.69 ± 0.09 and $0.61 \pm 0.02 \mu\text{g}$ at 1.54 and 0.54 $\mu\text{g}/\text{mL}$ for *C. quadrangula*. Each of these

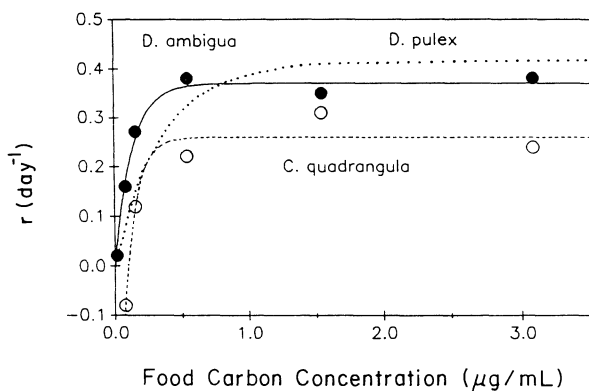


FIG. 1. Response of the rate of increase, r , to food carbon concentration, C . The curve for *Daphnia pulex* is taken from Lynch (1989).

TABLE 1. Parameter estimates for Eqs. 1–6 and their standard errors obtained by jackknifing.

	<i>Ceriodaphnia quadrangula</i>	<i>Daphnia ambigua</i>	<i>Daphnia pulex</i>
Population growth rate (Eq. 1)			
r_{\max}	0.26 (0.01)	0.37 (0.03)	0.41 (0.001)
k_r	11.41 (4.17)	7.65 (2.84)	2.93 (0.41)
C_r	0.100 (0.066)	0.000 (0.025)	0.004 (0.023)
Instar duration function (Eq. 2)			
D_{\max}	2.42 (0.00)	2.34 (0.01)	2.75 (0.00)
b_D	4.21 (0.78)	0.89 (0.05)	2.17 (0.21)
k_D	0.77 (0.03)	0.33 (0.00)	0.32 (0.01)
Net energy intake functions (Eqs. 4 and 5)			
F_{\max}	5.41 (0.31)	10.19 (0.21)	49.23 (5.26)
k_f	3.24 (1.13)	6.18 (6.75)	0.56 (0.10)
C_f	0.02 (0.06)	-0.05 (0.13)	-0.20 (0.04)
k_u	8.19 (7.43)	...	1.63 (0.59)
b_u	1.78 (3.60)	...	0.14 (0.04)
a_{\min}	0.52 (0.06)	0.21 (0.01)	0.06 (0.00)
Reproductive investment function (Eq. 7)			
R_{\max}	0.97 (0.01)	0.94 (0.00)	0.89 (0.00)
k_R	0.51 (0.02)	0.63 (0.02)	0.08 (0.00)
B_{\min}	1.54 (0.02)	1.18 (0.03)	7.06 (0.16)

estimates is an average of five weighings of groups of 10–35 eggs, i.e., of ≈ 100 total eggs. With no evidence of a significant food effect, the pooled estimates for *C. quadrangula* and *D. ambigua* were taken to be 0.62 ± 0.07 and $0.85 \pm 0.05 \mu\text{g}/\text{egg}$.

The relationship between the dry mass of the molt (in micrograms) and length (in millimetres) was of the standard allometric form $M = \alpha_1 L^{\alpha_2}$. To obtain this relationship, several dozen molts were obtained from different size classes ($n = 7$ for *D. ambigua*, $n = 4$ for *C. quadrangula*), washed in distilled water, dried, and weighed. For *D. ambigua*, the least squares parameter estimates are $\ln(\alpha_1) = 0.14 \pm 0.20$ and $\alpha_2 = 4.62 \pm 0.61$ ($r^2 = 0.89$, $P < .01$). For *C. quadrangula*, they are $\ln(\alpha_1) = 0.20 \pm 0.43$ and $\alpha_2 = 2.46 \pm 0.47$ ($r^2 = 0.87$, NS). These may be compared with the estimates obtained earlier for *D. pulex*: $\ln(\alpha_1) = -0.66 \pm 0.48$ and $\alpha_2 = 3.08 \pm 0.24$ (Lynch et al. 1986).

RESULTS

Demography.—The response of the intrinsic rate of increase (obtained from the stable age equation) to food concentration is adequately described by the hyperbolic function

$$r = r_{\max} \{1 - \exp[-k_r(C - C_r)]\}, \quad (1)$$

where r_{\max} is the maximum rate of increase, C is the food carbon concentration, C_r is the threshold food carbon concentration above which r is positive, and k_r determines the rate of approach to the asymptote (Fig. 1). Least squares fits of the parameters to this equation and their standard errors obtained by jackknifing are given in Table 1. Using twice the standard error of a difference for a criterion for significance at the .05 level,

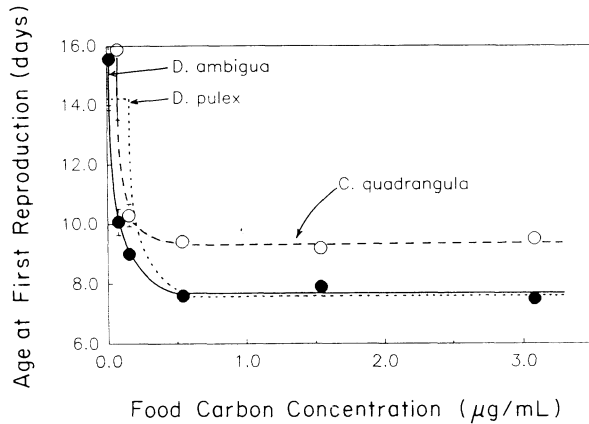


FIG. 2. The response of the average age at first reproduction to food carbon concentration. Curves fitted by eye; standard errors are narrower than the radius of most points. The response for *Daphnia pulex* is taken from Lynch (1989).

the r_{max} estimates for *D. ambigua* and *D. pulex* are significantly different, and *D. ambigua* has substantially higher values of r at low food levels. *C. quadrangula* has lower values of r than the *Daphnia* species at all food concentrations.

Three factors contribute to the response of r to food concentration. First, there is an inverse hyperbolic relationship between the age at first reproduction and food concentration (Fig. 2). *C. quadrangula* consistently initiates reproduction at a later age than does *D. ambigua*. At high food carbon concentrations *D. ambigua* initiates reproduction at essentially the same age as *D. pulex*, but below 0.2 µg/mL *D. pulex* exhibits an abrupt increase to a higher and constant age at first reproduction, whereas *D. ambigua* exhibits a more gradual and continuous increase. Second, below 0.5 µg/mL there is a decline in the instar-specific clutch

TABLE 2. Probabilities of survival through the first 10 d of life and their standard errors.

Food carbon concentration (µg/mL)	<i>Ceriodaphnia quadrangula</i>	<i>Daphnia ambigua</i>	<i>Daphnia pulex</i>
3.08	0.88 (0.05)	0.93 (0.04)	1.00 (0.00)
2.31	0.92 (0.04)
1.54	0.96 (0.03)	0.81 (0.06)	0.78 (0.06)
0.77	0.95 (0.03)
0.54	0.64 (0.07)	0.98 (0.02)	0.96 (0.03)
0.31	0.83 (0.05)
0.154	0.52 (0.07)	0.70 (0.60)	0.21 (0.04)
0.077	0.27 (0.06)	0.33 (0.06)	0.53 (0.07)
0.015	...	0.16 (0.04)	0.57 (0.07)

sizes (Fig. 3). This decline is much more pronounced in *C. quadrangula*. As in the case of *D. pulex* (Lynch 1989), there is typically an initial increase in clutch size with age followed by a plateau and an eventual decline. Third, there is a dramatic increase in juvenile mortality as food availability declines (Table 2). Qualitatively similar results were obtained with *D. pulex* (Lynch 1989).

As in the case of *D. pulex* (Lynch 1989), instar durations can be fit by the function

$$D_x = \frac{D_{max}}{b_D \exp(-k_D x) + 1}, \quad (2)$$

where x denotes the instar. All individuals that completed at least five instars were subjected to least squares analysis to obtain estimates for k_D , b_D , and D_{max} . The food-specific means of the log-transformed parameter estimates were regressed on the logarithm of food concentration, but none of these regressions were significant (at the .05 level) for either species. Thus, the pa-

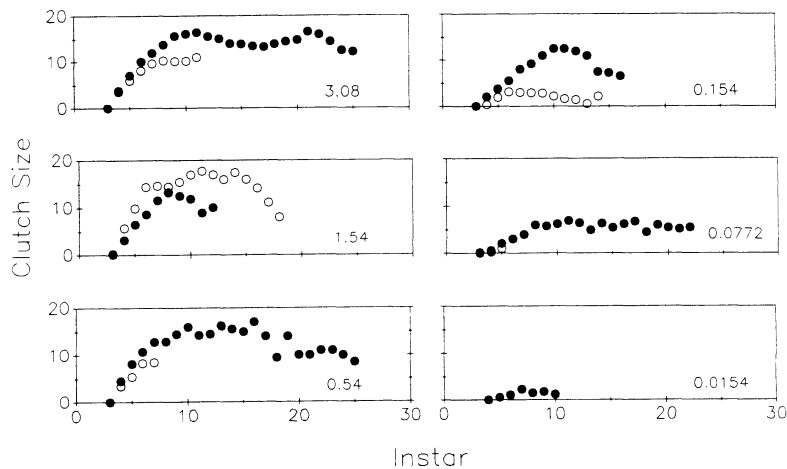


FIG. 3. The response of instar-specific clutch sizes to food carbon concentration. The latter is given at lower right in each graph, in micrograms per millilitre. The sample sizes for all plotted points are ≥ 5 , and for most points, the SE is less than the radius of the point. Solid points refer to *Daphnia ambigua*, and open points to *Ceriodaphnia quadrangula*.

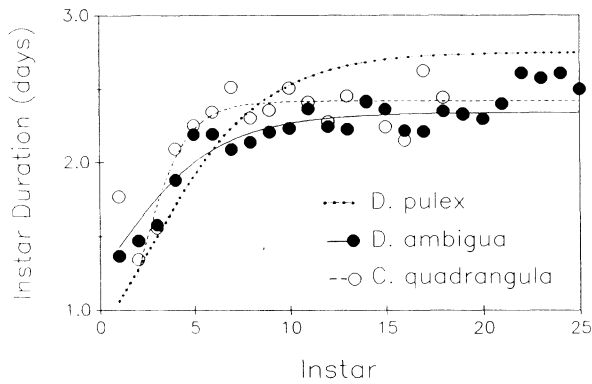


FIG. 4. Mean instar-specific durations and the functions described by Eq. 2 using the parameter estimates in Table 1. Each point represents a pooled mean of the data from all food carbon concentrations; the standard errors are on the order of the radius of the points. The curve for *Daphnia pulex* is taken from Lynch (1989).

rameters of the instar duration function appear to be independent of food level, as in the case of *D. pulex* (Lynch 1989). The instar-duration estimates given in Fig. 4 are means over all food levels, with each food-specific estimate being weighted by the inverse of its sampling variance. The estimated values of k_{1j} , b_{1j} , and D_{max} , and their standard errors obtained by jackknifing, are given in Table 1. Notice that relative to the larger *D. pulex*, both small species have longer durations in early instars (consistently through instar 6) but shorter durations in late instars (compare the D_{max} in Table 1).

Energetics.—Both species exhibit continuous growth, but there is a reduction in the growth rate with age (Fig. 5). This is particularly noticeable in *Ceriodaphnia* beyond the fifth instar. As in the case of *Daphnia pulex* (Lynch 1988), the variance in length levels off after the first few instars and in most cases exhibits a later decline with age. Since there is between-individual variation for all instar-specific growth rates, such a pattern

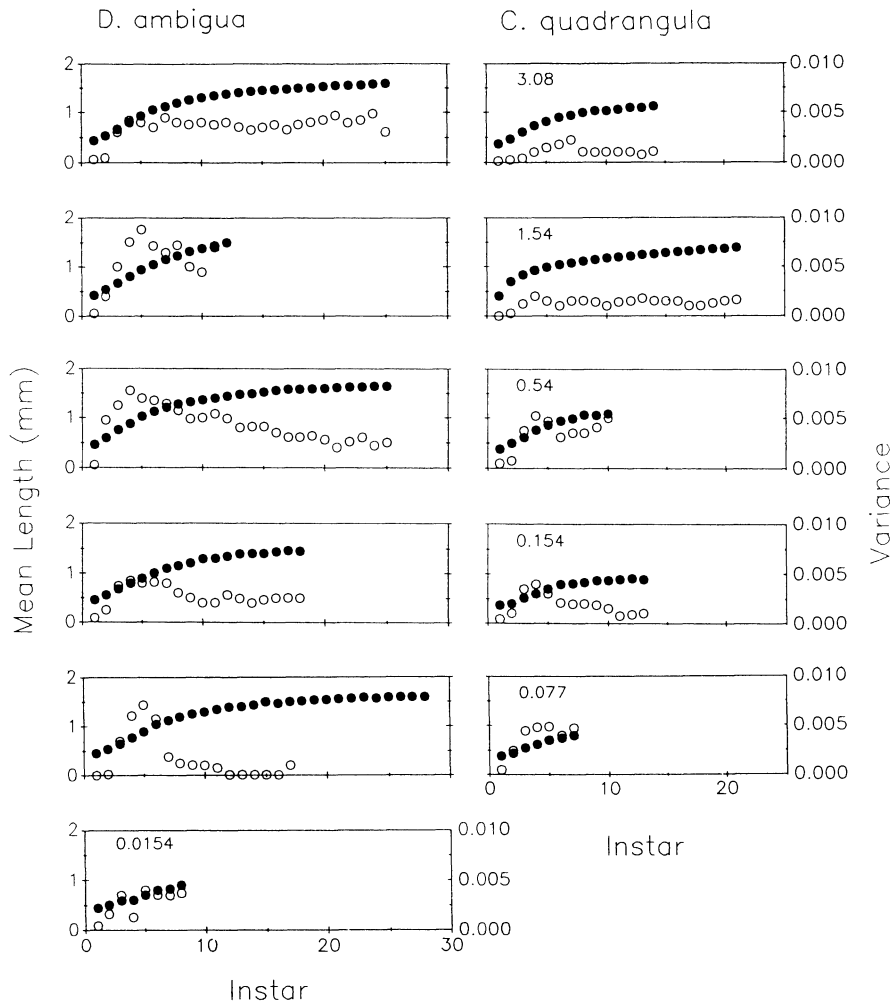


FIG. 5. Means (●) and variances (○) of instar-specific lengths at the six food carbon concentration levels (inset at upper left in graphs, in micrograms per millilitre). Sample sizes for all data points are ≥ 10 .

TABLE 3. Summary of the significant correlations between dry mass investments in reproduction and growth.*

Food carbon concentration ($\mu\text{g/mL}$)	Repro. vs. repro.		Growth vs. reproduction				
	+1	+2	-2	-1	0	+1	+2
	+/- (N)	+/- (N)	+/- (N)	+/- (N)	+/- (N)	+/- (N)	+/- (N)
<i>Daphnia ambigua</i>							
3.08	2/1 (18)	3/0 (17)	1/1 (17)	0/3 (18)	15/0 (19)	1/1 (19)	1/1 (18)
1.54	5/0 (11)	2/0 (10)	0/0 (10)	0/0 (11)	7/0 (12)	2/0 (12)	0/0 (11)
0.54	3/1 (18)	4/0 (17)	1/0 (17)	0/2 (18)	9/1 (19)	3/1 (19)	1/0 (18)
0.15	3/1 (17)	1/0 (16)	0/1 (17)	0/1 (17)	3/0 (18)	4/0 (18)	2/0 (17)
0.08	1/2 (16)	0/1 (8)	0/0 (9)	1/1 (9)	4/0 (10)	1/0 (9)	0/0 (9)
<i>Ceriodaphnia quadrangula</i>							
3.08	0/1 (8)	2/0 (7)	0/2 (8)	0/1 (8)	5/0 (9)	0/1 (9)	1/0 (8)
1.54	0/0 (17)	2/0 (16)	0/2 (17)	0/2 (17)	8/0 (18)	1/2 (18)	1/1 (17)
0.54	0/0 (7)	0/0 (6)	0/0 (6)	0/2 (7)	3/0 (8)	0/0 (8)	2/0 (8)
0.15	1/0 (12)	0/1 (11)	0/2 (11)	0/3 (12)	2/0 (13)	2/0 (13)	1/0 (12)
0.08	2/0 (2)	1/0 (3)	0/0 (2)	0/0 (3)	0/0 (5)	1/0 (4)	0/0 (4)

* Within each life table analysis, the correlations among the first 20 instars were computed. The entries in the table are the numbers of significantly ($P < .05$) positive (+) and negative (-) correlations, followed by the number of computed correlations, N . The first two columns summarize the correlations between reproduction in instar x and $x + 1$, and x and $x + 2$. The next five columns summarize the correlations between growth in instar x and reproduction in instar $x + i$ where i is the integer at the top of the column.

implies compensatory growth, i.e., negative correlations between the size increments in different instars.

To evaluate whether there are energy costs associated with reproduction, the correlations between the dry mass invested in eggs in different instars were estimated. Since the display of this information is rather difficult, Table 3 simply summarizes the number of significantly positive and negative correlations between reproductive investments one and two instars apart. Each instar combination was evaluated separately at each food level. Only a small fraction of these correlations were significant, but of those that were, the vast majority (32 of 40) were positive. This result is not qualitatively altered when comparisons are made between more distant instars. Thus, as in the case of *D. pulex* (Lynch 1989), there is no compelling evidence that an unusually high investment in reproduction in one instar results in a reduction in future reproduction. If anything, there is a slight tendency for some individuals to reproduce at a high rate throughout life and others to reproduce at a consistently low rate.

Of the 57 significant correlations observed between growth and reproduction in the same instar, 56 were positive (Table 3). Thus, there is no evidence of a trade-off between energy budget components within an instar. On the other hand, consistent with the relationships between growth in different instars, there is a definite tendency for reproductive investment to have a negative influence on future growth (23 of the 26 significant correlations were negative). The same result was found in *D. pulex* (Lynch 1989).

The rate of total net energy intake (assimilation in excess of metabolic requirements) of an individual is the sum of its investment in growth, reproduction, and molt replacement. The relation of this quantity to body size (B , dry mass) is approximately hyperbolic (Fig. 6),

following the function

$$F = F_{\max} \{1 - \exp[-a(B - B_{F,\min})]\}. \quad (3)$$

The parameters of this formula were estimated by least squares analysis for all individuals that survived at least six instars, and these were pooled to provide food-specific estimates.

The maximum rate of net energy intake F_{\max} is hyperbolically related to food concentration in both species (Fig. 7). The parameter estimates of the function

$$F_{\max} = F_{\text{Max}} \{1 - \exp[-k_f(C - C_f)]\} \quad (4)$$

are given in Table 1. Note that the estimates of F_{\max} for *D. ambigua* are approximately twice as large as those for *C. quadrangula* at all food levels but substantially below those for *D. pulex* at all but the lowest food concentrations.

In *C. quadrangula*, the constant a declines exponentially with increasing food carbon concentration following the pattern

$$a = b_a \exp(-k_a C) + a_{\min} \quad (5)$$

(Fig. 7, Table 1). A qualitatively similar situation exists in *D. pulex* (Lynch 1989), although it exhibits substantially lower values of a (Fig. 7). On the other hand, a is independent of food level in *D. ambigua* with an average value of 0.15 ± 0.03 .

The threshold size for $F > 0$, $B_{F,\min}$, is $\approx 0.6 \mu\text{g}$ dry mass for both *D. ambigua* ($0.58 \pm 0.03 \mu\text{g}$) and *C. quadrangula* ($0.64 \pm 0.45 \mu\text{g}$), independent of food concentration (Fig. 7, Table 1). However, while $B_{F,\min}$ in *D. pulex* has nearly this same value at very low food levels, it increases to an asymptotic value of $\approx 1.8 \mu\text{g}$ at high food levels, following the function

$$B_{F,\min} = 1.76 \{1 - \exp[-3.91(C + 0.11)]\}. \quad (6)$$

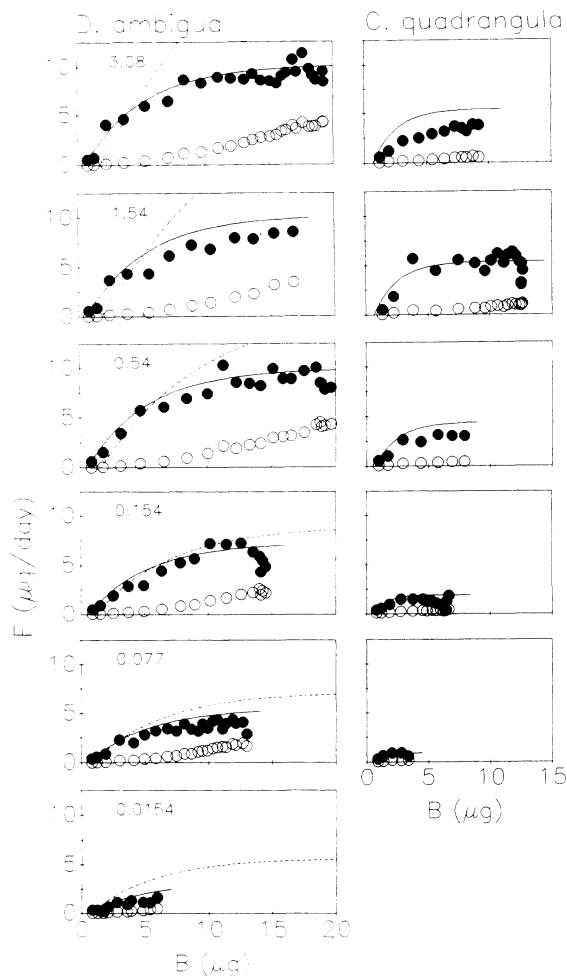


FIG. 6. Total daily net increment in dry mass, F (growth + reproduction + molt replacement) as a function of mean instar-specific sizes. The food carbon concentration levels are inset at the upper left in graphs, in micrograms per millilitre. The fitted hyperbolic functions (—) are generated by Eqs. 3–5 using the parameter estimates in Table 1. The investment in molt replacement is represented by \circ . Sample sizes are ≥ 5 for all plotted data. --- are the fitted F functions for *Daphnia pulex*.

[Note that $B_{F,\min}$ was assumed to be zero in Lynch (1989).]

The fitted curves in Fig. 6 are obtained by substituting the parameter estimates in Table 1 into Eqs. 3–5. In general, the size-specific rates of net energy intake are greater for *D. pulex* than for equivalent-sized individuals of the smaller species.

The proportion of dry mass available for growth and reproduction that is invested in reproduction can be represented by a hyperbolic function of body mass,

$$R = R_{\max} \{1 - \exp[-k_R(B - B_{R,\min})]\}, \quad (7)$$

where R_{\max} is the maximum proportional investment in reproduction, $B_{R,\min}$ is the mass at first investment in reproduction, and k_R is the rate of approach to the

maximum investment in reproduction. The parameters to this equation were estimated at each food concentration for each individual that was reproductive for at least four instars. The mean food-specific parameter estimates were then regressed on food concentration. None of the regressions reached significance at the 5% level for either species. Thus, as in *D. pulex* (Lynch 1989), the size-specific pattern of investment in reproduction appears to be independent of food concentration (Fig. 8). The pooled parameter estimates for Eq. 7 are given in Table 1. Like *D. pulex* (Lynch 1989), *D. ambigua* exhibits an increase in offspring size throughout life, and this tendency weakens at low food levels (Fig. 9). The data are less extensive for *C. quadrangula*, but there is no compelling evidence for such a pattern in this species.

DISCUSSION

Recently I reviewed the literature on the influence of resource availability on cladoceran life histories (Lynch 1989). Of the previous work, my study on *Daphnia pulex* provides the only extensive analysis of demography and energetics. The objective of the current study was to evaluate the extent to which the

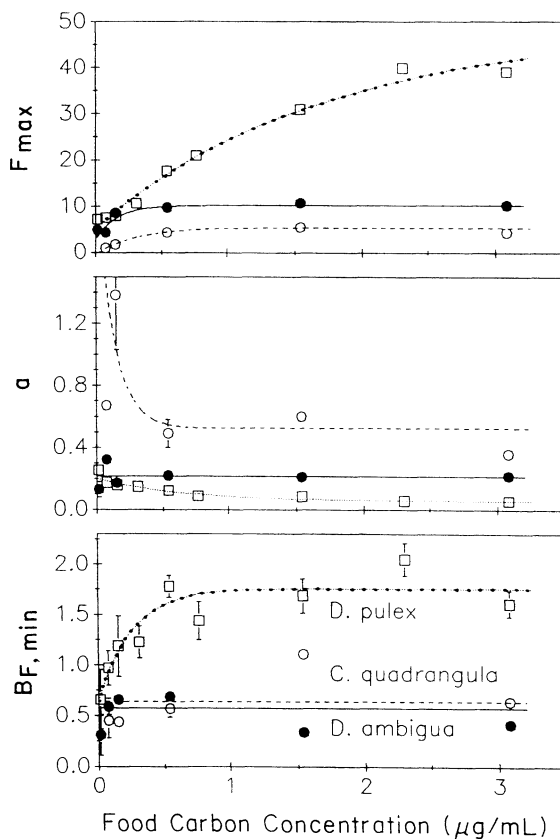


FIG. 7. Relationship of the parameters of the net energy intake function to food carbon concentration level. Standard errors for the food-specific estimates were obtained by fitting Eq. 3 to individuals; in most cases these are less than the radius of the data points.

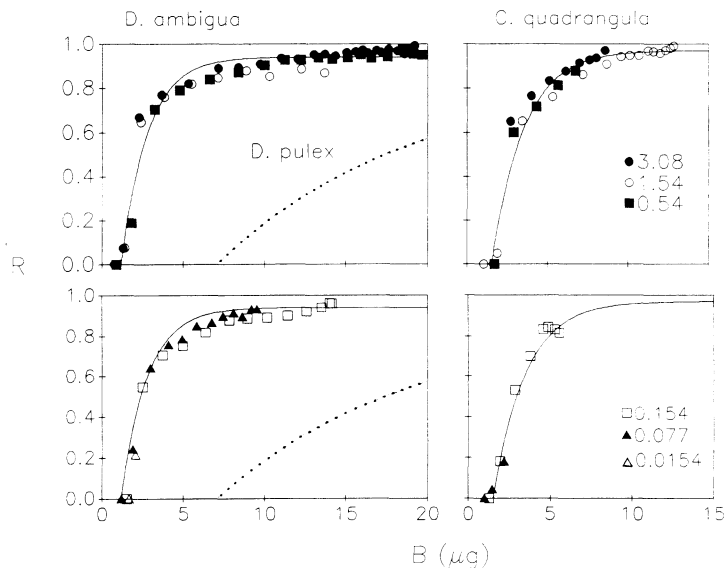


FIG. 8. Proportion of net dry mass invested in (growth + reproduction) that is allocated to reproduction, as a function of body mass. Different types of data symbols refer to means for different food carbon concentration levels, given in micrograms per millilitre. Sample size is ≥ 10 for all data points. The function for *Daphnia pulex* is taken from Lynch (1989). Note that the curves are the means of the R function fitted to individuals. For a nonlinear function, the mean of the function is not equal to the function of the means. Hence, the slight discordance between the fitted functions and the plotted data.

conclusions of that work can be extended to other species. *Daphnia ambigua* and *Ceriodaphnia quadrangula* were chosen because they are much smaller in size than *D. pulex* and because one of them is a member of a different genus.

As in the case of *D. pulex*, both species exhibit two fundamental properties that are essentially independent of food concentration: the relation between instar number and duration, and the size-specific fraction of energy available for (growth + reproduction) that is allocated to reproduction. Each of these functions follows the same approximate mathematical form in all three species. Both of the small species also exhibit size-specific net energy intake functions with the same hyperbolic form as found in *D. pulex*. However, contrary to the situation in *D. pulex* and *C. quadrangula*, the slope parameter does not depend upon food level in *D. ambigua*, and only in *D. pulex* does the threshold size for $F > 0$ change with food level.

Combined with the low F_{\max} , the cost of molting puts a severe constraint on the growth potential of *D. ambigua* and *C. quadrangula*, effectively preventing them from ever attaining the sizes that are common in *D. pulex*. The allometric functions for the molt mass for the three species are $M = 1.2L^{4.6}$, $M = 1.2L^{2.5}$, and $M = 0.5L^{3.1}$, respectively. Thus, the masses of the molts of 1-mm *D. ambigua* or *C. quadrangula* are more than twice that of the same-sized *D. pulex*.

Because the net rate of energy intake levels off shortly after maturation, while the cost of molting continues to increase with further growth (Fig. 6), a size is eventually reached at which the net energy intake is just

sufficient to cover the cost of the molt, with nothing left over for growth or reproduction. Under all but very low food concentrations, the critical size for *D. ambigua* is 1.9 mm, and at very low food levels, it drops to ≈ 1.3 mm (Fig. 10). For *C. quadrangula*, the maximum attainable size declines from 2.4 mm to 1.2 mm with decreasing food concentration. This type of analysis assumes that dry mass is an appropriate currency for all three components of the energy budget (growth, reproduction, and molting). Nevertheless, it is noteworthy that the critical sizes are not greatly beyond observed sizes in old individuals (Fig. 5). Moreover, there is a tendency for the instar-specific clutch sizes to decline with age after the first few instars (Fig. 3), which is consistent with an increased cost of molting.

Although the computation of the maximum attainable size is a straightforward application of the allometric function for the molt and the net energy intake function in the region of the maximum, it is less clear that the data in this study can be used to compute the minimum energetically feasible size. Unlike F_{\max} , which is used to compute the upper size limit, the estimates of $B_{F,\min}$ (Fig. 7) fall in a region where F is changing rapidly with size. So strictly speaking, $B_{F,\min}$ should be viewed as a parameter that allows the F function to closely fit the data at low body masses. Certainly, it seems rather unlikely that the minimum viable size of *D. pulex* actually increases with food concentration, as the pattern for $B_{F,\min}$ would suggest (Fig. 7). Nevertheless, it is interesting that $B_{F,\min}$ converges to $\approx 0.6 \mu\text{g}$ at low food levels in all three species.

It has been common to view the body sizes of plank-

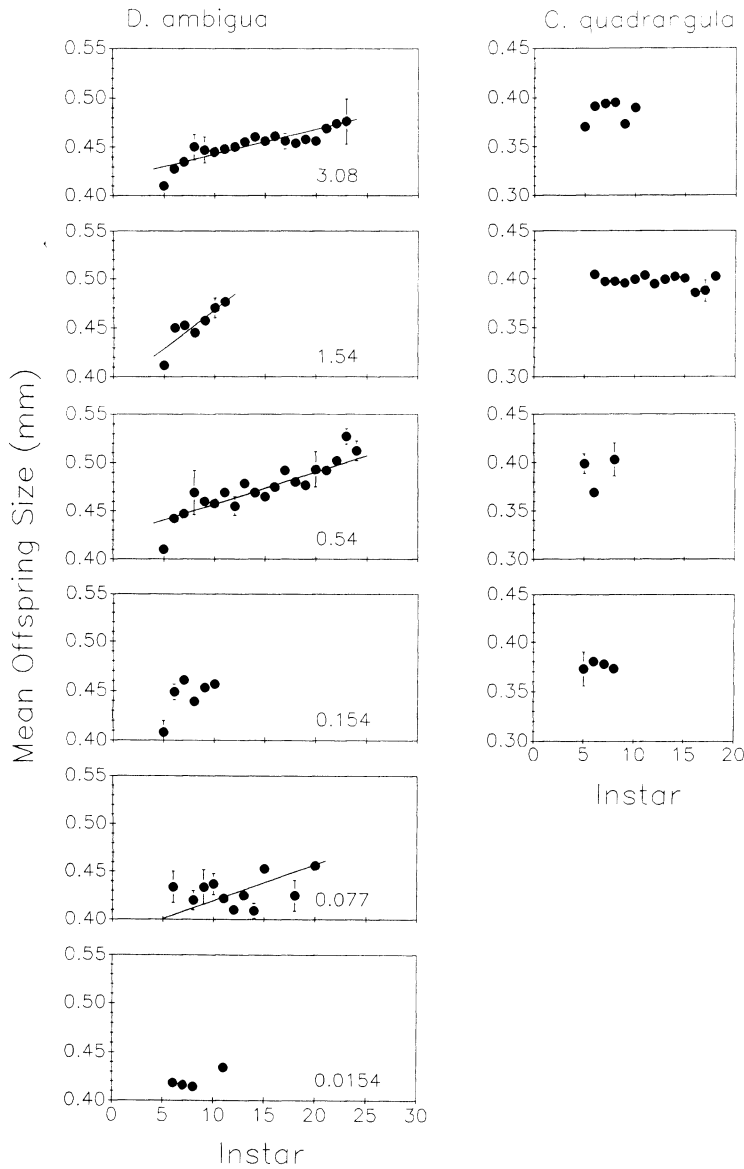


FIG. 9. The relationship between mean offspring size and maternal age in two daphnid species. Food carbon concentration levels are inset at lower right in graphs, in micrograms per millilitre. Only significant regressions are shown.

tonic cladocerans as evolutionary outcomes to selection on size per se (Hall et al. 1976, Lynch 1980a, b, Gabriel 1982, Dorazio and Lehman 1983). The results of this study and of Lynch (1989) suggest that the generality of this explanation needs to be reconsidered. From a mechanistic point of view, three things conspire to determine the size of a planktonic cladoceran: (1) the ability to harvest energy, and the diversion of energy away from growth into (2) reproduction and (3) molt replacement. Clearly, all three attributes are evolutionarily labile since they differ between species. However, there is a chicken vs. egg problem. On the one hand, the species-specific energy-related properties may be an outcome of (non-size-related) selection op-

erating directly on them, with body size evolving passively as a correlated response (Lande and Arnold 1983, Lynch and Arnold 1988). On the other hand, observed suites of energy-related characters may represent evolutionary solutions to selection for specific body sizes or growth trajectories.

Thus, the question arises as to whether *D. ambigua*, the smallest of the North American *Daphnia* species, is so diminutive because of selection for small size per se. An alternative explanation is that selection for a heavy carapace, which might serve as a useful defense against invertebrate predators (Dodson 1984), induces a correlated selection response for body size. Likewise, *C. quadrangula*, which is one of the largest species of

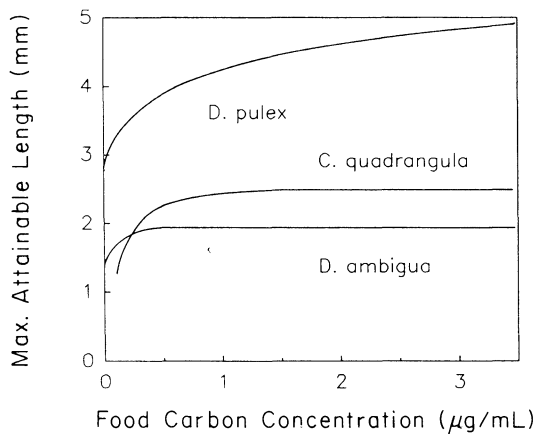


FIG. 10. Maximum attainable length as a function of food carbon concentration level.

Ceriodaphnia, may owe its size to selection for increased F or reduced R or M .

Two major problems that remain to be understood are why some species have much lower energy utilization capabilities than others and why F levels off with increasing size (Lynch et al. 1986). It may be argued that because offspring length increases with maternal age in some cases (Fig. 9) the computation of F using a constant egg mass has led to an artificial asymptote to the net energy intake function. For example, if the length-mass regression can be assumed to be fully accurate in the range of observed offspring sizes (0.40–0.53 mm) in *D. ambigua*, then there might be as much as a twofold difference in egg masses between first- and late-instar adults. Recently, Tessier and Consolatti (1989) demonstrated positive correlations between mass and length at birth within three species of *Daphnia*. It remains to be seen whether there is a significant correlation between masses of eggs and hatchlings, although it will be surprising if there is not. Thus, in future studies of the sort reported here, it will be useful to monitor changes in mean egg mass with maternal age directly, but that will require considerable labor.

Despite this potential shortcoming, the hyperbolic form of F appears to be a biologically significant phenomenon in planktonic daphnids. The full range of offspring length variation noted above for *D. ambigua* is not seen at most food levels, and the observed range is much smaller beyond instar 10 when the asymptote in F becomes most apparent (Fig. 9). Thus, a change in egg mass with maternal age does not provide an entirely satisfactory explanation for the leveling off of F with age in *D. ambigua*, and it is not an argument that applies to *C. quadrangula*, for which offspring size does not vary with maternal age.

Because this study involves only a single clone of each of three species, it is premature to draw any strong conclusions as to the patterns of energy-related and

demographic properties in large and small species. Earlier, drawing from a survey of experiments performed under a diversity of conditions, I suggested that small species may tend to allocate larger proportions of their energy budgets into growth following maturity than do large species and that some small species may never grow to their optimal foraging size (the approximate size at which F attains its maximum) (Lynch 1980a). The clones in this study do not bear those conclusions out, although it is possible that they are isolated exceptions.

The fact that the three species described in this study have rather different size-specific net energy intake functions at most food concentrations raises special problems for studies concerned with the identification of optimal life history strategies. All optimization models are built around some kind of energy constraint that is assumed to be fixed. In models of cladoceran life histories, the strategy has usually been to search for the optimal size at birth and maturity in the face of various patterns of size-specific mortality under the assumption that the F function or some close relative to it is constant (Lynch 1980b, Gabriel 1982, Dorazio and Lehman 1983). This is clearly not the case.

Recently, Gliwicz (1990) presented strong evidence that the minimum food concentration necessary for growth declines with increasing body size in interspecific comparisons of daphnids, consistent with Brooks and Dodson's (1965) size-efficiency hypothesis. Although the observations in this paper are based on only single clones of three species, they are in rough accord with Gliwicz's results. The threshold food concentration for positive F is significantly lower in *D. pulex* than in the much smaller species *D. ambigua* and *C. quadrangula* (Table 1). Since different-sized species allocate their energy to reproduction in rather different ways, it does not necessarily follow that the threshold food concentration for positive population growth is an increasing function of body size. Nevertheless, in this study, the two *Daphnia* species do have significantly lower food requirements for $r > 0$ than does *C. quadrangula* (the smallest of the three).

ACKNOWLEDGMENTS

Many thanks to B. Hecht, G. Henderson, B. Monson, L. Nass, L. Schmitt, and K. Spitze for helpful assistance in the lab, and to K. Spitze for helpful comments. The project was supported by NSF grants BSR 83-06072 and BSR 89-11038.

LITERATURE CITED

- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* **150**:28–35.
- Burns, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particles ingested. *Limnology and Oceanography* **13**:675–678.
- . 1969. Relation between filtering rate, temperature and body size in four species of *Daphnia*. *Limnology and Oceanography* **14**:693–700.
- Dodson, S. I. 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: morphological defenses and their cost. *Ecology* **65**:1249–1257.

- Dorazio, R. M., and J. T. Lehman. 1983. Optimal reproductive strategies in age-structured populations of zooplankton. *Freshwater Biology* **13**:157-175.
- Gabriel, W. 1982. Modelling reproductive strategies in *Daphnia*. *Archiv für Hydrobiologie* **95**:69-80.
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. *Nature* **343**:638-640.
- Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* **7**:177-208.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* **37**:1210-1236.
- Lynch, M. 1980a. The evolution of cladoceran life histories. *Quarterly Review of Biology* **55**:23-42.
- . 1980b. Predation, enrichment, and the evolution of cladoceran life histories: a theoretical approach. Pages 367-376 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, New Hampshire, USA.
- . 1985. Spontaneous mutations for life history characters in an obligate parthenogen. *Evolution* **39**:804-818.
- . 1988. Path analysis of ontogenetic data. Pages 30-46 in B. Ebenman and L. Persson, editors. *Size-structured populations*. Springer-Verlag, Berlin, Germany.
- . 1989. The life history consequences of resource depression in *Daphnia pulex*. *Ecology* **70**:246-256.
- Lynch, M., and S. J. Arnold. 1988. The measurement of selection on size and growth. Pages 47-59 in B. Ebenman and L. Persson, editors. *Size-structured populations*. Springer-Verlag, Berlin, Germany.
- Lynch, M., L. J. Weider, and W. Lampert. 1986. Measurement of the carbon balance in *Daphnia*. *Limnology and Oceanography* **31**:17-33.
- Tessier, A. J., and N. L. Consolatti. 1989. Variation in offspring size in *Daphnia* and consequences for individual fitness. *Oikos* **56**:269-279.