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Michael Lynch

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THE LIFE HISTORY CONSEQUENCES OF RESOURCE DEPRESSION IN *DAPHNIA PULEX*¹

MICHAEL LYNCH

Department of Ecology, Ethology, and Evolution, Shelford Vivarium, University of Illinois, Champaign, Illinois 61820 USA

Abstract. The life history response of a clone of *Daphnia pulex* to nine concentrations of a defined food supply is described and combined with an energy analysis. Three features of this clone were essentially invariant with respect to food level: the length-mass regression, the durations of instars, and the size-specific fractions of net energy intake invested in reproduction. The main response to food limitation was a reduction in size-specific net energy intake and in egg size. Simple mathematical functions are fit to the data on these relationships and combined to produce a model that reconstructs the age-specific patterns of growth and reproduction quite accurately. The energy cost of molting is shown to be a major constraint on the evolution of body size in *Daphnia*.

Key words: cost of reproduction; *Daphnia*; energetics; life history; reproductive effort; resource depression.

INTRODUCTION

Investigations of life history variation and competition have dominated ecological research for several years. Yet except for domesticated mammals and poultry, there is remarkably little information on the detailed responses of life histories to resource availability. Most studies concerned with resource depression have focused on physiological or behavioral attributes (metabolic and functional responses), a limited phase of the life history (juvenile development or adult reproduction), or on population rather than individual parameters (population growth rate). Interpretation of many of the studies is difficult because of inadequate control of qualitative aspects of the food supply or other environmental attributes, the failure to control for maternal effects, or the use of mixed genotypes and/or age classes.

Information on the developmental response of life history characters to resource depression is essential for understanding the ways in which species cope with short-term environmental change. Studies of this response should focus on the entire life histories of many individuals since characters generally will respond to environmental changes in concert and since different individuals may solve the same problem in different ways. It is also useful if measures can be made on replicated members of the same genotype rather than on genetically heterogeneous populations. In the latter case, the source of between-individual variation is hopelessly obscured unless a well-designed quantitative genetic analysis is carried out, and differences between experiments may be complicated by genetic differences in the study populations.

Planktonic cladocerans provide a useful model system for investigating the response of life history traits

to resource availability. Individual genotypes may be maintained indefinitely since females reproduce by ameiotic parthenogenesis. Such lines are maintained easily in controlled environments on defined media. Since individuals are live-bearers with rigid, transparent carapaces, it is easy to measure individual investments in growth and reproduction. The entire life history can be determined in a modest amount of time because of the short lifespan of individuals (<100 d).

This study combines a descriptive analysis of the life history response of a single clone of *Daphnia pulex* to food limitation with an energy analysis. Several properties of this clone will be shown to be essentially invariant with respect to food level, while others are expressed adequately by simple functions. This allows the development of a simple model that closely portrays age-specific patterns of growth and reproduction.

METHODS

The clone used in this study, an obligate ameiotic parthenogen, has been reported on extensively elsewhere (Lynch and Ennis 1983, Lynch 1985, Lynch et al. 1986, Toline 1986). Over the course of 2 yr, complete life tables were determined for ≈ 50 individuals at each of nine food concentrations, spanning two orders of magnitude. The general culture methods are outlined in Lynch et al. (1986). Briefly, all animals were raised in 40 mL of a defined medium containing a standard mixture of *Scenedesmus* and *Chlamydomonas* and maintained in clear, covered boxes in an environmental chamber set at 20°C, light:dark, 12:12 schedule. Food was replenished and experimental containers cleaned every other day. Two generations of acclimation preceded each analysis. All members of the experimental cohort were then examined daily for growth, survival, and reproduction.

Ideally, the nine life history assays should have been performed at the same time to control for nonobvious

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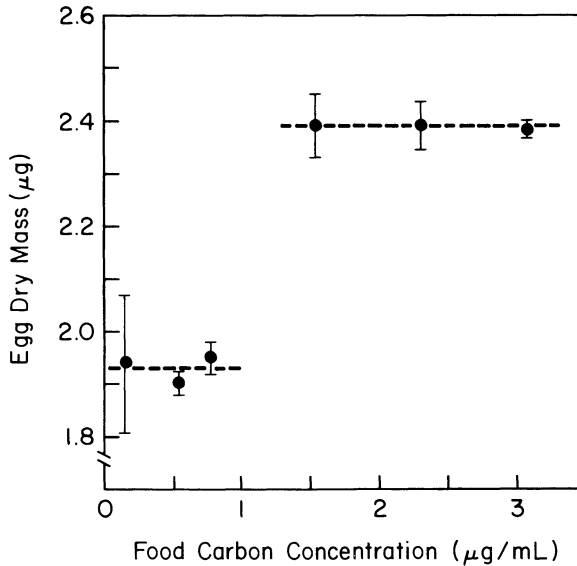


FIG. 1. Relationship of egg dry mass to food carbon concentration. Vertical bars represent ± 1 SE of means.

changes in the environmental background. However, such a treatment would have been difficult for an experiment of this size unless the entire experimental design had been broken down into several blocks, and even then there would have been difficulties in synchronizing all of the starting populations. It is also nearly impossible in a study of this nature to prevent the colonization of experimental vessels by some bacteria. The results indicate that neither of these potential sources of error had a serious influence on the general outcome of this study. The presence of bacteria in the food supply, if significant, can simply be viewed as a scaling factor.

For cladocerans, energy and nutrient intake in excess of metabolic requirements may be invested in growth, molt replacement, and/or reproduction. Dry mass will be used as the unit of investment in these categories. The use of dry mass as a surrogate for energy and nutrients implicitly assumes that the compositions of somatic tissues and eggs are equivalent. This is unlikely to be true. However, the results will indicate that the use of dry mass to measure production costs leads to a model that adequately describes the life history response to food limitation.

The growth rate in instar x is $G_x = (B_{x+1} - B_x)/D_x$, where B_x is the dry mass (in micrograms) of an individual at the beginning of instar x and D_x is the instar duration (in days). The dry masses are extrapolated from length measures (top of the head to base of the tail spine, in millimetres) using the relation $B = \alpha_1 L^{\alpha_2}$ obtained from juveniles and adults with freshly depleted ovaries and with eggs removed (Lynch et al. 1986). The constants α_1 and α_2 were estimated at all but the lowest food concentrations in this study, each with sample sizes on the order of 80 individuals. No relation of these constants to food concentration

emerged. Therefore, the entire data set was pooled to yield the general estimates (mean \pm SE: $\ln(\alpha_1) = 1.874 \pm 0.005$; $\alpha_2 = 2.632 \pm 0.032$ ($r^2 = 0.91$, $n = 651$).

The rate of investment in eggs by an individual in instar x is $R_x = E \cdot C_{x+1}/D_x$, where C_{x+1} is the observed number of eggs carried in instar $x + 1$ and E is the dry mass per egg. Egg dry masses were obtained at six food concentrations after pooling freshly extruded clutches from adults of various ages (Lynch et al. 1986). A discontinuous shift in investment per offspring emerged (Fig. 1). At food carbon levels $> 1.5 \mu\text{g/mL}$, the three highest food treatments in this study, the mean dry mass per egg was $2.39 \mu\text{g}$. At $0.8 \mu\text{g/mL}$ and lower, the mean dry mass per egg was $1.93 \mu\text{g}$. Since all of the egg masses were determined at the same time, this shift in egg mass with food carbon concentration cannot be attributed to a genetic change in the *Daphnia* culture.

The dry mass (in micrograms) of the ephippium (resting egg) of this clone has been shown previously to scale to length (in millimetres) according to the relation $EP_x = 2.90 L_x^{2.60}$ (Lynch et al. 1986). It has not yet been determined whether this regression changes significantly with food concentration, but the effects of any such dependence on the conclusions of this study would be minor since very few individuals ever produced ephippia. Under the assumption that ephippia are produced from energy reserves accumulated over the two preceding instars (Lynch et al. 1986), the rate of investment (micrograms dry mass per day) is approximately $Q_x = EP_{x+1}/2D_x$ or $EP_{x+2}/2D_x$.

Finally, from the allometric relationship given in Lynch et al. (1986), the dry mass investment required to replace the molt in instar x is $M_x = 0.52 L_x^{3.08}/D_x$.

RESULTS

Demography

As in most other organisms, the response of the intrinsic rate of increase, estimated with the stable age equation, to food carbon level was hyperbolic (Fig. 2). The asymptote was reached at $\approx 1 \mu\text{g/mL}$, and the intercept ($0.05 \mu\text{g/mL}^{-1}$) was very close to zero. The pre-

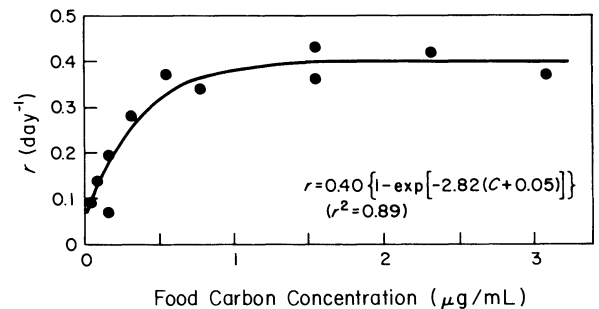


FIG. 2. Response of the steady-state rate of increase, r , to food carbon concentration, C . Additional data at 0.154 and $1.54 \mu\text{g/mL}$ are taken from Lynch and Ennis (1983); these were not used in the energy analysis.

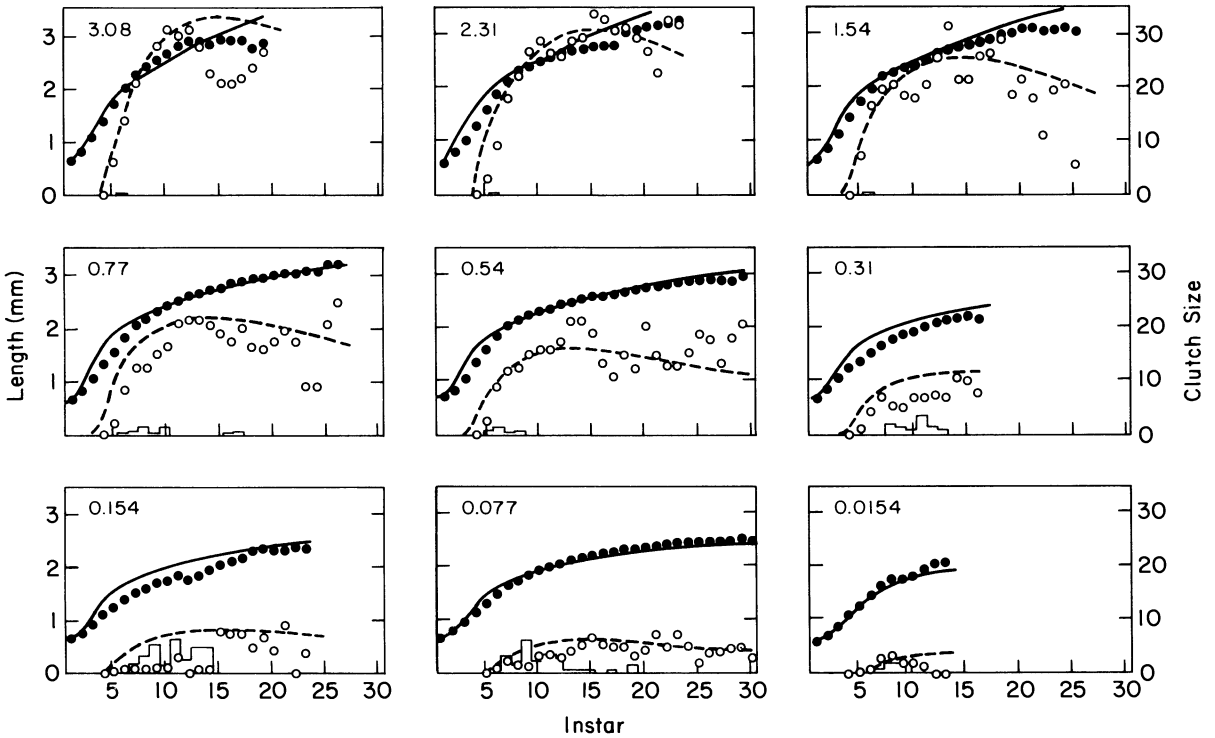


FIG. 3. Mean instar-specific lengths (●) and clutch sizes (○) under the nine food carbon concentrations ($\mu\text{g/mL}$). The histogram bars show the mean number of ephippia produced per individual per instar, which can be read on the scale on the left of the graphs. Curves are the growth (—) and reproductive (---) functions generated by the energy model described in Results: Energy Analysis. Sample sizes decline with increasing instar number.

dicted positive growth rate (0.05 d^{-1}) at zero algal concentration was presumably caused by colonization of the culture medium by bacteria, despite autoclaving.

A number of changes in age-specific rates of growth, survival, and reproduction were responsible for the form of Fig. 2. Growth was continuous at all food carbon concentrations, with a decline in instar-specific growth occurring slightly after the onset of reproduction (Fig. 3). The rate of growth declined in response to food limitation. At the highest food levels some animals attained lengths of 3.5 mm, while individuals that were extremely food-limited rarely reached 2.5 mm.

Instar durations were independent of food level but increased with instar number in a sigmoid fashion (Fig. 4). Ninety-five percent of the variance in mean instar durations obtained over all food concentrations was accounted for by the function

$$D_x = \frac{2.23}{2.03 \exp(-0.30x) + 0.79}, \quad (1)$$

where D_x is the duration of instar x in days.

Not surprisingly, reproductive output declined with resource depression (Fig. 3). Typically, within a food level, clutch sizes initially increased with instar number and reached a plateau near instar 10. In very late instars, particularly at the highest food levels, a decline in clutch size was observed. Ephippium production was

negligible at the three highest food concentrations and relatively low under all other conditions, generally being most intense in instars 6–12.

While the minimum age at first reproduction was nearly constant across all food carbon levels (Fig. 3), the mean exhibited a discontinuous shift (Fig. 5). At food carbon levels of $0.25 \mu\text{g/mL}$ and greater, the mean age at which offspring were first released was 7.6 d. At lower food levels, it nearly doubled (14.3 d) but remained essentially constant.

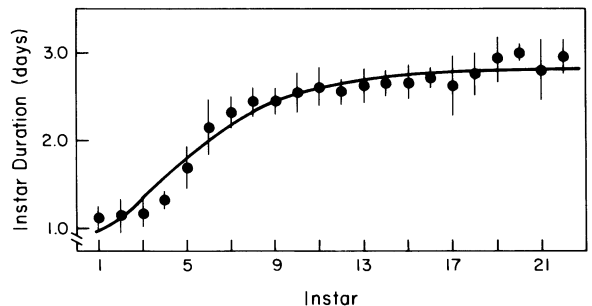


FIG. 4. Mean instar-specific durations D_x and the fitted function described by Eq. 1: $D_x = \frac{2.23}{2.03 \exp(-0.30x) + 0.79}$. The vertical bars are ± 1 SD of the nine mean estimates for each instar.

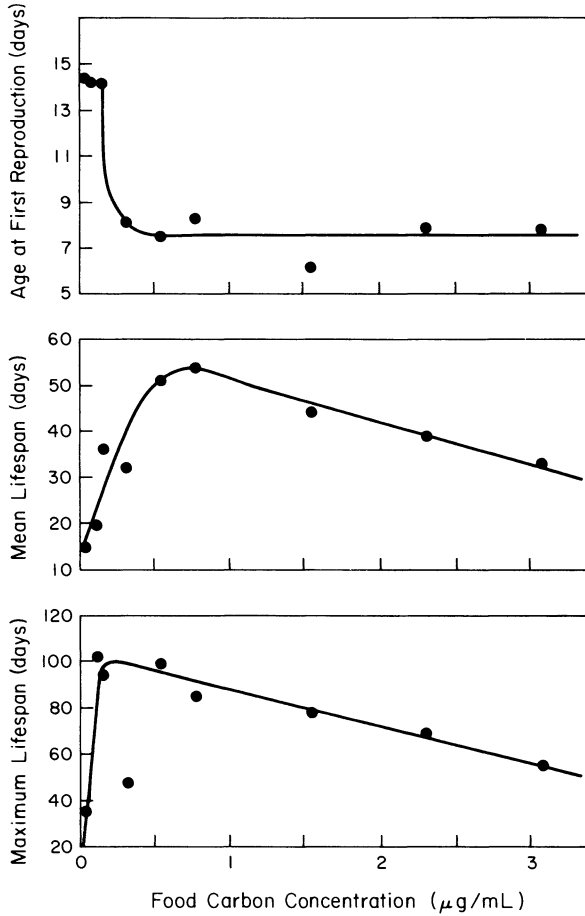


FIG. 5. The response of mean age at first reproduction, mean and maximum lifespan to food carbon concentration. Curves fitted by eye.

There was a gradual shift in age-specific survival throughout the entire range of food concentrations observed (Fig. 6). The general pattern consisted of an approximately constant age-specific mortality through the juvenile instars, followed by a plateau of relatively low and constant mortality, followed by a final phase of more pronounced and constant mortality. Juvenile mortality was most intense at low food concentrations, but the intense phase of adult mortality occurred earlier at the highest food levels. Consequently, both the mean and maximum longevity increased initially with food carbon concentration and then declined (Fig. 5).

Energy Analysis

Mean instar-specific net rates of energy (dry mass) intake, F , are plotted as functions of instar-specific dry mass, B , in Fig. 7. As a precaution against the inclusion of senescent individuals in the computation of these means, the data for each individual were truncated arbitrarily four instars prior to mortality. The data for each of the nine food carbon concentrations are approximated reasonably well by the hyperbolic function

$$F = F_{\max}[1 - \exp(-aB)]. \quad (2)$$

Moreover, the fitted constants (obtained by weighted least-squares analysis) are closely related to food carbon concentration (Fig. 8). F_{\max} increases hyperbolically with food availability according to the relationship

$$F_{\max} = 45.83\{1 - \exp[-0.66(C + 0.16)]\} \quad (3)$$

($r^2 = 0.99$), where C is the carbon concentration of algae in micrograms per millilitre. The apparent positive value of F_{\max} at $C = 0$ is not unreasonable if the

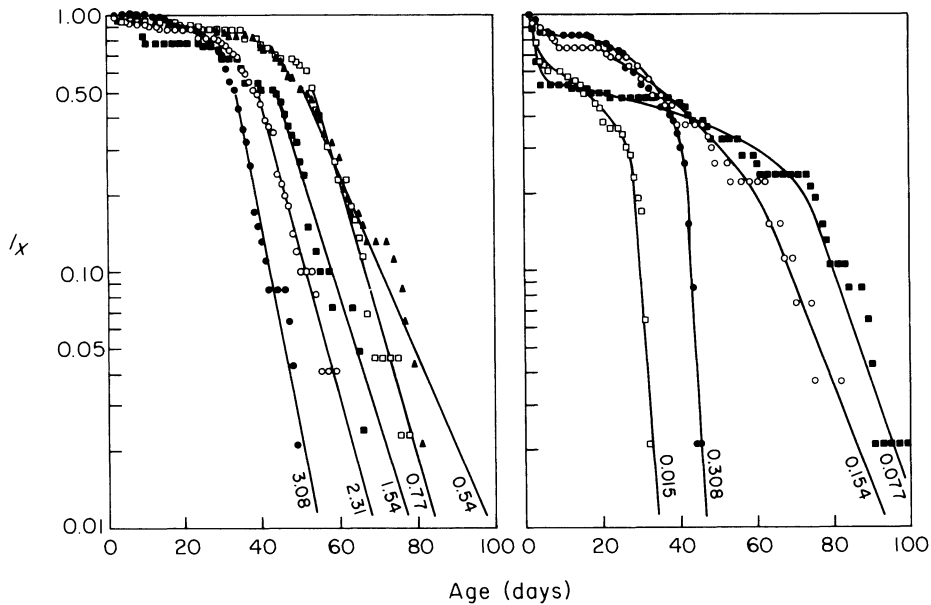


FIG. 6. Age-specific survival in response to food concentration. Curves fitted by eye, and denoted according to food carbon level ($\mu\text{g/mL}^{-1}$).

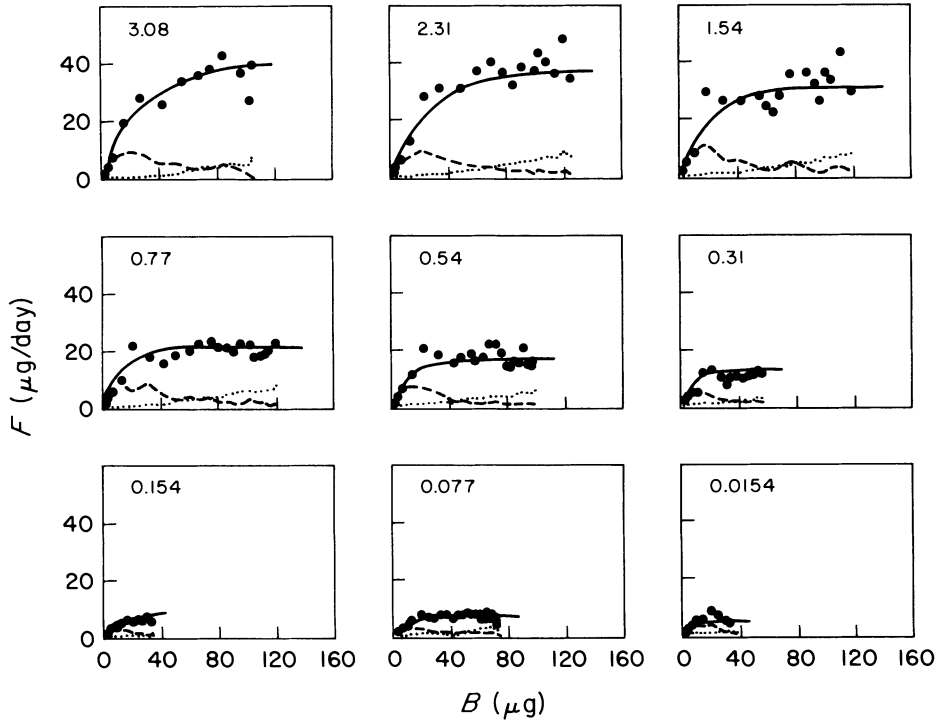


FIG. 7. Total net increment in dry mass per day (●) as a function of instar-specific mean dry mass at nine food carbon concentrations (inset numbers, in $\mu\text{g}/\text{mL}^{-1}$). The hyperbolic functions (—) are generated by Eq. 2–4. Interrupted curves show the investment in growth (---) and molt replacement (.....). Sample size is ≥ 10 for all plotted data.

experimental medium contains some bacteria and/or protozoa. The coefficient a declines exponentially with increasing food carbon concentration,

$$a = 0.107 \exp(-1.076C) + 0.028 \quad (4)$$

($r^2 = 0.92$). Thus, while the asymptotic net rate of energy intake (F_{max}) increases with food concentration, it is not reached until larger sizes have been attained.

Also illustrated in Fig. 7 are the portions of F invested in growth (---) and molt replacement (.....). The growth rate typically peaks in the fourth or fifth instar and subsequently declines to very low levels. The proportional investment in molt replacement is of minor significance early in life, but it is a major cost of large size, particularly at low food concentrations.

The clone employed in this study was characterized by a size-specific function for reproductive investment that was largely independent of food concentration (Fig. 9). The proportion of net energy intake devoted to growth or reproduction that was allocated to reproduction is described reasonably well by the size-specific function

$$R = 0.89\{1 - \exp[-0.075(B - 7.06)]\} \quad (5)$$

($r^2 = 0.96$). Investment in reproduction begins at a dry biomass of $\approx 7 \mu\text{g}$ and thereafter rapidly approaches a limit of $\approx 89\%$.

At high food carbon concentrations, individuals

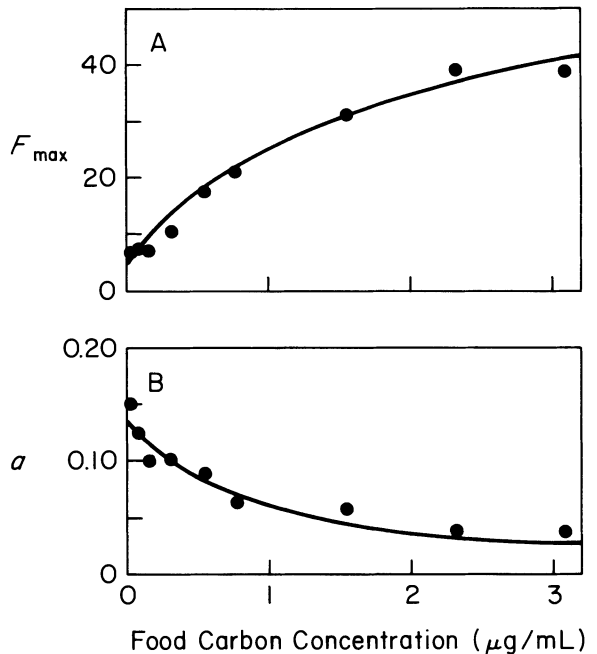


FIG. 8. Relationship of the parameters of the net energy (dry mass) intake function [$F = F_{\text{max}}[1 - \exp(-aB)]$] to food carbon concentration. Curves in A and B are from Eq. 3 and Eq. 4, respectively.

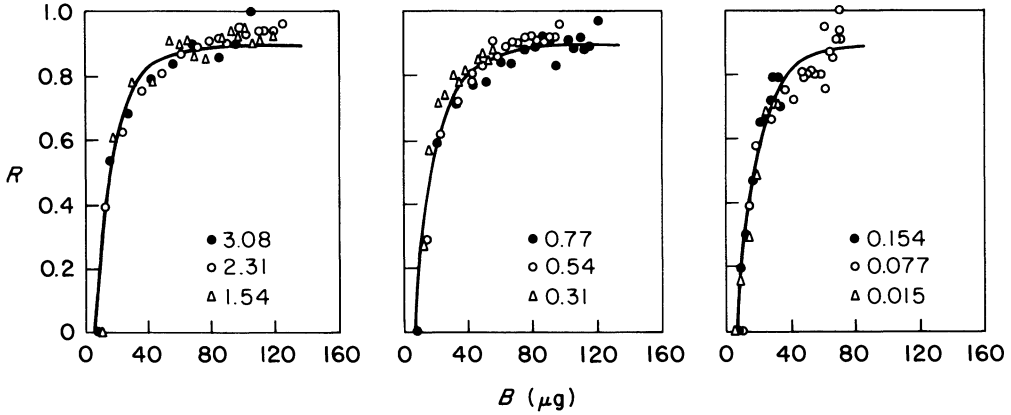


FIG. 9. Proportion of net dry mass invested in (growth + reproduction) that is allocated to reproduction, R , at the indicated food carbon concentrations ($\mu\text{g}/\text{mL}$). Solid lines are generated with Eq. 5: $R = 0.89 \{1 - \exp[-0.075(B - 7.06)]\}$.

tended to produce progeny of increasing sizes in subsequent clutches (Fig. 10). At lower food carbon levels, offspring size tended to constancy with parity, although a significant positive correlation appeared at 0.31 $\mu\text{g}/\text{mL}$.

Given the previous functions for (1) total net energy intake, molt dry mass, and proportional reproductive investment as functions of individual dry mass, (2) instar durations, (3) egg dry mass, and (4) size at birth, it is possible to project the growth curves and instar-

specific clutch sizes for the nine life tables. These are compared with the actual data in Fig. 3. Such comparisons do not constitute an entirely adequate test of the model since some of the parameter estimates are functions of the plotted data. However, the close fits obtained for all nine food concentrations are remarkable considering that all of the fitted functions are subject to errors that could act synergistically when applied jointly.

Of special interest in Fig. 3 are the declines in clutch

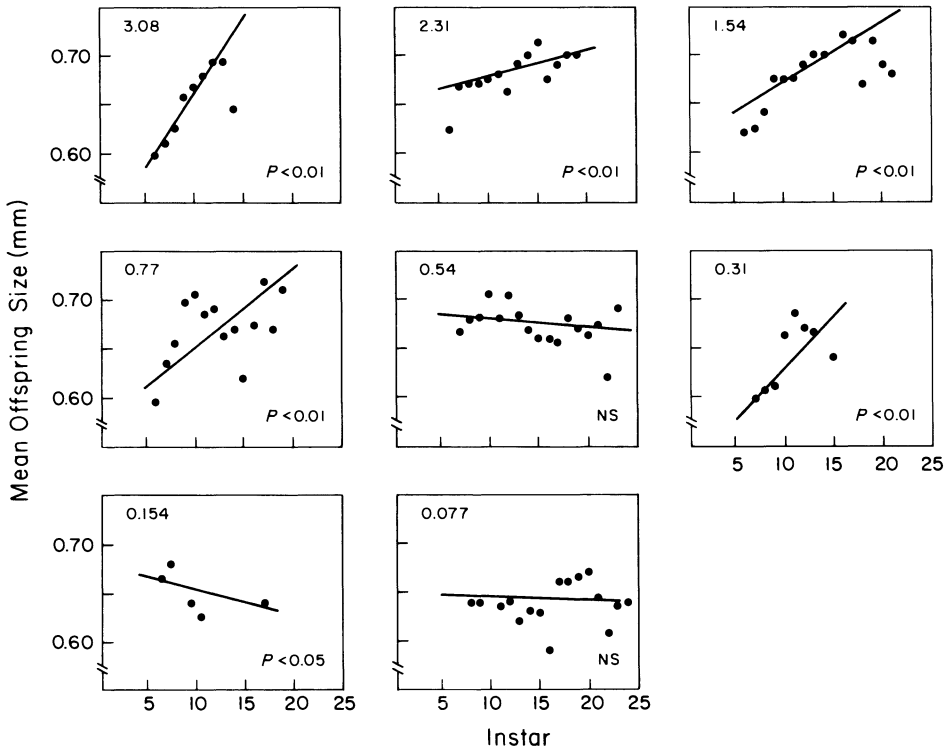


FIG. 10. Least-squares regressions of mean offspring size as a function of instar. The individual data points were weighted by sample size in the regression analysis.

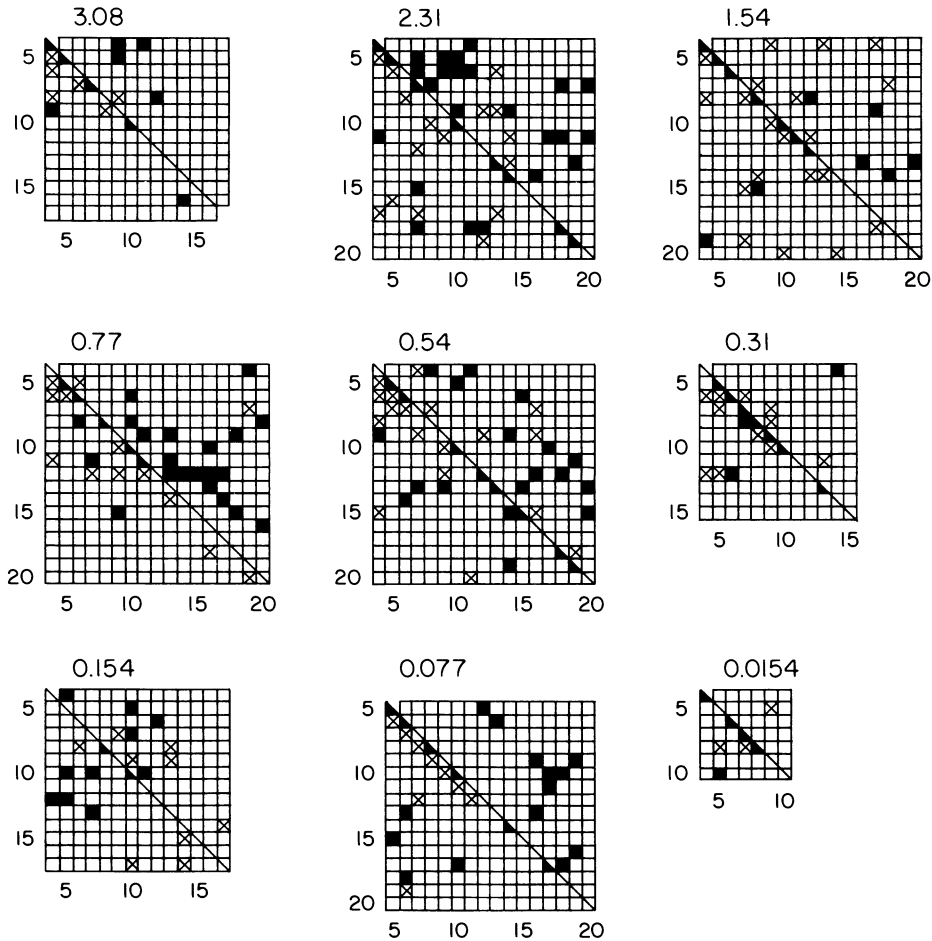


FIG. 11. Correlation matrices for instar-specific dry mass investments ($\mu\text{g}/\text{d}$) in reproduction and growth. Above diagonal: reproduction vs. reproduction in each subsequent instar; below diagonal: reproduction (columns) vs. growth in the same and each subsequent instar (rows). Positive correlations with $P \leq .05$ are darkened in; significant negative correlations are indicated with \times . Sample sizes decrease with increasing column and row numbers. Instars are denoted in the left and bottom margins; food carbon levels ($\mu\text{g}/\text{mL}^{-1}$) are given at the top of each matrix.

sizes observed in late instars and predicted by the model. These are not a consequence of senescence, but of the exponential increase in the cost of molting with increasing size. In late instars, individuals have achieved the maximal rate of net energy intake, but are also continuing to grow. Because the total energy devoted to molt replacement increases with each instar, the energy devoted to reproduction must eventually decline since the reproductive effort is essentially a constant 89% of intake.

The cost of reproduction

The energy costs of reproduction were assessed in two ways: correlations between the dry mass invested in reproduction in each instar and all subsequent instars, and between reproduction and growth in the same and all subsequent instars. Since a large amount of data was generated by this analysis, an attempt has been made to summarize the results in diagrammatic fash-

ion. Significant ($P < .05$) positive and negative correlations are denoted by shaded and \times -ed cells in the matrices of Fig. 11.

In brief, there is no compelling evidence that an increase in reproduction in a particular instar is associated with a reduction in future reproduction. Of the 106 significant correlations between reproductive investments, 73 were positive. Overall, the number of significant positive correlations between reproduction and growth were approximately equal to the number of significant negative correlations (82 vs. 73). All of the 51 significant correlations between reproduction and growth in the same instar (triangles below the diagonals in the matrices) were positive, a clear rejection of the cost argument. However, of 35 significant correlations between current reproduction and growth in the next instar, 33 were negative. Thus, while reproduction and growth within the same instar are modified in the same direction by environmental factors, an

overall increase in energy investment in one instar has a negative influence on growth, but not necessarily reproduction, in the following instar.

DISCUSSION

Although this study focused on only a single clone raised in a laboratory environment, it revealed a number of relationships that, if generally true, could greatly facilitate attempts to explain patterns of variation in cladoceran life histories as well as the tolerance of different species to various ecological settings. The close fit of the predictive model to observed growth and reproductive schedules over two orders of magnitude of food carbon concentration was accomplished by treating four functions as invariant with respect to food availability: the length-mass regression, the size-specific cost of molting, the relation between instar number and duration, and the size-specific fraction of net energy intake (exclusive of molt replacement) invested in reproduction. The response of the life history to resource depression was primarily caused by changes in the net energy intake function (F) and egg mass. Clearly, future work in this area would be eased greatly if the former functions did not have to be measured anew each time the study organism is raised on a new food supply. However, it is perhaps premature to rely fully on this strategy.

Although the literature is now replete with length-mass regressions for many species in many environments (Bottrell et al. 1976, McCauley 1984, Culver et al. 1985), they are for the most part uninterpretable from the standpoint of this study. With a few recent exceptions (Lemcke and Lampert 1975, Lampert 1977, Persson and Ekbohm 1980, Taylor 1985, Lynch et al. 1986, Tessier 1986), most investigators have included ovigerous females in their analysis. Since the clutch can account for 50% or more of the total mass of a female, it is not surprising that length-mass regressions computed in this manner often exhibit dramatic seasonal changes in concert with shifts in the food supply (Geller and Müller 1985). Such observations do not necessarily imply that the fundamental relation between length and mass of somatic tissues is flexible. Lemcke and Lampert (1975) and Persson and Ekbohm (1980) have observed temporal changes in this relationship, but it is conceivable that their results were at least in part caused by genetic changes. Taylor (1985) has documented significant reductions in the somatic masses of pure clones of *D. pulex* and *D. pulicaria* raised at food carbon concentrations of 0.1 as opposed to 1.0 $\mu\text{g}/\text{mL}$, but the differences in length-specific masses that she recorded were no greater than 1 μg . Such variation would have a negligible influence on the type of analysis presented above.

The assumption that the size-specific molt masses are independent of the food carbon level seems reasonable given the results for the length-mass regressions. The allometric relationship indicates that 6% of

the dry mass of a 2- μg *Daphnia pulex* and 12% of a 150- μg individual are lost as molts. There are no other data on the cost of molting in cladocerans except Wissing and Hasler's (1968) unelaborated statement that *Daphnia* molts are equivalent to 15–20% of individual energy values. This may be an overestimate. Data for marine amphipods (Dagg 1976), copepods (Mullin and Brooks 1967, Vidal 1980), euphausiids (Sameoto 1976), and mysids (Clutter and Theilacker 1971) indicate that molts constitute 3–10% of total body carbon. Mathias (1971) has obtained similar results for two freshwater amphipods, both of which exhibit a slight decline in molt mass to body mass.

The cost of molting is an important constraint on life history evolution in *Daphnia*. For example, the molt of a 2-mm individual in this study is roughly 4 μg dry mass, which is equivalent to approximately two eggs. The molt masses for 3- and 4-mm individuals are equivalent to 7 and 17 eggs, respectively. Since the cost of molting increases with size, while the net energy intake eventually levels off, a size must eventually be reached at which an insufficient amount of energy can be harvested for reproduction. This problem could be avoided to some extent by prolonging the instar duration as size increases, which is what *Daphnia* do (below). However, for the clone in this study, it can be shown that at a high food carbon level of 3 $\mu\text{g}/\text{mL}$, individuals exceeding 4.8 mm in length would be incapable of producing an egg. At the lowest food carbon level observed (0.0154 $\mu\text{g}/\text{mL}$), this upper limit to size becomes 2.7 mm. In some environments there are advantages to attaining such sizes as a means of avoiding invertebrate predation (Lynch 1980b), but such a strategy is evolutionarily unobtainable if reproduction is impossible.

There has long been general agreement among workers who study Cladocera that instar duration depends only on temperature and not on food level (Hall 1964, Korinek 1970, Bottrell 1975a, b). The results of this study are entirely consistent with this idea. Ingle et al. (1937) reported a dependence of instar duration on food availability in *Daphnia laevis*, but the variation is so minor that it can safely be ignored. Recently, however, Orcutt and Porter (1984) have claimed that the time between brood releases in *Daphnia parvula* depends on both temperature and food, exhibiting a nearly fourfold increase with food limitation at 25°C. Their results would be brought into line with all other observations if food-limited individuals were frequently barren during adult instars.

The primacy of temperature as a determinant of instar duration has been very helpful for zooplankton demographers, since it permits the estimation of birth rates from observed egg ratios and water temperatures (Edmondson 1968, Taylor and Slatkin 1981, Lynch 1982). However, in the case of *Daphnia pulex*, it is clear that the duration of an adult instar is also a function of adult age, increasing from ≈ 2 to 3 d at 20°.

Such increases are common to studies on other species of *Daphnia* (Fig. 12; and Lynch et al. 1986), as well as other Cladocera (Montu 1976, Murugan and Job 1982). Since the release of offspring is generally coincident with molting in cladocerans, this is a potentially serious source of error in birth rate estimation. Moreover, there is little that can be done about it, since it is not currently possible to age field-collected animals.

The finding that the proportion of net energy intake (in excess of requirements for molt replacement) invested in reproduction is a simple hyperbolic function of body mass, independent of food level, has greatly facilitated the modelling of this clone's life history. Again, further work will be required to evaluate whether this function is also invariant with respect to food type, temperature, etc. However, other data for the same clone indicate that the reproductive investment function is independent of maternal nutritional effects (Lynch and Ennis 1983). In the only other study of the subject, Taylor (1985) recorded small reductions in size-specific reproductive effort ($\approx 5\%$) in food-limited clones of *D. pulex* and *D. pulicaria*. Less extensive data from other studies (Anderson et al. 1937, Ingle et al. 1937, Frey and Hann 1985) are generally consistent with the notion that the onset of reproduction is more closely related to size than age in cladocerans. The reproductive investment functions of other *Daphnia* species are very similar to that of *D. pulex* in that they all rapidly reach asymptotes of $\approx 90\%$ (Lei and Armitage 1980b, Lynch 1980a, Tessier et al. 1983).

F(B) functions have now been estimated for several *Daphnia* species in several different environmental settings (Lampert 1977, Lynch 1980a, b, Paloheimo et al. 1982, Lynch and Ennis 1983, Taylor 1985, Lynch et al. 1986). The form of these functions is always approximately hyperbolic, although a physiological explanation for the plateau is not yet available. This study has gone a bit further in demonstrating that the parameter estimates of the hyperbolic model can be expressed as simple functions of food carbon concentration. These results were obtained with fully acclimated animals, however, and sometimes can be modified greatly when offspring are raised in environments different from their parents' (Lynch and Ennis 1983).

Many studies with various *Daphnia* species have reported that the age and size at first reproduction increase and decrease respectively in response to food limitation (e.g., Hrbáčková-Esslová 1963, Wegleńska 1971, Hrbáčková 1974, Vijverberg 1976, Hrbáčková and Hrbáček 1978, Goulden et al. 1982, Porter et al. 1983, Orcutt and Porter 1984, Romanovsky 1984, Tillman and Lampert 1984). Indeed, there appear to be no exceptions to this pattern. Such a response is entirely consistent with the model suggested in this paper. With declining food carbon levels, a longer time is required to attain the critical size for the onset of reproductive investment. Although this critical size is the same at all food carbon concentrations, the size in

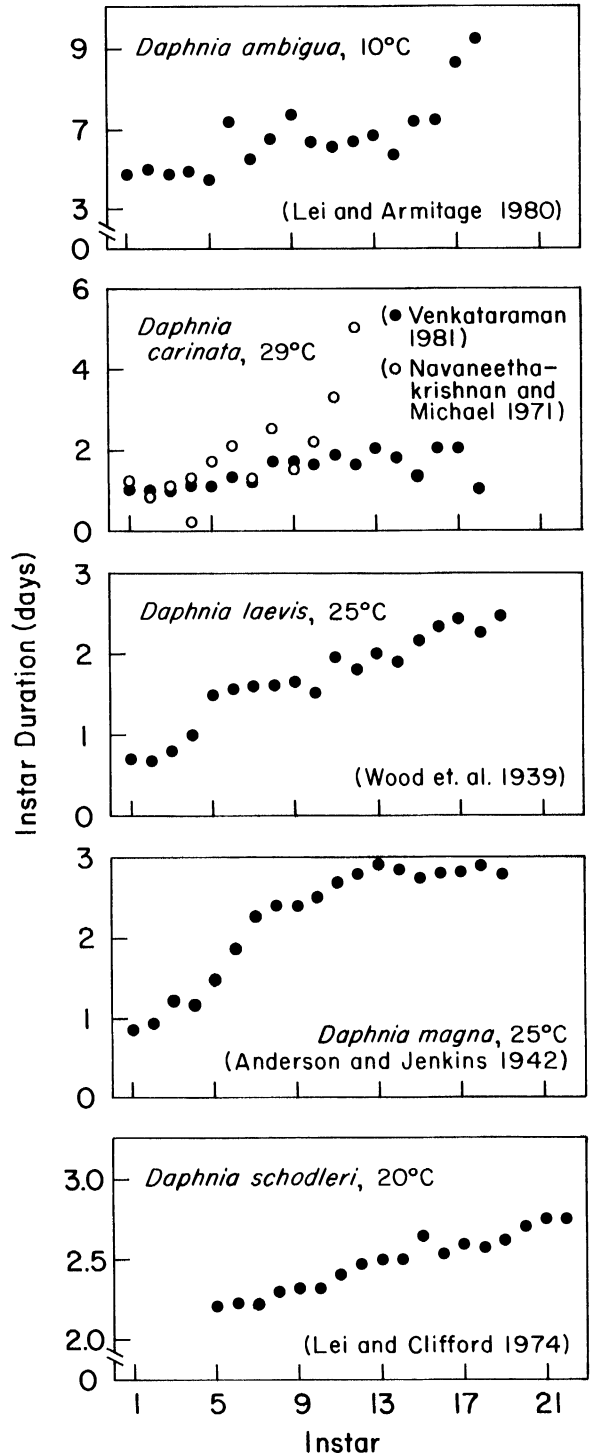


FIG. 12. Instar durations for several species of *Daphnia*.

the next instar (at which the first clutch is carried) is reduced at low food carbon levels because of the lower size-specific growth rates.

The reduction in egg volume with resource depression observed in this study is consistent with descrip-

tive data for *D. magna* (Green 1956), but no more data appear to have been published on this matter. Interestingly, a change in the length of hatchlings did not accompany the change in egg volume, at least in early clutches. In late clutches, neonate size was slightly larger at higher food levels because of the increase in size with parity. Similar results have been reported for *D. hyalina* (Hrbáčková 1974). The decoupling of egg volume from neonate length is most likely a result of the variance in the former being determined primarily by variation in lipid stores that enhance postembryonic survival but not embryonic growth (Tessier et al. 1983).

Since this study dealt with a single clone, the observed correlations between reproduction and growth are purely environmental in nature. They therefore can contribute little to the ongoing debate about the evolutionary cost of reproduction (Tuomi et al. 1983, Reznick 1985, Service and Rose 1985, Bell 1986, Bell and Koufopanou 1986, Reznick et al. 1986), since there is no necessary correspondence between environmental and genetic correlations. It is of interest, however, that there were no obvious changes in the covariance structure (Fig. 11) with a reduction in the food supply. This provides further support for the idea that the physiological mechanism that governs reproductive investment is essentially independent of the food level.

Since patterns of mortality in the laboratory may only remotely resemble those of natural populations, less emphasis has been placed on the response of the survivorship curve to resource depression than on other life history features. The response of the growth curve to food limitation may be of special relevance here, since much of the mortality of *Daphnia* in natural environments is caused by size-selective predators (Lynch 1980a). Because the reproductive investment function of this clone is independent of the food level, any reduction in food level will necessarily result in smaller size at all ages. Thus, for example, while well-fed individuals are capable of growing to large enough sizes to avoid predation from large invertebrate predators such as *Chaoborus*, this is less likely at extremely low food levels. Size-dependent mortality is readily incorporated into models such as the one presented above (Lynch 1980b, Dorazio and Lehman 1983). Unfortunately, reliable data on size-specific mortality rates are difficult to obtain for cladocerans (Lynch 1983) and are almost completely lacking.

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