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TO GROW OR NOT TO GROW: OPTIMAL RESOURCE ALLOCATION FOR *DAPHNIA*

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Abstract.—We constructed a discrete-time model for growth and reproduction of the cladoceran *Daphnia* and solved it numerically for resource allocation patterns to maximize the intrinsic rate of increase r under various environmental conditions. Conditions modeled include different functional forms for the size dependencies of predation risk and net production. Growth after maturity can maximize r when net production and survival rate increase with body size. The optimal period for growth after maturity increases with the reproductive life span, but the life span need not be long to favor growth. The shape of the net production curve influences the extent to which body size is increased by delaying maturity or by growing after maturity. When net production increases with body size but survival rate does not, growth after maturity is not optimal. However, simultaneous allocation to growth and reproduction can occur in the instar (time step) preceding maturity.

Many organisms, including various crustaceans, fish, reptiles, amphibians, trees, and other long-lived plants, continue to grow after attaining reproductive maturity. When an organism grows as an adult, the investment in growth detracts from the immediate investment in reproduction. Whether growth ultimately enhances an organism's reproductive output or fitness depends on the effects of body size on the abilities of the organism (and its offspring) to survive, acquire resources, and reproduce. With information about demography and energetics, the life history can be modeled as a problem in optimizing the allocation of resources to reproduction (see, e.g., Schaffer 1983). By specifying a mechanism for trade-off between activities affecting different components of fitness, such as survival rate and reproduction, we can determine a basis for predicting not only directions but also magnitudes of expected differences in life histories under various selective regimes.

Despite the wide occurrence of growth after maturity among both animals and plants, analyses of many life-history models show that optimal allocation of resources is achieved if somatic growth is completed before reproduction begins: a "bang-bang" or "on-off" allocation strategy, which results in a determinate pattern of growth. This result has been obtained with models for organisms with nonoverlapping generations, such as annual plants, for which fitness is measured by the number of offspring produced (Vincent and Pulliam 1980; Iwasa and

Roughgarden 1984; Cohen 1987). Simultaneous allocation to growth and reproduction, also termed intermediate or graded allocation, is sometimes optimal when length of the growing season varies randomly (King and Roughgarden 1982).

Optimal allocation patterns become more interesting in models for organisms with overlapping generations, although the on-off strategy or its near equivalent is still often the result. For models of perennial plants that die back to storage organs between growing seasons, Pugliese (1988*a*) maximized the intrinsic rate of increase $\lambda = e^r$, and Iwasa and Cohen (1989) maximized the expected number of seeds. The energetic resource is allocated to growth and metabolism of vegetation, storage reserves, or seeds. In the optimal allocation, the number of seeds produced may increase from the first reproductive year to the second but remains constant subsequently. When reproductive success is a nonlinear function of the energetic investment in seeds, the optimal strategy may include more seasons of increasing seed production or cycles of a season of seed production that alternate with several seasons of vegetative growth (Pugliese 1988*b*).

In Charlesworth's (1980) analysis of reproductive effort, which builds on earlier work by Schaffer (1974), Charlesworth and León (1976), and others, resources may be allocated to reproduction or to maintenance and growth. The model is formulated in discrete time, and conditions are found that maximize fitness, as measured by r . Either semelparity (a single episode of reproduction) or iteroparity (repeated episodes of reproduction) is optimal, depending on the form of the relation between survival and fecundity. Complete allocation of resources to reproduction causes death due to lack of maintenance; this condition thus precludes iteroparity without intermediate allocation.

The allocation problem in the model of Sibly et al. (1985) concerns reproduction and growth. The model is formulated in continuous time, and optimal control theory is used to determine the forms of resource allocation patterns that will maximize r . Under some conditions, the intrinsic rate of increase r is maximized by an on-off allocation strategy, which results in determinate growth. An intermediate allocation strategy may be optimal, depending on the forms and parameters of functions relating the number of offspring produced to the energetic investment in reproduction and relating mortality and energy investment in growth.

Cladocerans, which are small aquatic crustaceans, present an interesting example of the general life-history problem. Although conducted on a small scale of size and short scale of time, the cladoceran life history has attributes that are common among animals, including iteroparity, growth after maturity, and overlapping generations. Cladoceran growth has intrigued aquatic ecologists (e.g., Lynch 1980) because body size and growth patterns vary substantially among taxa. Resource acquisition (reviewed by Lynch 1980) and mortality (reviewed by Zaret 1980) are often strongly size-dependent. Adult growth is greatest in the family Daphnidae, which includes common planktonic and littoral genera such as *Daphnia*, *Ceriodaphnia*, *Simocephalus*, and *Scapholeberis*. The body mass of an adult *Daphnia* may triple or quadruple after maturity (Taylor 1985). The investment in reproduction is also large: a well-fed *Daphnia* will repeatedly produce broods of eggs with mass equivalent to her own body mass (data in Taylor 1985).

From the models reviewed above, we do not obtain clear predictions about

resource allocation patterns for an animal, such as *Daphnia*, with a resource to be apportioned between growth and reproduction, overlapping generations, and size dependencies of both production and mortality. The deficiency of applicable theory reflects in part the difficulty and complexity of solutions to the optimizations (Schaffer 1983), especially when r is the appropriate measure of fitness. Analyses of cladoceran growth have worked around the problem of maximizing r by using more tractable measures of performance, such as the expected number of offspring produced (Gabriel 1982) or a simple function of production and survival rate (Lynch 1977, 1980). Unfortunately, these alternatives have limited or uncertain applicability as measures of fitness under demographic conditions that are plausible for cladoceran populations. Other studies have shown that observed growth patterns of cladocerans do not maximize r under various conditions but have not found the optima (Taylor and Gabriel 1985; Perrin et al. 1987).

In this article, we explore resource allocation patterns that maximize r for a model of growth and reproduction of the cladoceran *Daphnia*. The model is derived from laboratory data for *Daphnia pulex* (Taylor 1985). Time steps in the model correspond to instars, which are the intervals between molts. Optimal allocation strategies were obtained numerically. We consider the effects of size-selective predation, food limitation, and life span on the optimal strategy. We also analyze the sensitivity of optimal strategies to variations in allocation patterns and to the form of size-selective predation. Because r is the measure of fitness, the analyses here apply to environments in which conditions remain constant for extended periods. Our results provide insight into the demographic properties of cladoceran life histories and suggest some general conditions that may favor evolution of growth after reproductive maturity.

DAPHNIA LIFE HISTORY

Cladocerans of the genus *Daphnia* are small (0.3–5.0 mm) crustaceans that form a major component of communities in freshwater lakes and ponds. Their life histories are well studied (Hebert 1978; Lynch 1980; Threlkeld 1987a). They lead short, productive lives, with few diversions from the basic activities of feeding, growing, and reproducing. In terms of a lifetime energy budget for a well-fed *Daphnia pulex*, respiration consumes 27% of the assimilated energy, reproduction consumes 68%, and growth consumes 5% (Richman 1958); 39% of the growth occurs during the preadult stage. *Daphnia* are iteroparous and can produce 10–20 or more broods of young at intervals of 2–5 d after maturing at age 3–7 d. Their abundances are usually seasonal and often highly variable (Allan 1976; Threlkeld 1987b). Normal or subitaneous eggs are produced parthenogenetically. When conditions become adverse, resting eggs may be produced. In most populations, production of males occurs contemporaneously, and the resting eggs are fertilized (Hebert 1978).

In adult females the molt cycle and egg production are closely linked. Shortly after the animal molts, a brood of eggs is produced from material accumulated in the ovaries during the previous instar. These eggs are carried in a dorsal brood chamber formed by the carapace. Resting or ephippial eggs remain in the brood

chamber until the next molt. Then they become enclosed in a chitinous case, the ephippium, and are shed with the molt. Subitaneous eggs hatch and progress through embryonic development in the brood chamber. When released, the young are free-swimming and have the general appearance of miniature adults. The young usually mature after four or five molts. The animal usually increases in length with each molt, but growth slows as the animal becomes larger. The number of eggs in a subitaneous brood is strongly correlated with body size if food is abundant, but only two eggs are produced in an ephippial brood. Poor environmental conditions reduce growth and fecundity and delay maturity (Taylor 1985; Threlkeld 1987a; Lynch 1989).

MODELS

Our models describe growth, reproduction, and mortality of *Daphnia*. Net production is determined by body size, and the allocation of this production between growth and reproduction may be changed at each reproductive instar. A discrete-time formulation is used: production of eggs, hatching of young, and changes in length occur at time intervals corresponding to instars. The allocation of net production to growth and reproduction during one instar determines size and fecundity at the beginning of the next instar. Although mass increases continuously during the instar, this growth can be translated into changes in length only at the molt.

Functions and parameters of the models, unless noted otherwise, were estimated from experimental data for *Daphnia pulex* (Taylor 1985). The animals were cultured in a flow-through system designed by Lampert (Lampert et al. 1988) that provided constant food concentration (the green alga *Scenedesmus acutus* at 1 mg carbon/L) and temperature (20°C). Net production during each reproductive instar was calculated from the change in body mass and the mass of eggs produced at the beginning of the next instar. We converted growth and reproduction from mass to energy using factors (given below) estimated from Richman's (1958) data for *D. pulex*. Animals to be weighed were collected just after molting and egg laying so that reproductive and somatic tissues could be separated.

The model life history includes two juvenile instars J_1 and J_2 , a prereproductive instar A_0 , and n adult instars A_1, A_2, \dots, A_n . Lengths during the juvenile instars are 0.72 mm and 1.07 mm. Length during instar A_0 is 1.42 mm. The relation between length L in millimeters and dry mass W in micrograms at the beginning of any adult instar (including A_0) is

$$L = (\log W - 1)/1.2. \quad (1)$$

Duration D_A of an adult instar (including A_0) is 2.5 d; duration D_J of a juvenile instar is 1 d when food does not limit production.

Production is an asymptotic function of body size (fig. 1). For *Daphnia* of prereproductive size ($L = 1.42$ mm, $W = 15$ μ g) or greater, production (E) in joules per adult instar is

$$E(W) = F \{2.73 [1 - (0.731 + 0.0318 W)^{-1}]\}. \quad (2)$$

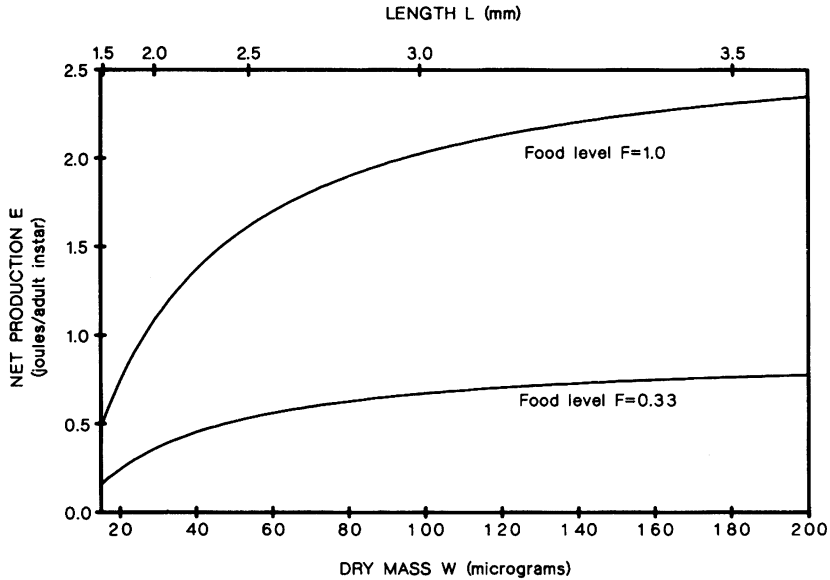


FIG. 1.—Net production E as a function of body size. $E(W)$ is given by eq. (2). Food level $F = 1$ corresponds to a phytoplankton concentration of ≈ 1 mg carbon/L; $F = 0.33 \approx 0.1$ mg carbon/L. Food level also affects duration of juvenile instars (eq. [3]). The relation between length L and mass W is given by eq. (1).

Production under food-limited conditions is described as a fraction F of the production under conditions of optimal food. Food limitation also affects juvenile growth. Duration in days of a juvenile instar decreases as the food level increases:

$$D_j = -4.5 F + 5.5. \quad (3)$$

For each adult instar k ($k = 0, 1, 2, \dots, n$), the proportion of the net production allocated to reproduction is α_{k+1} , and $(1 - \alpha_{k+1})$ is the proportion allocated to growth. The α_k are subscripted to indicate the instar in which their effects on fecundity and size are expressed. The mass of a single egg is $W_{\text{egg}} = 2.5 \mu\text{g}$. Then, at the beginning of the next adult instar, the mass of the animal in micrograms and the number of eggs m_{k+1} in its brood are

$$W_{k+1} = W_k + (1 - \alpha_{k+1})c_{\text{som}}E_k \quad (4)$$

and

$$m_{k+1} = \alpha_{k+1}c_{\text{rep}}E_k/W_{\text{egg}}. \quad (5)$$

Because reproductive and somatic tissues differ in energetic content, the constants $c_{\text{rep}} = 40 \mu\text{g/J}$ and $c_{\text{som}} = 60 \mu\text{g/J}$ (from Richman 1958) are used to convert net production to biomass. The brood m_{k+1} is carried until age t_{k+1} d, the end of adult instar $k + 1$, when the fully developed young are released. From laboratory data, the observed resource allocation pattern is

$$\alpha_k = 1 - (1.80 k + 2.44)^{-1}. \quad (6)$$

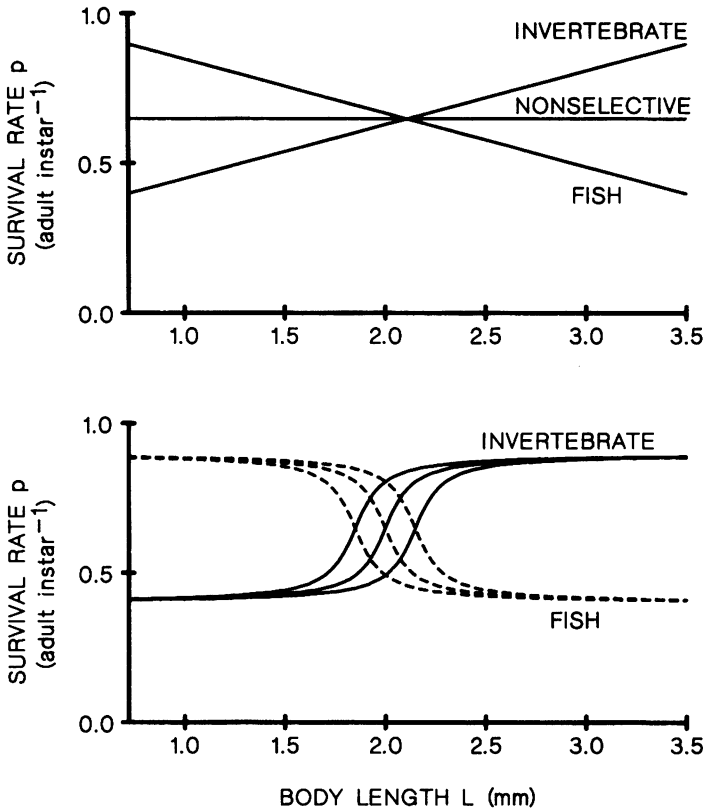


FIG. 2.—Survival rate as a function of body length L . Linear functions (upper panel; eq. [7]) are shown for the stereotypical nonselective, invertebrate, and fish predators. Arc-tangent functions (lower panel; eq. [8]) model invertebrate and fish predators with thresholds for perceiving or capturing prey. Dashed lines show the effect of shifting the midpoint L_{mid} of the predator's threshold.

Survival rate p is defined as a function of body size. An increasing or decreasing size dependency of survival rate describes the general effect of an invertebrate predator, such as larvae of the phantom midge *Chaoborus*, or a fish (Zaret 1980). We consider two forms of size-dependent survival rate (fig. 2). In the linear models, survival rate over an instar of duration D days is a function of length L in millimeters:

$$p(L) = (aL + b)^{(D/2.5)}. \quad (7)$$

Parameter values are $a = 0$, $b = 0.65$ for the nonselective predator; $a = 0.180$, $b = 0.271$ for the invertebrate; and $a = -0.180$, $b = 1.03$ for the fish. (Note that eq. [7] is linear for an adult instar, when $D = 2.5$ d.) The arc-tangent functions model the effect of a threshold in the predator's ability to detect or capture prey:

$$p(L) = \{a \arctan [b(L - L_{mid})] + c\}^{(D/2.5)}, \quad (8)$$

where L_{mid} is the midpoint of the threshold region. Parameter values are $a = 0.5/\pi$, $b = 10$ (invertebrate predator) or $b = -10$ (fish), and $c = 0.65$; L_{mid} varies. With the threshold models, survival rates for *Daphnia* shift from high to low over a narrow size range: about 75% of the change occurs with a 0.5-mm change in length.

The probability of surviving from birth to the end of prereproductive instar A_0 is

$$\ell_{A_0} = p_{J_1} p_{J_2} p_{A_0}. \quad (9)$$

The probability of surviving from birth to the end of adult instar k is

$$\ell_k = \ell_{A_0} \prod_{i=1}^k p_i. \quad (10)$$

Fitness

For an age-structured population in a constant environment, the intrinsic rate of increase r is an appropriate measure of fitness when the conditions affecting survival and reproduction remain constant for sufficiently long that the age distribution of the population becomes stable. We calculated r (t in days, r in days⁻¹) using the discrete-time formulation of the renewal equation (Keyfitz 1977):

$$1 = \sum_{k=1}^n \ell_k m_k e^{-rk}. \quad (11)$$

Optimizations and Tests of Fitness

Resource allocation was treated as a problem in constrained optimization with the number of variables n set by the number of adult instars. The optimizations were performed using the double precision version of subroutine ZXMIN, which uses a quasi-Newton method to search for the minimum of a function (IMSL Library, IMSL, Houston, Tex.). The program minimized $-r$, the negative of the measure of fitness. Values of α were constrained to the range [0, 1]. Because r becomes numerically insensitive to variations in the α values under some conditions, optimization results were checked by examining sign-determining portions of the derivatives of $\lambda = e^r$ with respect to various α_k , particularly as α_k approached one. This is equivalent to testing whether reproductive value (Goodman 1982) has been maximized at that instar (see Appendix).

Fortran programs for the models and other computations were written by the authors. Graphs were produced using RS/1 (BBN Software Products, Cambridge, Mass.).

RESULTS

The actual life history for a well-fed *Daphnia*, as described by our model, exhibits increasing but always intermediate allocation of resources to reproduction (fig. 3). The increments to length and fecundity diminish with age. Body mass increases from 15 μg at instar A_0 , when allocation to reproduction begins, to 21.7

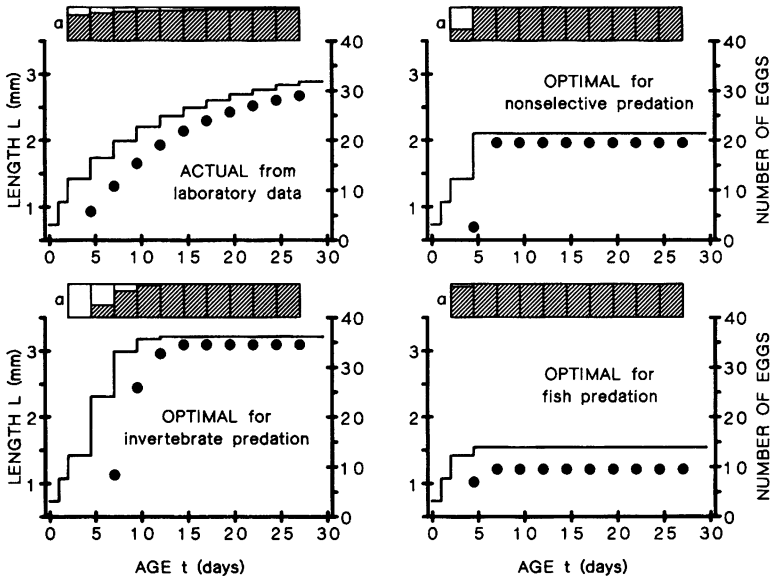


FIG. 3.—Schedules of fecundity, body size, and resource allocation for actual and optimal life histories. Optimal allocations maximize r for the nonselective model of predation and linear models of invertebrate and fish predation. Actual allocation is described by eq. (6). Length is shown by the step function; number of eggs (filled circles) is shown at time of egg laying. Proportion of net production allocated to reproduction (α) at each instar is shown by shaded portions of boxes on the strip above each panel.

μg at instar A_1 and to a final mass of $86.2 \mu\text{g}$ at instar A_{10} . If no mortality occurs until the end of the life span, the intrinsic rate of increase for this life history is $r = 0.379 \text{ d}^{-1}$.

Predation

When r is maximized, the optimal life history varies substantially with the predation model (fig. 3). None of these optimal strategies duplicates the prolonged growth that is characteristic of real *Daphnia*, but all include at least one instar of intermediate allocation. The optimal pattern under fish predation, which shows only a small allocation to growth in prereproductive instar A_0 ($0 < \alpha_1 < 1$), most closely resembles an on-off strategy. The largest size is attained in the optimal invertebrate strategy, in which prereproductive growth is extended through instar A_1 ($\alpha_1 = 0$), which thus delays reproductive maturity by one instar. Partial allocation to growth occurs in three subsequent instars.

Optimal strategies for the threshold predation models are quite sensitive to the location of the midpoint of the threshold, L_{mid} (fig. 4, upper panel). For the invertebrate models, there are one to three adult instars with intermediate allocation. Maturity may be delayed by as many as three instars ($\alpha_1 = \alpha_2 = \alpha_3 = 0$). For the fish predation models, intermediate allocation is restricted to one instar at maximum, and reproduction is never delayed. Complete allocation to reproduction in all possible instars occurs in the region where $L_{\text{mid}} = 1.2\text{--}1.6 \text{ mm}$. Length

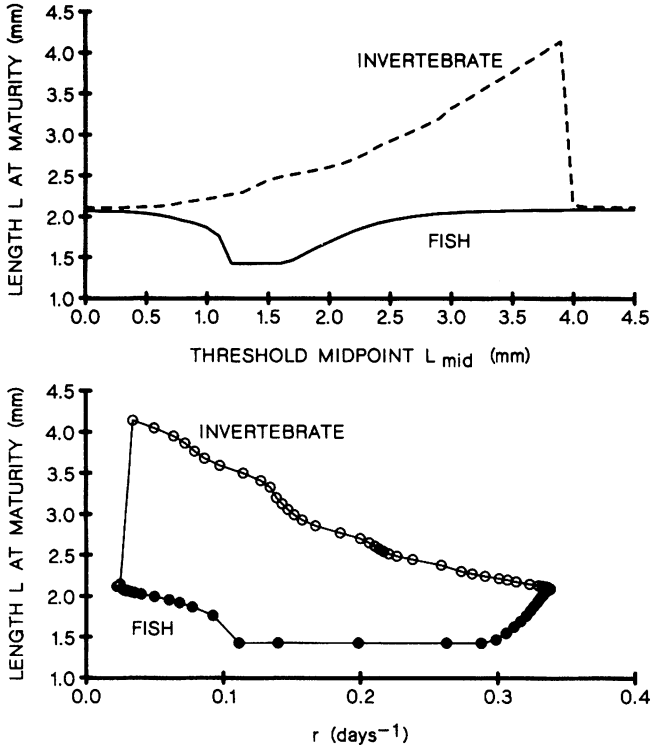


FIG. 4.—Effect of threshold in invertebrate and fish predation models on the optimal life history. *Upper panel* shows optimal length at maturity as a function of the midpoint of the threshold. *Lower panel* shows variation in length at maturity with r . Symbols show values for optimal life histories with L_{mid} ranging from 0–4.5 mm in increments of 0.1 mm.

at first reproduction decreases abruptly as L_{mid} approaches this range from below, but it increases gradually with L_{mid} above this range. For the invertebrate predation models, length at first reproduction increases until $L_{mid} = 3.9$ mm, then drops abruptly.

The abrupt drop in optimal length at maturity for the invertebrate predation model is the consequence of a shift in relative values of two local optima in r with respect to resource allocation. One local optimum occurs with maturity at instar A_1 ; the other occurs with delayed maturity. As L_{mid} increases, the delay increases. In a narrow region around $L_{mid} = 4$ mm, the optimal allocation pattern shows features of both patterns: the animal begins egg production at a small size, then resumes full growth, and finally resumes egg production at a much larger size. (The optimal allocations for $L_{mid} = 4$ mm are $\alpha_1 = 0.2825$, $\alpha_2 = 0.1225$, $\alpha_3 = 0.0000$, $\alpha_4 = 0.0000$, $\alpha_5 = 0.5856$, $\alpha_6 = \dots = \alpha_{10} = 1.0000$.)

When L_{mid} is outside the range of 1–4 mm, optimal life histories for both kinds of threshold predation models converge to the optimal life history for nonselective predation, although the optimal strategy for invertebrate predation retains an additional instar of intermediate allocation. For the fish predation model, $r \rightarrow$

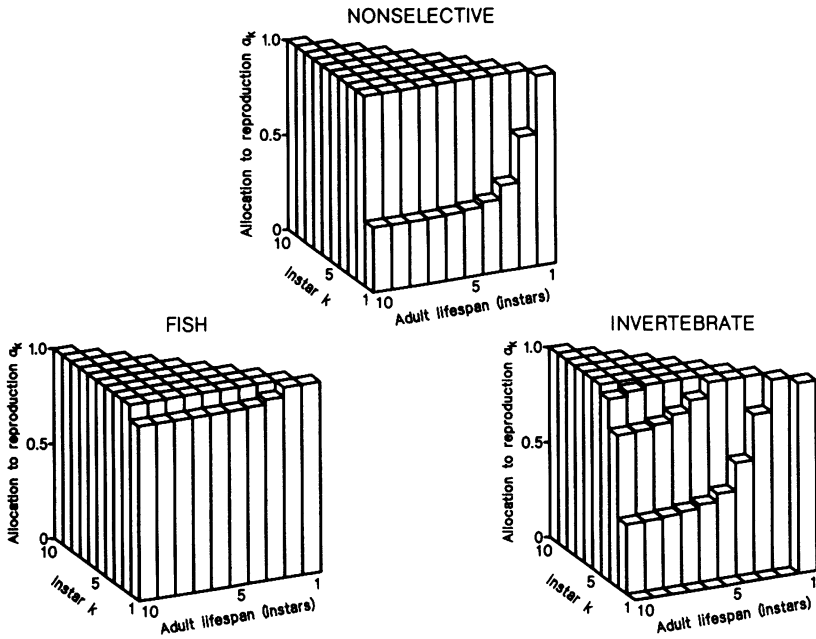


FIG. 5.—Effect of adult life span on optimal resource allocation. Optimal allocations maximize r for the nonselective model of predation and linear models of invertebrate and fish predation.

0.02 d^{-1} as L_{mid} decreases, and $r \rightarrow 0.34 \text{ d}^{-1}$ as it increases; the reverse holds for the invertebrate predation model. At either of these extremes in intensity of predation, the optimal life histories are similar (fig. 4, lower panel).

Adult Life Span

When the life span is very short, the optimal pattern is complete allocation of resources to reproduction for each of the linear predation models (fig. 5). Intermediate allocation begins when the adult life span exceeds one instar for the nonselective predation model or two instars for the other two models. If survival rate increases steeply enough with size, an optimal allocation of $\alpha_1 < 1$ is possible even when the animal can reproduce only once, because survival of the egg during its development depends on the survival of its mother.

The maximum number of instars with intermediate allocation is only one for the nonselective and fish predation models, and reproduction is not delayed. The allocation pattern changes very little when life span increases beyond four adult instars for the fish model or beyond five adult instars for the nonselective predation model. An increase in the life span from 10 to 30 adult instars also has little effect.

The optimal pattern for the invertebrate predator is more sensitive to life span. When it increases from one to two adult instars, reproduction is delayed by one instar. The number of instars with intermediate allocation increases with life span,

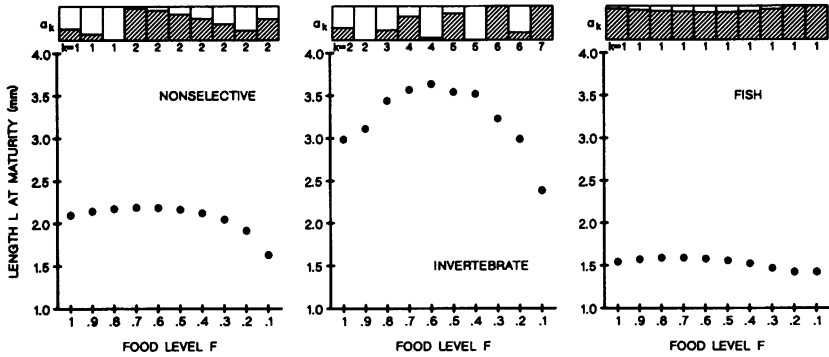


FIG. 6.—Effect of food level on the optimal life history. Plots show length at maturity as a function of food level for the three linear predation models. The earliest adult instar i for which $\alpha_i > 0$ is shown by the shaded portion of the box above the graph; the number of the instar is below the box.

beginning with one instar of intermediate allocation when the life span is three adult instars and increasing to three instars of intermediate allocation when the life span is 10 adult instars. When life span is extended to 30 adult instars, reproduction is delayed by one instar, and there are seven instars of intermediate allocation, although the maximum size attained is only 0.05 mm longer than that attained in the optimal 10-instar strategy.

Food Limitation

The optimal size at maturity is highest with moderate food limitation for all three linear predation models (fig. 6). In the optimal allocation strategy for invertebrate predation, intermediate allocation occurs for as many as three instars under invertebrate predation when the food level is $F < 0.7$ but for only one instar or none when the food level is lower. Under nonselective and invertebrate predation, the optimal strategy includes at most one instar of intermediate allocation. Production of the first brood is postponed from the second to the seventh adult instar as the food level drops from 1.0 to 0.1 under invertebrate predation and from the first to the second adult instar under nonselective predation. There is no delay with decreasing food level under fish predation.

Sensitivity of r to Allocation Pattern and Predation

We tested sensitivity of r to allocation patterns with both optimal and arbitrarily constructed life histories. According to the general results (fig. 7), variations in α have greater effects in earlier instars. Each optimal allocation pattern was tested with the predation model for which it was optimized (fig. 8). The optimal patterns for the size-selective predators are more sensitive than those for the nonselective predator. For all three life histories, little variation in r occurs with variation in α after the fourth adult instar, and the time required to produce a significant reduction in population size, relative to a population growing with the optimal life history, becomes very long (>15 yr for a 50% reduction).

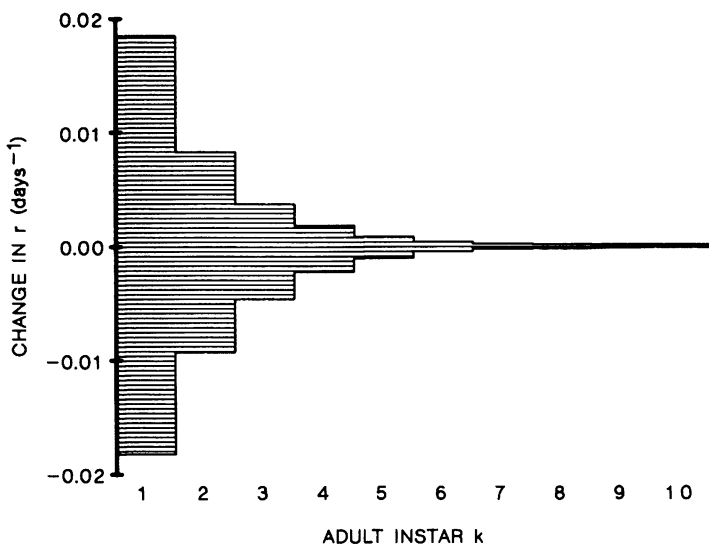


FIG. 7.—General sensitivity of r to variation in α . Range of variation in r is shown for deviations of ± 0.1 in α_i . Fecundity schedules were calculated using $\alpha_i = C$ for adult instars $i = 1, 2, \dots, 10$ with $C = 0.7, 0.8,$ or 0.9 . Variation in r with variation in α_i was calculated using each of the three linear predation models separately to determine survival rate.

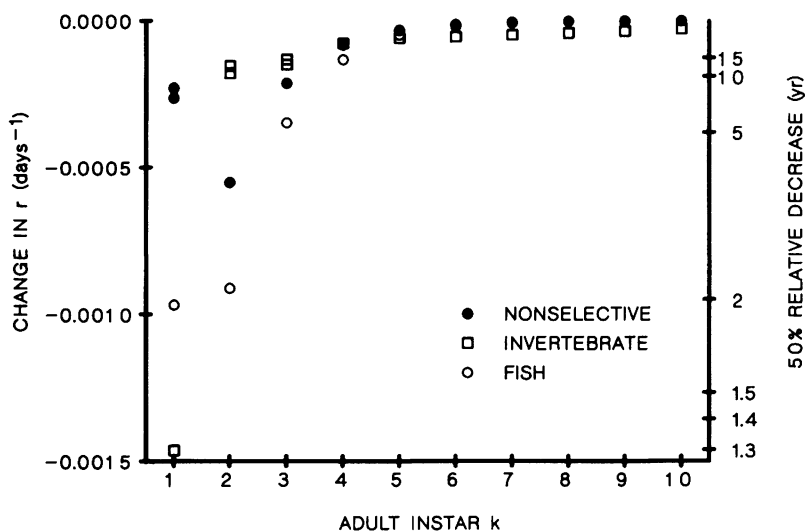


FIG. 8.—Sensitivity of r for optimal life histories to variation in α . Results are shown for deviations of ± 0.1 in α_i . The second Y-axis shows the decrease in r translated into the time required to observe a 50% reduction in population size for a population growing with the perturbed life history, relative to a population growing with the optimal life history. (This projection assumes initial populations of equal size at stable age distribution.)

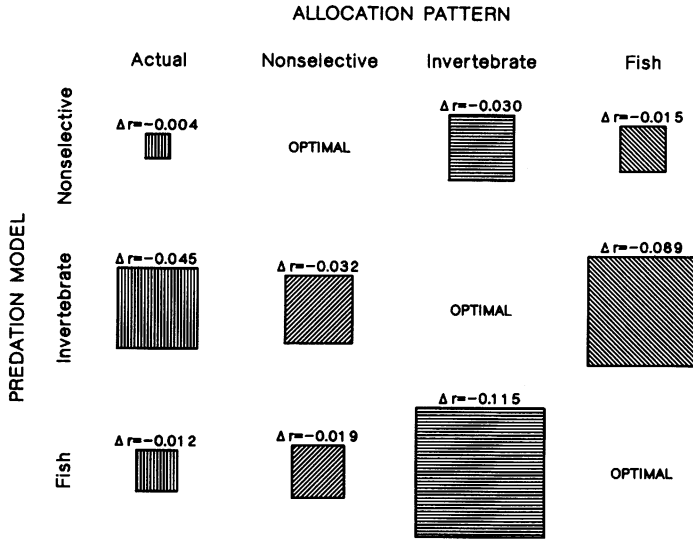


FIG. 9.—Test of actual and optimal resource allocation patterns with different predation models in a constant environment. Deviations from the optimal r for each predation model are shown in analogue format: area of square is proportional to deviation from r .

We calculated fitnesses of four life histories (actual, optimal for nonselective predation, optimal for invertebrate predation, and optimal for fish predation; fig. 3) for *Daphnia* exposed to predation according to each of the three linear predation models (fig. 2, upper panel). In a constant environment where r is the appropriate measure of fitness, the worst combination is the optimal invertebrate life history with the fish predation model (fig. 9). The optimal fish life history fares nearly as badly with the invertebrate predation model. Neither the optimal nonselective nor the natural life history is worst in any case.

DISCUSSION

The optimal *Daphnia*, according to our models, will usually grow after it begins to allocate resources to reproduction. Allocations to growth and reproduction are thus not usually separated temporally, unlike the predicted strategies for organisms such as annual plants. In our models, simultaneous allocation to growth and reproduction is limited to the instar preceding maturity if mortality is nonselective or increases with body size (fish predation). Even in the latter case, *Daphnia* grows slightly after beginning to allocate resources to reproduction, because the advantage in productivity compensates for the disadvantage in mortality. For the optimal *Daphnia*, growth may extend through several instars if mortality decreases with body size (invertebrate predation).

The single instar of intermediate allocation has a precedent in the optimization literature: Pugliese's (1988a) perennial plant model shows seemingly analogous behavior. Mortality is constant with age and size for the plant. In the optimal

strategy, seed production and the maximum size of the vegetative part may increase from the first reproductive year to the second but are constant for subsequent years; the reserve at the end of the growing season is constant for all reproductive years. The optimal allocation is simpler for *Daphnia* because body mass is retained from one reproductive period to the next, not re-created from stored resources. However, after a certain body size is achieved, no further growth occurs, and, as for the plant among years, reproductive output is constant for all instars after the first reproductive instar.

Intermediate allocation in the optimal strategy for *Daphnia* may be a consequence, in part, of the discrete structure of the model, which imposes time delays between the allocation of resources and their effects on fecundity and survival rate. Our model for *Daphnia* under nonselective predation is analogous to the continuous-time model of Sibly et al. (1985) in the case where the trade-offs between fecundity and growth and between mortality and growth are both linear. The trade-off between nonselective predation and growth can be graphed as a horizontal straight line. Their graphical analysis for the continuous-time model shows that the optimal allocation is always on-off when the trade-offs are linear, in contrast to our discrete-time model, which yields examples of intermediate allocation.

The conditions favoring multiple instars of intermediate allocation and thus growth after maturity are unclear. Our results suggest that survival rate, as well as productivity, must increase with body size for growth after maturity to maximize r , although a steep slope for either function should favor continued growth and delayed reproduction (see Appendix). However, for a perennial plant with a constant annual survival rate, Pugliese (1988*b*) found that nonlinearity in the relation between reproductive success and investment in seeds could favor a pattern analogous to growth after maturity in *Daphnia*. This pattern (initiation of seed production in a year preceding the year that maximum vegetative size is first attained) is optimal only if the relation between reproductive success and investment in seeds shows concave downward nonlinearity, so that the benefit from additional investment decreases as the amount of investment increases.

Our results on optimal adult size are broadly consistent with the variety of models that predict that delayed maturity occurs if survival rate or fecundity increases with size (see, e.g., Stearns and Crandall 1981; Kozłowski and Wiegert 1987). However, our results demonstrate potential difficulties in making testable predictions about the life history if only general characteristics of the predator's preferences are known. Simply knowing whether an agent of mortality more strongly affects larger or smaller organisms will not suffice. Although the optimal strategy for an invertebrate predation model never exhibits earlier maturity or smaller size at maturity than the optimal strategy for the corresponding fish predation model (figs. 3, 4), the response of the optimal life history to predation may be negligible if most of the change in mortality with size is outside some critical range (fig. 4). Constraints may also strongly influence the response of the optimal life history, as demonstrated in our models by the limit that the minimum size at maturity imposes on response of optimal size at maturity to a changing threshold for fish predation (fig. 4).

The evolutionary response of the model life history to a predator is not necessarily correlated with the demographic response of the population. Relations between intensity of predation, measured by its effect on r , and traits of the optimal life history, such as size at maturity, in figure 4 are not simple or even monotonic. The extreme ranges of L_{mid} (low values for the fish model, high values for the invertebrate model) that produce the greatest effects on population growth are also the ranges where the life history is least affected. Furthermore, the lack of correlation between responses of life history and population implies discordance between responses of the life history and the community. If a predator that prefers large prey is introduced into a community of cladocerans of various sizes, a simple prediction is that the larger species will be reduced in importance relative to the smaller species. This prediction has been supported empirically (see Zaret 1980). Whatever the effect of the predator on the population or the community, if the range of body sizes for the largest species lies entirely within the size range at maximum risk of predation, the model predicts that size at maturity will not change.

A corollary effect, which is often unrecognized, concerns changing the intensity of predation. If intensity of predation is altered uniformly across age or size classes, there is no effect on the optimal life history. This lack of effect can be demonstrated easily by considering the expression for $d\lambda/d\alpha_k$ in the Appendix. When the survival rate coefficients p_i are multiplied by a constant C , the rate of increase for the altered survival rate schedule is $C\lambda$, if λ and the p_i are expressed in the same units of time. The constants cancel in the expression for the sign-determining portion of $d\lambda/d\alpha_k$, and the optimum is thus unchanged. More generally, whether the population is increasing or decreasing has no specific influence on the optimal life history, if intrinsic rate of increase is the measure of fitness.

Food limitation generates an apparent paradox: animals grow more in size to gain less in productive capacity. This effect occurs with mild to moderate food limitation for all three predation models. The gain in net production per unit growth at any body size is smaller at lower food levels, according to our model of net production. But the contribution to future reproduction is discounted by powers of r (see Appendix), which diminishes with the extended juvenile stage and reduced fecundity. Thus, the greater investment in growth is favored. However, with severe food limitation and flatter net production functions, growth is reduced. In general, but depending on the other parameters that determine reproductive value and on the shapes of the production and survival rate functions, resources at a given instar will be allocated entirely to growth if the slope of the production function is steep, to both growth and reproduction if the slope is moderate, or entirely to reproduction if the slope is shallow.

According to Lynch (1980), small cladoceran species show greater adult growth than large ones. He explained the growth patterns as strategies to attain optimal foraging size in the face of fish predation for the small species or invertebrate predation for the large species. Results from our models suggest that reversing these strategies would be more likely to maximize r , because growth after maturity does not occur with fish predation but with invertebrate predation under a variety of conditions. Although Lynch proposed that optimal body size at matu-

ity should maximize the product of net production and instar-specific survival, optimal sizes to begin reproduction or cease growth are not simple functions of net production and survival rate. The timing of reproduction strongly influences fitness, and postponing reproduction to grow larger can be demographically expensive. For example, in the optimal life history for nonselective predation (fig. 3), the rate of change in net production E with body mass W is still strongly positive when growth stops: at instar A_0 , $dE/dW = 0.059 \text{ J}/\mu\text{g}$; at the final mass, $dE/dW = 0.027 \text{ J}/\mu\text{g}$. Perrin et al. (1987) also demonstrate with a model for *Simocephalus*, a large daphnid cladoceran, that fitness is enhanced by stopping growth at sizes much smaller than those predicted by Lynch's model.

None of the strategies to maximize r produces growth during the entire adult life. In this respect, the optimal strategies are unlike growth patterns of real *Daphnia*. Optimal life histories for invertebrate predation show the richest variation and include the examples that most closely approximate natural, indeterminate growth. It is tempting to speculate from this similarity that cladoceran life histories evolved under invertebrate predation. Alternatively, the observed intermediate allocation patterns may be favored by environmental variation or other conditions that we did not test. Growth patterns do have large effects on fitness in the models (fig. 9), and we would thus predict that growth patterns will respond to selection. For any predation model, however, r becomes insensitive to small variations in resource allocation after the first few reproductive instars (figs. 7, 8). A morphological or other constraint that forced continued growth would not be demographically expensive, so long as the actual growth pattern approximated the optimal pattern during the first few reproductive instars. Thus, if the prolonged growth of real *Daphnia* is not optimal, it may not be significantly suboptimal.

For a cladoceran or its analogue, in an environment that remains stable for some length of time, conditions that should favor evolution of growth following reproductive maturity are abundant food resources, so that productive capacity increases with body size (but not too steeply) and a lower risk of mortality for larger animals. Growth after maturity does not maximize fitness if risk of mortality does not decrease with increasing body size. Although growth is continuous for plants and most animals, except arthropods, reproduction at intervals is common, so results from discrete-time models (not necessarily of the exact form as our *Daphnia* model) should have wide applicability.

For cladocerans, however, the environment is typically quite unstable. Physical conditions in lakes and ponds follow seasonal cycles, and abundances of food and predators fluctuate. Because it assumes stable conditions, the intrinsic rate of increase r becomes a poorer predictor of performance as the duration of those conditions decreases. In an environment with limited season for growth and reproduction, r is a reliable predictor of relative success of a *Daphnia* life history only if the mean season length is greater than 30–40 d (B. E. Taylor and W. Gabriel, unpublished results with the models presented here; fitness was measured by the geometrical mean number of resting eggs).

Several sets of results suggest that more complex growth patterns may be favored in limited or variable environments. In models for annual plants, the

introduction of variance in the length of the growing season can produce optimal intermediate allocation for models that otherwise give only on-off allocation patterns (King and Roughgarden 1982). In apparent contradiction to the general results for annual plants and to our results here, the maximization of the total number of eggs produced by an individual *Daphnia* yielded indeterminate growth when risk of predation increased with size (Gabriel 1982; continuous growth, production described by Bertalanffy function). When the mean value of r (geometrical mean value of λ) is used to measure fitness, alternation of predation schedules can also favor extended adult growth in *Daphnia* (Gabriel and Taylor, in press; model essentially identical to that described here).

Little is yet known about the effect of magnitude or temporal scale of environmental variation on resource allocation. Exploring models for optimal resource allocation in variable environments and discovering whether they yield general, testable predictions about growth will be an interesting task.

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APPENDIX

The renewal equation G defines $\lambda = e^r$ as an implicit function of the resource allocation parameters α_k for adult instars $k = 1, 2, \dots, n$.

$$G = \sum_{k=1}^n \ell_k m_k \lambda^{-k} = 1, \quad (\text{A1})$$

where $\ell_k = \ell_{A_0} p_1 p_2 \dots p_k$, $p_k = p_k(\alpha_1, \alpha_2, \dots, \alpha_k)$, and $m_k = m_k(\alpha_1, \alpha_2, \dots, \alpha_k)$. Derivatives of λ with respect to α are obtained by differentiating G .

$$dG = \frac{\delta G}{\delta \alpha_1} d\alpha_1 + \frac{\delta G}{\delta \alpha_2} d\alpha_2 + \dots + \frac{\delta G}{\delta \alpha_n} d\alpha_n + \frac{\delta G}{\delta \lambda} d\lambda.$$

Then,

$$\frac{d\lambda}{d\alpha_k} = - \frac{\delta G / \delta \alpha_k}{\delta G / \delta \lambda}.$$

Because the denominator is always negative, the sign of $d\lambda/d\alpha_k$ is determined by the sign of the numerator, $\delta G/\delta \alpha_k$.

As an example, we derive the expression for $\delta G/\delta \alpha_k$ when $k = n - i$ and growth does not occur after instar k . In this case, $\alpha_{k+1} = \alpha_{k+2} = \dots = \alpha_n = 1$, $p_k = p_{k+1} = \dots =$

p_n , and $m_{k+1} = m_{k+2} = \dots = m_n$. Note that $m_{k+1} \neq m_k$ if $\alpha_k < 1$. Equation (A1) can be rewritten as

$$G = \sum_{j=1}^{k-1} \ell_j m_j \lambda^{-t_j} + \ell_{k-1} \lambda^{-t_k} [p_k m_k + m_{k+1} (p_k^2 \lambda^{t_k - t_{k+1}} + p_k^3 \lambda^{t_k - t_{k+2}} + \dots + p_k^{i+1} \lambda^{t_k - t_{k+i}})].$$

Multiplying the expression inside brackets by $\lambda^{t_{k-1} - t_k}$ converts it to the reproductive value for an animal of age t_{k-1} at the beginning of instar k . Then,

$$\frac{\delta G}{\delta \alpha_k} = \ell_{k-1} \lambda^{-t_k} \left\{ p_k \frac{\delta m_k}{\delta \alpha_k} + (p_k^2 \lambda^{t_k - t_{k+1}} + p_k^3 \lambda^{t_k - t_{k+2}} + \dots + p_k^{i+1} \lambda^{t_k - t_{k+i}}) \frac{\delta m_{k+1}}{\delta \alpha_k} + [m_k + m_{k+1} (2p_k \lambda^{t_k - t_{k+1}} + 3p_k^2 \lambda^{t_k - t_{k+2}} + \dots + (i+1) p_k^i \lambda^{t_k - t_{k+i}})] \frac{\delta p_k}{\delta \alpha_k} \right\}.$$

The partial derivatives of m_k , m_{k+1} , and p_k depend on the forms of the net production function $E(W)$, the length-weight function $L(W)$, and the survival rate function $p(L)$ (e.g., eqq. [1], [2], and [6] or [7]).

Because λ and ℓ are always positive, the sign of the partial derivative $\delta G/\delta \alpha_k$, and thus of $d\lambda/d\alpha_k$, is determined by the portion inside the outermost brackets. For the *Daphnia* model, the first term inside the brackets is positive, because current fecundity m_k always increases with the current allocation to reproduction α_k . The second term is negative because future fecundity m_{k+1} is reduced by increasing the current allocation to reproduction and thus decreasing the current allocation to growth. The third term is negative for invertebrate predation, positive for fish predation, and zero for nonselective predation.

When $d\lambda/d\alpha_k$ is positive for all α_k in the range $[0, 1]$, $\alpha_k = 1$ is the optimal allocation; when $d\lambda/d\alpha_k$ is negative for all α_k in the range $[0, 1]$, $\alpha_k = 0$ is the optimal allocation. An intermediate allocation $0 < \alpha_k < 1$ is optimal if $d\lambda/d\alpha_k = 0$ and gives a local maximum of λ , which occurs when $d^2\lambda/d\alpha_k^2 < 0$. Otherwise, an allocation of $\alpha_k = 1$ or $\alpha_k = 0$ is optimal.

Some models yield only on-off patterns in the optimal allocation. If $d^2\lambda/d\alpha_k^2$ is always positive, then optimal intermediate allocation is not possible, because the extremum is a local minimum. For example, $d^2\lambda/d\alpha_k^2$ is always positive when the production function is a quadratic function ($E = aW^2 + b$, $a > 0$) and mortality is nonselective. Thus, the optimal allocation is always $\alpha_k = 1$ or $\alpha_k = 0$, whether or not $d\lambda/d\alpha_k = 0$ for $0 < \alpha_k < 1$. A linear production function ($E = aW + b$) and nonselective mortality provide a similar result. Here, $d\lambda/d\alpha_k$ is constant. Intermediate allocation is possible only in the unlikely case that $d\lambda/d\alpha_k = 0$, when any value of α_k would give the same value of λ .

LITERATURE CITED

- Allan, J. D. 1976. Life history patterns in zooplankton. *American Naturalist* 110:165-180.
- Cohen, Y. 1987. Optimal reproductive strategies in annual plants. *Lecture Notes in Biomathematics* 73:19-37.
- Charlesworth, B. 1980. *Evolution in age-structured populations*. Cambridge University Press, Cambridge.
- Charlesworth, B., and J. A. León. 1976. The relation of reproductive effort to age. *American Naturalist* 110:449-459.
- Gabriel, W. 1982. Modelling reproductive strategies of *Daphnia*. *Archiv für Hydrobiologie* 95:69-80.
- Gabriel, W., and B. E. Taylor. In press. Optimal resource allocation in cladocerans. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen*.
- Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *American Naturalist* 119:803-823.

- Hebert, P. D. N. 1978. The population biology of *Daphnia* (Crustacea, Daphnidae). *Biological Reviews of the Cambridge Philosophical Society* 53:387–426.
- Iwasa, Y., and D. Cohen. 1989. Optimal growth schedule of a perennial plant. *American Naturalist* 133:480–505.
- Iwasa, Y., and J. Roughgarden. 1984. Shoot/root balance of plants: optimal growth of a system with many vegetative organs. *Theoretical Population Biology* 25:78–105.
- Keyfitz, N. 1977. *Introduction to the mathematics of population* (with revisions). Addison-Wesley, Reading, Mass.
- King, D., and J. Roughgarden. 1982. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theoretical Population Biology* 22:1–16.
- Kozlowski, J., and R. G. Wiegert. 1987. Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology* 1:231–244.
- Lampert, W., R.-D. Schmitt, and P. Muck. 1988. Vertical migration of freshwater zooplankton: test of some hypotheses predicting a metabolic advantage. *Bulletin of Marine Science* 43:620–640.
- Lynch, M. 1977. Fitness and optimal body size in zooplankton populations. *Ecology* 58:763–774.
- . 1980. The evolution of cladoceran life histories. *Quarterly Review of Biology* 55:23–42.
- . 1989. The life history consequences of resource depression in *Daphnia pulex*. *Ecology* 70:246–256.
- Perrin, N., M. Ruedi, and H. Saiah. 1987. Why is the cladoceran *Simocephalus vetulus* (Müller) not a “bang-bang strategist”? a critique of the optimal-body-size model. *Functional Ecology* 1:223–228.
- Pugliese, A. 1988a. Optimal resource allocation in perennial plants: a continuous-time model. *Theoretical Population Biology* 34:215–247.
- . 1988b. Optimal life history models: effects of nonlinearities in the response of reproductive success to investment. Pages 223–235 in L. M. Ricciardi, ed. *Biomathematics and related computational problems*. Kluwer, Dordrecht.
- Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecological Monographs* 28:273–291.
- Schaffer, W. M. 1983. The application of optimal control theory to the general life history problem. *American Naturalist* 121:418–431.
- . 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303.
- Sibly, R., P. Calow, and N. Nichols. 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* 112:553–574.
- Stearns, S. C., and R. E. Crandall. 1981. Quantitative predictions of delayed maturity. *Evolution* 35:455–463.
- Taylor, B. E. 1985. Effects of food limitation on growth and reproduction of *Daphnia*. *Archiv für Hydrobiologie Beihefte* 21:285–296.
- Taylor, B. E., and W. Gabriel. 1985. Reproductive strategies of two similar *Daphnia* species. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 22: 3047–3050.
- Threlkeld, S. T. 1987a. *Daphnia* life history strategies and resource allocation patterns. *Memorie dell’Istituto Italiano di Idrobiologia Dott. Marco de Marchi* 45:353–366.
- . 1987b. *Daphnia* population fluctuations: patterns and mechanisms. *Memorie dell’Istituto Italiano di Idrobiologia Dott. Marco de Marchi* 45:367–388.
- Vincent, T. L., and H. R. Pulliam. 1980. Evolution of life history strategies for an asexual annual plant model. *Theoretical Population Biology* 17:215–231.
- Zaret, T. M. 1980. *Predation and freshwater communities*. Yale University Press, New Haven, Conn.