



Fitness and Optimal Body Size in Zooplankton Population

Michael Lynch

Ecology, Vol. 58, No. 4. (Jul., 1977), pp. 763-774.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197707%2958%3A4%3C763%3AFAOBSI%3E2.0.CO%3B2-K>

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.

FITNESS AND OPTIMAL BODY SIZE IN ZOOPLANKTON POPULATIONS^{1,2}

MICHAEL LYNCH³

Department of Ecology and Behavioral Biology and Limnological Research Center,
University of Minnesota, Minneapolis, Minnesota 55455 USA

Abstract. A measure of fitness which is an explicit function of feeding efficiency and vulnerability to predation is introduced. Feeding efficiency is a function of feeding and respiration rates and the nature of the food supply. Defining fitness as a function of body size reveals several potential explanations for the evolution of life-histories and for mechanisms of competition in zooplankton populations. Utilizing available data for *Daphnia pulex* and evaluating fitness for several temperatures, food-size distributions, and predatory regimes gives results which are very consistent with what is known of the ecology and demography of this species. A large variability in fitness is shown to exist between size classes, very small and very large individuals being particularly prone to food limitation. Thus, for a specified environment, there is an optimal body size at which an organism maximizes its contribution to the persistence of the population in terms of survival and/or reproduction. I suggest that natural selection should lead to maximum reproductive effort at this size at the expense of growth, and present several examples which support this idea. As alternatives to the size-efficiency hypothesis, I suggest several mechanisms whereby small species may outcompete or coexist with larger ones.

Key words: Body size; competition; *Daphnia pulex*; feeding efficiency; fitness; life-history strategy; size-efficiency; zooplankton.

The primary forces molding zooplankton community structure have been supposed to follow the concepts of size-selective predation and size-efficiency proposed by Brooks and Dodson (1965). They argue that although large zooplankton species are more vulnerable to visual predators, they are the superior competitors when predation is not intense. They attribute the competitive superiority of the large herbivores to their greater effectiveness of food collection and to a reduced metabolic demand per unit mass (the size-efficiency hypothesis).

Selective feeding on large zooplankton by vertebrate planktivores is a very well-documented phenomenon (Dodson 1970; Galbraith 1967; Brooks 1968; Wells 1970; Werner and Hall 1974). Recent work on invertebrate predators (cyclopoids, midges) suggests that they also feed size-selectively, but specializing instead on small zooplankton (Dodson 1970; Fedorenko 1975). Zaret (1975) and Dodson (1974) assemble a great deal of support indicting predation as the primary selective factor responsible for the morphological characteristics of zooplankton species. Emphasis on the importance of selective predation has become so strong that Dodson (1974, Dodson et al. 1976) suggests that the predatory regime alone can account for zooplankton community structure.

Competition has not been generally accepted as important in structuring zooplankton communities. In fact, little information exists to account for the dynamics of zooplankton communities in response to

their food supply. However, the experimental evidence which does exist is less than supportive of the size-efficiency hypothesis. Dodson (1974) reports that *Daphnia middendorffiana* is unable to exclude the smaller *Daphnia minnehaha* when enclosed in a Rocky Mountain pond for 1 mo. In laboratory microcosms, *Ceriodaphnia quadrangula* is able to exclude the much larger *Daphnia magna* by outcompeting the latter's offspring for food (Neill 1975a). Field experiments I have done (M. Lynch, *personal observation*) demonstrate that the outcome of competition between enclosed populations of *Daphnia pulex* and the smaller *Ceriodaphnia reticulata* varies temporally, *Daphnia* often being excluded by *Ceriodaphnia*. Nonetheless, theoretical treatments continue to suggest that competitive ability should generally be size-related (Hall et al. 1976; Wilson 1975).

Considering the many assumptions of the size-efficiency hypothesis, it is not surprising that it is not supported by experimental evidence. (1) A shortcoming of the hypothesis and of competition theory in general is the failure to consider age structure of the interacting populations. The size-efficiency hypothesis maintains that the important competitive interactions occur between adults. (2) The hypothesis assumes that all zooplankton species have similar energetics, and feeding mechanics, i.e., that metabolic requirement and feeding rate are the same function of body size for all species. It does not recognize adaptations to temperature or other environmental circumstances as being important in mediating the outcome of competition. (3) Resource partitioning and interspecific differences in assimilatory capabilities are assumed to be negligible. (4) The large suspended particles available only to large species are assumed to convey some nutritional advantage to these species. (5) Finally, as

¹ Manuscript received 10 July 1975; accepted 24 February 1977.

² Contribution No. 144 from the Limnological Research Center.

³ Present address: Dept. of Ecology, Ethology and Evolution, Morrill Hall, University of Illinois, Urbana, Ill. 61801.

stated, the size-efficiency hypothesis places no restriction on the upper limit to body size in the absence of vertebrate predators.

Below I pose a specific example to illustrate how the fitness of a zooplankton population may vary with its environment. The graphical analysis I present centers on *Daphnia pulex* simply because the information necessary for developing a model is available. This species is a relatively large cladoceran (up to 3.5 mm in length) which is a common inhabitant of ponds and some lakes (Brooks 1957; Brandlova et al. 1972). I use a technique which estimates fitness as a function of body size, and predicts an optimal size given the predatory regime, the food-size distribution, and the temperature. This technique is quite simple, and does a very adequate job in describing the distribution and demography of *Daphnia pulex*.

The precise outcome of this analysis is not intended to be of general applicability to other zooplankton species. However, it provides several interesting insights into the characteristics of a particular species, variations of which may be extended to other types.

This approach leads to an understanding of competitive interactions independent of the assumptions of the size-efficiency hypothesis, and suggests several reasons why large individuals may be particularly prone to food limitation. Relying on the outcome of this analysis and the results of several recent studies, I suggest several mechanisms whereby small species may outcompete or coexist with larger ones.

Most work done to evaluate factors determining zooplankton distribution has been on a relatively local scale or within a specific lake. No general theory exists to explain large-scale, geographical distributions of species. The form of analysis I present provides a framework for approaching these problems.

The concept of fitness and optimal body size

Dobzhansky (1968) points out the very serious problems in measuring fitness of populations. Reproduction is a necessary but not sufficient condition for perpetuation of the population. The fate of a population may be most dependent upon its ability to survive under temporary conditions during which reproduction is impossible. The few survivors may be genetically more important to the population than those genotypes which develop rapidly under more favorable conditions. Nevertheless, while survival is a necessary condition for reproduction, an individual may spend its entire life in a nonreproductive state if sufficient food conditions are never met.

For these reasons, I employ a measure of fitness which defines the relative amount of energy an individual will be expected to harvest and contribute to the future population in terms of growth or reproduction. Each individual will have one fitness component associated with feeding efficiency (F) and another as-

sociated with vulnerability to predation (P , an inverse function of vulnerability). Feeding efficiency is a relative estimate of an individual's harvest of energy in excess of that required for basal metabolism. When a surplus of energy is acquired, it can be utilized for growth and/or reproduction. Since F and P may be different functions of body size, their product is used as an estimate of fitness (W):

$$W(x) = F(x) \cdot P(x) \quad (1)$$

where x = carapace length. Thus, an individual with a high feeding efficiency (and perhaps large clutch size) will nonetheless be of low fitness if it is highly vulnerable to predation.

The optimal body size for an individual is the size at which W attains its maximum. In the absence of predation, the optimal body size would be the optimal foraging size (i.e., the size at which F attains its maximum).

Below I utilize this approach to describe various *Daphnia pulex* populations. I first derive a measure of feeding efficiency (F) based on food-size distribution and concentration, and temperature, and solve it as a function of body size. I then pose 3 possible functions for P . Combining F and P as in equation 1 gives a series of curves describing fitness as a function of body size.

Feeding efficiency

As defined here, fitness associated with feeding efficiency (F) is a dimensionless parameter equal to the feeding rate (energy ingested/animal/time) divided by the basal metabolic rate (energy expended/animal/time). It is a function of food-size distribution and concentration, energy extractable from the various food items, and the temperature-dependent rates for filtering and respiration:

$$F(x, t, c) = \frac{\text{feeding rate } (x, t, c)}{\text{respiration rate } (x, t)} \quad (2)$$

$$= \frac{f(x, t, c) \int_{z=0}^{z_{\max}(x)} a(z) dz}{R(x, t)}$$

where F = feeding efficiency

x = carapace length

t = temperature

c = food concentration

$f(x, t, c)$ = filtering rate

$z_{\max}(x)$ = diameter of maximum sized particle ingested

$a(z)$ = caloric concentration of food particles of diameter z

$R(x, t)$ = respiration rate.

Schoener (1969, 1971) reviews the literature and finds that active metabolism is generally a multiple of basal metabolism. For this reason, I define F in terms of proportional excess rather than absolute surplus of energy intake. Thus, F values for different body-sizes

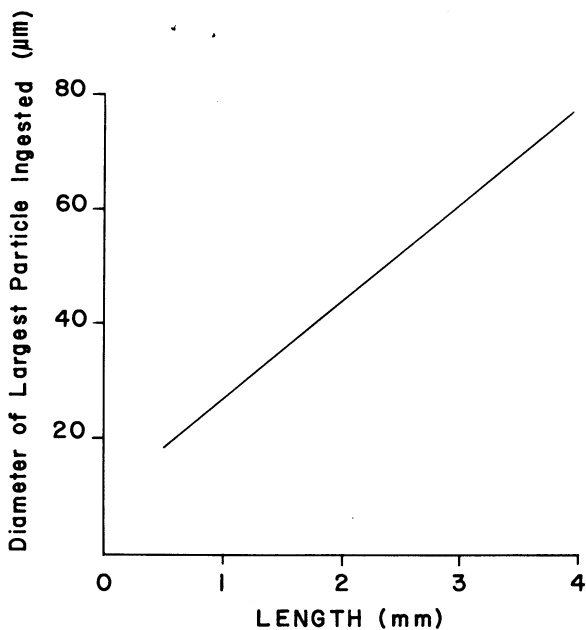


FIG. 1. The relationship between cladoceran carapace length and the diameter of the largest particle ingested (from Burns 1968).

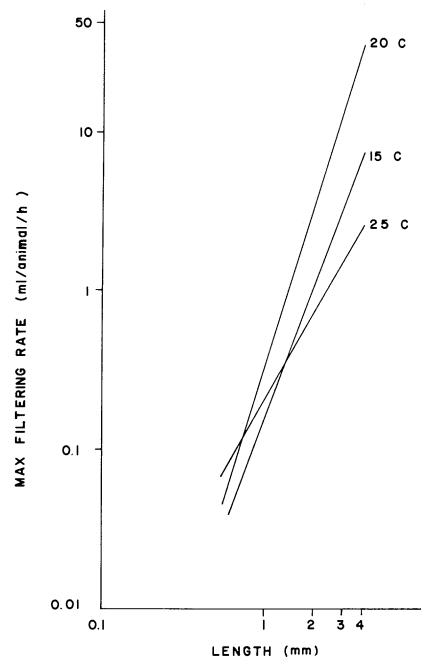


FIG. 2. The relationship between carapace length and maximum filtering rate for *Daphnia pulex* (from Burns 1969).

will remain unchanged relative to each other regardless of metabolic state.

Figure 1 (based on Burns' 1968 data) shows that the maximum particle size ingested by cladocerans ($z_{\max}[x]$) increases linearly with carapace length. Since Gellis and Clarke (1935) report removal of colloidal-sized particles by *D. magna* (the largest daphnid), I assume that all particles below an upper size limit are available and filtered randomly. The implications of selective feeding will be discussed later.

Maximum filtering rates for *D. pulex* acclimated to 15, 20, and 25°C for a range of body sizes are available in Burns (1969). In Fig. 2 regression lines are logarithmically fitted to her data and extended to a length of 3.5 mm. Each regression is highly significant ($P < .01$). Rigler (1961) first demonstrated for *Daphnia magna* that filtering rate is dependent on food concentration. Below an incipient limiting concentration filtering rate is maximal and feeding rate is a linear function of food concentration. McMahon (1965) finds that the incipient limiting concentration is independent of temperature, and that smaller daphnids diverge from their maximal filtering rate at lower food concentrations than do larger ones. Since the feeding efficiency curves should be most applicable when food concentrations are low, these circumstances should not affect the interpretation of the model. At food levels above the incipient limiting concentration, a more precise feeding efficiency could be determined directly using the feeding rates.

In order to measure fitness associated with consumptive activities, feeding rates must be standardized

with respiration rates. Richman (1958) provides measurements of respiration of *D. pulex* starved for 24 h prior to manipulation. His values for nongravid females at 20°C are fitted ($P < .01$) and extended to a carapace length of 3.5 mm in Fig. 3. Richman's data are probably close to basal metabolism, and their incorporation into the model is reasonable since they will partially account for adaptations to low food conditions. Q_{10} values can be estimated from Tonolli's (1947) measurements of *D. pulex* heartbeat rates, and are available for heartbeat rate and longevity in *D. magna* (MacArthur and Baillie 1929), and length of generation cycle (beginning of first instar to end of first adult instar) for *D. pulex* (Brown 1929). As an approximation to these values I have chosen to use $Q_{10} = 1.5$ to fit respiration values to 25°C, and 2.5 to estimate those at 15°C (Fig. 3).

In order to simplify terms, respiration and food ingested are computed on an energy basis. To convert respiration values to their energy equivalents, $1 \mu\text{l O}_2$ is taken to be equivalent to 0.021 joules (Richman 1958). For lack of more precise information, energy content of a specific food item is taken to be a simple function of particle mass. A reasonable approximation of energy values reported for several algal species is 23.01 J/mg dry wt (Ketchum and Redfield 1949; Richman 1958; Ryther 1959; Schindler 1968). Algal cell weights are estimated in Schindler (1968) for *Chlorella* (0.12×10^{-6} mg dry wt/cell) and in Richman (1958) for *Chlamydomonas* (0.25×10^{-6} mg dry wt/cell). Since much limnetic particulate matter is larger than these small algae, I have used 0.5×10^{-6} mg dry

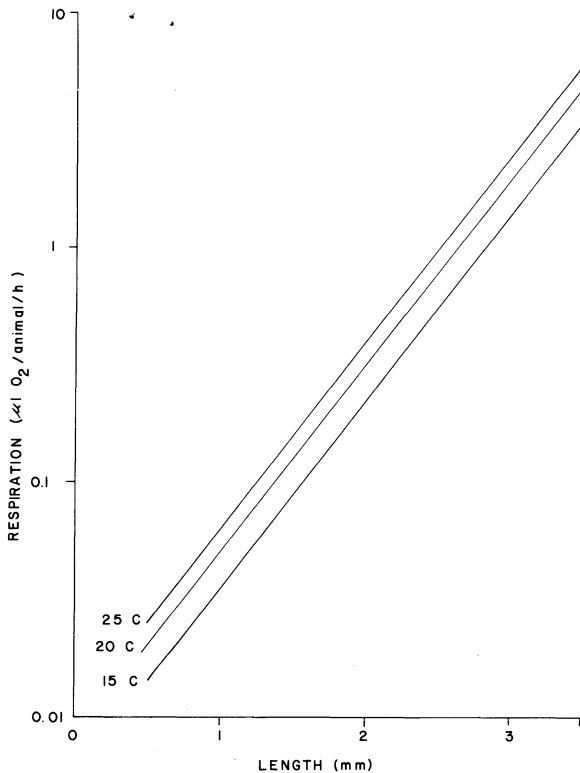


FIG. 3. Respiration rate vs. carapace length for *Daphnia pulex*. Values for 20°C from Richman (1958); values fitted to 25°C using $Q_{10} = 1.5$, to 15°C using $Q_{10} = 2.5$.

wt/cell as an estimate of average planktonic cell mass. Using the above data, a food concentration of 1×10^4 cells/ml, which is well below the incipient limiting concentration for *D. pulex* (Burns and Rigler 1967; McMahon 1965; Rigler 1961), is equivalent to .1151 J/ml. This value will be used as a measure of the total available food supply, independent of the size distribution.

Taking 3.5 mm as the hypothetical maximum length of an individual daphnid, the food available to a *D. pulex* population will include particles with diameters $< 65 \mu\text{m}$ (from Fig. 1). To demonstrate the close relationship between optimal body size, fitness, and food supply, I have incorporated 3 food-size distributions into the model (Fig. 4). Thus, feeding rates for a given size are calculated from the filtering rates (Fig. 2), the available food-size range (Fig. 1), and the biomass within that range (Fig. 4) based on:

$$\text{Feeding rate } (x, t, c) = f(x, t, c) \int_{z=0}^{z_{\max}(x)} a(z) dz. \quad (3)$$

F values are estimated by dividing the size-specific feeding rates by the respiration values.

The relationships of assimilation efficiency to food quantity and quality, temperature, and body size are not clear. Assuming a constant 100% assimilation efficiency results in deviations from actual feeding eff-

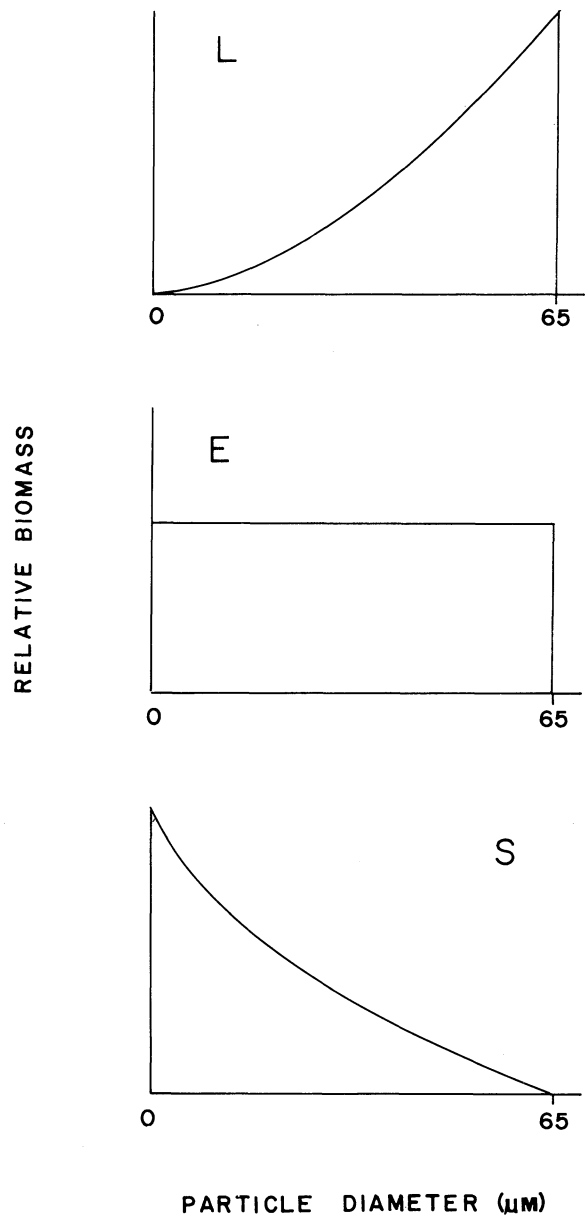


FIG. 4. Different size distributions of food available to *D. pulex* populations used in the model. Total food biomass is the same in each case. L—biomass concentrated in large particles, E—biomass equal for all particle sizes, S—biomass concentrated in small particles.

ficiencies but does not alter the interpretation of the model.

The dependence of feeding efficiency on body length, food-size distribution, and temperature is shown in Fig. 5. For specific food and thermal conditions, there is an optimal size for extracting energy from the environment. For *Daphnia pulex* respiration rate increases with body size more rapidly than does feeding rate. Thus, feeding efficiency increases with size to a certain point and then begins to decline (i.e.,

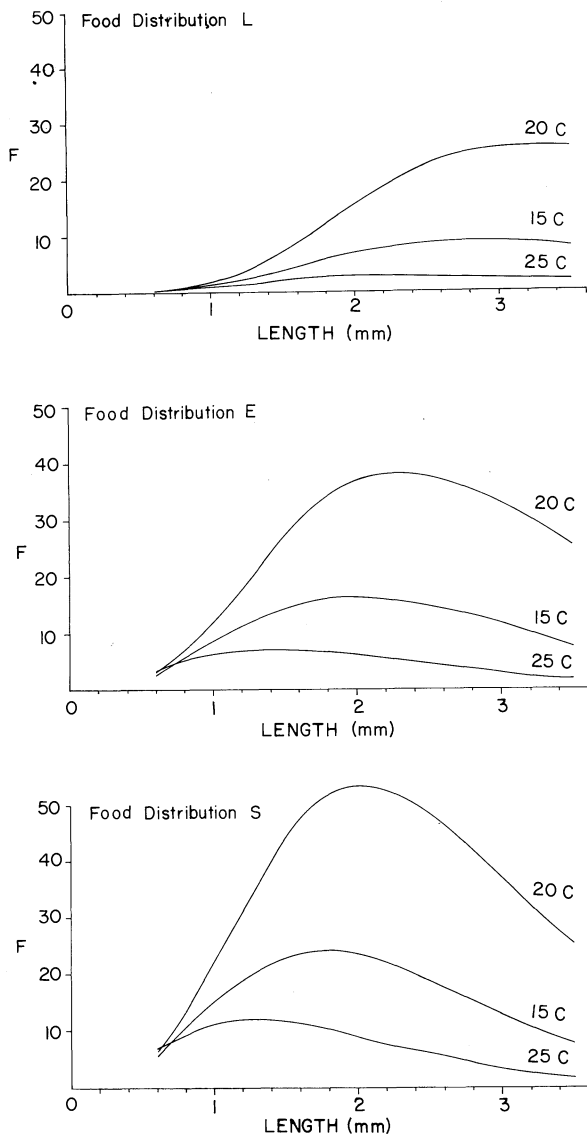


FIG. 5. Fitness associated with feeding efficiency (feeding rate/basal metabolic rate) for *Daphnia pulex* vs. carapace length as a function of food-size distribution and temperature (relative importance of small food particles increasing from top to bottom).

the largest individuals are not necessarily the most efficient feeders). As the food supply becomes enriched with smaller food particles, feeding efficiency increases for small and intermediate-sized animals, and optimal foraging size decreases. Feeding efficiency of large individuals is relatively insensitive to changes in the food-size distribution since a greater proportion of the food-size range is available. A change in food abundance simply has the effect of moving the feeding efficiency curves vertically. High filtering rates produce maximum feeding efficiency at 20°C, but at 25°C filtering rates decrease and respiration rates increase to produce a much lower feeding efficiency. Optimal

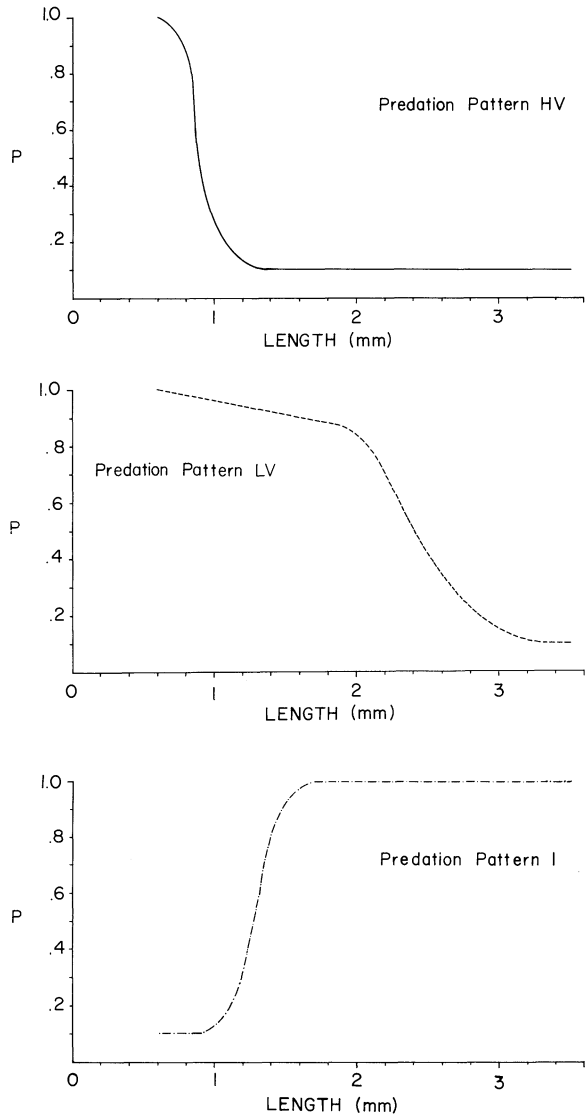


FIG. 6. Fitness associated with vulnerability to predators (P) for *Daphnia pulex* vs. carapace length; HV—vertebrate predator interest high relative to prey availability, LV—vertebrate predator interest low relative to prey availability, I—invertebrate predation.

foraging size is always smallest at 25°C and largest at 20°C.

Vulnerability to predation

In the absence of predation, the feeding efficiency curve should adequately describe relative fitness for a size range of individuals. In most cases, however, cladocerans will be subject to some form of predation.

The correlation of zooplankton body size with vulnerability to fish predation has been demonstrated in the field (Galbraith 1967; Wells 1970) as well as in laboratory experiments (Ivlev 1961; Brooks 1968; Werner and Hall 1974). Werner and Hall (1974) also

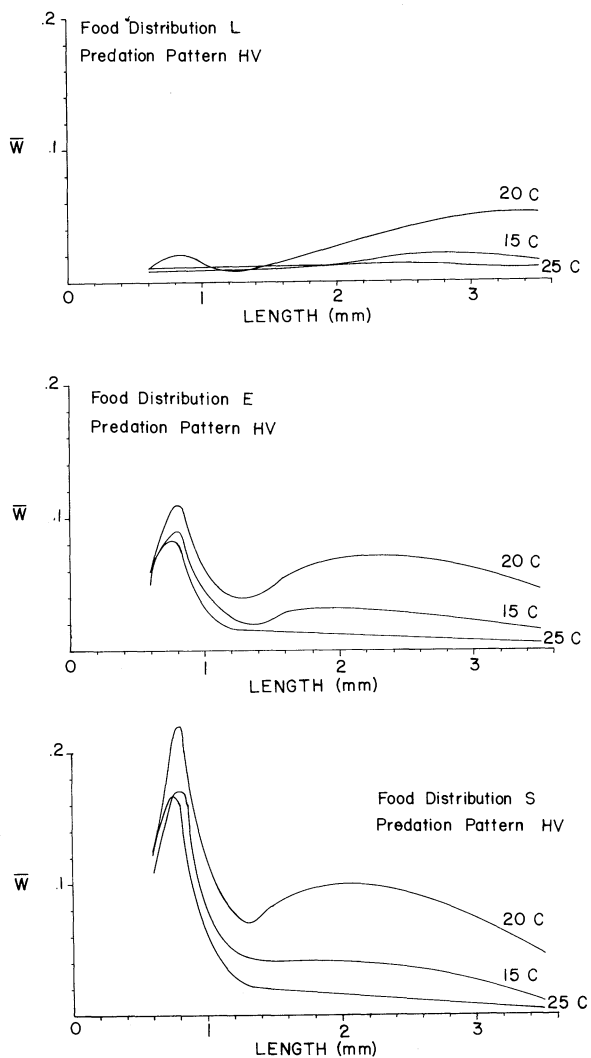


FIG. 7. Relative fitness ($W = F \cdot P$) vs. carapace length when vertebrate predation is high relative to prey availability (relative importance of small food particles increasing from top to bottom).

find that smaller size classes of prey are sequentially dropped from the diet as prey abundance increases. Diet breadth increases at lower temperatures because fish search more slowly, decreasing their rates of encounter. A decrease in light or an increase in turbidity should also increase diet breadth by decreasing searching effectiveness. Experiments by Ware (1972) and Werner (1974) show in addition that the intensity of predation increases with hunger as a result of a decrease in handling time.

To demonstrate the influence of predation upon cladoceran fitness in a variety of communities, I have constructed three possible curves for fitness associated with predators (Fig. 6). The first two curves are based on data of Galbraith (1967) and Werner and Hall (1974) and describe vulnerability to predation when vertebrate predators are dominant. Curve HV

illustrates vulnerability when vertebrate interest is high relative to prey density. Although different-sized fish specialize on different-sized prey (Wong and Ward 1972), large predators generally feed more on larger prey. For this example I have taken P to be a decreasing function of body size, with maximum vulnerability (minimum P) above a body length of 1.3 mm.

Curve LV represents a case of very high prey availability. Fitness associated with predators begins to drop sharply at a length of 2.0 mm and decreases to a minimum at 3.5 mm. Prey <2.0 mm are available to the predator, but are dropped from the diet when larger items are very abundant. This threshold value may vary depending upon the availability of the prey. Such a curve might also be expected when an alternate preferred prey is present.

Although vertebrate predation is a common cause of cladoceran mortality in many situations, invertebrate predation has also been implicated as a major mortality source in several bodies of water (Wright 1965; Dodson 1972). Individuals above a certain size will be relatively immune to predation when invertebrates are the primary predators. Dodson (1970, 1974) notes that the phantom midge (*Chaoborus*) specializes on zooplankters between 0.7 and 1.5 mm in length. He also finds that when offered *D. pulex*, the predaceous copepod *Diaptomus shoshone* selectively takes individuals between 0.5 and 1.0 mm. Curve I in Fig. 6 represents a case where invertebrate predators are dominant. Individuals <0.9 mm long are most vulnerable to invertebrate predation, with P increasing to a maximum for those >1.7 mm.

Fitness curves for *Daphnia pulex*

The product of the fitness components for feeding efficiency (F converted to a scale of 0 to 1) and vulnerability to predation (P) provides a measure of W for *Daphnia pulex* in Figs. 7–9. When vertebrate predation is intense (Fig. 7) there is a tendency for the fitness curves to be bimodal. This results because the smallest individuals with low feeding efficiencies are able to avoid predation, while the larger individuals which are heavily predated have higher feeding efficiencies. Fitness for all individuals is very low (note the lower scale in Fig. 7), and optimal body size is very small except when the food supply is biased towards large particles; then there may be an advantage to being large despite extreme vulnerability to predators.

As vertebrate predation becomes less intense (Fig. 8), fitness and optimal body size increase. Optimal size varies with the food-size distribution, but it is most dependent upon temperature.

When invertebrates are the main source of predation (Fig. 9) the fitness curves are broadly domed in the upper size range. Fitness values for adults are high, but those for small animals are extremely low. In this case food-size distribution is a very important determinant of optimal size. When small food particles are

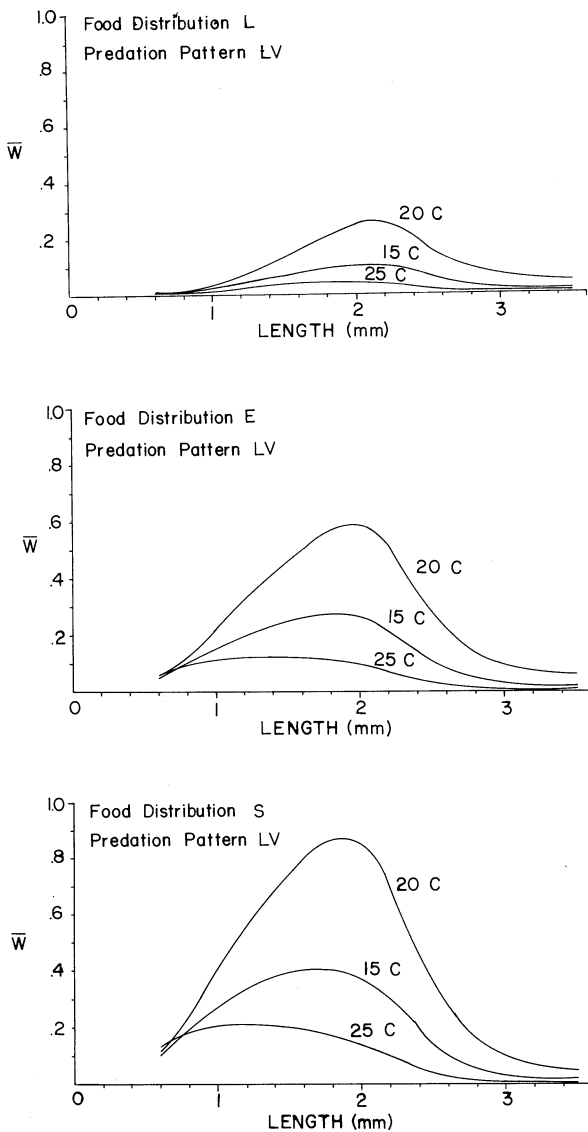


FIG. 8. Relative fitness ($\bar{W} = F \cdot P$) vs. carapace length when vertebrate predation is low relative to prey availability (relative importance of small food particles increasing from top to bottom).

relatively scarce it is advantageous to be very large. However, when small particles become more common, optimal body size decreases by ≈ 1 mm. This suggests that when vertebrate predators are rare food-size distribution may be a very important selective factor.

Several simplifying assumptions have been made in order to facilitate construction of the fitness curves. However, deviations from most of these tend to reinforce the interpretations of the model. Several factors further emphasize the decline in feeding efficiency at the smallest and largest sizes. (1) Although the model predicts that an increase in frequency of large food particles will favor large body size, these particles include the inedible forms such as gelatinous green algae

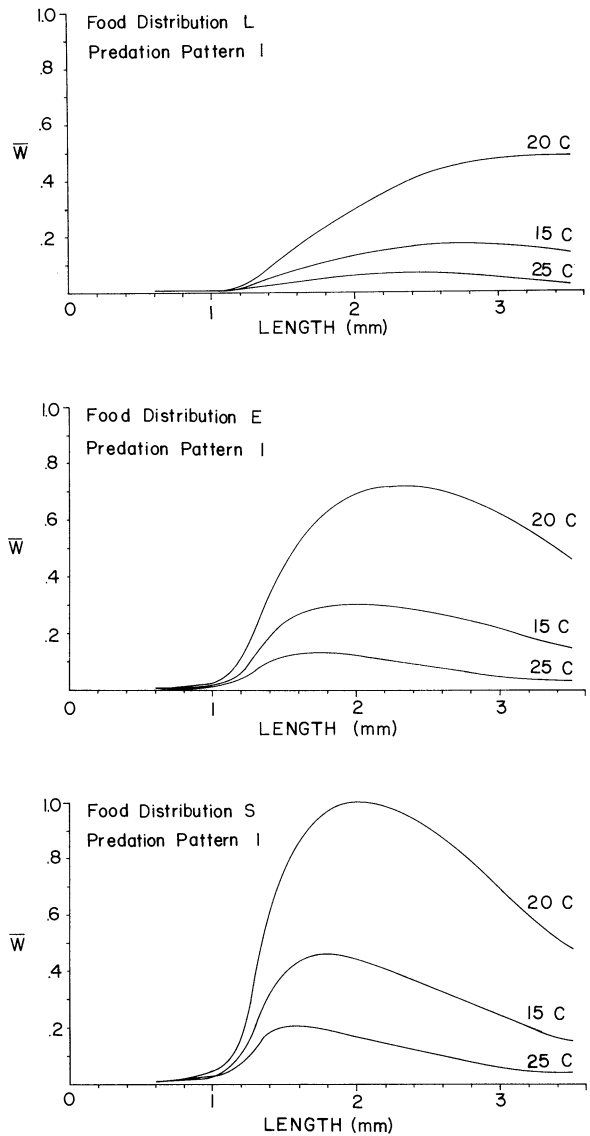


FIG. 9. Relative fitness ($\bar{W} = F \cdot P$) vs. carapace length in the face of pure invertebrate predation (relative importance of small food particles increasing from top to bottom).

(Porter 1973), forms that are poorly assimilated (Arnold 1971), or forms with hard, protective outer walls (i.e., dinoflagellates and desmids). (2) If larger animals are less efficient at filtering small particles, as Neill (1975a, b) suggests, the F values for large animals are further overestimated. (3) Richman (1958) reports higher assimilation efficiencies for adult *Daphnia pulex* than for preadults. If this is so, the F values for small animals are overestimated more than those for larger individuals because I have assumed 100% assimilation efficiency for all animals.

If Q_{10} for respiration increases with body size as the literature suggests (Edwards and Irving 1943a,b; Rao and Bullock 1954; Conover 1960), the feeding efficiency curve for 25°C will be tilted down and to the

right, giving larger animals lower F values. At 15°C, the effect will be reversed, giving larger animals slightly higher F values than indicated.

In deriving the fitness values I have assumed predator avoidance to be independent of temperature. If predation rates do increase with temperature, the fitness of *D. pulex* at 25°C should be even lower relative to that at 15 and 20°C.

Finally, the model assumes random filtering. Sufficient information does not exist to generalize on the relation of selective feeding to body size, although it could conceivably affect the feeding efficiencies. Selection for certain-sized food particles will not necessarily increase fitness if the feeding rate on alternate-sized particles is reduced. Berman and Richman (1974) note that when *D. pulex* selects for a certain size-range of particles it reduces its filtering rate on all other sized particles. Nonetheless, selective feeding might convey an advantage to an individual if the preferred particles have a higher energetic value per unit biomass than the neglected particles.

Before proceeding to elaborate on the implications of such fitness functions for other species, I summarize data available for *Daphnia pulex* to demonstrate that these curves present a reasonable description of the nature of this species. I will not attempt to further rationalize the particular P curves I have employed, since their precise shape will vary widely in nature. I have simply chosen an arbitrary 3 which have the effect of decreasing the fitness of large individuals as the intensity of vertebrate predation increases relative to that of invertebrates.

The general form of the feeding efficiency curves will be more directly dependent on the biology of the species and should vary less between lakes. Therefore, the validity of their predictions may be tested by examining field and laboratory studies on *Daphnia pulex*.

The feeding efficiency curves (Fig. 5) suggest that for most conditions there is an optimal foraging size, with smaller and larger animals being more sensitive to food limitation. Consistent with this is the decrease in maximum body size with a lowered food supply noted in a laboratory population of *Daphnia pulex* (Richman 1958). Since this same result is obtained with other cladocerans (Hall 1964; Weglenska 1971), similar-shaped functions may exist for other species. The sensitivity of juvenile survivorship to low food levels has been demonstrated for several cladocerans in laboratory microcosms (Neill 1975a). Information on this aspect is equivocal for laboratory populations of *Daphnia pulex* (Anderson et al. 1937; LeSeur 1960; Richman 1958) probably because of the variety of foods and temperature utilized. Unfortunately, suitable data do not exist to test whether size-strategies vary with food-size distribution, but field investigations are in progress to collect the information needed.

By migrating to an energetically advantageous tem-

perature, an organism may increase its feeding efficiency, and ultimately its reproductive rate (McLaren 1963, 1974). The feeding efficiency curves for *Daphnia pulex* predict that as water temperature increases above 20°C, fitness and optimal body size rapidly decline. Hall (1964) reports that in Base Line Lake *D. pulex* reaches peak abundance in surface waters in the spring (15–20°C), and then retreats to the thermocline as summer epilimnetic temperatures rise to 25°C. Similarly, Bell and Ward (1970) note that in West Blue Lake, Manitoba, *D. pulex* remains in the cool deeper waters as summer epilimnetic temperatures rise to 22°C. In environments where high summer temperatures cannot be avoided (i.e., eutrophic lakes with anaerobic hypolimnia, or shallow unstratified waters), the fitness curves for *Daphnia pulex* predict that optimal body size will be small and fitness low. Relatively low reproductive output would be expected in such environments, and *D. pulex* would be particularly sensitive to an unsuitable food supply or moderate levels of predation. These predictions are supported by studies on populations of *D. pulex* in several shallow Minnesota ponds (M. Lynch, *personal observation*). Thus, the feeding efficiency curves indicate a metabolism for *Daphnia pulex* which is consistent with its distributional pattern.

Finally, several laboratory studies of the fecundity patterns in *Daphnia pulex* are in accord with the optimal body sizes predicted in Fig. 5. LeSeur (1960) finds that clutch size is maximized between 2.0 and 2.5 mm when *D. pulex* is fed *Ankistrodesmus* at 15°C. A population raised on *Chlamydomonas* at 20°C has a maximum clutch size at 2.4 mm (Richman 1958). Using a manure-soil media as a food at 15–20°C, Anderson et al. (1937) find that clutch size peaks at 2.4 mm and then declines. These maxima in clutch size are in rough accord with the peaks in the feeding efficiency curves (Fig. 5). Reductions in fecundity at the larger sizes further supports the existence of diminishing fitness in the largest individuals.

I now proceed to a more general treatment of size-related fitness in zooplankton populations. The remainder of my discussion rests on two assumptions: (1) significant differences in fitness may exist between size classes in zooplankton populations, and (2) there is an optimal body size for any species in a specified environment.

DISCUSSION

The optimal life-history strategy of an organism is to allocate its resources to maintenance, growth, and reproduction so as to maximize its contribution to the persistence of the population. Schaffer (1974) proposes that an optimal life-history should maximize for each age the sum of the expected fecundity of that age plus all future expected fecundities (each discounted by an appropriate power of λ). For any age class, it becomes advantageous to devote a large share of re-

TABLE 1. Life history characteristics of *Ceriodaphnia cornuta* morphs from Gatun Lake, Panama Canal Zone determined in the laboratory in the absence of predators (modified from Zaret 1972a). The culture medium was enriched in 1969. Unhorned morphs predominate in offshore waters where fish predation is low; horned morphs are more common in near-shore waters where the zooplanktivorous *Melaniris* are concentrated. (Numbers in parentheses are sample sizes)

Life history parameter	1968		1969	
	Uhorned	Horned	Uhorned	Horned
Days to maturity	5.7 (9)	9.4 (5)	4.9 (12)	6.4 (9)
Average lifespan (days)	16.0 (7)	14.0 (2)	18.1 (9)	11.2 (9)
Reproductive period (days)	11.3	4.6	13.2	4.8
Fecundity (eggs/lifespan)	9.1 (7)	4.3 (3)	28.1 (10)	11.1 (9)
Reproductive effort (fecundity/reproductive period) (eggs/day)	.81	.93	2.13	2.31

sources to growth and survival when future reproductive output is sufficiently enhanced. Increasing reproductive effort at any age will augment fecundity at that age, but only at the expense of future growth. Thus, while cladocerans continue to grow throughout their life, the rate of growth declines with the onset of reproduction (Anderson et al. 1937; Green 1956; Richman 1958; Hrbáček and Hrbáčková-Esslová 1960).

When fitness is examined as a function of body size, it has interesting implications for the life-history strategies of cladocerans. Although it is unlikely that fitness curves for other species will be similar in shape to those for *Daphnia pulex*, it does not seem unreasonable to assume that there is an optimal body size for any species in a specified environment. Since an individual of optimal body size will maximize its contribution to the persistence of the population (either in terms of survival or reproduction), the optimal strategy will be to remain at that size. There will be a premium for young individuals to allocate energy for growth to the optimal body size. Growth beyond that size, however, will result in a loss of fitness. Thus, once the optimal body size has been reached, reproductive effort should be maximized at the expense of future growth. The greater the slopes of the fitness curves, the greater should be the selective pressure to follow these strategies.

As previously discussed, it is particularly clear that an increase in vertebrate predation leads to a decline in optimal body size. In that case, there would be an advantage to initiating reproduction at a smaller size and to maximizing reproductive effort in subsequent

age classes. In addition to maintaining a reproducing population, this will defer growth to the larger more vulnerable sizes.

Several examples support the existence of such size-strategies. (1) There are two phenotypes of *Ceriodaphnia cornuta* in Gatun Lake, Panama Canal Zone (Zaret 1972a). Unhorned forms predominate in the open-water areas where *Melaniris* (the most significant zooplanktivorous fish in the lake) is virtually absent. In near-shore areas, *Melaniris* concentrates its feeding on unhorned forms, and the less vulnerable, horned forms are more abundant. Table 1 summarizes data from Zaret (1972a). The horned morphs produce smaller offspring (Zaret 1972b) which grow more slowly, but upon reaching maturity they maximize energy input into reproduction rather than into growth and survival. The unhorned morphs mature more rapidly, invest less energy per unit time in reproduction, and survive longer. Zaret's (1972b) discovery that the horned forms have much lower ingestion rates than their unhorned counterparts further emphasizes their greater allocation of energy intake to reproduction (assuming they have similar efficiencies). (2) In Lake Albert, East Africa, *Daphnia lumholtzi* is found in two forms (Green 1967). The *monacha* type has a longer carapace and is most abundant near the middle of the lake where zooplanktivorous fish are rare. In Ndaiga Lagoon, where the zooplanktivorous *Alestes* selectively feed on large *Daphnia*, the smaller helmeted type is more abundant. Table 2 shows that despite being much smaller, the Ndaiga forms carry more eggs. The fact that the smaller Ndaiga forms have greater ratios of brood volume to carapace length

TABLE 2. Life history parameters of *Daphnia lumholtzi*, Lake Albert (modified from Green 1967). Mean carapace length was determined from a random sample of 20 adult ♀♀; brood data are means for 30 adult ♀♀. Ndaiga forms were exposed to much greater fish predation than midlake forms

Locality	Form	\bar{x} carapace length (μm)	Eggs/♀	Egg vol ($\mu\text{m}^3 \times 10^6$)	Total brood vol ($\mu\text{m}^3 \times 10^6$)	Total brood vol/mean carapace length ($\times 10^4$)
Ndaiga	helmeted	850	3.95	2.18	8.61	1.01
Ndaiga	<i>monacha</i>	940	2.10	3.94	8.27	0.88
Midlake	<i>monacha</i>	1,270	1.60	5.64	9.02	0.71

suggests that they are allocating greater amounts of energy to reproduction. (3) Galbraith (1967) and Wells (1970) note for several daphnids a decrease in the size at first reproduction following an increase in predation. (4) Finally, Hrbáček and Hrbáčková-Esslóvá (1960) demonstrate in controlled laboratory experiments with several species of *Daphnia* that clones from ponds with high fish stock have slower growth rates than those from ponds with low fish stock.

When invertebrates are the primary cause of mortality the premium for rapid growth to larger, less vulnerable sizes should be great (i.e., small initial increments in length result in large increases in fitness). This could also be accomplished by producing larger, less vulnerable offspring. Dodson (1974) notes that in alpine ponds with few vertebrate predators, *Daphnia middendorffiana* produces fewer but larger offspring when the predatory copepod, *Diaptomus shoshone*, becomes abundant. Kerfoot (1974) describes the egg-size cycle of *Bosmina longirostris* in Frains Lake, Michigan, where the primary predators are fish in the summer and invertebrates in the winter. He noted an increase in both adult carapace length and yolk volume/egg in the winter.

The size-specific selective factors discussed in the previous sections suggest several mechanisms that preclude the universality of the size-efficiency hypothesis. Two species compete when the food-size distribution, quality, or abundance is altered by either species in such a way that the fitness of the other is reduced. Since such interactions may be modified by temperature (and very likely other physical factors), the direction and intensity of competition between two species will be subject to seasonal alterations. In a purely competitive system, the outcome will depend directly on the feeding efficiencies of the interacting species (as functions of body size, food supply, and temperature). However, such competition can be alleviated by resource partitioning on a coarse scale (i.e., temporal or spatial segregation) or on a fine scale (i.e., food particle size), or by selective predation on the superior competitor.

In a homogeneous environment, if two species are generalized with respect to food, the one with the lowest feeding efficiency (regardless of its size) will be excluded if the food supply is lowered below its critical level (the lowest food concentration at which it can maintain itself). However, when the fitness of different species varies temporally and spatially, coexistence of potential competitors may be maintained (Armstrong and McGehee 1976). As Richerson et al. (1970) point out, many lake waters are temporally and spatially heterogeneous with respect to both phytoplankton and zooplankton. Temperate lakes are all obviously subject to changing temperatures. It is also unlikely that filtering rates of any two species will be identical functions of food concentration. Should one species be a more efficient harvester at low food concentrations

and the other at high concentrations, coexistence may occur in a heterogeneous environment.

Selective removal of large particles by one species may permit coexistence of smaller species. Figure 5 shows that when the food supply is enriched with relatively small particles, feeding efficiency increases for all sizes. If very large species are less efficient at removing small food particles, then small species might coexist by feeding on their "scraps." Several recent studies show that resource partitioning may be important in zooplankton communities. In an experimental study of competition between two similar-sized species (*Daphnia parvula* and *Holopedium gibberum*), Allan (1973) shows *H. gibberum* to be the poorer competitor for mutually shared resources, but also to be less reliant on those shared resources as a result of its larger feeding niche. His results suggest that some resource partitioning may occur—*Holopedium* feeding on algal populations unimportant to the daphnid, *D. parvula*, feeding more efficiently on bacteria. In stable laboratory microcosms Neill (1975b) demonstrates extensive resource partitioning by cladocerans. Small species such as *Alonella*, *Ceriodaphnia*, and *Pseudosida* feed selectively on small cells with little separation by age-class. Adults of larger forms such as *Daphnia* and *Simocephalus* feed more selectively on larger food particles and overlap very little with the small species in resource utilization. Furthermore, the adults and young of the large species appear to partition their resources, the offspring being in more direct competition with the smaller species. Berman and Richman (1974) demonstrate the capability of *D. pulex* to graze selectively on size-classes of abundant food particles, and similar observations have been made for a marine copepod (Wilson 1973).

When the breadth of a small species' diet is a subset of that of a larger species, the size-efficiency hypothesis predicts that the larger species should competitively exclude the smaller one. This argument assumes that the important competitive interactions occur between adults or that size classes of different species do not overlap. However, Neill (1975a) shows that when the adults of a small species share the food of the offspring of a larger species, they might lower the viability of the larger species' offspring to a greater extent than their own. One laboratory study by Neill in particular strongly disputes the size-efficiency hypothesis. Despite the production of young and good adult survivorship, *Daphnia magna* was consistently excluded by several smaller species because its young failed to survive to maturity. Thus, a "competitive bottleneck" at an early stage in an organism's life history may limit the number of individuals reaching maturity regardless of the adults' ability to survive (Neill 1975a).

Finally, unlike the simplified predators upon which classical competition theory is based (MacArthur 1972), zooplankton exploit a spectrum of resources which interact with each other. In theory, this compli-

cation can lead to several interesting results (M. Lynch, *personal observation*). For instance, suppose that in the absence of any exploiters, resource A outcompetes resource B. Further suppose that exploiter X depends most on resource A as a food source, and that exploiter Y specializes on resource B. Then by lowering the abundance of resource A and relieving the competitive pressure on B, X might actually accommodate Y (i.e., the environment would be more favorable for Y when X is present even if they overlapped in resource utilization to some extent). It would appear that interactions of this sort might have particular bearing on zooplankton community structure. The necessary data to evaluate its relevance are not yet available, and it would certainly merit further study.

The mechanisms causing successional changes in zooplankton communities with eutrophication have not been well explained. Several changes which accompany enrichment of lakes may have important effects on zooplankton community structure: loss of cold-water refuges as a result of hypolimnetic anoxia, increased importance of small zooplanktivores in the fish community, and decreased transparency, which might lead to wider diet breadth for zooplanktivores. Modification of phytoplankton community structure by enrichment is well documented (Hutchinson 1967), and various hypotheses for changes in phytoplankton size distribution have been proposed (Parsons and Takahashi 1973; Hecky and Kilham 1974). Such changes might affect fitness of different zooplankton populations to the extent that dominance could shift to alternate species.

The concepts of fitness and optimal body size remain somewhat nebulous unless they can be measured in natural populations. I have suggested the product of an individual's intake of surplus energy and its ability to avoid predation as a measure of fitness. (In certain cases, it might be desirable to include other mortality factors which are independent of metabolism in the P function.) I posit that natural selection should maximize reproductive effort/energy intake in excess of metabolic requirements at the optimal body size. The feeding efficiency function may be evaluated when estimates of growth and brood volume for different sized animals of the population are available (using their sum as a relative measure of feeding efficiency). The P function will necessarily be somewhat more arbitrary, unless detailed information on predator abundances, distributions, and feeding preferences are available. Size-specific clutch size or total brood volumes cannot be used alone as fitness estimators because one must also account for the probability of surviving to release those offspring. Since they are functions of the food supply and temperature (and any other factors influencing metabolism), clutch size measurements cannot be used to evaluate the life-history strategy of a species unless simultaneous growth measurements are available.

ACKNOWLEDGMENTS

I am particularly grateful to Tom Zaret for encouragement and criticism which contributed to the content and clarity of this paper. Discussions with several friends led to various improvements of the manuscript. I thank Robert Armstrong, Robert Carlson, Stanley Dodson, George Jacobson, Joseph Shapiro, Edward Swain, Robert Taylor, Stephen Threlkeld, and the University of Minnesota Limnology Discussion Group. During the preparation of this manuscript, I was supported by a National Science Foundation grant to Joseph Shapiro.

LITERATURE CITED

- Allan, J. D. 1973. Competition and the relative abundances of two cladocerans. *Ecology* **54**:484-498.
- Anderson, B. G., H. Lumer, and L. J. Zupancic, Jr. 1937. Growth and variability in *Daphnia pulex*. *Biol. Bull.* **73**:444-463.
- Arnold, D. E. 1971. Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. *Limnol. Oceanogr.* **16**:906-920.
- Armstrong, R. A., and R. McGehee. 1976. Coexistence of species competing for shared resources. *Theor. Popul. Biol.* **9**:317-328.
- Bell, R. K., and F. J. Ward. 1970. Incorporation of organic carbon by *Daphnia pulex*. *Limnol. Oceanogr.* **15**:713-726.
- Berman, M. S., and S. Richman. 1974. The feeding behavior of *Daphnia pulex* from Lake Winnebago, Wisconsin. *Limnol. Oceanogr.* **19**:105-109.
- Brandlova, J., Z. Brandl, and C. H. Fernando. 1972. The Cladocera of Ontario with remarks on some species and distribution. *Can. J. Zool.* **50**:1373-1403.
- Brooks, J. L. 1957. The systematics of North American *Daphnia*. *Mem. Conn. Acad. Arts Sci.* **13**:1-180.
- . 1968. The effects of prey size selection by lake planktivores. *Syst. Zool.* **17**:273-291.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* **150**:28-35.
- Brown, L. A. 1929. The natural history of cladocerans in relation to temperature. II. Temperature coefficients for development. *Am. Nat.* **63**:346-352.
- Burns, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particles ingested. *Limnol. Oceanogr.* **13**:675-678.
- . 1969. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. *Limnol. Oceanogr.* **14**:693-700.
- Burns, C. W., and F. H. Rigler. 1967. Comparison of filtering rates of *Daphnia rosea* in lake water and in suspensions of yeast. *Limnol. Oceanogr.* **12**:492-502.
- Conover, R. J. 1960. The feeding behavior and respiration of some marine planktonic crustacea. *Biol. Bull.* **119**:399-415.
- Dobzhansky, T. 1968. On some fundamental concepts of Darwinian biology. *Evol. Biol.* **2**:1-34.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.* **15**:131-137.
- . 1972. Mortality in a population of *Daphnia rosea*. *Ecology* **53**:1011-1023.
- . 1974. Zooplankton competition and predation: An experimental test of the size efficiency hypothesis. *Ecology* **55**:605-613.
- . 1974. Adaptive change in plankton morphology in response to size-selective predation: A new hypothesis of cyclomorphosis. *Limnol. Oceanogr.* **19**:721-729.
- Dodson, S. I., C. Edwards, F. Wiman, and J. C. Normandin. 1976. Zooplankton: Specific distribution and food abundance. *Limnol. Oceanogr.* **21**:309-313.
- Edwards, G. A., and L. Irving. 1943a. The influence of

- temperature and season upon the oxygen consumption of the sand crab, *Emerita talpoida* Say. J. Cell. Comp. Physiol. 21:169-182.
- . 1943b. The influence of season and temperature upon the oxygen consumption of the beach flea, *Talorchestia magalophalma*. J. Cell. Comp. Physiol. 21:183-189.
- Fedorenko, A. Y. 1975. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20:250-258.
- Galbraith, M. G., Jr. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96:1-10.
- Gellis, S. S., and G. L. Clarke. 1935. Organic matter in dissolved and colloidal form as food for *Daphnia magna*. Physiol. Zool. 8:127-138.
- Green, J. 1956. Growth, size, and reproduction in *Daphnia* (Crustacea: Cladocera). Proc. Zool. Soc. Lond. 126:173-204.
- Hall, D. J. 1967. The distribution and variation of *Daphnia lumholtzi* (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. J. Zool. 151:181-197.
- . 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology 45:94-112.
- 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. Annu. Rev. Ecol. Syst. 7:177-208.
- Hutchinson, G. E. 1967. A treatise on limnology: volume 2. Introduction to lake biology and the limnoplankton. John Wiley & Sons, Inc., New York. 1,115 p.
- Hecky, R. E., and P. Kilham. 1974. Environmental control of phytoplankton cell size. Limnol. Oceanogr. 19:361-366.
- Hrbáček, J., and M. Hrbáčková-Esslová. 1960. Fish stock as a protective agent in the occurrence of slow-developing dwarf species and strains of the genus *Daphnia*. Int. Revue Gesamten Hydrobiol. 45:355-358.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. 302 p.
- Kerfoot, W. C. 1974. Egg-size cycle of a cladoceran. Ecology 55:1259-1270.
- Ketchum, B. H., and A. C. Redfield. 1949. Some physical and chemical characteristics of algae grown in mass culture. J. Cell. Comp. Physiol. 33:281-300.
- LeSeur, B. W. 1960. The life history of *Daphnia pulex* spp. *pulicoides*. Proc. Mont. Acad. Sci. 19:80-83.
- MacArthur, J. W., and W. H. T. Baillie. 1929. Metabolic activity and duration of life. I. Influence of temperature on longevity in *Daphnia magna*. J. Exp. Zool. 53:221-268.
- MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York 269 p.
- McLaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. 20:685-727.
- . 1974. Demographic strategy of vertical migration by a marine copepod. Am. Nat. 108:91-102.
- McMahon, J. W. 1965. Some physical factors influencing the feeding behavior of *Daphnia magna* Straus. Can. J. Zool. 43:603-612.
- Neill, W. E. 1975a. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56:809-826.
- . 1975b. Resource partitioning by competing microcrustaceans in stable laboratory microecosystems. Verh. Internat. Verein. Limnol. 19:2885-2890.
- Parsons, T. R., and M. Takahashi. 1973. Environmental control of phytoplankton cell size. Limnol. Oceanogr. 18:511-515.
- Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244:179-180.
- Rao, K. P., and T. H. Bullock. 1954. Q_{10} as a function of size and habitat temperature in poikilotherms. Am. Nat. 88:33-44.
- Richerson, P., R. Armstrong, and C. R. Goldman. 1970. Contemporaneous disequilibrium, a new hypothesis to explain the "paradox of the plankton." Proc. Nat. Acad. Sci. 67:1710-1714.
- Richman, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. 28:275-291.
- Rigler, F. H. 1961. The relation between concentration of food and feeding rate of *Daphnia magna* Straus. Can. J. Zool. 39:857-868.
- Ryther, J. H. 1959. Potential productivity of the sea. Science 130:602-608.
- Schaffer, W. M. 1974. Selection for optimal life histories: The effects of age structure. Ecology 55:291-303.
- Schindler, D. W. 1968. Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. J. Anim. Ecol. 37:369-385.
- Schoener, T. W. 1969. Models of optimal size for solitary predators. Am. Nat. 103:277-313.
- . 1971. The theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.
- Tonolli, V. 1947. Il ritmo cardiaco della *Daphnia pulex* de Geer. Mem. Ist. Ital. Idrobiol. 3:415-429.
- Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): The influence of hunger, prey density, and prey size. J. Fish. Res. Board Can. 29:1193-1201.
- Weglenska, T. 1971. The influence of various concentrations of natural food on the development, fecundity, and production of planktonic crustacean filtrators. Ekol. Pol. 19:427-471.
- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15:556-565.
- Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31:1531-1536.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.
- Wilson, D. S. 1973. Food size selection among copepods. Ecology 54:909-914.
- . 1975. The adequacy of body size as a niche difference. Am. Nat. 109:769-784.
- Wong, B., and F. J. Ward. 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29:1761-1764.
- Wright, J. C. 1965. The population dynamics and production of *Daphnia* in Canyon Ferry Reservoir, Montana. Limnol. Oceanogr. 10:583-590.
- Zaret, T. M. 1972a. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 53:248-257.
- . 1972b. Predators, invisible prey, and the nature of polymorphism in the Cladocera (class Crustacea). Limnol. Oceanogr. 17:171-184.
- . 1975. Strategies for existence of zooplankton prey in homogeneous environments. Verh. Int. Ver. Limnol. 19:1484-1489.