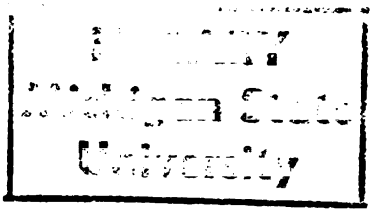

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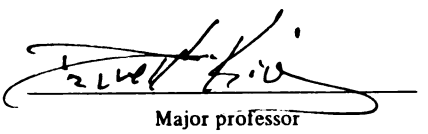

Major professor

Date May 16, 1986

FEEDING, FILTERING, FECUNDITY, AND GROWTH KINETICS AS LIMITS TO POPULATION DYNAMICS OF *DAPHNIA PULEX*

By

Mike Allan Wessels

A THESIS

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ABSTRACT

FEEDING, FILTERING, FECUNDITY, AND
GROWTH KINETICS AS LIMITS
TO POPULATION DYNAMICS OF
DAPHNIA PULEX

By

Mike Allan Wessels

Laboratory determined feeding, filtering, fecundity, and individual and population growth rate kinetics of *Daphnia pulex* fed *Chlamydomonas reinhardi* at 27 C were used to explain the mechanisms which allow these filter-feeding cladocerans to simultaneously maintain both viable populations and reduced algal densities in eutrophic lakes. Survival of the cladoceran population at suppressed food levels was dependent on allocation to the neonates of maternal energy reserves which in turn were dependent on the ratio of the mass of algae available to the total daphnid population biomass. Variation in food to mass ratios and the related variation in fecundity combined to yield a final state of oscillating dynamic population equilibrium where the population possessed significant unrealized grazing, growth, and reproductive potentials which would prevent proliferation of any phytoplankton which could be assimilated by the cladocerans.

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INTRODUCTION

Cultural eutrophication of freshwater lakes is a primary environmental concern. It represents a serious threat to the maintenance of acceptable water quality standards. Cultural eutrophication simply defined, involves the detrimental unnatural increase in plant production of a lake as a consequence of human activities. This human induced increase in plant production in most cases can be related directly to an excessively high input of a previously limiting essential nutrient. Of the potentially limiting nutrients, phosphorus most often has been identified as the primary causative factor (Vollenweider 1968; Schindler and Fee 1974; Smith 1982; Premo et.al. 1985). The most conspicuous and objectionable symptom of such phosphorus enrichment in most lakes, is increased phytoplankton abundance and the resulting decrease in water clarity.

Conventional physical and chemical lake management techniques implemented to permanently regulate and rectify cultural eutrophication by effectively moderating phosphorus inputs have included; waste nutrient diversion (Edmondson 1972 a,b), advanced wastewater treatment (Malueg et.al. 1973), preventitive watershed land management practices (Christensen and Wilson 1976; Goldman 1981), dredging (Bengtsson etl. al. 1975), and aluminum sulfate application (Soltero et.al. 1981). However, in lake watersheds where nutrient deposition originates from many uncontrollable, diffuse, nonpoint sources or,

where diversion or reduction of nutrient loading is impractical or cost prohibitive or, in instances where internal lake nutrient loading rates exceed defined standards making nutrient control impossible, other management methods are required. In this case the methods utilized treat the symptoms of cultural eutrophication rather than the base cause and include; artificial aeration (Bernhardt 1967; Pastorok et.al. 1981), hydrologic flushing (Welch et.al. 1972), algal harvesting (Oswald 1976), and algacide application (Horne and Goldman 1974).

Biomanipulation has been suggested as a feasible alternative technique to such chemical and physical procedures applied for the purpose of reducing undesirable plant production in eutrophic lakes (Fott et.al. 1974; Shapiro et.al. 1975; Andersson et.al. 1978; U.S. Environ. Prot. Ag. 1979, 1981; Shapiro 1980; Goad 1984; Shapiro and Wright 1984). The potential of biomanipulation as an alternative management technique originated from studies of the alterations of fish populations and the resulting changes in zooplankton and phytoplankton communities. Hrbacek et.al. (1961) observed this interactive biological phenomena in his seminal investigation, while other researchers (Grygierek et.al. 1966; Hurlbert et.al. 1972; Losos and Hetesa 1973; Helfrich 1976; Stenson et.al. 1978; Lynch and Shapiro 1981; Hurlbert and Mulla 1981; Spencer and King 1984), subsequently substantiated the beneficial practicality of this technique.

Biomanipulation involves the control of natural limnetic trophic levels, primarily upper order trophic levels, to regulate algal biomass. Biomanipulation relies on biological factors to

control nuisance algal blooms, as opposed to the more conventional dependence on control of physical and chemical factors.

The presence of significant populations of large filter-feeding cladocerans appears to be pivotal to successful biological control of nuisance phytoplankton populations. The positive correlation that exists between low phytoplankton biomass and uninhibited grazing intensity characteristic of a viable, large, herbivorous filter-feeding cladoceran species has been documented by Lampert (1978a), Edmondson and Litt (1982), Elliot et.al. (1983), Osgood (1984), Schoenberg and Carlson (1984), Vanni (1984), and Sterner (1986).

In aquatic ecosystems where this cladoceran control of phytoplankton is functioning, zooplanktivorous fish predation pressure on the cladocerans has been reduced, usually by piscivorous fish. This balanced equilibrated biological state can persist only if piscivorous fish densities are not critically reduced and catastrophic physical, chemical, or biological events do not decimate the cladoceran populations.

However, even if predation on the cladocerans is relaxed by maintenance of large numbers of piscivorous fish, control of algal abundance by cladocerans involves consideration of a great many interacting rate functions. Clearly, Cladocera population dynamics involve interactions and feedbacks between feeding and filtering rate kinetics, individual growth and fecundity rates, cladoceran population dynamics, and the production rate of the algae.

Feeding and filtering rate kinetics of Daphnia have been studied extensively for various purposes ranging from physiological

inquiries to incorporation of descriptive relationships into simulation models of trophic dynamics.

To obtain such information on daphnid feeding and filtering rate kinetics, experimentation has involved both laboratory trials with controlled environmental variables (Ryther 1954; Rigler 1961; Mc Mahon and Rigler 1963, 1965; Mc Mahon 1965; Burns and Rigler 1967; Burns 1968a, 1968b, 1969; Arnold 1971; Berman and Richman 1974; Hayward and Gallup 1976; Lampert 1977a, Watts and Young 1980; Porter et.al. 1982, 1983; Paloheimo et.al. 1982; Richman and Dodson 1983; Holm et.al. 1983; Muck and Lampert 1980, 1984; Meise et.al. 1985), and field investigations with relatively uncontrolled variables (Haney 1973; Crowley 1973; Haney and Hall 1975; Chow-Fraser and Knoechel 1985; Knoechel and Blair 1986), to mention just a few. Also, Lehman (1976) and Peters and Downing (1984) present articles containing a survey of published literature regarding this topic. Some of the variables and reference parameters examined and utilized include; animal species composition and abundance, diet resource effects, particle size and volume effects, behavioral versus mechanistic feeding processes, temperature, blue-green algal toxicity and manageability, diet resource concentrations, animal size relationships, diel vertical migration, and photoperiod.

Generally, from the reviewed literature, empirical models describing the feeding rate functional response curves for Daphnia are of three basic types (Mullin et.al. 1975; Lehman 1976; Lampert 1977a; Porter et.al. 1982). These are; the rectilinear model, the Ivlev model, and the Michaelis-Menten model. Regardless of the model utilized, the shape of the feeding rate curve as a function of food

concentration is uniformly depicted as a hyperbolic function assuming a constant rate after the discrete incipient limiting food concentration is exceeded.

Conceptual mechanistic models describing filtering rate processes and kinetics are usually expressed as a function of food concentration and body length. However, filtering rate functional response curves and derived empirical and theoretical models vary considerably.

Mc Mahon (1965), Burns and Rigler (1967), Burns (1969), Paloheimo et.al. (1982), Chow-Fraser and Knoechel (1985), and Knoechel and Blair (1986), all empirically model daphnid filtering rate functional responses as a power function of daphnid body size. Hayward and Gallup's (1976) filtering rate relationship as a function of algal concentration for two daphnid species was determined to be the inverse obtained for their feeding rate data and is equivalent to a negative exponential function of food concentration. Rigler (1961), Mc Mahon and Rigler (1963, 1965), Crowley (1973), and Porter et.al. (1982), concluded that daphnid filtering rates increased with decreasing food concentrations becoming constant at food concentrations below the discrete incipient limiting food concentration. Henry and Peters (1984) suggested that cladoceran filtering rates can best be computed by utilizing a multivariate empirical model with filtering rate calculated as a function of animal dry weight, food concentration, experimental volume, and experimental volume per animal. Finally, Lehman (1976) hypothesized that an appropriate theoretical model capable of predicting filtering rates for filter-feeding zooplankton, would include the fundamentals of energy optimization.

Lehman's model is predicated on theoretical filtering behavior of a zooplankter to maximize its net gain of energy in a particulate suspension of known composition. His model depicts a filtering rate functional response, in relation to food concentration, that increases with decreasing food concentration, attains a physiological maximum, and then declines proportionately with decreasing food concentration, ultimately intersecting at the origin. Lehman also provides a feeding rate model based on the same precepts as his filtering rate model. In this instance, his theoretical feeding rate functional response curve approximates a hyperbolic function of food concentration, similar to that presented by Mullin et.al. (1975), Lampert (1977a), and Porter et.al. (1982).

The general concensus from the reviewed literature is that the filtering rate of cladocerans increases with increased body size of the organism, and decreases with increased food concentration, although there is some debate about the functional response at low food concentrations.

The main point of debate in the literature concerning filter-feeding zooplankton filtering and therefore, feeding rate functional responses at decreased food concentrations, revolves around the existence or non-existence of a threshold food concentration. A food concentration threshold is defined as the food concentration where filter-feeding activities of zooplankton cease as a physiological reaction to minimize energy expenditures during periods of depleted food resources. The base of this argument revolves around whether or not filter-feeding cladoceran behavior is characteristic of

theoretical optimal foraging and energy optimization models. According to Parson et.al. (1967), Mullin et.al. (1975), Frost (1975, 1980), Lehman (1976), and Lam and Frost (1976), filter-feeding zooplankton do indeed, comply with the theoretical energy optimization models and exhibit a threshold food concentration. However, Crowley (1973), Muck and Lampert (1980, 1984), and Porter et.al. (1982, 1983), provide experimental data supporting a diametrically opposite position, suggesting no need to correct empirical filtering and feeding rate models for threshold food concentrations.

From the literature, it appears that the primary factors affecting growth and fecundity rates of individual daphnids, are temperature and food concentration (Richman 1958; Kryutchkova and Sladecek 1968; Arnold 1971; Weglenska 1971; Vijverberg 1976; Lampert 1977a,b,c; Porter and Orcutt 1980; Neill 1981; Paloheimo et.al. 1982; Lynch and Ennis 1983; Orcutt and Peter 1983; Porter et.al. 1983; Holm and Shapiro 1984; Stich and Lampert 1984; Orcutt and Porter 1984; Meise et.al. 1985).

While food and temperature have been demonstrated to be two very significant factors affecting daphnid growth and fecundity rates, Goulden et.al. (1982), Tessier et.al. (1983), and Goulden and Henry (1984), suggest that the ability of Daphnia to accumulate lipid energy reserves in a manner which allows these lipid deposits to be allocated to their progeny is of equal importance in determining the growth rate potential of cladocerans. Additionally, the study conducted by Lynch and Ennis (1983) demonstrated that such maternal energy reserves, as a function of maternal nutritional environment,

are of import to neonate physiology, morphology, and potential fecundity rates, as well as potential growth rates.

Of the thirty-one papers reviewed dealing with zooplankton population dynamics, fifteen were studies of naturally occurring zooplankton assemblages (Hall 1964; Wright 1965; Tappa 1965; Clark and Carter 1974; George and Edwards 1974; Kwik and Carter 1975; Allan 1977; Lynch 1978; Threlkeld 1979; Goldman et.al. 1979; Lynch 1979; Brambilla 1980; Taylor and Gerking 1980, 1985, De Mott 1983), while the remainder were laboratory population studies of which two were conducted on rotifer populations (Ingle et.al. 1937; Anderson 1937; Dunham 1938; Pratt 1943; Frank 1952; Slobodkin 1954, 1959; Frank et.al. 1957; Smith 1963; King 1967; Neill 1975; Goulden and Hornig 1980; Elliot et.al. 1983; Romanovsky 1984; Stemberger and Gilbert 1985). Regardless of the approach taken toward the study and analysis of zooplankton populations, it appears that the primary factor limiting these assemblages is food availability. Prominent in Slobodkin's (1954) classical work, is the remarkably linear relationship obtained when mean number of organisms at equilibrium is graphed as a function of the relative quantities of food provided to each population. This linearity was later substantiated and verified by King (1967), with his laboratory cultured rotifer populations.

In addition to food availability, other, often synergistic, elements impacting on zooplankton populations include vulnerability to size-selective predation and temperature influences (Hall 1964; Wright 1965; Allan 1977; Goldman et.al. 1979; Threlkeld 1979; Elliot et.al. 1983).

Emanating from the available and voluminous quantity of zooplankton literature previously reviewed, are excellent but, diverse examples of significant applied research. However, due to the heterogeneous composition of these studies when collated, the compilation of the requisite data for purposes of deriving quantitative kinetic rate relationships between food availability and daphnid feeding, filtering, fecundity, and individual and population growth dynamics, is impossible. And yet, such kinetic rate relationships are absolutely necessary to develop a mechanistic understanding of the feedback limits which allow cladocerans to simultaneously maintain both their population growth and the control of phytoplankton biomass. This interaction is essential for successful biomanipulative management efforts of eutrophic lakes.

The objectives of this conducted research therefore, are to develop such quantitative kinetic rate relationships for a single cladoceran fed one alga at a constant temperature. The experimental temperature chosen was 27 C. The daphnid species utilized was *Daphnia pulex* and the diet algal species provided as food was *Chlamydomonas reinhardi*. The objectives included formulation of quantitative relationships between rates of feeding, filtering, fecundity, and individual and population growth all as a function of food availability at one constant temperature.

MATERIALS AND METHODS

As defined in the introduction, the objectives of this thesis required three distinct but, complementary experimental phases. Despite the existence of some differences among the various experimental phases, there are several commonalities presented as follows.

COMMON EXPERIMENTAL METHODS

Daphnia pulex was collected from the permanent ponds south of the Michigan State University main campus at the Inland Lakes Research and Study Center. Stock daphnid populations were cultured in the laboratory in a 25 liter aquarium filled with a mixture of aerated, aged tap water, algal nutrient media, and pond water. Air temperature varied between 19 and 28 C. The daphnid culture water mixture was replenished periodically and all cultures were supplied regularly with the experimental diet algal species. The original stock culture from which daphnid clones were selected for the required laboratory experiments, were raised from two female daphnids obtained from the initial zooplankton field sample. Species identification was verified according to Edmondson (1959).

The diet algal species used in this study was *Chlamdomonas reinhardi*. The strain, wild type (+), was purchased from the Carolina Biological Supply Company. This alga was cultured in a standard defined inorganic nutrient medium and maintained at the ambient

environmental laboratory conditions described for the daphnid stock cultures. The chemical composition of the algal nutrient media is identical to that used by Spencer and King (1985), except that vitamin supplements were not included for this algal media formula. Algal cultures were decanted, replenished with media, and reseeded regularly to avoid excessive bacterial contamination (Stemberger and Gilbert 1985). The alga was cultured in constant illumination and continuously aerated.

Individual daphnid growth and fecundity, feeding and filtering, and population growth kinetic rate experiments were conducted at four to six food concentrations ranging from zero to 400,000 algal cells/ml. Experimental daphnid cultures were supplied daily with fresh cell suspensions utilizing the renewed batch culture method.

All feeding, filtering, individual growth and fecundity, and population growth kinetic rate studies were performed at 27 C. in a LAB-LINE AMBI-HI-LO CHAMBER 3550 incubator. Experiments were conducted in the dark. All study organisms were acclimated to the experimental conditions prior to experimental analysis for a time period ranging from 12-16 hours. An experimental temperature of 27 C. was chosen because it was typical of mean summer temperatures experienced by the natural daphnid populations in the M.S.U. ponds from which the study organism was obtained (Spencer and King 1984). Additionally, by maintaining a relatively high but, tolerable, experimental temperature, daphnid population kinetic rate dynamics can be accelerated; thereby, reducing the time required for the population study.

The dilution water used for all experiments was aged, aerated Millipore membrane filtered (0.45 um), tap water. Glass distilled

water was utilized for the dilution of the algal nutrient media.

Preparation of the appropriate algal food suspensions for the individual and population growth rate experimental cultures and the feeding and filtering kinetic rate experimental trials proceeded as follows. An adequate experimental volume of concentrated algal cell suspension was removed from the established stock algal culture and placed in a clean volumetric flask. Algal stock cultures were composed of fresh, exponentially growing algae in early to mid log growth phase. The volumetric flask containing the concentrated stock algal culture was diluted and allowed to stand overnight in the dark under constant aeration. The next day, a 10.1 ml aliquot of diluted stock algal cell solution was removed and preserved with 1 drop of Lugol's solution. From this preserved sample, 1.0 ml was transferred by graduated pipet to a Sedgewick-Rafter algal counting cell. Algal cells were enumerated using a phase contrast Leitz compound microscope equipped with a calibrated Whipple-grid algal counting field at 100X or 210X. Algal cell concentration was calculated from a series of algal cell counts (n = 40). The equation used to calculate algal cell concentration is presented as Equation 1.

algal cell concentration (algal cells/ml) = (mean number of algal cells counted/Whipple-grid) (1000 mm^2/ml, Sedgewick-Rafter cell area per unit volume of the algal sample)/ (Whipple-grid area (mm^2)) (1)

Following algal cell enumeration of the diluted stock algal cell solution, desired serial algal cell dilutions were prepared to provide greater accuracy. Verification of the desired algal cell

suspensions was accomplished by counting each dilution once more. The algal food suspensions were then transferred to the experimental culture vessels, and the daphnids were added.

Algal cell suspensions were subjected to constant aeration without illumination for a 24 hour period prior to serial dilution because this treatment enhanced algal motility, and suppressed algal reproduction through nutrient and light deprivation. Effectiveness of this technique was verified by algal cell enumeration and direct observation. Inhibited algal cell growth and motility stimulation was further augmented by decreasing the nitrogen reagent weight when preparing the algal nutrient culture media (12.5 mg KNO_3/L). The experimental advantage of culturing a motile C. reinhardi algal population, lies in the ability to maintain a homogeneous algal food suspension without having to resort to physical and, potentially disruptive, circulation techniques to prevent algal cell sedimentation.

Daphnids utilized for any of the experimental analyses in these study phases were selected based on subjective physiological appearance and behavioral criteria. Physiologically impaired or morphologically damaged organisms were disposed. Adult daphnids utilized were all in a non-gravid state prior to the initiation of an experiment.

Eight daphnid size classes were defined: 0.69-0.8% mm, 0.89-1.00 mm, 1.01-1.25 mm, 1.26-1.38 mm, 1.39-1.50 mm, 1.51-1.75 mm, 1.76-2.00 mm, and 2.01-2.25 mm. These length defined size classes were utilized to examine individual and population kinetic rate dynamics as a function of daphnid size.

Daphnids were transferred individually at random from the daphnid culture aquarium with a large mouthed pipet into a beaker, and then placed on a glass depression plate cell. Excess water was removed to immobilize the daphnids for length measurement. Lenth was measured using an American Optical binocular dissecting microscope equipped with a calibrated occular micrometer at 15X. Daphnix carapace length was determined by measuring from the anterior most apex of the head to the point of inflection on the posteroventral margin of the carapace.

An allometric length-weight relationship index equation was developed for the D. pulex strain used. The technique consisted of removing healthy non-ovigorous daphnids from the stock cultures and placing them in a beaker containing prepared algal cell suspension dilution water. Daphnids remained in the beaker for approximately two hours. This was done primarily to rinse the organism and allow for the egestion of their gut contents before weight determination (Paloheimo et.al. 1982). Daphnids were then rinsed with distilled water. Following the second rinsing, the daphnids were transferred to a glass depression plate cell and measured to the nearest 0.025 mm. Following carapace length measurement, the experimental organisms were placed on a tared weighing pan constructed from thin aluminum foil. The organisms were then dried to constant weight in a drying oven for 24 hours at 60 C., cooled in a dessicator, and weighed with a Cahn Model G electrobalance sensitive to 0.05 ug on the 0-to-5-mg range setting.

A double log plot was made relating weight vs. carapace length of the organism (Figure 1). A linear regression analysis of

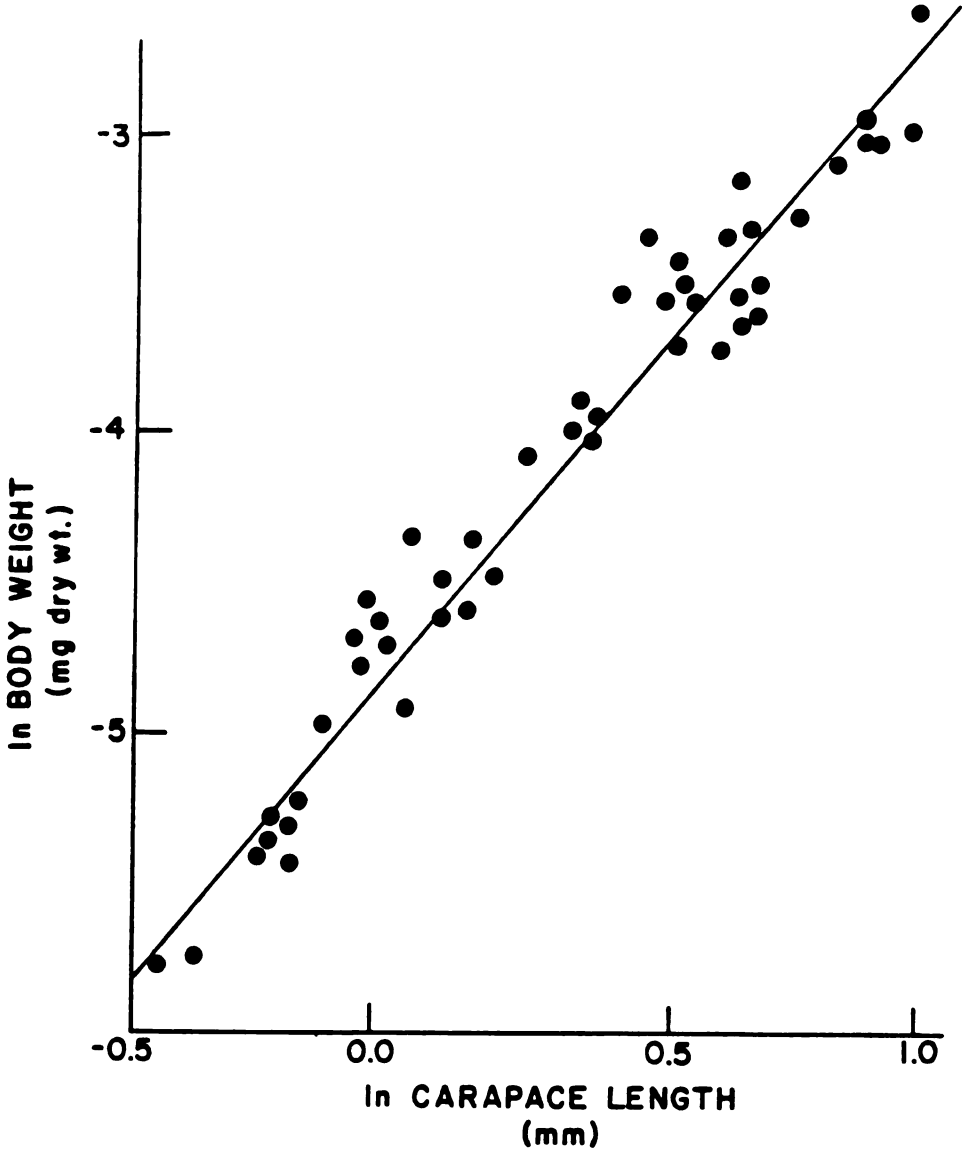


Figure 1. Relationship between in body weight and in carapace length for D. pulex. Equation 2; $W=7.69X10^{-3}L^{2.39}$, is indicated by a solid straight line.

ln (weight) against ln (length) yielded a transformed power equation describing the length per dry weight index relationship. The equation fit to the resulting power curve is a function expressed by Equation 2 with a coefficient of determination of 0.96.

$$W = 7.69 \times 10^{-3} L^{2.39} \quad (2)$$

where,

W = weight of daphnid in mg

L = carapace length of a daphnid in mm

This transformed expression provided a convenient and expedient conversion method for systematically calculating either individual or population daphnid biomass as a function of carapace length.

The weight of the experimental diet alga Chlamydomonas reinhardi was determined in multiple replicates (h = 5) by filtering, drying, and weighing a known volume of an algal cell suspension at specific concentrations. A stock solution of algae was prepared as previously described, a subsample aliquot pipeted into a receiving flask and preserved with 1 drop of Lugol's solution, and algal cell concentration determined by obtaining a mean value from a series of Sedgewick-Rafter algal cell counts. Ten to 100 mls of the algal cell suspension were filtered through a tared 0.45 um sterilized gridded Millipore filter, dried at 60 C. for 24 hours, weighed, and the weight per algal cell calculated. Algal cell weight, determined regularly throughout the period of laboratory experimentation, was calculated to be 3.00×10^{-8} mg dry weight per algal cell (S.E. = 1.75×10^{-9}).

FEEDING AND FILTERING RATE DETERMINATION EXPERIMENTAL METHODS

Feeding and filtering kinetic rates were estimated utilizing the "differential algal cell count" method, the general format of which has been applied and described previously by Gauld (1951) and Ryther (1954). Typically, the differential algal cell count method involves microscopically estimating algal cell concentrations from the experimental cultures before, during, and after a defined period in which selected known experimental daphnid size classes were allowed to graze in suspensions of known algal cell concentration. This technique consisted of pipeting a two, three, or five ml aliquot of sample from the experimental filter-feeding flask, preserving it with one drop of Lugol's solution, and then determining the algal cell concentration at each time period.

Prior to any feeding and filtering rate experiment, daphnids of the approximate size class range desired were transferred individually at random from the stock culture with a large mouthed eye dropper into a beaker containing algal cell suspension dilution water. Study organisms were then measured according to the previously described technique to the nearest $\pm$ 0.05 mm. After appropriate experimental size selection, the daphnids were placed in variable dense concentrations of algal cell suspensions and left overnight without illumination at the experimental temperature (27 C.).

Before the actual feeding and filtering kinetic rate experiments, the daphnids were re-measured for length and then transferred into aerated, aged tap water for approximately one hour. This was done to rinse the organisms and to allow for egestion prior to the experimental trial.

Following preparation of the serial algal cell dilutions for the feeding and filtering kinetic rate trials, the daphnids were transferred from the aerated, aged tap water into their respective experimental containers. A volume of 50 mls was used for all feeding and filtering kinetic rate experiments which were conducted in 50 ml Erlenmeyer flasks. Feeding and filtering kinetic rate experiments were performed for all eight daphnid size classes. The number of daphnids per experimental vessel varied for each size class, depending on the size of the daphnid under investigation and the algal cell suspension concentration. The experimental feeding and filtering flasks were swirled gently periodically to resuspend any sedimenting cells and create a homogeneous algal cell distribution. Sample aliquots from the experimental feeding and filtering kinetic rate trial containers for algal cell enumeration were obtained with a graduated pipet at regular intervals as necessitated by experimental design requirements.

For the feeding and filtering kinetic rate trials, daphnids were allowed to graze in the experimental cultures for time periods ranging from one to 12 hours, depending upon algal cell suspension concentration, experimental objectives, and daphnid size and number. Beginning experimental algal cell concentrations utilized for the feeding and filtering kinetic rate experiments ranged from 7,500 to 400,000 algal cells/ml.

Filtering rate expresses the volume of algal cell suspension passed through the filtering appendages per organism per unit time, assuming a 100% capture efficiency of algae. Feeding rate provides

the estimation of the quantity of algal cells removed from the algal suspension per organism per time.

The calculation utilized for measuring observed daphnid feeding rates is described by Equation 3.

$$A/D/T \quad \frac{\frac{C_1 - C_2}{T_1 - T_2}(V)}{} \tag{3}$$

where,

A/D/T = algal cells consumed per daphnid per hour (daphnid feeding rate)
C_1 = algal cell concentration at time 1 (algal cells/ml)
C_2 = algal cell concentration at time 2 (algal cells/ml)
T_1 = experimental time 1 (hours)
T_2 = experimental time 2 (hours)
V = experimental filter-feeding volume (mls)
D = number of experimental daphnids per filter-feeding trial vessel

Measured daphnid filtering rates expressed as volume filtered (ml) per daphnid per unit time was calculated according to Equation 4.

$$V/D/T \quad \frac{A/D/T}{C_1} \tag{4}$$

where,

V/D/T = daphnid filtering rate (mls algal cell suspension filtered per daphnid per time)

For each daphnid size class, four separate algal cell concentrations were used. Multiple trials (Table 1) were performed for each daphnid size class.

Feeding rate kinetics for the eight different size classes, were calculated utilizing a threshold corrected and non-threshold corrected right rectangular hyperbolic function as the conceptual models. These conceptual empirical models represent a modification of the often used Michaelis-Menten equation. The threshold corrected model used in this research is presented in Equation 5.

$$A/D/T = A/D/T_{max.} \frac{C - C_q}{C + K_C - 2(C_q)} \quad (5)$$

where,

$A/D/T$ = daphnid feeding rate (algal cells/daphnid/hour)

$A/D/T_{max.}$ = maximum daphnid feeding rate (algal cells/daphnid/hour)

C = algal cell concentration (algal cells/ml)

C_q = feeding rate threshold algal cell concentration (algal cells/ml)

K_C = half saturation constant (algal cells/ml)

An alternative conceptual empirical feeding rate model, uncorrected for a threshold feeding rate food concentration, is presented in Equation 6.

$$A/D/T = A/D/T_{max.} \frac{C}{C + K_C} \quad (6)$$

Regardless of the conceptual empirical model utilized, either approach provides a mathematical fit of the hyperbolic functional response curve for daphnid feeding rate as a function of algal cell concentration. Differences in the empirical models are exhibited in hyperbola abscissa intersection coordinates. Threshold food concentration corrected empirical models intersect the abscissa at some characteristic coordinate (x,0), while non-threshold food concentration

corrected empirical models intersect at the origin.

Calculation of the daphnid feeding rate kinetic constants for the non-threshold model (Equation 6), were calculated with data from Equation 3 and the linear transformation of Equation 6 given as Equation 7.

$$\frac{C}{A/D/T} = \frac{K_C}{A/D/T_{max.}} (C_1) \qquad (7)$$

Thus, a linear regression of $(C_1/(A/D/T))$ as a function of (C_1) yields a slope equal to the reciprocal of $(A/D/T_{max.})$ and the intercept multiplied by $A/D/T/_{max.}$ yields K_C.

Determination of the kinetic rate constants for the threshold food concentration corrected hyperbolic feeding rate model (Equation 5), is accomplished in a manner similar to that described in Equation 7, after calculation and correction for the threshold value.

The threshold concentration was approximated by fitting feeding rate and algal cell concentration data to Equation 8.

$$A/D/T = a + b\log C \qquad (8)$$

where,

A/D/T = daphnid feeding rate (algal cells/daphnid/hour)
log C = common logarithm of algal cell concentration (algal cells/ml).

Since the threshold is reached when (A/D/T) equals zero, solving for (C) in Equation 8, with (A/D/T) equal to zero yields the threshold concentration. Correction of Equation 5 for the threshold concenctration yields Equation 9, from which $(A/D/T_{max.})$ and (K_C) can be calculated in the same manner described for Equation 7.

$$\frac{C - C_q}{A/D/T} = \frac{C - C_q}{A/D/T/_{max.}} + \frac{1}{A/D/T/_{max.}} (C - C_q) \qquad (9)$$

Completing this procedure for all eight experimental daphnid size classes, resulted in 16 empirical models from which calculated feeding rates can be obtained as a function of algal cell concentration, for any algal cell concentration within the experimental range.

Measured filtering rates for the eight size classes of D. pulex also were calculated from the observed data (Equation 4).

Similar to the feeding rate empirical model presentation, it is possible to describe filtering rate functional response by two conceptual mathematical expressions. The first empirical model described includes energy optimization considerations, where a threshold food concentration is assumed at which point daphnid filter-feeding processes cease. The second and third models presented, do not include the above theoretical suppositions and therefore, are derived independent of energy optimization considerations.

Expression of daphnid filtering rate as a function of algal cell concentration with a threshold food concentration involves dividing both sides of Equation 5 by algal cell concentration to yield Equation 10.

$$V/D/T = A/D/T_{max.} \frac{1 - C_q/C}{C + K_C - 2C_q} \qquad (10)$$

The functional response of filtering rate against algal cell concentration for this model takes the form of line A in Figure 2. Similarly, Equation 6 can be divided through by algal cell concentration resulting in Equation 11. This expression also can predict daphnid filtering rates as a function of algal cell concentration.

$$V/D/T = A/D/T_{max.} \frac{1}{C + K_C} \quad (11)$$

The daphnid filtering rate functional response curve described by Equation 11 as a function of algal cell concentration, is represented by line B in Figure 2.

The alternative expression used to empirically model the response of daphnid filtering activities as a function of algal cell concentration, was the negative exponential function (Equation 12).

$$V/D/T = ae^{-bc} \quad (12)$$

where,

V/D/T = daphnid filtering rate (ml algal suspension filtered/daphnid/hour)

C = algal cell concentration (algal cells/ml)

e = base of the natural logarithm

Determination of the empirical constants (a) and (b) in Equation 12 was accomplished by linear regression of the natural log transformed data in the manner shown in Equation 13.

$$\ln V/D/T = \ln a + bC \quad (13)$$

where,

lnV/D/T = natural log of daphnid filtering rate

C = algal cell concentration (algal cells/ml)

The functional response of this model to algal cell concentration takes the form of line C on Figure 2.

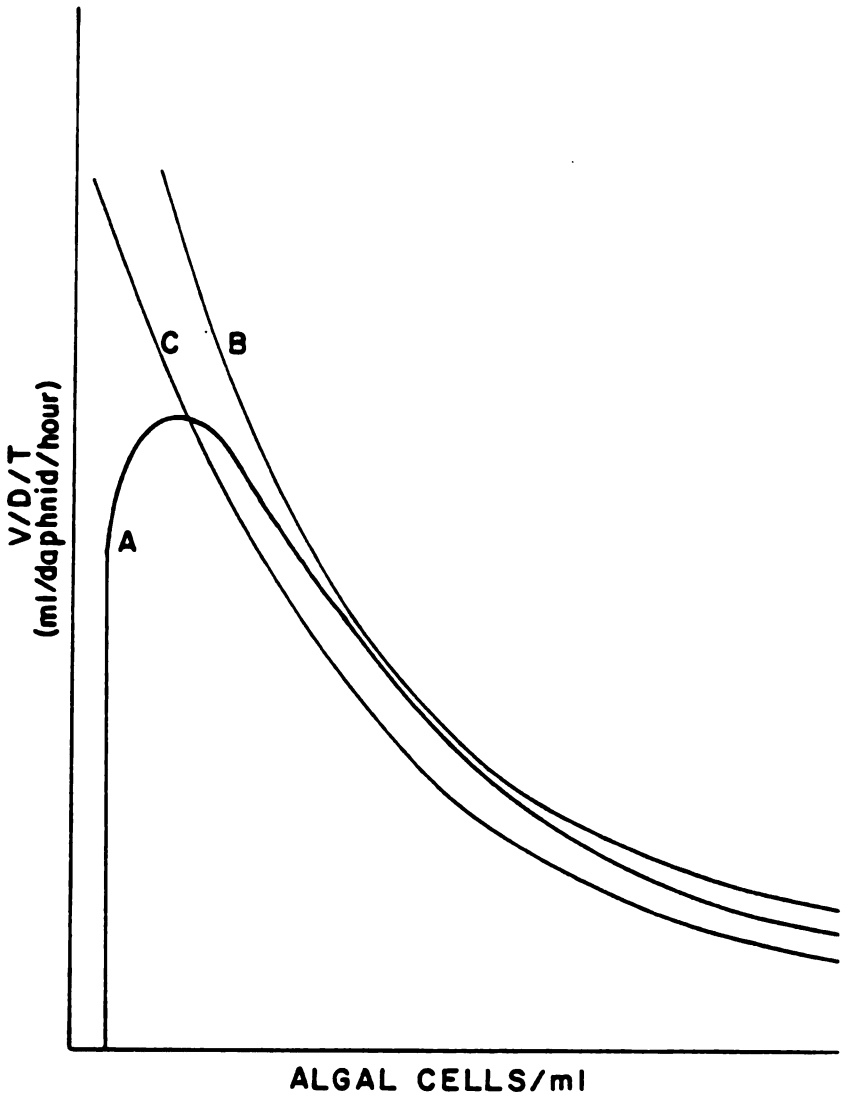


Figure 2. Functional response filtering rate curves for D. pulex as related to algal cell concentration. Line A illustrates filtering rate response described by Equation 10, line B depicts filtering rate response expected from Equation 11, and line C exemplifies filtering rate response as predicted by Equation 12.

INDIVIDUAL GROWTH AND FECUNDITY RATE DETERMINATION EXPERIMENTAL METHODS

Individual growth and fecundity rates of the daphnids were determined as functions of algal cell concentration using many of the previously discussed methods.

For this study phase, individual daphnids were randomly selected from the stock culture tank, measured for uniformity of length and inoculated into an experimental culture containing a known concentration of algal cells. These studies were initiated by placing five daphnids of a given size class in algal cell cultures of various concentrations and allowing them to grow for a period of seven to eleven days. All neonates produced were removed. The volume of algal cell suspension utilized for this experimental phase was 200 ml and the culture container was a 250 ml beaker. The algal cell concentrations used for growth and fecundity rate experiments were; 0, 10,000, 20,000, 40,000, 80,000, 100,000, and 200,000 algal cells/ml. The beginning size classes used were; neonates (less than 8 hours old), 0.825 mm, 1.00 mm, 1.25 mm, and 1.75 mm. Daphnids comprising the original inoculated cohort were not replaced with equivalently sized organisms upon their death. The algal cell suspension was renewed daily.

Daily measures from each culture included; length of both living and dead daphnids, number of eggs per reproductive female, total eggs per culture, number of neonates, and observation of general morphological and physiological developmental characteristics and states.

After the daily measurements were recorded, daphnids (minus the neonates), were transferred from the old algal cell culture solution into a fresh algal cell culture solution.

The computation of individual daphnid growth rate, it was assumed that the growth of the daphnid at each algal cell concentration was exponential hence, the application of the exponential growth rate equation (Equation 14).

$$W_t = W_o e^{ut} \tag{14}$$

where,

W_t = population biomass at time t (mg)

W_o = population biomass at time o (mg)

t = experimental time interval (day)

u = specific growth rate (day^{-1})

Daphnid growth rates were calculated on a biomass basis with individual biomass being determined from the daily length measures and Equation 2. The specific growth rate (u) was calculated with Equation 15.

$$u = \frac{\ln Wt_{t1} - \ln Wt_{to}}{t1 - to} \tag{15}$$

Fecundity was expressed as total egg production observed for a daphnid culture over the experimental time period and number of eggs per reproductive female measured at each census.

POPULATION GROWTH RATE DYNAMICS DETERMINATION EXPERIMENTAL METHODS

Evaluation of daphnid population growth rate dynamics was the final phase of this study. This examination of daphnid population dynamics was conducted essentially within the same procedural framework as that explained for the individual size class growth rate and

fecundity rate experiments. There were three primary experimental design differences between this study phase and the previously described investigation. The first involved inoculating experimental daphnid cultures with newly released neonates (less than eight hours old), from a single isolated female. This practice was used to reduce existing genetic growth and reproductive variability. The second significant difference was that neonates were allowed to remain in the culture. Only dead organisms were removed. The final difference was that the culture volume was reduced to 100 mls.

Duplicate daphnid populations each initiated with five neonates were cultured at algal cell concentrations of 0, 10,000, 20,000, 40,000, and 80,000 algal cells/ml in the dark at 27 C. These cultures were provided fresh algal cell suspension solutions daily. Initially, these cultures were censused daily, but once the daphnid population cultures began expanding, the duplicate population cultures were censused on alternate days. Population parameters measured included; daphnid fecundity rates in terms of number of eggs per female and number of reproductive females in the population, number of free infertile eggs, number and length of living and dead daphnids in each of the eight size classes, total eggs produced in the population, juvenile survivorship, and embryonic development and post embryonic development time. The experiment was terminated after the viable daphnid populations experienced their third oscillation around some mean daphnid population biomass value. This was observed to occur following the 60th day of cultured daphnid population growth.

RESULTS AND DISCUSSION

To satisfy the research objectives of this thesis, a series of laboratory experiments were conducted as indicated in the introduction, using the study organism, Daphnia pulex, and the diet algal species Chlamydomonas reinhardi, at one constant temperature of 27 C. To facilitate the discussion of the results from these experiments the study was separated into three distinct experimental phases these included; feeding and filtering rate trials, individual growth and fecundity rate experiments, and population growth rate studies. Data presentation and discussion of the experimental results are provided for these three experimental phases in this section.

FEEDING AND FILTERING RATE TRIALS

Feeding rate trials were performed as detailed earlier with observed rates computed using Equation 3. From the measured feeding rate data, two conceptual continuous empirical hyperbolic models were applied and fit as a function of algal cell concentration. The first empirical model used, Equation 5, is a threshold food concentration corrected hyperbolic function and is representative of theoretical energy optimization assumptions. The second feeding rate empirical model, Equation 6, is a non-threshold food concentration corrected hyperbolic function.

Daphnid filtering kinetic rates were analyzed concomitantly with daphnid feeding rate kinetics. Measured daphnid filtering rates were calculated using Equation 4. Resulting observed filtering rates were fit to three conceptual continuous models as a function of algal cell concentration. The first empirical filtering rate model incorporated energy optimization considerations given by Equation 10. The second was fit by Equation 11. The third was the exponential form illustrated by Equation 12.

Application of the observed feeding rate data to Equations 5 and 6, for all experimental daphnid size classes, yielded Table 1. Included in Table 1 are the derived kinetic rate constants and corresponding coefficients of determination for the two conceptual empirical models as indicated. It appears from the coefficients of determination that the threshold food concentration corrected hyperbolic model provides a slightly better fit to the observed data.

Observed feeding rate data and the fit of the two empirical conceptual models to the measured data (Equations 5 and 6), are given as functional response curves in Figure 3, for the 1.76-2.00 mm experimental daphnid size class. All other daphnid size classes yield generally similar functional response curves.

Companion observed filtering rate data as a function of algal cell concentration for the 1.76-2.00 mm size class are presented in Figure 4. Included in Figure 4, are the filtering rate functional response curves obtained from the three empirical conceptual models. The first was threshold food concentration corrected (Equation 10), the second with no threshold food concentration correction (Equation 11),

Table 1. Kinetic rate constants derived from observed daphnid feeding rates as a function of algal cell concentration provided for both empirical feeding rate hyperbolic models (Equation 5 and 6) as differentiated for the eight experimental daphnid size classes. Also given are the coefficients of determination (r^2) obtained for each model as fit to the measured data.

		WITH THRESHOLD CORRECTION				WITHOUT THRESHOLD CORRECTION		
Daphnid Carapace Length (mm)	Data Points	$A.D.T._{max.}$ (algal cells/ daphnid/time maximum	K_C (algal cells/ml)	S_q (algal cells/ml)	r^2	$A/D/T_{max.}$ (algal cells/ daphnid/time maximum)	K_C (algal cells/ml)	r^2
0.69-0.88	58	20,464	90,785	11,075	0.75	25,642	168,132	0.64
0.89-1.00	34	31,684	65,758	5,571	0.51	37,261	119,786	0.30
1.01-1.25	34	38,354	34,133	2,758	0.84	41,496	40,858	0.82
1.26-1.38	25	51,265	22,894	2,988	0.93	54,907	29,769	0.90
1.39-1.50	41	76,897	47,349	4,089	0.59	89,067	71,461	0.48
1.51-1.75	40	82,379	56,262	5,170	0.91	91,580	65,432	0.80
1.76-2.00	85	88,129	37,059	2,676	0.85	94,356	49,321	0.82
2.01-2.25	30	116,176	61,947	5,422	0.81	130,494	75,243	0.73

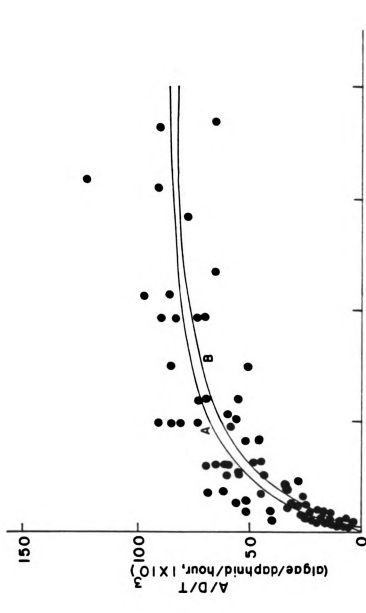


Figure 3. Relationship between daphnid feeding rate (algae/daphnid/hour) as a function of algal cell concentration (algal cells/ml) for the 1.76-2.00 mm daphnid size class. Line A represents the functional response curve for Equation 5 (threshold food concentration corrected) and Line B represents the functional response curve for Equation 6 (non-threshold food concentration corrected), using kinetic rate constants given in Table 1.

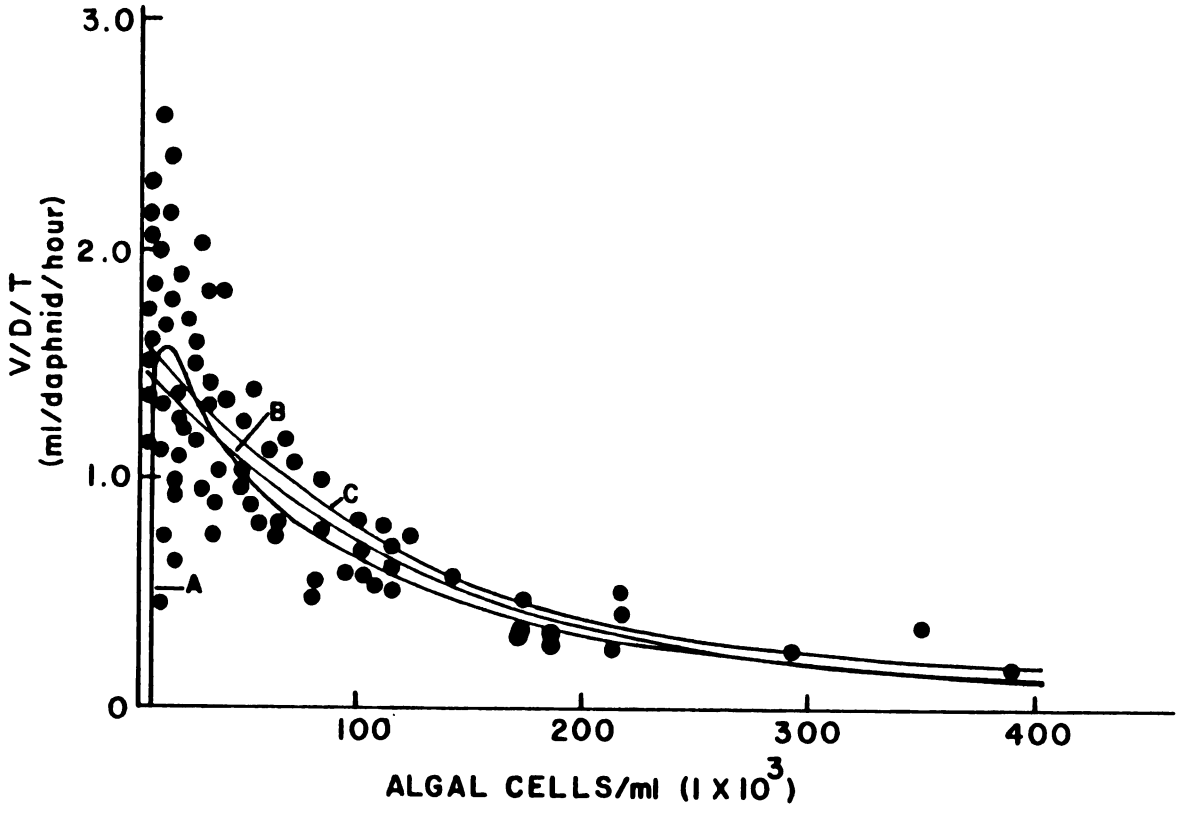


Figure 4. Relationship between daphnid filtering rates (ml/daphnid/hour) as a function of algal cell concentration (algal cells/ml) for the 1.76-2.00 mm daphnid size class. Line A represents the functional response curve for Equation 10 (threshold food concentration corrected), line B represents the functional response curve for Equation 11 (non-threshold food concentration corrected), and line C represents the functional response curve for Equation 12 (non-threshold food concentration corrected), using kinetic rate constants given in Table 1 (Equations 10 and 11) and regression coefficients presented in Table 2 (Equation 12).

and the third uncorrected for threshold food concentration (Equation 12) as derived from the measured filtering rate data.

As discussed earlier there is a disagreement in the literature concerning the shape of the predicted functional response filtering and feeding rate curves, primarily at low food concentrations. The debate revolves around the dispute as to whether the predicted feeding and filtering rate curves should be corrected for a threshold food concentration, with threshold food concentration indicating resource conditions where cladoceran filter-feeding activities cease. Presently, this is regarded as a hypothetical behavioral response for zooplankton when basal metabolic demands are not energetically satisfied due to a severely food limited environment.

Threshold food concentration correction of empirical feeding and filtering rate models, originates from researchers who assume that filter-feeders comply with theoretical optimal foraging and energy optimization models (Parson et.al. 1967; Mullin et.al. 1975; Frost 1975, 1980; Lehman 1976; Lam and Frost 1976). These models imply that a filter-feeder maximizes the net rate of energy gained from its food as a function of energy expended in filtering food particles. This theory fits well with predicted relations between filtering rate, feeding rate, and abundance of food with empirical models at high resource concentrations, but not at low particle densities, hence, the debate as suggested earlier.

However, those authors espousing theoretical foraging and energy optimization models apply them almost exclusively to a different type of organism, the calanoid copepods. These organisms, as opposed

to a continuous filter-feeding cladoceran, have been shown to employ alternative feeding and filtering mechanisms and strategies (Richman and Dodson 1983). Therefore, the suitability of the foraging and energy optimization models, exemplified by Equations 5 and 10, may not fit well when applied to filter-feeding cladocerans.

In addition, the inhalant current produced by movement of the thoracic appendages subserves respiration as well as feeding in filter-feeding zooplankton (Jorgensen 1966; Crowley 1973). Therefore, it is essential that filtering continue even if net energy expenditure is greater than net energy intake during the filter-feeding process at low food densities. This demand for respiration suggests that filter-feeding continues and that no threshold food concentration is reached.

Supplemental evidence substantiating this position is provided in studies conducted by Muck and Lampert (1980, 1984) and Porter et.al. (1982, 1983) in direct refutation of Lehman (1976). In fact, Muck and Lampert (1980) failed to demonstrate a threshold food concentration feeding or filtering behavior even for Eudiaptomus, a calanoid copepod.

Upon examination of Figures 3 and 4, it is apparent that there is little difference between the feeding and filtering rate functional response curves, suggesting little real difference in the various empirical models fit to the measured data. Discrepancies are only observed to exist at the lowest algal cell concentrations which, especially for Figure 4, is the region demonstrating the most data point scatter and variability. The variability is of sufficient magnitude at the low concentrations that no clear choice of model can be justified.

Thus, there is no distinct evidence for a threshold correction and models represented by Equation 5 and 10 do not seem appropriate for filter-feeding cladocerans.

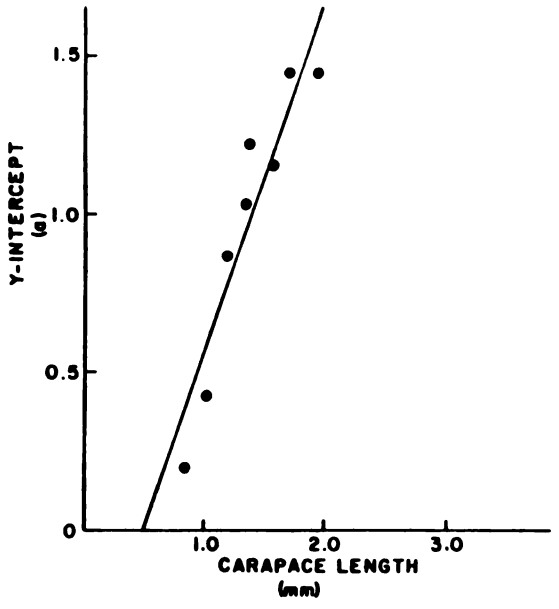
Calculation of filtering rate for the various size classes of daphnids using Equation 11 and the kinetic constants for the non-threshold food concentration corrected model given in Table 1 yields filtering rate values which appear to decline with increased food concentration in a negative exponential manner similar to that of Equation 12 (Figure 4). Separate exponential relationships were determined for both such calculated filtering rates and observed filtering rates for each size class of daphnids. The constants for these equations are given in Table 2. To determine if the two negative exponential curves were coincident, two separate statistical Student's t-tests were utilized. These two tests consisted of a test for parallelism of slope and a test for common y-intercept (Kleinbaum and Kupper 1978). In all instances the null hypotheses were not rejected (significance level = 0.05), indicating coincidence of the two curves (Table 2). Therefore, either Equation 11 or 12 can be used to calculate filtering rates of daphnids as a function of food concentration.

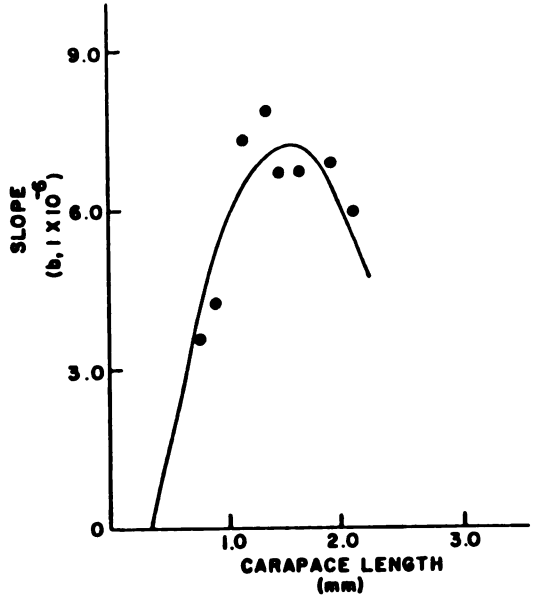
Regardless of the model chosen, daphnid filtering rates for any size class varies as a function of algal cell concentration. However, the regression coefficients (slope and y-intercept, Table 2) vary as a function of carapace length of the organism (Figures 5a and b).

From Figure 5a it is apparent that the y-intercept (a) in the negative exponential filtering rate model (Equation 12) is a function of carapace length. The relationship between the y-intercept

Table 2. Regression coefficients derived from observed and calculated filtering rates as a function of algal cell concentration provided for Equation 11 (the negative exponential function developed from Equation 6) and for Equation 12 (the negative exponential function constructed from observed filtering rates), as differentiated for the eight experimental daphnid size classes. Also given are the coefficients of determination (r^2) obtained for each model as fit to the observed and calculated data and the P values associated with the two Student's t-tests for coincidence for two straight line regression models. Significance level = 0.05.

	OBSERVED FILTERING RATES			CALCULATED FILTERING RATES				
Daphnid Carapace Length (mm)	y-intercept (a)	Slope (b) ($1X10^{-6}$)	r^2	y-intercept (a)	Slope (b) ($1X10^{-6}$)	r^2	Student's t-test for parallelism	Student's t-test for common y-intercept
0.69-0.88	0.1441	-3.082	0.53	0.1434	-3.618	0.99	0.50<P<.0.70	P>0.90
0.89-1.00	0.3841	-5.932	0.33	0.3086	-4.442	0.98	0.30<P<0.50	0.70<P<0.90
1.01-1.25	0.8088	-8.740	0.70	0.7151	-7.360	0.94	0.30<P<0.50	0.50<P<0.70
1.26-1.38	1.285	-9.575	0.80	1.199	-8.211	0.93	0.20<P<0.30	0.50<P<0.70
1.39-1.50	1.220	-7.297	0.54	1.040	-5.817	0.96	0.30<P<0.50	0.50<P<0.70
1.51-1.75	1.143	-3.951	0.61	1.146	-6.061	0.95	0.10<P<0.20	P>0.90
1.76-2.00	1.603	-6.892	0.68	1.463	-6.844	0.95	P>0.90	0.30<P<0.50
2.01-2.25	1.494	-4.102	0.58	1.462	-5.676	0.97	0.20<P<0.30	P>0.90





Figures 5a and b. Relationship between the regression coefficients y-intercept (Figure 5a) and slope (Figure 5b) as a function of carapace length (mm) obtained from the daphnid filtering rate regression models given in Table 2. In Figure 5a, the solid straight line represents Equation 16; $a=-0.49+1.01(L)$, $r^2=0.87$. In Figure 5b, the solid parabolic curve represents Equation 17; $b=-5.82X10^{-6}+1.65X10^{-5}(L)-5.29X10^{-6}(L)^2$, $r^2=0.58$.

and daphnid carapace length can be fit to a straight line regression model by the least squares method yielding Equation 16.

$$a = -0.49 + 1.01(L) \qquad r^2 = 0.87 \tag{16}$$

where,

a = y-intercept (regression coefficient)
L = daphnid carapace length (mm)

Similarly, it is implied from Figure 5b that the slope (b) in the negative exponential empirical filtering rate model (Equation 12) also is a function of daphnid carapace length. The relationship between slope and carapace length can be fit to a quadratic expression by multiple regression analysis yielding Equation 17.

$$b = -5.82 \times 10^{-6} + 1.65 \times 10^{-5}(L) - 5.29 \times 10^{-6}(L)^2$$
$$r^2 = 0.58 \tag{17}$$

where,

b = slope (regression coefficient)
L = daphnid carapace length (mm)

Examining the coefficients of determination (r^2) for Equations 16 and 17, it is apparent that there is a strong linear relationship between y-intercept and daphnid carapace length but, a weaker transformed linear association between slope and carapace length. However, the correlation coefficient for Equation 17 is 0.76, which indicates a fairly significant association between slope and daphnid length. Despite the poorer coefficient of determination measured for Equation 17, it still can be seen that daphnid filtering rates are definitely a function of both algal cell concentration and

daphnid carapace length. Therefore, it is possible to develop the single negative exponential empirical filtering rate model that relates daphnid filtering rate, carapace length, and food concentration given as Equation 18.

$$V/D/T = -0.49 + 1.01(L)e^{-(-5.82 \times 10^{-6}) + 1.65 \times 10^{-5}(L) - 5.29 \times 10^{-6}(L)^2)(C)} \quad (18)$$

where,

V/D/T = daphnid filtering rate (ml algal suspension filtered/daphnid/hour)
L = daphnid carapace length (mm)
e = base of natural logarithm
C = algal cell concentration (algal cells/ml)

Depicting Equation 18 graphically, results in Figure 6, vividly demonstrating that daphnid filtering rates are most certainly a function of both algal cell concentration and carapace length.

It has been proposed recently that zooplankton community filtering rates can be predicted accurately by applying a simple power function model based on zooplankton body length, exclusive of other potentially important parameters (Knoechel and Holtby 1986a,b). They provided several models, each derived utilizing different diet food particles provided to a diverse assemblage of endemic zooplankton species occurring naturally in a pelagic lake community. Presented were separate power function models of filtering rate as function of body length for yeast (Knoechel and Holtby 1986a), bacteria, algae, and a combination of all three food types (Knoechel and Holtby 1986b). However, it is seen from this study (Figure 6) that cladoceran filtering rates are a function of both carapace length and food concentration.

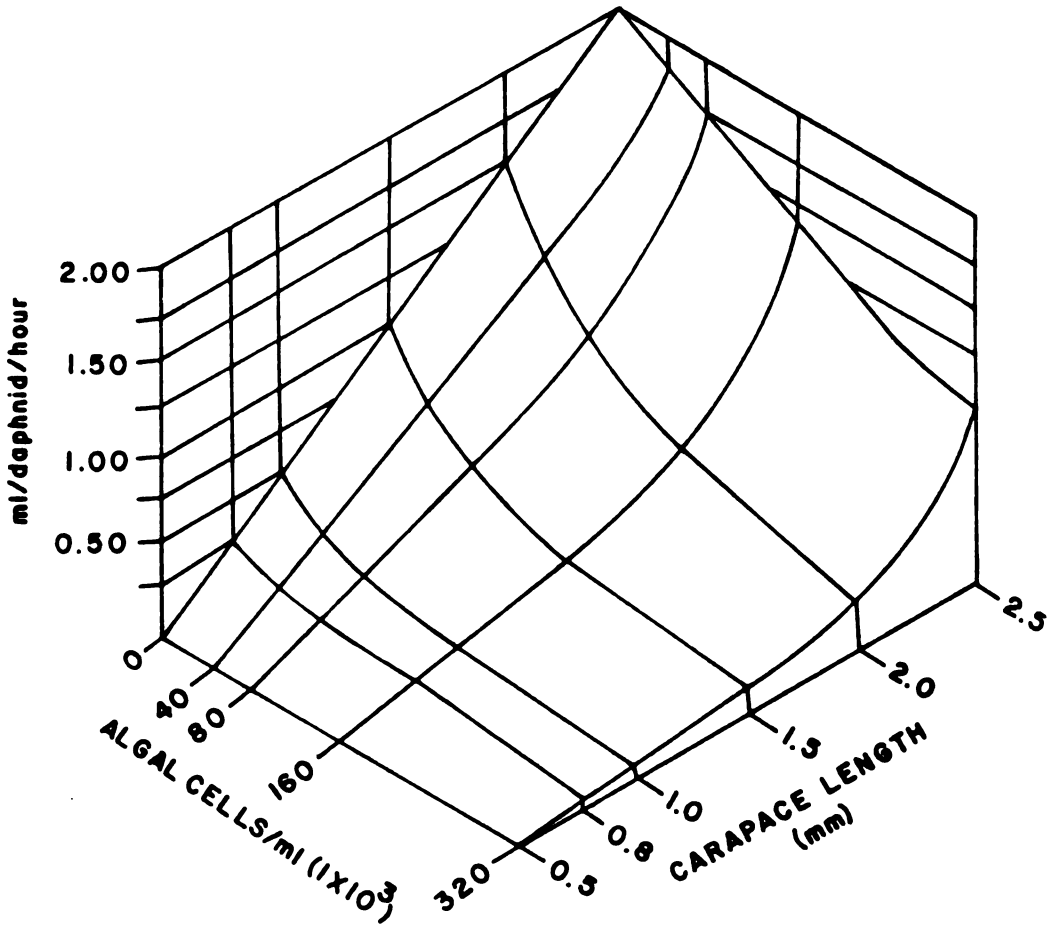


Figure 6. Daphnid filtering rate (ml/daphnid/hour) as a multivariate functional relationship between algal cell concentration (algal cells/ml) and carapace length (mm) as predicted by Equation 18; $V/D/T=-0.49+1.01(L)e^{-(-5.82X10^{-6}+1.65X10^{-5}(L)-5.29X10^{-6}(L)^2(C)}$.

This multivariate functional relationship has also been advocated by other researchers (Mc Mahon 1965; Crowley 1973; Geller 1975; Hayward and Gallup 1976; Porter et.al. 1982).

Figure 7 includes the filtering rate functional response of a 2.00 mm Daphnia pulex calculated for various food concentrations from Equation 12 presented with the filtering rate functional response of a 2.00 mm cladoceran calculated from Knoechel and Holtby's (1986a,b) models.

Clearly, Knoechel and Holtby's (1986a,b) approach is not particularly useful and their proposed models must be adjusted to include food concentration and type.

The preceding discussion has primarily emphasized the presentation of the feeding and filtering rate empirical models and their associated kinetics as applied to fit the measured experimental data. However, the critical issue as it pertains to the research objectives in this section, is not necessarily the proposed models themselves but, rather the energy return realized from daphnid filter-feeding activities as a function of food availability. Essential to developing a daphnid energetic relationship between food availability and feeding rate kinetic interactions, is the determination of the variable energy expenditures by an organism on respiration as a function of organism biomass.

Equation 19 was used to calculate daphnid respiration rate as a function of body weight. Equation 19 was obtained from Lampert (1977b) who used the exponent from Richman (1958) for an experimental temperature of 25 C.

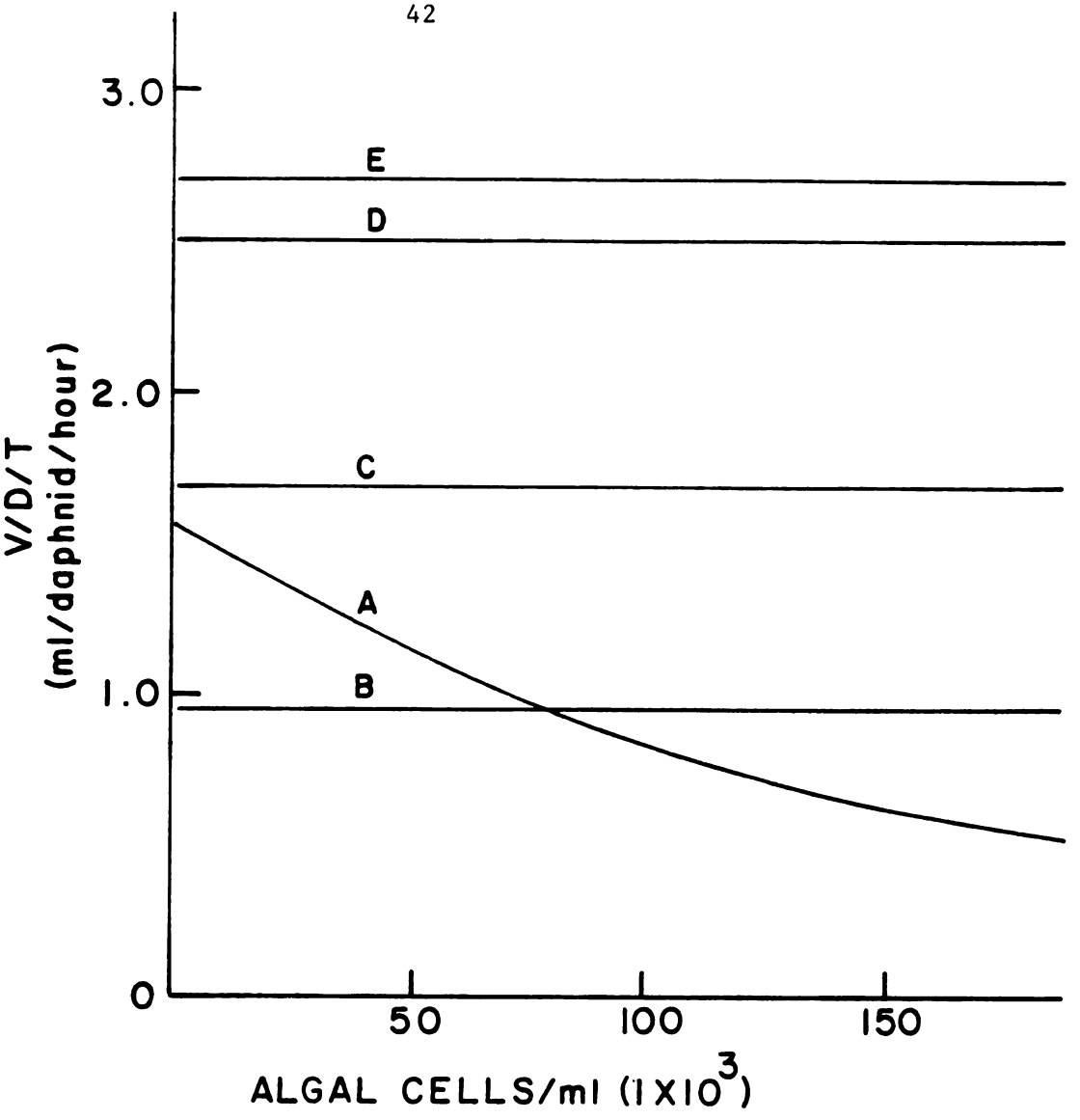


Figure 7. Relationship between daphnid filtering rate (ml/daphnid/hour) as a function of algal cell concentration (algal cells/ml) for a 2.00 mm daphnid applying Equation 12 and the empirical filtering rate models presented by Knoechel and Holtby (1986a,b). Line A represents the functional response curve for Equation 12 (Table 2), line B represents the functional response for $V/D/T = 5.105L^{2.176}$ (food type, bacteria), line C represents the functional response for $V/D/T = 7.396L^{2.403}$ (combined models), line D represents the functional response for $V/D/T = 7.534L^{3.002}$ (food type, large algae), and line E represents the functional response for $V/D/T = 11.695L^{2.480}$ (food type, yeast).

$$R = aW^b \tag{19}$$

where,

R = daphnid respiration rate (ul O_2/daphnid/hour)
W = daphnid body weight (mg dry weight)
a = 6.39 @ 25 C.
b = 0.88

Figure 8 illustrates daphnid respiration rates as a function of carapace length indicating that neonates possess considerably higher relative respiration rates than any other size class as a function of body weight. This indicates potential competitive inhibition for the neonates.

Since Equation 19 is based on a function of biomass, it is necessary to express daphnid feeding rate kinetics in biomass units, too. The procedure used to convert daphnid feeding rates from conventional measurement units (as calculated from Equation 6 and Table 1), into normalized biomass units is given in Equation 20.

$$mg/mg/T = A/D/T \times \frac{3.00 \times 10^{-8} \text{ mg/algal cell}}{\text{mg/daphnid}} \tag{20}$$

where,

A/D/T = daphnid feeding rate (algal cells/daphnid/hour calculated from Equation 6 and Table 1)
mg/mg/T = mass normalized daphnid feeding rate (mg algae consumed/mg daphnid/hour)

Relating mass normalized daphnid feeding rates as a function of carapace length calculated for various algal cell concentrations yields Figure 9. It is evident from Figure 9 that the intermediate daphnid size classes possess an advantage at the lowest food

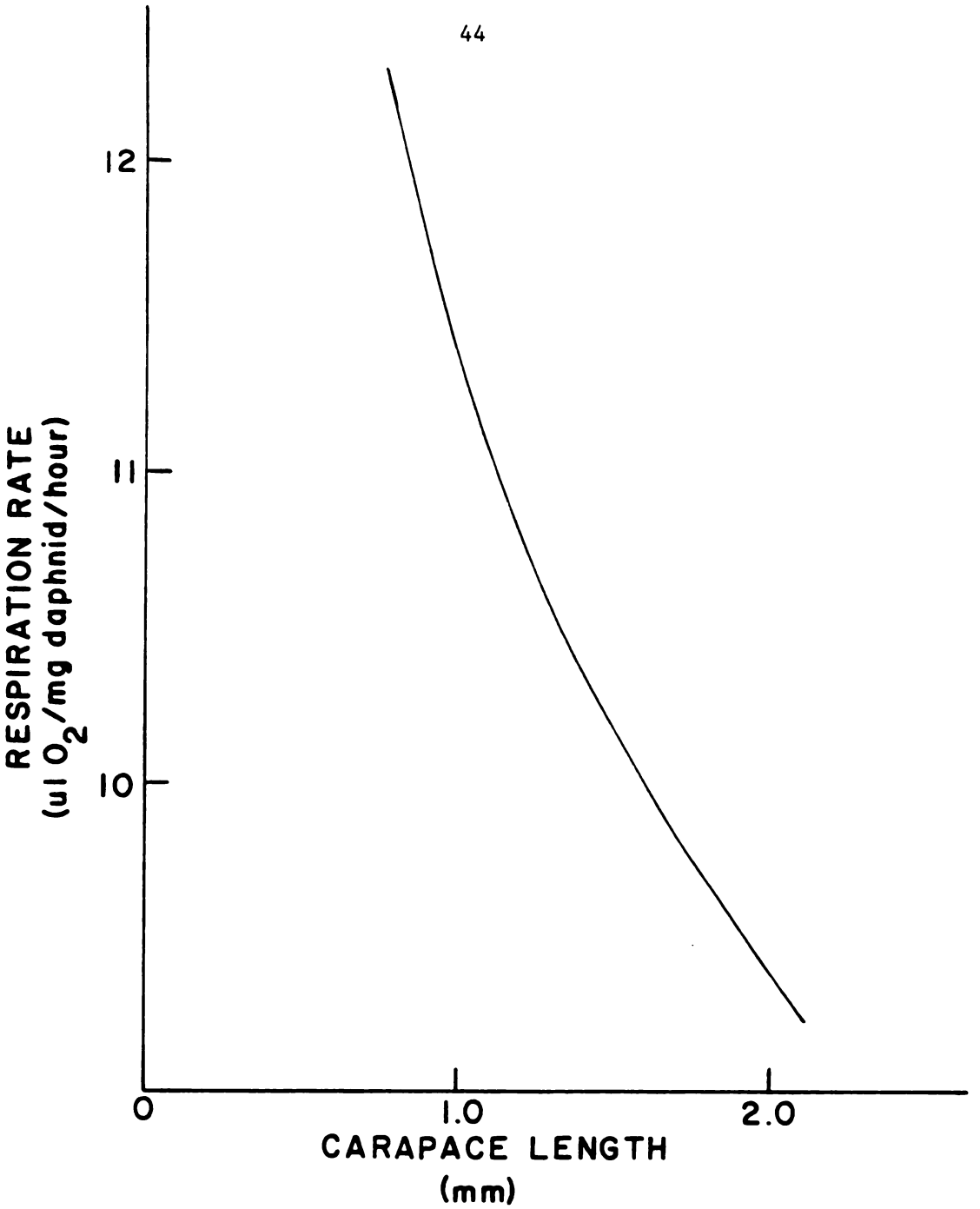


Figure 8. Relationship between discrete mass-specific daphnid respiration rate (ul O_2/mg daphnid/hour) as a function of carapace length (mm).

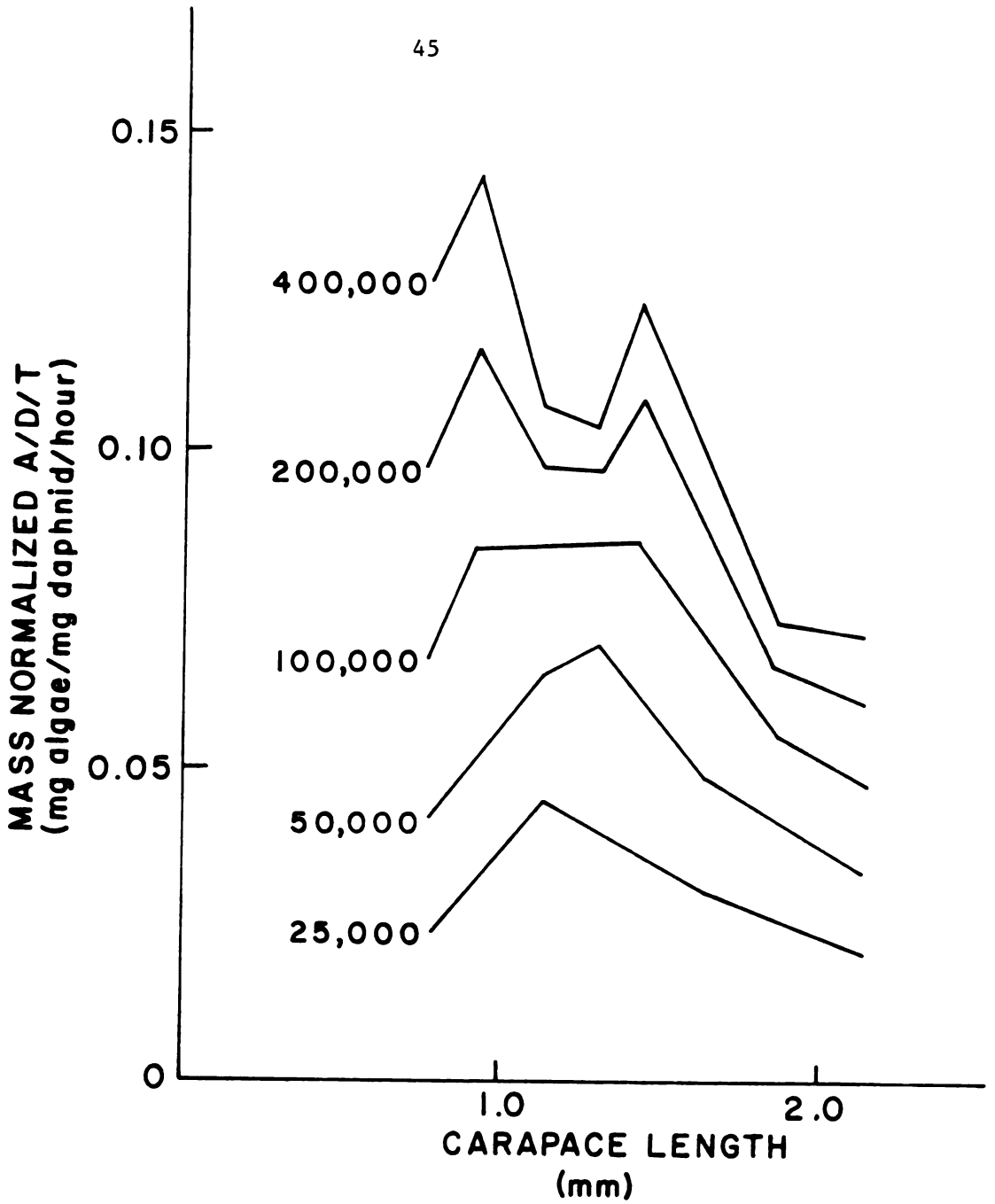


Figure 9. Relationship between mass normalized daphnid feeding rates (mg algae/mg daphnid/hour) as a function of carapace length (mm) calculated for five algal cell concentrations (algal cells/ml).

concentrations. At these limiting food concentrations, the immature and largest daphnid size classes are seen to maintain the least relative competitive positions. It has been observed that at decreased algal cell concentrations, inter- and intra-specific competition for food by cladocerans is significant (Neill 1975a,b; Lynch 1978, 1979). At the highest calculated algal cell concentration, the relative position of the normalized daphnid feeding rates for the different size classes changes appreciably. At high algal cell concentrations the relative competitive position of the neonate size class improves greatly while the relative competitive position of the largest daphnid size classes remains essentially the same. However, at such an elevated algal cell density, food availability would not be considered a limiting element and daphnid competitive interactions for food would be reduced significantly.

It is suggested by Figure 9 that at critical food limiting concentrations, intermediate daphnid size classes are able to ingest proportionately more algal biomass per unit body biomass than the largest and smallest experimental daphnid size classes. As will be shown later, this is of crucial importance in competitive daphnid population dynamics.

Lynch and Ennis (1983), demonstrated that a similar parabolic relationship existed between net energy intake or ingestion (ug dry weight/day), and body length for D. pulex. In other words, net energy intake as a function of feeding rate, increased and then decreased with increasing size. This functional relationship is equivalent to the results given in Figure 9, especially at the low to moderate algal

cell concentrations which were in the concentration range that Lynch and Ennis (1983) utilized for their study.

Kryutchkova and Sladecek (1968) and Lampert (1977a) concluded that an asymptotic function best described the relationship observed between assimilation and consumption rates and daphnid body weight. They illustrated this fit graphically as an increase in assimilation and consumption rates with incremental decreases in daphnid body biomass reaching maxima at the smallest size. While such a fit is similar to the mass normalized feeding rate curves presented in Figure 9 for the highest food concentration, a discrepancy does exist. By not including experimental daphnid size classes below about 1.00 mm, Kryutchkova and Sladecek (1968) and Lampert (1977a) were unable to examine if immature daphnid size classes possess inhibited competitive feeding capabilities at low food concentrations.

Dividing daphnid respiration rate as presented in Figure 8 (ul O_2/mg daphnid/hour) by mass normalized feeding rates (mg algae/mg daphnid/hour) yields daphnid respiration rates expressed in units standardized for the mass of algae consumed (ul $^{O}2$/mg algae). This relationship is plotted as a function of carapace length in Figure 10 for high and low algal cell concentrations. Such normalization of respiration for the mass of algae consumed indicates the vulnerable position occupied by very small and very large daphnids and the superior ability of mid-sized daphnids at low food concentrations (Figure 10). However, this size-dependent variability in efficiency disappears at high food concentrations (Figure 10).

Lynch (1977) in his study on optimal daphnid body size and fitness, presented similar findings. He was able to demonstrate

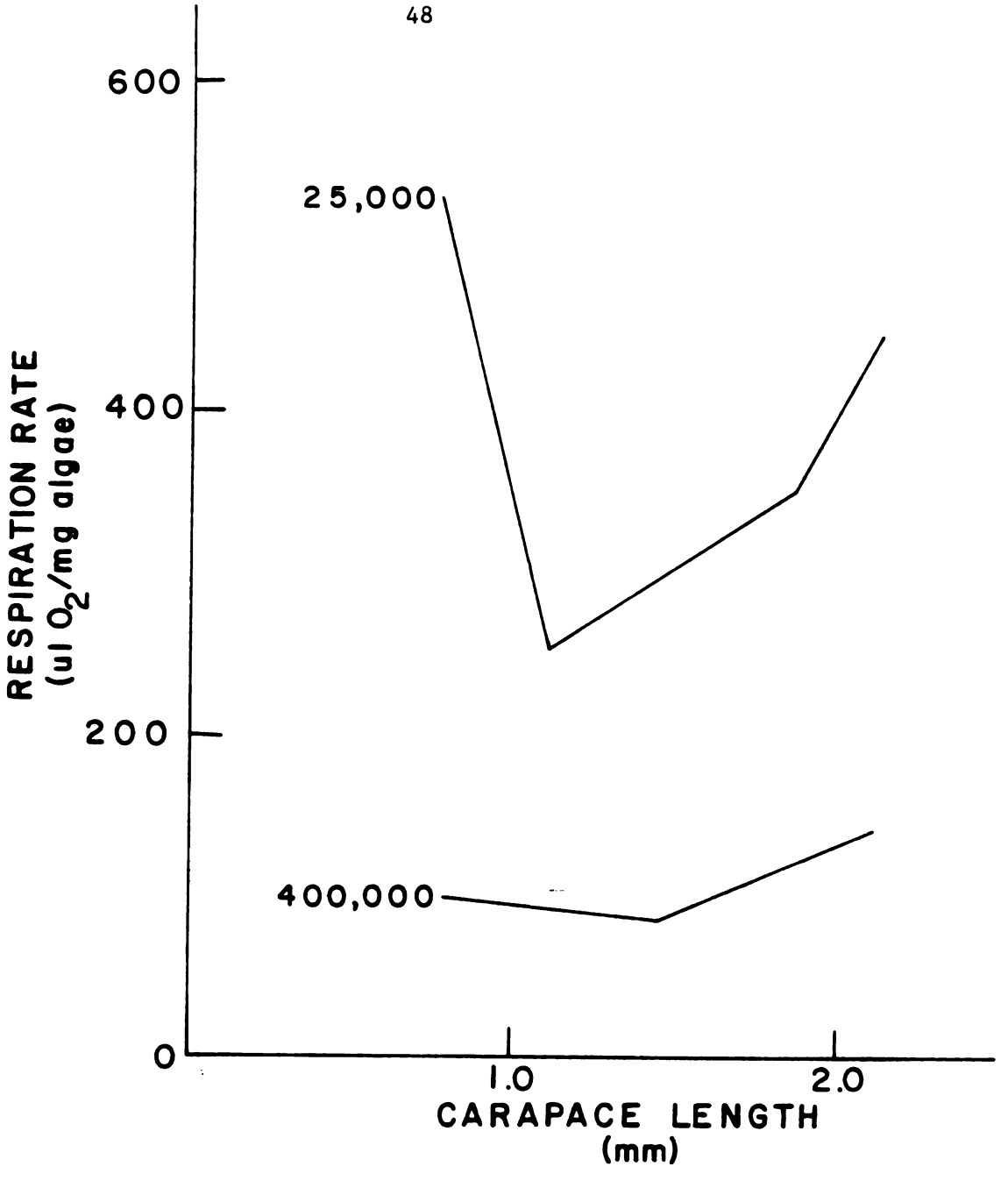


Figure 10. Relationship between discrete mass-specific daphnid respiration rate standardized for the amount of algae consumed (ul O_2/mg algae) as a function of carapace length (mm) calculated for a high and low algal cell concentration (algal cells/ml).

that the dependence of daphnid fitness associated with feeding efficiency for D. pulex on body length, exhibited a parabolic relationship. Lynch (1977) expressed feeding efficiency as daphnid feeding rate divided by basal metabolic rate, the reciprocal of the approach used in Figure 10. His feeding efficiency was observed to increase with size to a size equivalent to the intermediate daphnid size classes in this study before it began to decline. Therefore, the mid-sized daphnids were more competitive than the largest and smallest individuals at low algal cell concentrations. His observation agrees well with the relationship shown in Figure 10.

Dividing the respiration rates standardized for the mass of algae consumed (ul O_2/mass algae) by daphnid body biomass yields; ul O_2/mg algae/mg daphnid, as is presented in Figure 11 as a function of carapace length for high and low algal cell concentrations. Again, the smallest size classes possess the most inferior competitive efficiencies particularly at the lowest algal cell concentration. Larger sized and senescing adult daphnids, despite their relative inefficiencies when respiration rates were standardized for mass of algae consumed (Figure 10), exhibit improved relative efficiencies at the low algal cell concentration (Figure 11). This is due to their lower calculated respiration rates as adjusted for a larger body mass. This increased body biomass represents a significantly larger potential energy reserve available for utilization to maintain basal metabolic requirements during periods of low food densities thereby, enhancing survival.

At the high algal cell concentration, the relative competitive disadvantages of the smallest daphnid size classes are reduced

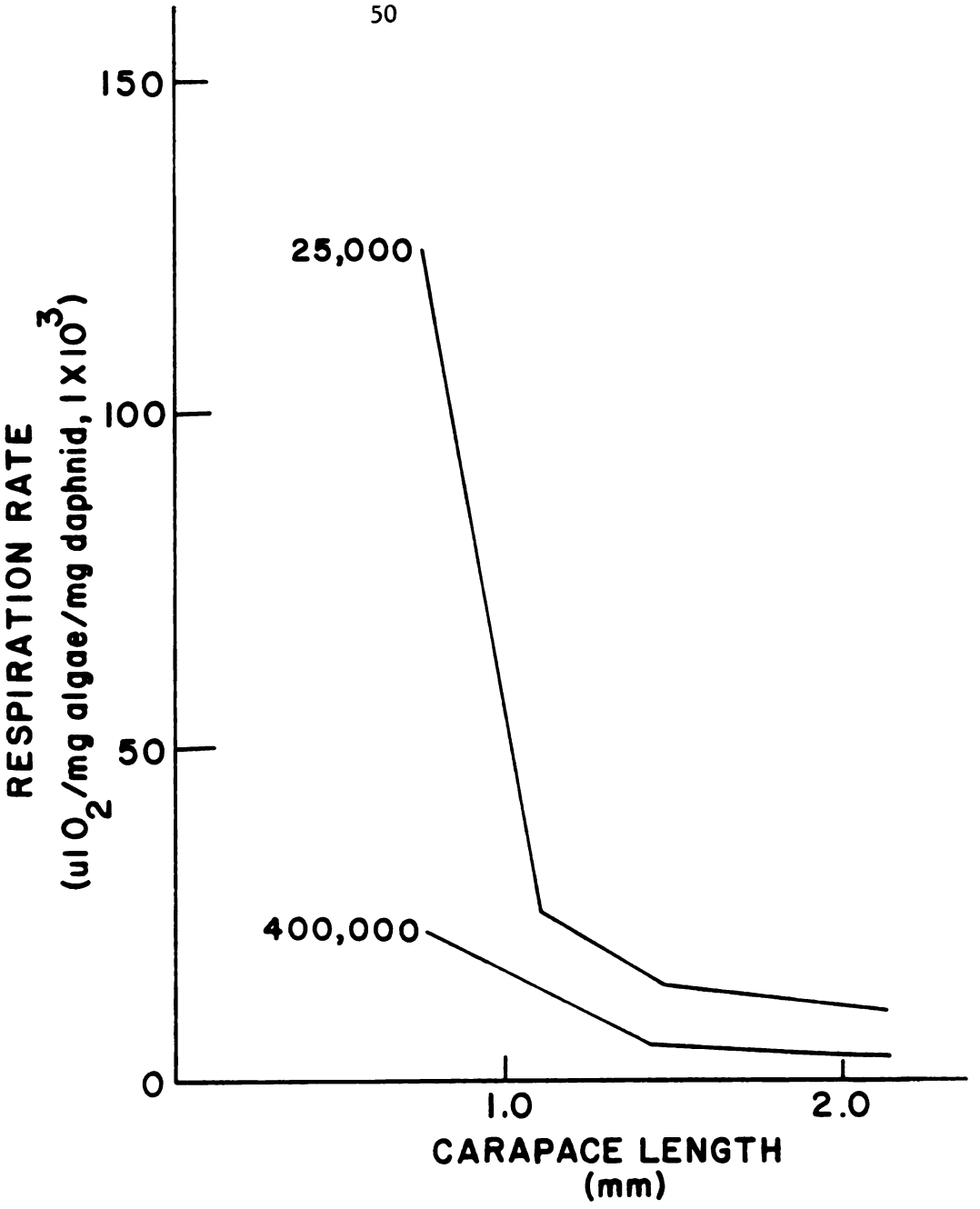


Figure 11. Relationship between discrete mass-specific daphnid respiration rate standardized for the amount of algae consumed and adjusted for daphnid biomass (ul O_2/mg algae/mg daphnid) as a function of carapace length (mm) calculated for a high and low algal cell concentration (algal cells/ml).

substantially. In fact, adjusted daphnid respiration rates throughout the different size classes are fairly equivalent, almost eliminating noticeable competitive advantages and disadvantages (Figure 11).

The vulnerability of the immature daphnids and the physiological advantage of a large body biomass possessed by adult daphnids also was noted by Threlkeld (1976). For his study, Threlkeld (1976) investigated various zooplankton species under conditions of starvation. He expressed zooplankton survival time as a function of weight specific respiration rates and the fraction of initial body weight catabolized prior to death. Survival time therefore, was determined to be approximately proportional to body weight, as would be expected in regards to the quantitative efficiencies presented in this study.

Of primary importance throughout this discussion is the concept of the relative competitive ability of different size classes of daphnids as a function of food concentration. The relative competitive inefficiencies of immature daphnids as related to their inferior mass standardized and adjusted respiration rate efficiencies at low food concentrations is of particular import. Their inhibited competitive ability would imply poor survivorship when food availability is suppressed. When their respiration rates are standardized for mass of algae consumed the largest daphnid size classes also demonstrate inferior competitive physiological rate kinetics at low food concentrations (Figure 10). However, they can physiologically compensate for this kinetic rate deficiency by expending a relatively lower quantity of energy per unit body biomass to maintain their basal metabolic rate. With their superior efficiencies the intermediate

daphnid size classes appear to possess the greatest competitive potential at low food concentrations (Figure 10). Ultimately, this would suggest that intermediate sized daphnids would possess the best innate competitive dynamics on a population level if the daphnid population were to become food stressed.

INDIVIDUAL GROWTH AND FECUNDITY RATE EXPERIMENTS

The second experimental research phase involved the measurement of individual growth and fecundity rates as functions of algal cell concentration. These studies were conducted to examine daphnid growth and reproductive rates and to develop rate relationships at various stages of daphnid life history over a representative range of algal cell concentrations at one constant temperature of 27 C.

Data to be presented in this subsection were obtained from duplicate individual growth and fecundity rate experiments performed using a cohort of five daphnids whose average carapace lengths upon inoculation approximated C.825 mm. The technical procedures and the individual daphnid parameters measured used to conduct this experimental analysis were described in the materials and methods section. The experimental algal cell concentrations utilized for this study phase ranged from zero to 200,000 algal cells/ml and were renewed daily.

Individual growth and fecundity rate parameters were censused daily and neonates were removed each day. After the eleventh day the experiment was terminated. Measured daphnid carapace lengths were converted to dry weight by applying Equation 2. These calculated daphnid weights obtained from consecutive daily censuses for each

culture beaker were totaled and converted to specific growth rates, u day^{-1}, utilizing Equation 15. Daily measured daphnid specific growth rates were computed and then summed for the entire experimental period and divided by the number of days the cultures were censused producing an average measured specific growth rate at each algal cell concentration. This procedure was performed to determine average measured daphnid specific growth rates for the 11 day study period including and excluding the contribution of egg biomass to total daphnid body biomass in each culture. Egg biomass was estimated to be 0.00184 mg, the weight calculated for a 0.55 mm neonate, the smallest size observed during this study. This egg weight value is very close to a median egg weight value presented by Lynch and Ennis (1983) for D. pulex eggs produced by females maintained at high and low food conditions. Average measured daphnid specific growth rates are given in Table 3 along with their associated standard errors for the various algal cell concentrations used.

As observed from Table 3, positive average specific growth rates were recorded for all experimental algal cell cultures, except for the zero algal cell concentration food level. However, even though negative specific growth rates were calculated at a zero algal cell concentration, daphnid body growth was allowed by accumulated and maternally allocated energy reserves (lipid deposits) that the experimental daphnids possessed prior to their incoulation. Residual energy reserves, maternally allocated or accumulated in the hemocoel of daphnids when food is abundant, are later metabolized when food is scarce to temporarily sustain daphnid basal metabolism, body growth, and even reproduction as suggested by Goulden and Hornig (1980),

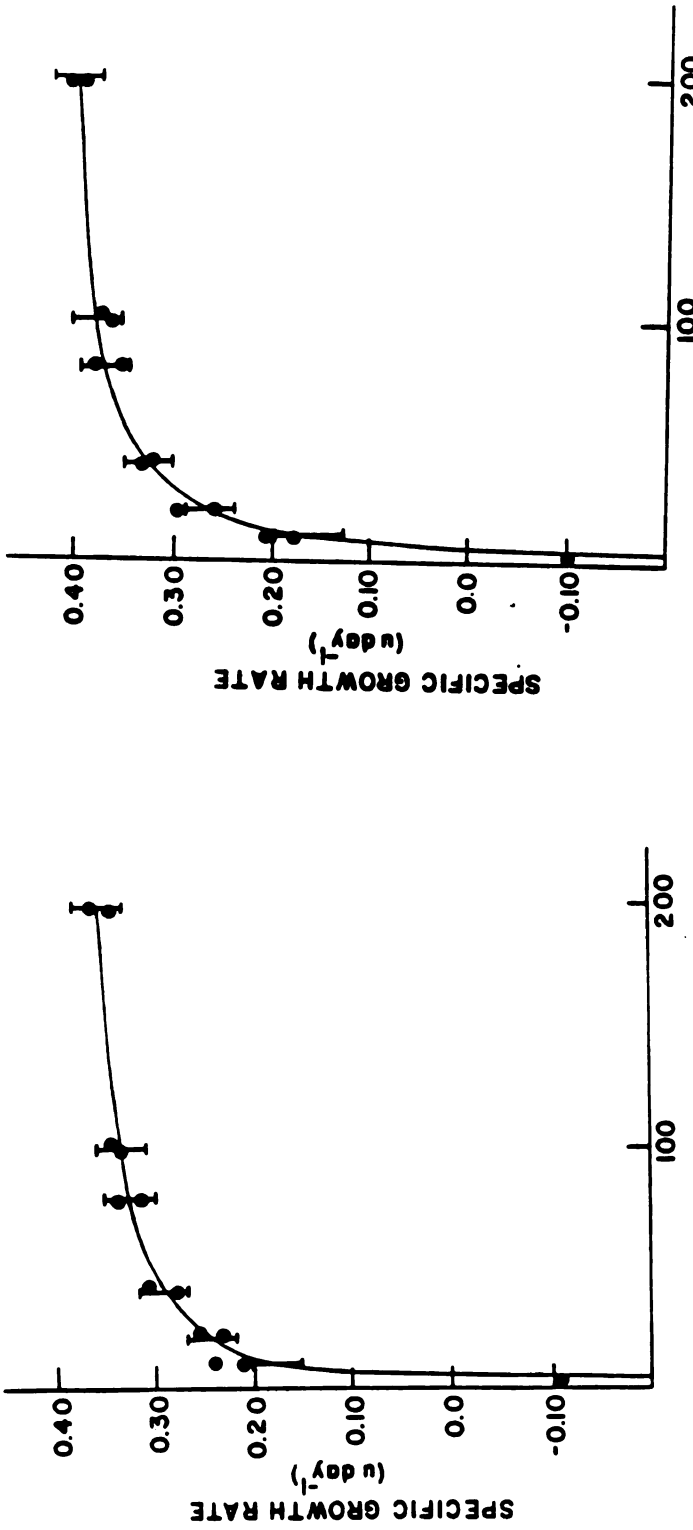
Table 3. Average measured daphnid specific growth rates calculated including and excluding egg biomass contribution observed at the seven experimental algal cell concentrations provided with the estimated standard error of the mean ($\bar{X} \pm$ S.E. ($\bar{X}$)).

Algal Cell Concentration (algal cells/ml, $1X10^3$)	Experiment A $\bar{u}$ (day^{-1}) $\bar{X} \pm$ S.E. ($\bar{X}$)		Experiment B $\bar{u}$ (day^{-1}) $\bar{X} \pm$ S.E. ($\bar{X}$)	
	Without Egg Biomass	With Egg Biomass	Without Egg Biomass	With Egg Biomass
0	-0.4946 ± 0.3534	-0.4946 ± 0.3534	-0.2137 ± 0.3491	-0.2137 ± 0.3491
10	0.1053 ± 0.0638	0.1053 ± 0.0612	0.1379 ± 0.0527	0.1468 ± 0.0524
20	0.1837 ± 0.0523	0.2009 ± 0.0503	0.1343 ± 0.669	0.1520 ± 0.0652
40	0.1914 ± 0.0524	0.2228 ± 0.0538	0.1829 ± 0.0628	0.2147 ± 0.0643
80	0.2118 ± 0.0695	0.2489 ± 0.0805	0.2297 ± 0.0597	0.2799 ± 0.0569
100	0.2313 ± 0.0628	0.2609 ± 0.0773	0.2347 ± 0.0659	0.2793 ± 0.0708
200	0.2536 ± 0.0639	0.2920 ± 0.0878	0.2406 ± 0.0589	0.2935 ± 0.0697

Goulden et.al. (1982), Tessier and Goulden (1982), Tessier et.al. (1983), and Goulden and Henry (1984). Negative average measured daphnid specific growth rates were obtained upon the death of the entire inoculated daphnid cohort.

To predict daphnid specific growth rates as a function of algal cell concentration, average measured daphnid specific growth rates (including and excluding the egg biomass contribution), were fit to the hyperbolic threshold food concentration corrected empirical model, Equation 5. This fit was completed in relation to the algal cell concentration from which the average measured daphnid specific growth rates were obtained. Though the mathematical structure of Equation 5 was unmodified for this application, it was necessary to substitute for the correct terminology; (u) for (A/D/T) and ($u_{max.}$) for ($A/D/T_{max.}$).

The linear transformation presented in Equation 9 was used to calculate the kinetic rate constants, $u_{max.}$ and K_C. A single threshold food concentration quantity (C_q) required for the computation of the kinetic rate constants and subsequent implementation of Equation 5, was determined graphically from the data presented in Table 3 and Figures 12a and b for daphnid specific growth rates measured with and without the contribution of egg biomass. The individual daphnid threshold food concentration was estimated to be 7,250 algal cells/ml for a daphnid specific growth rate of zero. Calculated kinetic rate constants for Equation 5 are presented in Table 4, along with their corresponding coefficients of determination. The curves illustrating predicted daphnid specific growth rate (including and excluding egg biomass contribution), calculated as a function of algal cell concentration utilizing Equation 5, are provided in Figures 12a and b.



Figures 12a and b. Relationship between average measured daphnid specific growth rate (based on daphnid culture biomass, u day^{-1}), calculated exclusive (Figure 12a) and inclusive (Figure 12b) of egg biomass as a function of algal cell concentration (algal cells/ml). The continuous hyperbolic curves in Figures 12a and b are diagrammed as given by Equation 5 (Table 4). The vertical bars indicate the standard error of the mean for the average measured daphnid specific growth rates ($\bar{X} \pm$ S.E.($\bar{X}$).

Table 4. Kinetic rate constants derived from measured daphnid specific growth rates, including and excluding egg biomass, as a function of algal cell concentration provided for the threshold food concentration corrected hyperbolic empirical specific growth rate model (modified Equation 5, $u=u_{max.}(C-C_q)/(C+K_C-2C_q)$). Also given are the associated coefficients of determination (r2).

	$u_{maximum}$	K_C (algal cells/ml)	S_q (algal cells/ml)	r^2
Without Egg Biomass	0.2547	15,305	7,250	1.00
With Egg Biomass	0.3036	16,619	7,250	1.00

Three important features are illustrated in Figures 12a and b. The first is the establishment of an existing threshold food concentration. This food quantity indicates the minimum limit, on an individual daphnid basis, at which an organism is just able to equalize its metabolic losses by assimilation of food so that the body mass of the organism remains constant. Under these conditions biomass production or daphnid specific growth rate is zero. Therefore, if food conditions were to be suppressed below the threshold food concentration, daphnid survivorship would be imperiled.

Threshold food concentrations for individual D. pulex previously have been observed by Lampert (1977c) and Lampert and Schober (1980), and for a variety of rotifer species by Stemberger and Gilbert (1985). Additionally, Lampert (1978) and Lampert and Schober (1980) have identified and estimated a reproductive threshold food concentration defined as the food concentration that just maintains egg production in zooplankton. Such a threshold food concentration required to sustain egg production is defined more in the context of zooplankton population level dynamics where population biomass production must exceed mortality and not just compensate for metabolic losses. In this study, egg production was observed at all algal cell concentrations. This implies, that individual and reproductive threshold food concentrations, as estimated, could have coincided. However, neonate survivorship as a function of algal cell concentration was not evaluated, this could potentially influence the correct estimation of a reproductive threshold food concentration at which viable progeny are produced. This criticism extends also to the data of Lampert (1977c) and Lampert and Schober (1980).

The second important distinctive feature in Figures 12a and b, is the significant relative impact that the contribution of egg biomass has upon calculated daphnid specific growth rates. Including egg biomass in addition to total daphnid body biomass increased calculated specific growth rates by approximately 20% at the maximum point of divergence between the curves presented in Figures 12a and b. The coordinate where curve separation occurs, indicates the point when primiparous females were observed in the culture beakers. Divergence of the two curves in Figures 12a and b, represents the amount of productive energy, measured as specific growth rate, that a gravid female allocates towards reproduction as opposed to the energy partitioned for somatic growth as a function of algal cell concentration.

The final relationship given in Figures 12a and b, is the demonstration of the affect that food availability has upon individual daphnid growth. Daphnid individual specific growth rates increase with increasing algal cell concentration approaching an asymptote at 100,000 algal cells/ml beyond which the rate of daphnid specific growth as a function of increasing food concentration decreases. Increased cladoceran and rotifer growth as a function of increasing food concentration expressed as a hyperbolic functional response in the manner given in Figures 12a and b, has been observed by King (1967), Vijverberg (1976), Lampert (1977b), Porter and Orcutt (1980), Porter et.al. (1983), Orcutt and Porter (1984), and Stemberger and Gilbert (1985).

Daphnid fecundity, measured as eggs per female per clutch, was obtained for all experimental algal cell concentrations and

plotted as a function of carapace length yielding Figure 13. Separate straight line regression models were fit to these data by applying the least squares statistical analysis method (Kleinbaum and Kupper 1978) to predict daphnid fecundity as a function of carapace length at each of the six algal cell concentrations used. Figure 14 illustrates the discrete predictive empirical regression models fit to the fecundity parameters in Figure 13 for each algal cell concentration. Table 5 contains the estimated regression coefficients for the separate straight line regression models corresponding to algal cell concentration and their associated coefficients of determination. A statistical test for coincidence was performed as described earlier (Student's t-test for parallelism of slope and common y-intercept), to determine if significant differences existed among the various straight line regression models as a function of algal cell concentration. Results for the tests for coincidence between the models are presented in Table 6 along with the determined P values. While some of the fecundity regression models did exhibit coincidence, it still can be seen in Figures 13 and 14, that daphnid fecundity, as expressed by eggs per female per clutch, increases with increased carapace length and food concentration.

From Table 5, it is apparent that the regression coefficients (slope and y-intercept), estimated for the daphnid fecundity regression models, vary as a function of algal cell concentration as illustrated in Figures 15a and b. The association between the y-intercept (a) and algal cell concentration can be fit to a straight line regression model by the least squares method yielding Equation 21.

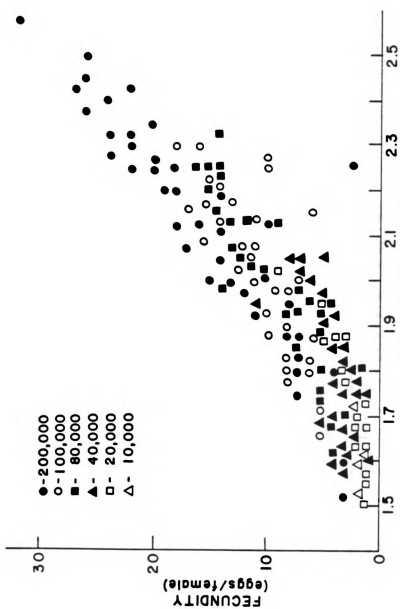


Figure 13. Relationship between daphnid fecundity (eggs/female) and carapace length (mm) as observed for the individual algal cell concentration culture suspensions (algal cells/ml).

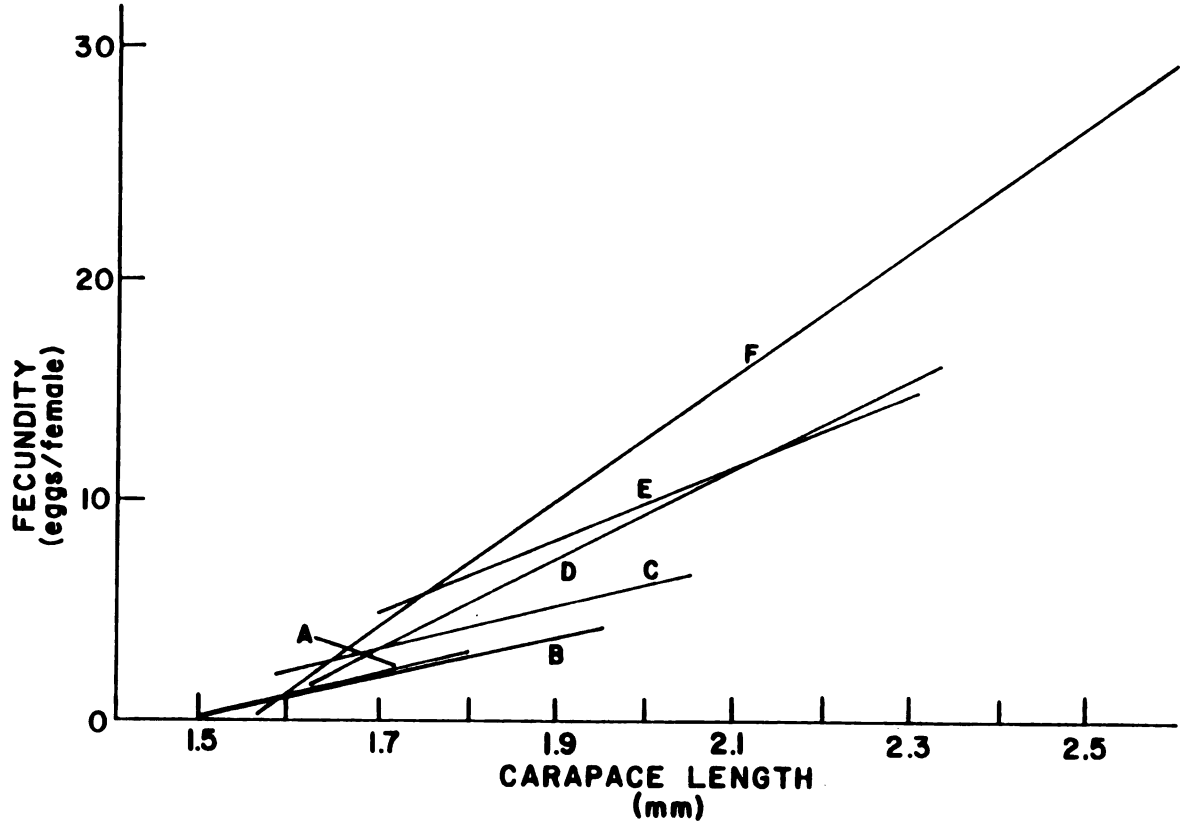


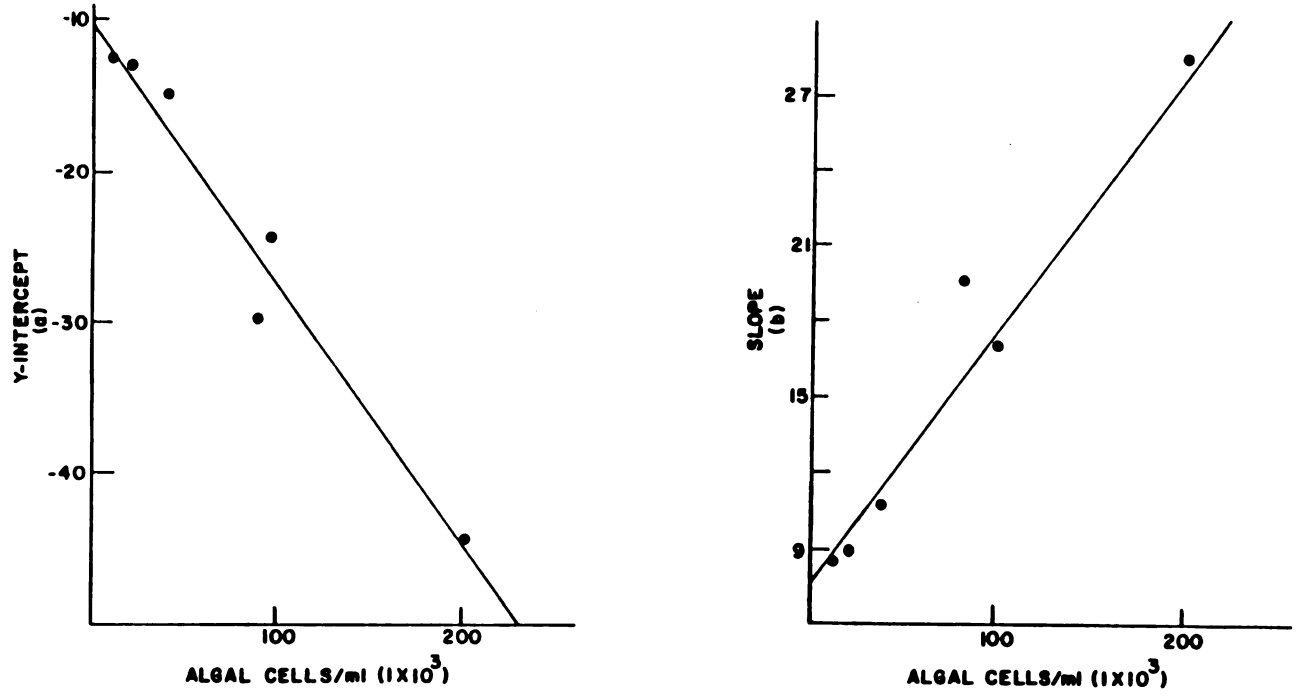
Figure 14. Daphnid fecundity empirical linear regression models (Table 5) graphed as eggs/female as a function of carapace length (mm) for each individual algal cell concentration culture suspension (algal cells/ml) Line A-10,000 algal cells/ml, line B-20,000 algal cells/ml, line C-40,000 algal cells/ml, line D-80,000 algal cells/ml, line E-100,000 algal cells/ml, line F-200,000 algal cells/ml.

Table 5. Regression coefficients for daphnid fecundity empirical models derived from observed daphnid clutch sizes as a function of carapace length for the six discrete experimental algal cell concentrations. Also given are the respective coefficients of determination (r^2) for the linear regression models.

Algal Cell Concentration (algal cells/ml, $1X10^3$)	y-intercept (a)	Slope (b)	r^2
10	-12.4762	8.5714	0.48
20	-12.9529	8.8019	0.69
40	-14.8350	10.4281	0.53
80	-30.8309	20.0716	0.80
100	-24.1441	16.9282	0.65
200	-44.2394	28.4173	0.81

Table 6. Statistical analysis results for the two Student's t-tests for coincidence from separate straight-line fits using the regression coefficients given in Table 5 for each algal cell concentration. Also provided are the corresponding P values for the individual t-tests for common y-intercept (a) and parallelism (b). Significance level = 0.05.

Algal Cell Concentration (algal cells/ml, $1X10^3$)	20	40	80	100	200
20	Coincident a - P>0.90 b - P>0.90				
40	Coincident a - 0<70<P 0.90 b - P>0.90	Coincident a - 0.30<P<0.50 b - 0.50<P<0.70			
80	Not Coincident a - P<0.001 b - NA	Not Coincident a - P<0.001 b - P<0.001	Not Coincident a - P<0.001 b - P<0.001		
100	Not Coincident a - P<0.001 b - NA	Not Coincident a - P<0.001 b - NA	Not Coincident a - 0.02<P<0.05 b - NA	Coincident a - 0.20<P<0.30 b - 0.20<P<0.30	
200	Not Coincident a - P<0.001 b - NA	Not Coincident a - P<0.001 b - NA	Not Coincident a - P 0.001 b - NA	Not Coincident a - 0.01<P<0.02 b - NA	Not Coincident a - 0.01<P<0.02 b - NA



Figures 15a and b. Relationship between the regression coefficients y-intercept (Figure 15a) and slope (Figure 15b) as a function of algal cell concentration (algal cells/ml) obtained from the daphnid fecundity regression models given in Table 5. In Figure 15a, the solid straight line represents Equation 21; $a=-10.38-1.72X10^{-4}(C)$, $r^2=0.92$. In Figure 15b, the solid straight line represents Equation 22; $b=7.45+1.08X10^{-4}(C)$, $r^2=0.93$.

$$a = -10.38 - 1.72 \times 10^{-4} (C) \qquad r^2 = 0.92 \qquad (21)$$

where,

a = y-intercept (regression coefficient)
C = algal cell concentration (algal cells/ml)

Similarly, the relationship between slope (b) and algal cell concentration can be fit to a straight line regression model by the least squares method producing Equation 22.

$$b = 7.45 + 1.08 \times 10^{-4} (C) \qquad r^2 = 0.93 \qquad (22)$$

where,

b = slope (regression coefficient)
C = algal cell concentration (algal cells/ml)

By combining Equations 21 and 22, it is possible to construct a single empirical linear regression model that predicts daphnid fecundity as a function of both carapace length and algal cell concentration as presented in Equation 23.

$$E/F = (-10.38 - 1.72 \times 10^{-4} (C)) + (7.45 + 1.08 \times 10^{-4} (C)) (L) \qquad (23)$$

where,

C = algal cell concentration (algal cells/ml)
L = daphnid carapace length (mm)
E/F = eggs per clutch (predicted daphnid fecundity)

Figure 16 graphically depicts the functional relationships described in Equation 23.

As seen in Figures 12a and b, daphnid growth rate clearly varies as a function of food concentration. Exhibited at the higher algal cell concentrations, is the potential for D. pulex to express

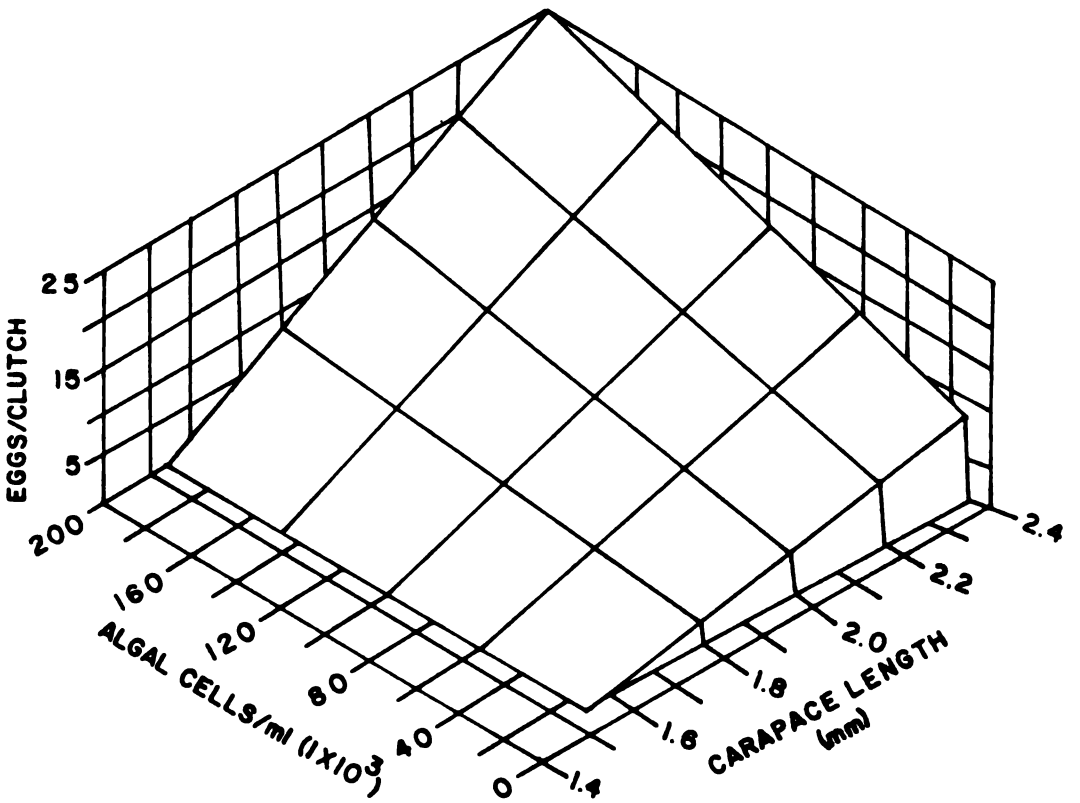


Figure 16. Daphnid fecundity (eggs/female) as a multivariate functional relationship between algal cell concentration (algal cells/ml) and daphnid carapace length (mm) as predicted by Equation 23; $E/F=(-10.38-1.72X10^{-4}(C))+(7.45+1.08X10^{-4}(C))(L)$.

their innate capacity for relatively rapid post embryonic development and attainment of primiparous size (approximately 1.50 mm), while experiencing little mortality.

Daphnid fecundity also is observed to vary as a function of food concentration, as well as with carapace length, as demonstrated in Figures 13 and 14. At all food concentrations, there is a positive linear relationship between daphnid carapace length and fecundity, with greatest size and fecundity observed at the highest food concentration. The functional relationship between daphnid carapace length and fecundity as related to food concentration was conveniently reduced to a single mathematical statement (Equation 23). Illustrating Equation 23 yielded Figure 16, which succinctly demonstrates the prolific reproductive potential of D. pulex with increasing carapace length at high food levels.

Combining the results presented in Figures 12a and b, 13, 14, and 16 for D. pulex, there exists a definite correlation between accelerated daphnid growth and realized prolific fecundity (as a function of carapace length), at elevated food concentrations. These inherent abilities possessed by D. pulex to exploit favorable food conditions and to rapidly incorporate net energy gain into biomass production (somatic and reproductive tissue formation), are very beneficial life history traits considering the ephemeral and dynamic environment in which the population naturally occurs. Of equal importance as demonstrated in this experimental phase, is the observed potential for daphnids to exist under less conducive food conditions which is also characteristic of the fluctuating environment the natural daphnid population is exposed to.

POPULATION GROWTH RATE STUDIES

As indicated in the introduction, the concluding research experimental phase involved the study of the dynamics of daphnid populations. To conduct this study, duplicate daphnid populations were cultured at algal cell concentrations of 0, 10,000, 20,000, 40,000, and 80,000 algal cells/ml at a constant temperature of 27 C., with the algal cell suspensions being renewed daily.

All daphnid population cultures were inoculated with five neonates less than eight hours old produced by a single isolated female maintained in a dense algal cell suspension. The study was terminated after 60 days, during which time viable daphnid populations experienced three oscillating growth and decline cycles. During the entire study period, only dead organisms were removed from the experimental population cultures.

Duplicate daphnid population cultures were censused on alternate days for the population parameters described in the materials and methods section. All surviving daphnids in each population culture were measured for length and size specific daphnid body mass was calculated with Equation 2. Following length to weight conversion, individual daphnid biomass was summed for each population culture yielding total daphnid population biomass for that census period. Daphnid population specific growth rates were calculated for each population culture applying Equation 15 using summed daphnid population biomass values obtained from two consecutive censuses. Also calculated at each census was a food per mass ratio of biomass of algae supplied to a population culture each day (mg) per daphnid population biomass existing when the census was taken (mg). Additional

technical procedures used to perform this experimental laboratory study of daphnid population dynamics were described previously in the methods and materials section.

Daphnid population size observed for the duplicate (A and B Series) population cultures maintained at the five algal cell concentrations are provided in Figures 17 and 18. Figure 17 illustrates daphnid population size expressed in units of number of daphnids in the population as a function of time. Figure 18 illustrates daphnid population size expressed in units of total daphnid population biomass (mg) as a function of time.

It was observed throughout the course of the daphnid population growth rate experiment, that analyzing viable daphnid population dynamics based on population numbers proved to be too variable. This is especially evident when daphnid population numbers were categorized into the eight different size classes for each census period and stable size-age frequency distributions were never attained for any culture population supplied any algal cell concentration. Also encountered were appreciable fluctuations in total population numbers conforming to no apparent pattern when the duplicate populations were compared. This made impossible data analyses and relevant biological conclusions concerning daphnid population numbers as a function of food availability over time.

Moreover, the magnitude of the mass differences exhibited and the unique size specific growth, reproductive, respiration, feeding, and filtering rate kinetics as a function of daphnid body mass noted previously for the eight daphnid size classes argues against using total population numbers. Thus, total population biomass rather than

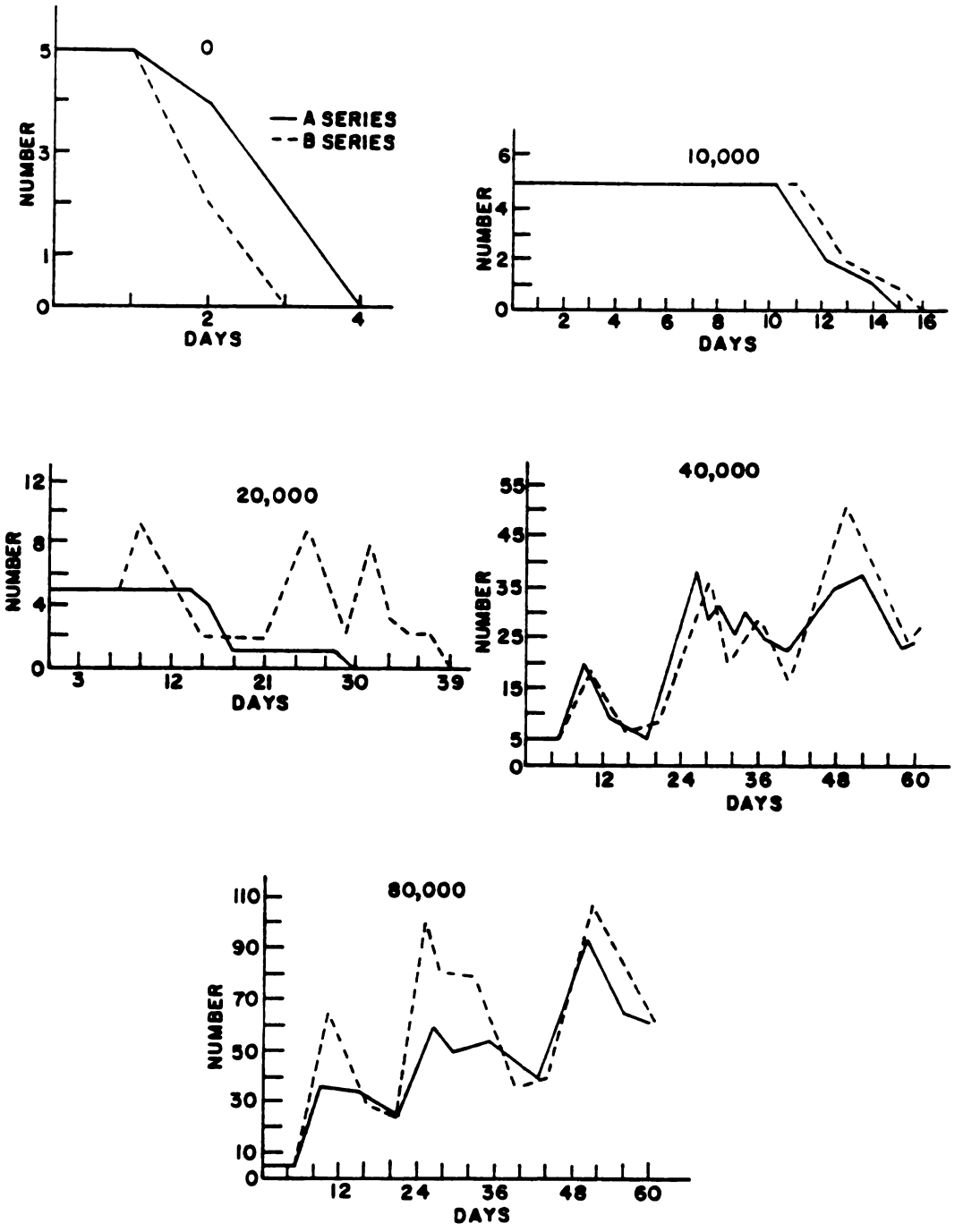


Table 17. Observed culture daphnid population size measured as total population numbers as a function of time (days) for all experimental algal cell food concentrations (algal cells/ml).

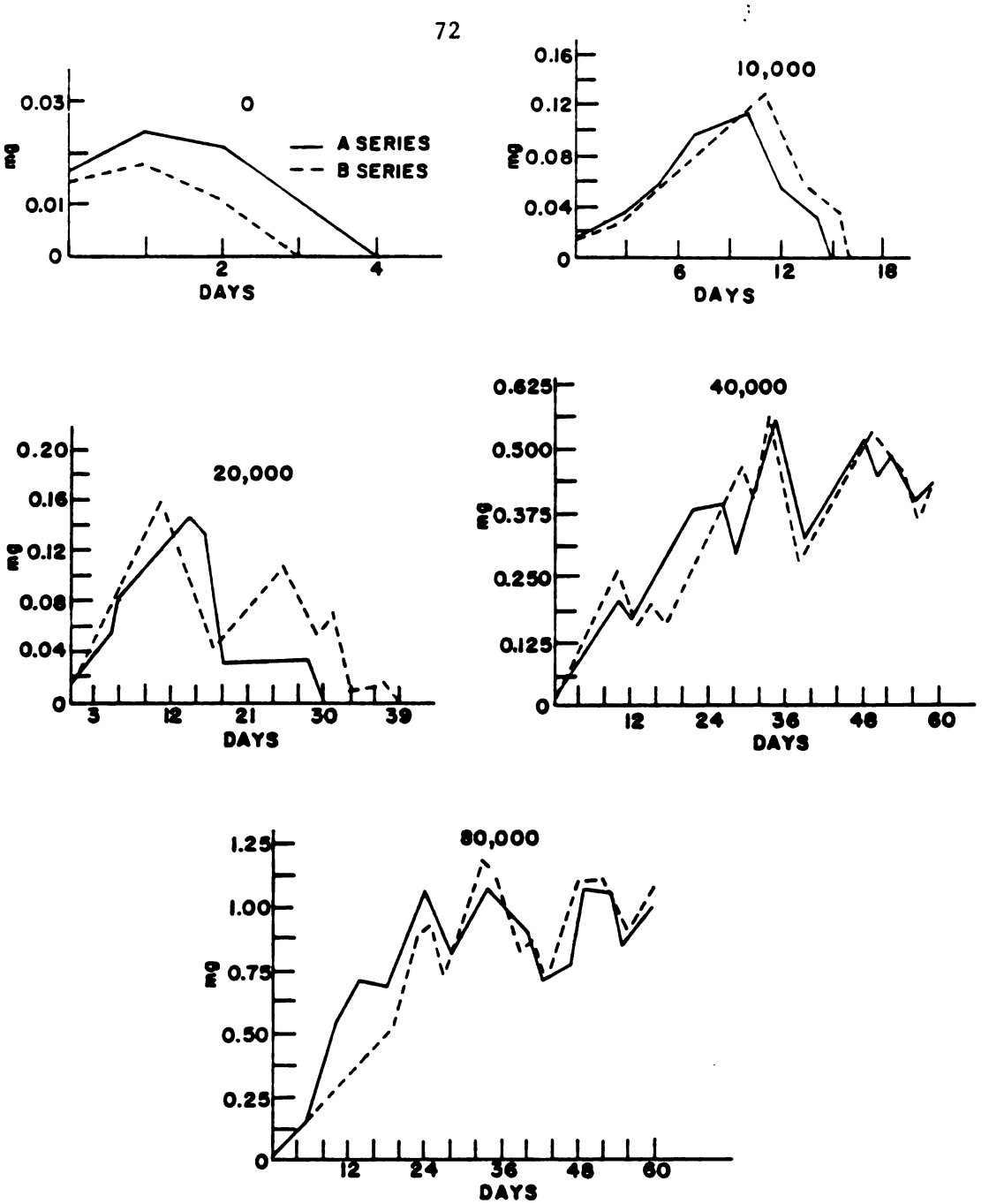


Figure 18. Observed cultured daphnid population size measured as summed population biomass as a function of time (days) for all experimental algal cell food concentrations (algal cells/ml).

numbers appears to be a more biologically meaningful unit upon which to express population dynamic phenomena in these unstable daphnid assemblages. The use of total population biomass units yielded much more regularly oscillating populations which enhanced population dynamic analyses as a function of food availability.

As depicted in either Figure 17 or 18, the daphnid population cultures supplied the three lowest algal cell concentrations (0, 10,000, and 20,000 algal cells/ml), all became extinct, with daphnid populations perishing in relative order of the algal cell concentration suspension provided to each culture.

Despite the extinction of these daphnid population cultures, population growth, measured in units of accrued biomass, occurred prior to culture population death as indicated in Figure 18. In fact, except for the zero algal cell concentration suspension, inoculated daphnid cohorts were observed to attain reproductive size (1.50 mm) and to produce eggs. However, neonates released by the inoculated female daphnid cohorts at these algal cell concentrations were unable to survive to reproductive size thereby, preventing the perpetuation of the population beyond the lifespan of the second generation daphnids.

Apparent neonate growth in the zero algal cell concentration, the growth of the inoculated neonate cohorts to a reproductive size in the 10,000 and 20,000 algal cell concentration suspension, and the failure of the neonate cohorts to produce viable progeny at the same algal cell concentrations can be explained in terms of the relative quantity of accumulated and maternally allocated energy reserves (Lipid deposits) available to each daphnid as suggested by Goulden and Hornig

(1980), Goulden et.al. (1982), Tessier and Goulden (1982), Tessier et. al.(1983), and Goulden and Henry (1984). These residual energy reserves, maternally allocated to the neonates as a function of the abundant food available to the seed female, can be metabolized to temporarily sustain basal metabolism and support body growth for several days even at a zero food concentration level. However, when these maternally allocated lipid deposits are completely metabolized and available body mass catabolized, the neonate expires quickly, since there is no food obtainable to assist in supplementing the required energy necessary to sustain bodily functions.

At the food concentrations of 10,000 and 20,000 algal cells/ml food availability was apparently sufficient for inoculated neonatal filter-feeding activities to supplement maternally allocated energy reserves in suppoying the necessary energy required to support neonatal basal metabolism and growth to reproductive size. However, the substantial impact that adequate maternally allocated energy reserves contribute to potential neonatal growth and survival at low food concentrations is not fully realized until the viability of the inoculated cohort's progeny is assessed.

Apparently, maternal energy reserves possessed by the original inoculated neonates allocated to them from the well fed seed female provided sufficient additional energy to sustain basal metabolism and growth through the most vulnerable daphnid size classes. Once this early critical size class was passed the relative mass normalized filter-feeding and adjusted respiration rate kinetics of the daphnids improved and the energetically superior intermediate sized daphnids could then

fully ruly upon their own abilities at these low food concentrations to obtain the necessary energy to sustain basal metabolism, accumulate energy reserves, support body growth, and initiate reproduction. However, as stated earlier, neonates produced by the females composing the original inoculated cohort at either 10,000 or 20,000 algal cells/ml never survived beyond the neonate and early juvenile size classes. The death of these second generation daphnids before they reproduced at 10,000 and 20,000 algal cells/ml can be attributed to the small quantities of maternal energy reserves allocated to them by their parents existing under conditions of low food availability.

Thus, daphnid population cultures maintained at 0, 10,000, and 20,000 algal cells/ml became extinct following the death of either original inoculated daphnid cohort members or second generation daphnids. Extinction occurred primarily because inoculated females could not allocate sufficient maternal energy reserves to their progeny at these low food levels. Adequate allocated maternal energy reserves are necessary at limiting food concentrations to sustain the relatively inefficient neonate until it develops into a more energetically efficient and competitively superior intermediate daphnid size class.

The existence of such a threshold food concentration required to sustain a viable daphnid population culture was not encountered in the reviewed literature. Previous laboratory studies conducted on zooplankton population dynamics (e.g., Ingle et.al. 1937; Slobodkin 1954; Smith 1963; King 1967; Goulden and Hornig 1980; Stemberger and Gilbert 1985) have all included food concentration ranges sufficient to sustain experimental culture populations where population biomass

production exceeded population metabolic losses and mortality. However, several field investigations did report zooplankton population extinction as a consequence of interspecific competition for a suppressed food base but, they failed to suggest a mechanism responsible for population extinction as a function of food availability (George and Edwards 1974; Kwik and Carter 1975; Allan 1977; Lynch 1978; De Mott 1983; Romanovsky 1984).

Since viable daphnid populations were cultured at a food concentration of 40,000 algal cells/ml and daphnid populations became extinct at a food concentration of 20,000 algal cells/ml (Figures 17 and 18), it can be inferred that the critical population threshold food concentration for D. pulex fed C. reinhardi at 27 C. lies between 20,000 and 40,000 algal cells/ml. This population threshold food concentration (perhaps approximately 30,000 algal cells/ml), is considerably higher than that obtained in the preceding section from Figures 12a abd b and Table 3 (7,250 algal cells/ml). The reason for this discrepancy is associated with the allocation of maternal energy reserves relative to food availability. In this study phase, second generation neonates were not supplied sufficient maternal energy reserves to survive at food concentrations below the threshold. Therefore, by continuously removing released progeny from the culture container and conducting an abbreviated experiment as was done in the individual growth and fecundity rate experiments, a population threshold food concentration was considerably underestimated.

Lampert (1977, 1978b) and Lampert and Schober (1980) defined population threshold food concentration as the quantity of available organic carbon sufficient to induce egg production. However, the

correlation of egg production to minimum resource concentration (Lampert and Schober's estimated reproductive threshold food concentration), is not necessarily an accurate determination of the ability of a daphnid population to persist at specific levels of food availability. Not only do eggs have to be produced but, neonates must also be able to survive given the existing limiting environmental conditions from which they were conceived. Therefore, a more biologically tenable estimation of a population threshold food concentration would include egg production and neonate survival. Neonate survival at limiting food concentrations is dependent upon the maternal energy reserves provided by the female. Maternal energy reserve allocation by the female is related to the energy available to her prior to egg extrusion. This interactive relationship between available energy, maternal energy reserve, and neonate survival is particularly important at lower resource concentrations. To provide an accurate estimate of a population's threshold food concentration, it is not enough to measure only egg production, for to maintain the population, the egg must hatch and the neonates must be able to survive and in turn, produce viable neonates.

Viable daphnid populations, capable of sustained reproductive activities, were cultured at food concentrations of 40,000 and 80,000 algal cells/ml for the entire study period as indicated in Figures 17 and 18. Both populations exhibited typical oscillating growth and decline cycles as observed by numerous researchers conducting similar laboratory zooplankton population studies. The moderating effect that population biomass has in assisting to dampen erratic daphnid population

fluctuations and to indicate the interacting relationships between daphnid population biomass, food availability, and time is apparent in these figures.

Oscillating daphnid population cycles have been discussed by Pratt (1943), Frank (1952), Slobodkin (1954), Smith (1963), and Goulden and Hornig (1980). Fundamental to the understanding of cyclical population oscillations, is the intrinsic biological mechanistic phenomena responsible for producing them. This phenomena has been attributed to a time period delay between an organism's present physiological state and the environmental conditions which provoked that state. Implied is an innate physiological mechanism that makes it impossible for daphnids to instantaneously respond to ephemeral environmental conditions when existing in a dynamic environment. Therefore, an absence of synchronization exists between the organism and its physiological state and the vagaries and vicissitudes of the environment.

In both the 40,000 and 80,000 algal cells/ml food concentrations, the general dynamic growth pattern exhibited was rapid biomass increase, followed by a decline in population biomass, and two subsequent population biomass oscillations of similar magnitude (Figure 18). A sustained, stable, steady-state population biomass equilibrium was never attained for any experimental culture. From the data presented in Figure 18 it appears that a continuing population biomass oscillation is as close as this organism gets to a steady-state equilibrium.

Upon inoculation of the initial five neonates in each culture, algal cell densities were sufficient and population biomass small enough that rapid neonate growth and development was promoted.

Reproductive size was attained quickly with sexually mature adults possessing large quantities of visible lipid deposits as they did throughout their life history. Fecundity rates were high during the early growth phases of each culture and neonate survival was enhanced by the ready availability of maternal energy reserves. With the elevated constant experimental temperature and continued abundant food availability, the population quickly expanded in the cultures fed at 40,000 and 80,000 algal cells/ml.

Since the amount of food fed was constant in each culture, such increases in biomass led to decreases in the food available per milligram of daphnid population biomass. This decrease in the food per mass ratio was accompanied by reductions in the visible oil accumulation within the daphnid hemocoel. This trend continued until the population biomass reached a maximum.

As a consequence of this reduction in food per mass, the amount of lipid deposits accumulated per individual daphnid decreased and the quantity of maternal energy reserve partitioned by ovigorous females to their progeny decreased considerably. Because of the reduced maternal energy reserves, suppressed food availability, and their inefficient mass normalized rate kinetics (Figures 9 and 10) the mortality of the smaller daphnid size classes increased appreciably. The adult size classes, having allocated all their residual energy reserves into reproduction, also experienced high mortality rates at this time as is suggested by Figure 10.

Therefore, with the existing daphnid population biomass apparently exceeding the energy capacity of the system, the population

suffered a crash in numbers as reflected in substantial mortality rates of both the largest and smallest daphnid size classes. A sharp decrease in daphnid fecundity rates occur simultaneously with increasing daphnid mortality rates during this period.

The decreased population biomass associated with such accelerated mortality leads to increased food per mass ratios and increased visible oil accumulation in the surviving daphnids. This assumulation of lipid deposits allows increased growth and increased allocation of maternal energy reserves to neonates in amounts which ensure their survival. The growth of these neonates leads to declining food per mass ratios thereby initiating the next oscillation. As seen in Figure 18 this process appears to be continuous.

Applying simple population dynamics theory to this study, an assumption can be made that an equilibrium biomass exists relative to the supply of available food, the mass of individuals in the population, and the birth rate and death rate of the population. As observed in this study, when food available exceeds population food demand, birth rate will be high and the biomass of the population will increase. As the biomass of the population increases the amount of food per individual decreases, birth rate correspondingly decreases and at some equilibrium population biomass the birth rate should approximately equal the death rate. However, in the populations of D. pulex studied here, a constant population biomass equilibrium is not realized because there is a time lag between the decrease of food concentrations and the delayed response of decreasing birth rates. Because excess fecundity is supported by residual energy reserves,

the daphnid population biomass will exceed the theoretical equilibrium biomass. As a result, the daphnid population starves and experiences high mortality rates. After this population biomass equilibrium point has been exceeded, the population declines in size coincidental to a decrease in population biomass.

The mechanism responsible for the time lag provoking population oscillations has been identified as accumulated or maternally allocated lipid deposits. These residual energy reserves accumulated and allocated during dynamic population phases when food is abundant can be metabolized at high population biomass levels when food is unavailable to temporarily sustain daphnid population activity and reproduction. A population culture system overstressed for energy ensues and the population reacts to deteriorating ambient resource conditions by sacrificing the most vulnerable fraction of its assemblage. Only the most energetically superior and physiologically efficient intermediate sized individuals emerge to perpetuate the population.

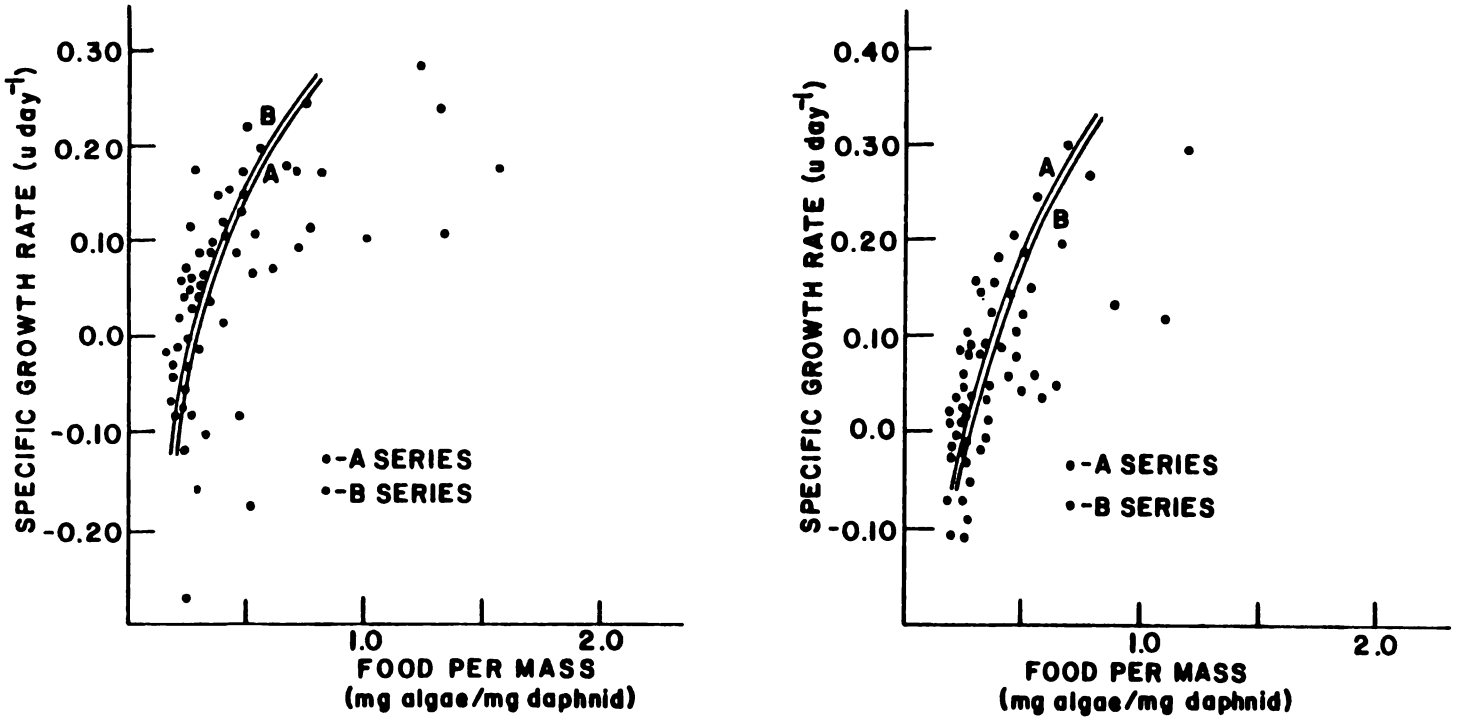
Responding to improved food conditions following the period of population biomass loss, the troughs in the population biomass curves in Figure 18, daphnids began forming lipid deposits necessary to supply the required energy to sustain continued growth, reproduction, and basal metabolism. This is indicative of another population time lag as the population continues its cyclical oscillation around the theoretical equilibrium population biomass (Figure 18).

The relationship between two of the population parameters measured at each census, population specific growth rate and the ratio of total mass of food supplied to existing total daphnid

population biomass is illustrated in Figures 19a and b. Observed throughout the oscillating population growth and decline phases of positive and negative rates of population biomass change (Figure 18), is a continuous fluctuation of the population specific growth rate above and below the theoretical population equilibrium value. Below this theoretical population equilibrium, the trouth in population curves in Figure 18, population specific growth rates are positive and above, the apex on the population curves in Figure 18, they are negative.

Using Figures 19a and b, it is possible to illustrate the biological relationship that exists between calculated population specific growth rates and the measured food per mass ratio. Upon inoculation of the initial daphnid cohort, calculated population specific growth rates are high as are the measured food per mass ratios. This implies excellent growth potential since there is sufficient algal biomass availability to promote and support high daphnid population biomass production rates. However, as the daphnid population biomass increases and the measured food per mass ratio decreases, the accompanying population specific growth rates decrease concurrently. Once the population begins its typical oscillating growth and decline cycle, population specific growth rate alternatives between positive and negative rates. Negative specific growth rates occur as the population biomass curve descends from apex to trough and positive specific growth rates occur as the population biomass curve ascends from the trough to the next apex.

Alternating positive and negative population specific growth rates also appear to be confined within a distinct food per mass range



Figures 19a and b. Relationship between measured daphnid population specific growth rate (u day^{-1}) and food per mass (mg algae/mg daphnid) obtained from the duplicate 40,000 (Figure 19a) and 80,000 (Figure 19b) algal cells/ml food concentration daphnid population cultures. The continuous hyperbolic curves were drawn using Equation 5 and the kinetic rate constants given in Table 8. Curve A represents the series A population duplicate and curve B represents the series B population duplicate in each figure.

characteristic for the experimental algal cell concentration fed each population culture (Figures 19a and b).

As proposed earlier, population dynamics theory assumes that an equilibrium biomass exists between the supply of available food and population biomass. Though this equilibrium biomass is never attained indefinitely for any daphnid culture assemblage exhibiting an oscillating population growth pattern, due to time lag effects, there is a maximum population biomass that can be supported provided a constant rate of energy availability. What eventuates, because of experimentally imposed energy constraints, is a daphnid population biomass incessantly fluctuating around this theoretical population biomass equilibrium point. Above which the population culture system is energy stressed and population biomass declines. Below which the population culture system has sufficient resources and population biomass increases.

Therefore, as presented, the theoretical daphnid population equilibrium biomass is defined by the amount of energy available to the culture system. The theoretical equilibrium biomass is the food per mass ratio where biomass of algae supplied to the system per maximum daphnid population biomass that can be sustained is equivalent to a population specific growth rate of zero. At this specific growth rate, daphnid population biomass production equals population mortality and metabolic losses; and the population exists at equilibrium. This food per mass ratio, where the daphnid population specific growth rate equals zero can be referred to as the population maintenance threshold. Whenever the daphnid population biomass and its

exerted energy demands increase beyond the capacity of the culture system's available energy supply, yielding a food per mass ratio below the threshold, negative specific growth rates occur. This indicates an energy deficient system and the daphnid population responds by experiencing high mortality rates, reduced fecundity rates, and decreasing population biomass. Completing the downward cyclic phase, the reduced daphnid population biomass and its associated decreased energy demand is underutilizing the culture system's capacity to supply available energy. The food per mass ratio increases to levels above the threshold and positive specific growth rates occur. This indicates the culture is able to support additional daphnid biomass production and the population responds by increasing its intrinsic birth rate and body growth and population biomass increases.

The population maintenance threshold food per mass ratios were calculated with Equation 8. Prior to estimating the population maintenance threshold food per mass ratios, necessary terminology substitutions in Equation 8 were made; (u) for (A/D/T) and log (food per mass) for log (C). The population maintenance threshold food per mass ratios were computed for the duplicate 40,000 and 80,000 algal cells/ml cultures and are given in Table 7 with their respective coefficients of determination (r^2).

Theoretically, it would be expected that the population maintenance threshold food per mass ratios calculated for each daphnid population supplied either algal cell food concentration would be equivalent. However, as observed in Table 7, the population maintenance threshold food per mass ratios calculated for the 40,000 algal cells/ml food concentration cultures are slightly higher than those calculated

Table 7. Population maintenance threshold food per mass ratios derived from measured daphnid population specific growth rates as a function of log algal biomass supplied per daphnid population biomass using Equation 8 for the duplicate 40,000 and 80,000 algal cells/ml food concentration daphnid population cultures. Also provided are the associated coefficients of determination (r^2).

	population cultures series A		population culture series B	
	40,000 algal cells/ml	80,000 algal cells/ml	40,000 algal cells/ml	80,000 algal cells/ml
AB/DB_q	0.3119	0.2602	0.3001	0.2829
r^2	0.71	0.82	0.69	0.86

for the 80,000 algal cells/ml cultures. This measured discrepancy might occur because of possible increased daphnid population energy requirements necessary to sustain elevated filtering activities at a more dilute algal cell suspension (40,000 algal cells/ml) than a more dense algal cell suspension (80,000 algal cells/ml). Regardless, the daphnid population cultured at either algal cell suspension appear to require approximately 29 percent of the population's body biomass in food per day when the populations are existing at theoretical equilibrium conditions. Other suggestions as to why a slight difference exists between the two sets of calculated population maintenance threshold food per mass ratios involve technical laboratory experimental error or fundamental experimental aberrations due to inherent biological variability.

The empirical threshold corrected hyperbolic model (Equation 5) was used to predict daphnid population specific growth rate as a function of algal biomass supplied per existing daphnid population biomass. To this model were fit measured daphnid population specific growth rates in relation to observed food per mass ratios obtained for both the 40,000 and 80,000 algal cells/ml cultures at each census. To correctly apply Equation 5 for this fit, it was necessary to substitute for the appropriate terminology in the model; (u) for (A/D/T), ($u_{max.}$) for ($A/D/T_{max.}$), (AB/DB) for (C), (AB/DB_q) for (C_q), and ($K_{AB/DB}$) for (K_C). AB/DB was defined as the food per mass ratio.

The linear transformation given by Equation 9 was used to calculate the kinetic rate constants; ($u_{max.}$) and ($K_{AB/DB}$). The population maintenance threshold food per mass ratio values used were those

in Table 7. Kinetic rate constants for Equation 5 calculated for both duplicate sets of daphnid population cultures are given in Table 8, along with the associated coefficients of determination (r^2). The population maintenance threshold corrected hyperbolic curves illustrating predicted daphnid population specific growth rates computed as a function of algal biomass supplied per daphnid population biomass are presented as the curves in Figures 19a and b.

Unique to this method of predicting daphnid population specific growth rates, is the ability to relate daphnid population specific growth rate to some function of resource availability. In this context, daphnid population dynamics expressed as specific growth rates are related to potentially controlling environmental factors such as the relative supply of some identified limiting resource. For this study, food was established as the limiting factor regulating daphnid population growth or biomass production. In the presented population specific growth rate model however, the limiting resource term is seen to be the food per mass ratio rather than absolute food concentration.

Demonstrating the importance of this relationship between available food and daphnid population biomass as observed for the viable daphnid populations, a population maintenance threshold food per mass ratio (AB/DB_q) was estimated for the daphnid population cultures existing at equilibrium (specific growth rate equalling zero). This ratio represents maximum daphnid population biomass that can be sustained given a defined concentration of food supplied daily to the daphnid population cultures (Table 7). Whenever total daphnid population biomass increased to cause food per mass ratios to fall below the

Table 8. Kinetic rate constants derived from observed daphnid population specific growth rates as a function of algal biomass supplied per daphnid population biomass obtained from the duplicate 40,000 and 80,000 algal cells/ml food concentration daphnid population cultures provided for the threshold corrected hyperbolic empirical model (modified Equation 5, $M = M_{max.}\frac{AB/DB - AB/DB_q}{AB/DB + K_{AB/DB} - 2(AB/DB_q)}$). Also given are the coefficients of determination (r^2) calculated for the model as fit to the measured data.

	population culture series A		population culture series B	
	40,000 algal cells/ml	80,000 algal cells/ml	40,000 algal cells/ml	80,000 algal cells/ml
$u_{max.}$	0.68	0.98	0.61	0.86
$K_{AB/DB}$	1.047	1.310	0.9245	1.224
AB/DB_q	0.3119	0.2602	0.3001	0.2829
r^2	0.97	0.99	0.98	0.99

theoretical threshold, negative population specific growth rates were calculated and observed (Figures 19a and b). When total daphnid population biomass decressed yielding food per mass ratios above this threshold value, positive population specific growth rates were calculated and observed (Figures 19a and b). This dynamic pattern results in a continuous oscillating population growth and decline cycle with daphnid population biomass fluctuating around the theoretical population biomass equilibrium quantity represented by the population maintenance threshold food per mass ratio derived for each population culture system for a certain level of food availability (Figure 18). Therefore, the food per mass ratio represents the primary controlling factor existing in this experimental phase.

Integral to this discussion of daphnid population dynamics as a function of food availability, is the quantification of the amount of food consumed by each mass specific daphnid size class in a day at various phases of the population cycle utilizing Equation 6 and the filter-feeding kinetic rate constants obtained in the first experimental section for both conventional and mass normalized filter-feeding rate units (Table 1). Of equal value is the relative daphnid size specific mass normalized food consumption efficiencies at suppressed food conditions affecting size specific daphnid survival expressed by calculated relative mass normalized respiration rate efficiencies (Figure 10).

To perform this exercise, a representative population biomass apex and trough (Figure 18) were selected for the 40,000 and 80,000 algal cells/ml cultures after the culture populations had attained their oscillating steady state existence.

Table 9 gives the relative statistics, parameters, and size-specific daphnid population composition distributions obtained from the respective census dates when daphnid population biomass is high (apex) and when it is low (trough) for all four daphnid population cultures used in this analysis. For each individual daphnid size lass present in the population for either biomass level, the amount of algae consumed per hour was determined with the kinetic rate constants. Following the discrete measurement of algal cell consumption for all individual daphnid size classes multiplied by the number of daphnids in each size class, total algal cell consumption for the population per hour was obtained and subtracted from the original algal cell concentrations supplied to each population. This adjusted food concentration represents the quantity of algae available for consumption beginning the second calculated hourly feeding interval. This iterative feeding rate process was continued until the algal cell concentration was reduced to less than 1,000 algal cells/ml. Iterative algal cell consumption computation below this food concentration was demonstrated to have a minimal quantitative effect on established daphnid size class consumption values.

Concluding the final iterative food consumption calculation, discrete algal cell consumption for each daphnid size class per hour was summed for the entire feeding interval, divided by the number of daphnids composing each individual size class, and algal cell concentration converted to mass (3.00×10^{-8} mg/C. reinhardi algal cell). A subsequent mass conversion involved normalizing discrete daphnid algal cell consumption per day by mean individual daphnid size class mass.

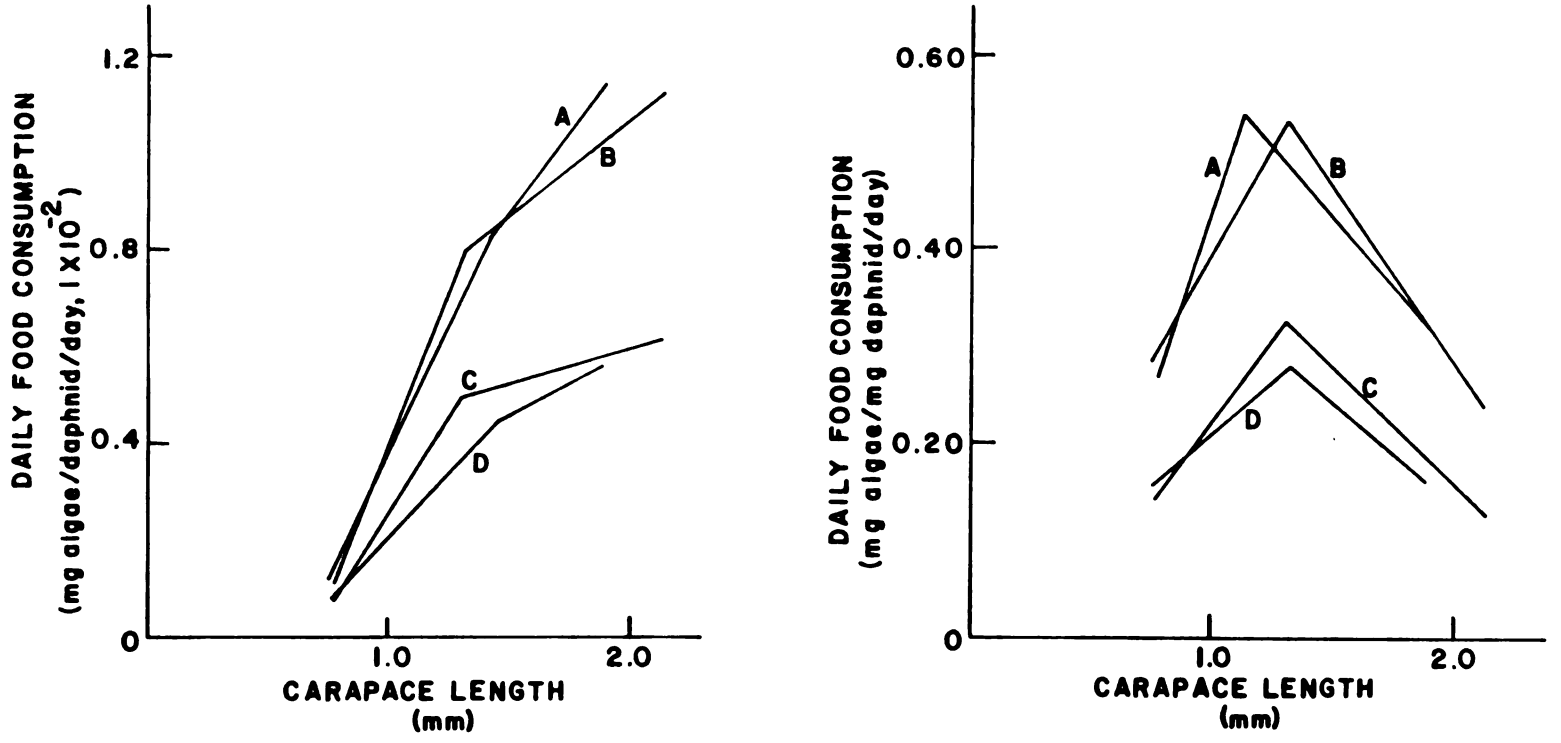
Table 9. Measured cultured daphnid population parameters and statistics obtained from representative census dates when population biomass levels were high (apex) and low (trough) for both 40,000 and 80,000 algal cells/ml food concentrations.

	40,000 (apex)	40,000 (trough)	80,000 (apex)	80,000 (trough)
mean carapace length ovigorous females (mm)	1.78	1.87	1.81	1.95
mean clutch size (eggs/female)	2	4	2	5
number ovigorous females	3	7	4	18
number females reproductive size	11	7	17	18
total eggs	6	31	9	83
predicted clutch size (eggs/female)	4	5	5	7
size class and number				
0.69-0.88 mm	2	11	13	10
0.89-1.00 mm	0	1	9	6
1.01-1.25 mm	8	3	26	3
1.26-1.38 mm	6	0	12	1
1.39-1.50 mm	2	2	4	2
1.51-1.75 mm	8	4	7	9
1.76-2.00 mm	2	3	9	8
2.01-2.25 mm	1	0	0	1
population number	29	24	80	40
population biomass (mg)	0.57	0.32	1.18	0.73

Illustrated in Figure 20a, is the mass of algae consumed per daphnid per day for the categorized daphnid size classes. As would be expected, the largest daphnid size classes because of their quantitatively superior filter-feeding rate capacities on an individual basis consumed more algal biomass than the smaller daphnid size classes at either high or low population biomass levels. However, all daphnid size classes are observed to consume a larger biomass of algae when population biomass levels are low (troughs in the population curves in Figure 18), than when population biomass levels are high (apexes in the population curves in Figure 18), regardless of supplied food concentration.

Normalizing the mass of algae consumed per daphnid size class individual per day by the mass of the average daphnid size class individual for both high (apex) and low (trough) population biomass levels, yields Figure 20b. By normalizing food consumption by daphnid body biomass, the relative competitive efficiencies of the various daphnid size classes can be exhibited when food is suppressed at higher levels of population biomass and when food is abundant at lower levels of population biomass.

As observed in Figure 20b, the intermediate daphnid size classes possess the most competitive and efficient daily mass normalized food consumption rates regardless of population biomass levels at either food concentration. Also demonstrated in Figure 20b, is the considerably increased quantity of food consumed by each daphnid size class when population biomass is low as compared to when population biomass is high. This difference in food consumption rates, as



Figures 20a and b. Relationship between calculated daily daphnid food consumption in both conventional (mg algae/daphnid/day, Figure 20a) and mass normalized (mg algae/mg daphnid/day, Figure 20b) feeding rate units as a function of carapace length (mm) determined using Equation 6 and the kinetic rate constants given in Table 1 for duplicate high and low cultured daphnid population biomass levels (Table 9) supplied 40,000 and 80,000 algal cells/ml each day. Curve A represents low population biomass supplied 40,000 algal cells/ml, curve B represents low population biomass supplied 80,000 algal cells/ml, curve C represents high population biomass supplied 40,000 algal cells/ml, and curve D represents high population biomass supplied 80,000 algal cells/ml, in each respective figure.

related to daphnid population biomass, indicates the mass of algae required per unit daphnid body mass for the population to experience positive rates of population biomass production which occurs at the trough.

Daphnids of any size class consume a larger mass of algae per individual or per unit body mass in a day when daphnid population biomass levels are low than they do when daphnid population biomass levels are high (Figures 20a and b). Also explicit, as presented in Figure 20b, is the increased relative efficiencies of the mass normalized intermediate daphnid size classes' daily food consumption rates implying a superior intraspecific competitive position and ability. This would appear to be very important when population biomass levels are high and food availability is low.

On a population level the results presented in Figures 20a and b would predict that at low population biomass levels and abundant food availability the daphnid population would be expected to; accumulate lipid deposits, allocate sufficient maternal energy reserves to the neonates, increase fecundity rates, decrease mortality rates, and exhibit positive rates of population biomass production changes. Indeed, all of the above daphnid population dynamic parameters indicative of low population biomass and increased food availability, were observed in the census data as would be predicted given the information contained in Figures 20a and b.

Predicted population dynamic parameters observed for a daphnid culture population existing at a high population biomass level and reduced food availability would be expected to be the reciprocal of

those presented above. Upon examination of the daphnid population census data, these parameters at this cyclic phase clearly show that given a high population biomass level and suppressed food conditions the inverse of those population dynamics measures presented above are realized.

Of particular interest is the remarkable similarity exhibited between the calculated daphnid daily food consumption rate curves adjusted for size class numbers as related to daphnid population biomass between the 40,000 and 80,000 algal cells/ml cultures (Figures 20a and b). This coincidence suggests that daphnids composing a viable population consume proportionately identical quantities of food per day supplied various concentrations of food above the population threshold food concentration when food consumption is adjusted for population numbers and therefore, that daphnid population biomass is certainly a function of algal biomass availability. Implied in the preceding statement, is that since daphnids characteristically consume equivalent discrete quantities of food per individual size class at distinct food levels, daphnid populations supplied a higher level of food availability should reflect a relative increase in population biomass production as is observed in Figure 18.

As discussed previously, daphnid mortality rates increase when daphnid population biomass has exceeded the carrying capacity of the food limited culture system. Daphnid size classes possessing the highest mortality rates during this population biomass decline phase were observed to be the smallest and largest daphnid size classes, while the intermediate daphnid size classes exhibited the lowest mortality rates.

This poor survivorship potential of the smallest and largest adult daphnid size classes at low food concentrations was predicted in the first experimental phase as illustrated in Figures 9 and 10. At the lowest food concentrations for which daphnid size class mass normalized feeding rates and feeding rate adjusted respiration rate efficiencies were calculated (Figures 9 and 10) the superior competitive positions of the intermediate daphnid size classes and the inferior competitive positions maintained by the smallest and largest daphnid size classes were evident. The smallest and largest daphnid size classes therefore, would be assumed to be most vulnerable to starvation at low food concentrations given their inferior relative mass normalized filter-feeding and respiration rate efficiencies. This corresponding fundamental assessment between predicted and observed differential daphnid size class survivorship when population biomass is high and food availability is suppressed is illustrated in Figures 20a and b for realized daily food consumption for each daphnid size class.

Effectively shown in Figures 20a and b, is the realized vulnerable position that the smallest and largest daphnid size classes were predicted to maintain from the results depicted earlier in Figure 9, based on individual mass normalized filter-feeding rate kinetics. It is clear, that the food per mass that the smallest and largest daphnid size classes are capable of consuming when food is suppressed is considerably inferior to that consumed per day by the intermediate daphnid size classes under the same environmental food conditions. By combining Figure 10 with Figures 20a and b, it is possible to explain the

observed differential size-specific daphnid mortality rates exhibited at the population biomass level when food is scarce. That being, on a per unit daphnid body biomass basis, the determination that the smallest and largest daphnid size classes possess the most inferior mass normalized filter-feeding rates at low food concentrations and therefore, are incapable of maintaining their inefficient feeding rate adjusted respiration rates when competing for a limited suppressed food base with more efficient intermediate daphnid size classes. Their vulnerable position is further exacerbated at low food densities by deficient maternally allocated and accumulated energy reserves.

Though the fundamental shapes of the curves illustrated in Figures 20a and b are identical for both food concentrations and population biomass levels, food consumption is apparently sufficient when population biomass is low to allow reduced mortality.

The average food consumption value of all daphnid size classes was 38 percent of daphnid body weight per day at low population biomass where population biomass production was occurring. At high population biomass this average value was 21 percent of daphnid body weight per day when population biomass production was decreasing. These values compare favorably with the theoretical population equilibrium threshold value of 29 percent of daphnid body weight per day calculated previously.

Daphnid fecundity also was observed to increase and decrease with the relative quantitative daily food consumption rates of the reproductive daphnid size classes (greater than 1.50 mm carapace length), during the respective periods of low and high population biomass levels

and food availability (Figures 20a and b). As would be expected, when reproductive daphnid size classes were calculated to consume a relatively greater proportion of food at low population biomass levels their measured mean fecundity increased as did the number of ovigorous females and mean carapace length (Table 9). At high population biomass levels and suppressed food conditions when relative daily food consumption rates of the reproductive daphnid size classes were low (Figures 20a and b) fecundity and carapace length were reduced (Table 9).

Of additional interest to this present discussion, is the applicability and accuracy of Equation 23 as it pertains to the observed data for the daphnid culture populations existing at high and low population biomass levels and thus suppressed and abundant food availability. Daphnid fecundity was estimated using mean daphnid carapace lengths and beginning food concentrations (40,000 and 80,000 algal cells/ml), for both food availability and population biomass ambient environmental conditions with these calculated results presented in Table 9. The predicted fecundity values obtained from Equation 23 slightly overestimated measured daphnid fecundity. However, the general trends exemplified in the census data for each food availability and population biomass environmental condition is duplicated in the predicted fecundity values.

Overall, daphnid fecundity, mean carapace length, and the number of ovigorous females in the populations were seen to increase with a decrease in population biomass and the resulting increase in food per mass ratios. At higher population biomass levels and thus lower food per mass ratios, daphnid fecundity, mean carapace length, and the number of ovigorous females were all reduced.

In the individual daphnid growth and fecundity rate experimental phase, a potential was observed for both rapid daphnid development to a large body size and for prolific reproductive output with increasing food concentrations (Figures 12a and b, and 16 and Tables 3 and 4). Similarly, in the feeding and filtering rate experimental phase, there was a substantial maximum potential ($A/D/T_{max.}$) for daphnid grazing pressure at any food concentration (Table 1 and 2). However, in the daphnid population studies these high potentials for daphnid growth, fecundity, and grazing were never realized after the culture populations began to oscillate.

Utilizing the data obtained for the 80,000 algal cells/ml individual daphnid growth and fecundity rate study and comparing it with the census parameters observed for the 80,000 algal cells/ml daphnid population experiment indicates disparities in both average maximum adult daphnid size attained and egg clutch size. An average daphnid carapace length of 1.88 mm and an average clutch size of four eggs per female for the ovigorous females in the population study were both much lower than the average carapace length of 2.35 mm and clutch size of 18 eggs per female observed for ovigorous females in the individual growth and fecundity study supplied the same algal cell concentration (Table 9).

Apparently, intense intraspecific competitive pressure for a limited suppressed food supply in a daphnid population where neonates are not removed leads to reductions in both daphnid carapace length and clutch size far below their potential.

Data provided in Table 10 gives the potential algal cell consumption by daphnid size class when their maximum grazing rates (Table 1) are multiplied by the number of daphnids in a particular size class extrapolated for an entire day. Also presented is the realized algal cell consumption for the particular daphnid size class as calculated iteratively for hourly decreases in algal cell concentration using the feeding rate kinetic constants in TAble 1. Total potential food consumed per day is considerably higher than what is realized by the individual daphnid size classes composing the populations. In fact, realized average daphnid population daily food consumption never exceeds 13 percent of the potential, even when population biomass levels are low. Therefore, this food consumption differential suggests that the daphnids composing a growing population are continuously exposed to a critically food limited environment as measured by their realized decreased maximum carapace lengths attained, reduced clutch sizes, and underutilized filter-feeding rate capacities expressed in terms of total daily food consumption as compared to their potential. By having to persist under less than optimum food conditions, which the daphnid population creates for itself through excess grazing and reproductive pressure supported by residual energy reserves, daphnid potentials are inhibited and a stunted daphnid population develops. Stunting as a function of food limitation is also encountered in natural cladoceran populations (Brambilla 1980).

Emphasized throughout this concluding experimental phase has been the substantial interactive relationship that has been observed to exist between algal biomass availability and daphnid population

Table 10. Calculated maximum potential and observed realized daily total food consumption using daphnid population composition size distribution data presented in Table 9 for high (apex) and low (trough) population biomass levels applying derived feeding rate kinetic constants given in Table 1 for Equation 6.

80,000 algal cells/ml (trough)

Size (mm)	Daphnid Number	Potential $A/D/T_{max.}$ (algal cells/day)	Realized A/D/T (algal cells/day)
A- 0.69-0.88	10	6,154,280	408,040
B- 0.89-1.00	6	5,869,728	505,926
C- 1.01-1.25	3	2,905,704	495,642
D- 1.26-1.38	1	1,317,768	263,660
E- 1.39-1.50	2	4,275,216	525,470
F- 1.51-1.75	9	19,781,280	2,570,400
G- 1.76-2.00	8	18,116,352	2,768,216
H- 2.01-2.25	1	3,131,856	372,361

80,000 algal cells/ml (apex)

Size (mm)	Daphnid Number	Potential $A/D/T_{max.}$ (algal cells/day)	Realized A/D/T (algal cells/day)
A	13	8,000,304	293,306
B	9	8,804,592	414,900
C	26	25,182,768	2,279,784
D	12	15,803,216	1,661,712
E	4	8,550,432	567,196
F	7	15,385,440	1,076,313
G	9	20,380,896	1,673,190
H	0		

Table 10 (Continued . . .)

40,000 algal cells/ml (trough)

Size (mm)	Daphnid Number	Potential $A/D/T_{max.}$ (algal cells/day)	Realized A/D/T (algal cells/day)
A	11	6,769,488	418,506
B	1	978,288	81,129
C	3	2,905,704	552,102
D	0		
E	2	4,275,216	539,708
F	4	8,791,680	1,187,820
G	3	6,793,632	1,131,468
H	0		

40,000 algal cells/ml (apex)

Size (mm)	Daphnid Number	Potential $A/D/T_{max.}$ (algal cells/day)	Realized A/D/T (algal cells/day)
A	2	1,230,816	163,008
B	0		
C	8	7,748,544	775,592
D	6	7,906,608	968,580
E	2	4,275,216	286,604
F	8	17,583,360	1,260,112
G	2	4,529,088	398,524
H	1	3,131,865	201,798

biomass. Clearly, all daphnid population parameters censused were influenced by food concentration. Two indices indicative and sensitive to food availability were measured daphnid population specific growth rate and the observed relative quantities of accumulated or maternally allocated residual energy reserves possessed by the various experimental daphnid size classes.

Since daphnid population specific growth rates were calculated in terms of population biomass production rates in a culture system where supplied food quantities were constant, it was possible to relate population specific growth rate as a function of food per mass. As presented earlier, when positive rates of population biomass changes were recorded (reflective of low population biomass and abundant food availability), food per mass ratios measured exceeded the estimated theoretical population maintenance threshold food per mass ratio. During this period of positive rates of daphnid population biomass production changes, daphnids of all size classes were observed to possess increased amounts of visible residual energy reserves (lipid deposit formation). This physiological phenomenon is characteristic of population biomass growth intervals when food is abundant.

However, when daphnid population biomass production surpassed the culture system's carrying capacity (indicating high population biomass and scarce food availability), measured food per mass ratios descended below the estimated theoretical population maintenance threshold food per mass ratio. This suggests that the food mass supplied to the culture system is insufficient to maintain the existing excess daphnid population biomass and negative rates of population biomass production occur as a consequence of population starvation.

Providing energetic support to daphnid population biomass overproduction when food availability per daphnid population biomass was progressively decreasing, was the metabolization and subsequent depletion of previously accumulated and maternally allocated residual energy reserves. Utilization of stored or conferred lipid deposits desensitizes the daphnid population to rapidly declining food conditions and provides energy to stimulate excess reproduction and grazing pressures beyond the culture system's limited energy capacity. This temporary support of excess daphnid reproduction and grazing pressures eventually creates starvation food levels and the daphnid population begins to crash.

Despite the apparent function that residual energy reserves have in causing negative daphnid population biomass production rates and possible population extinction, residual energy reserves were observed to possess a redeeming quality by providing a deposit from which necessary energy can be extracted to sustain the most efficient daphnid size classes through periods of food scarcity ensuring the population's continued existence.

Daphnid population dynamics during the period when the population is characterized by oscillating conditions of high and low daphnid population biomass levels and abundant and scarce food availability, could be considered the daphnid's vacillating steady-state existence. Daphnid population oscillations stimulated by organismal time lags induced by residual energy reserve accumulation or allocation and subsequent use delay daphnid physiological state response to the prevailing environmental conditions. Lipid deposit formation or allocation

and subsequent utilization corresponding to existing daphnid population food per mass ratios varies around the population maintenance threshold food per mass ratio.

Characteristic of growing daphnid population cultures are great latent unrealized grazing, growth, and reproductive potentials that only exhibited when algal biomass availability appreciably exceeds daphnid population biomass. As demonstrated, daphnid population cultures, once they attain their characteristic oscillating steady-state existence, are confined to the constraints of a population induced food limited environment as indicated in their sub-optimal population parameters mentioned previously. This latent potential represents a considerable unrealized population response mechanism should food availability increase dramatically.

It is these unrealized grazing, growth, and reproductive potentials which allows filter-feeding cladocerans to maintain the low phytoplankton abundance critical to biomanipulation of eutrophic lakes. It appears that once these cladocerans reach their oscillating steady-state and the accompanying low phytoplankton abundance, their significant unrealized grazing, growth, and reproductive potentials inhibits the development of blooms of any phytoplankton which can be ingested and assimilated by the cladocerans. Thus, if piscivorous fish can maintain control of zooplanktivorous fish predation upon filter-feeding cladocerans, the cladocerans will maintain phytoplankton biomass at desirable levels.

CONCLUSIONS

1. Feeding rate kinetics of *D. pulex* fed *C. reinhardi* at 27 C. can be empirically modeled to fit a Michaelis-Menten type hyperbolic function.

2. Filtering rate kinetics of *D. pulex* fed *C. reinhardi* at 27 C. can be empirically modeled to fit a negative exponential function.

3. There was no distinct experimental evidence supporting a feeding or filtering rate empirical model threshold food concentration correction for *D. pulex* fed *C. reinhardi* at 27 C.

4. Daphnid filtering rates can be predicted from a multivariate functional relationship of both algal cell concentration and daphnid carapace length.

5. Intermediate daphnid size classes were observed to possess the most efficient and competitive intra-specific mass normalized filter-feeding and respiration rate kinetics at low food concentrations.

6. All measured daphnid feeding and filtering rate kinetic quantities were observed to differ with daphnid carapace length and therefore, body mass.

7. At zero algal cell concentration food levels, daphnid body growth occurred, apparently supported by maternally allocated energy reserves possessed by the neonates prior to experimental inoculation.

8. To predict individual daphnid specific growth rates as a function of algal cell concentration, average measured daphnid specific growth rates and corresponding algal cell concentrations were fit to the threshold food concentration corrected hyperbolic empirical model.

9. It was demonstrated, that daphnid individual specific growth rates increase with increasing algal cell concentration approaching an asymptote at 100,000 algal cells/ml beyond which the rate of daphnid specific growth as a function of increasing food concentration decreases.

10. Daphnid fecundity (eggs per female per clutch), can be predicted from a multivariate functional relationship of both daphnid carapace length and algal cell concentration.

11. The measured accelerated daphnid growth and prolific fecundity as a function of carapace length, at elevated food concentrations explains the ability of D. pulex to explicit favorable food conditions and to rapidly incorporate net energy gain into biomass production.

12. Residual energy reserves, maternally allocated or accumulated in the hemocoel of daphnids when food is abundant, are later metabolized when food is scarce to temporarily sustain daphnid basal metabolism, body growth, and reproduction.

13. Observed high size-specific daphnid mortality rates exhibited by the largest and smallest daphnid size classes at high population biomass levels when food is scarce, is due to their inferior and

inefficient mass normalized filter-feeding and respiration rates, exacerbated by deficient maternally allocated and accumulated energy reserves.

14. All daphnid size classes composing a population culture were calculated to obtain a larger quantity of algal biomass per day when daphnid population biomass levels were low than when population biomass levels were high, with the most efficient intermediate daphnid size classes consuming the most algal biomass at either population biomass level.

15. Daphnid population specific growth rates along with other measured population dynamic parameters all varied as an interactive functional relationship of the calculated food per mass ratio and therefore, the food per mass ratio represents the primary controlling factor regulating daphnid population dynamics.

16. Daphnid populations cultured at the 40,000 and 80,000 algal cells/ml food levels appear to require 29 percent of the total body biomass in food per day just to maintain the population.

17. An empirical threshold corrected hyperbolic model was applied to predict daphnid population specific growth rate as a function of the food per mass ratio.

18. Total daphnid population biomass rather than daphnid population numbers appeared to be a more biologically meaningful measure upon which to express population dynamic phenomena in the unstable experimental daphnid assemblages.

19. Sufficient allocated maternal energy reserves are necessary at limiting food concentrations to sustain the relatively inefficient neonate until it develops into a more energetically efficient and competitively superior intermediate sized daphnid.

20. With the renewed batch culture system, it was demonstrated, that the critical population threshold food concentration for D. pulex fed C. reinhardi at 27 C. lies between 20,000 and 40,000 algal cells/ml.

21. To provide an accurate estimate of a daphnid population's threshold food concentration, it is not enough to measure only egg production as a function of food density, for to maintain daphnid population growth, the eggs must be able to survive and in turn, produce viable neonates.

22. In the populations of D. pulex studied, a constant population biomass equilibrium is not realized because there is a time lag between the decrease of food concentration and the delayed response of decreasing birth rates.

23. The mechanism responsible for the time lag provoking population oscillations has been identified as accumulated and maternally allocated lipid deposits.

24. From the presented data it appears that a continuing population biomass oscillation is as close as D. pulex gets to a steady-state equilibrium.

25. The average food consumption value of all daphnid size classes was 38 percent of daphnid body weight per day at low population

biomass where population biomass was increasing.

26. At high population biomass the average food consumption value of all daphnid size classes was 21 percent of daphnid body weight per day when population biomass production was decreasing.

27. Realized average daphnid population daily food consumption never exceeded 13 percent of the calculated potential daily food consumption, even when daphnid population biomass levels were low.

28. By having to persist under less than optimum food conditions, which the daphnid population creates for itself through excess grazing and reproductive pressure supported by residual energy reserves, daphnid growth, reproductive, and filter-feeding potentials are inhibited and a population of stunted daphnids develops.

29. Utilization of stored or conferred lipid deposits desensitizes the daphnid population to rapidly declining food conditions when population biomass is high and provides energy to stimulate excess reproduction and grazing pressures beyond the culture system's limited energy capacity creating starvation food conditions and subsequent negative population biomass production rates.

30. Despite the apparent function that residual energy reserves have in causing negative daphnid population biomass production rates and possible population extinction, residual energy reserves were observed to possess a redeeming quality by providing a deposit from which necessary energy can be extracted to sustain the most efficient daphnid size classes through periods of food scarcity ensuring the population's continued existence.

31. Daphnid population dynamics during the period when the population is characterized by oscillating conditions of high and low daphnid population biomass levels and abundant and scarce food availability, could be considered the daphnid's vacillating steady-state existence.

32. Daphnid population oscillations stimulated by organismal time lags induced by residual energy reserve accumulation or allocation and subsequent use delay daphnid physiological state response to the prevailing environmental conditions.

33. Lipid deposit formation or allocation and subsequent utilization corresponding to existing daphnid population food per mass ratios varies around the population maintenance threshold food per mass ratio.

34. Characteristic of viable evolving daphnid population cultures are great latent unrealized grazing, growth, and reproductive potentials that are only exhibited when algal biomass availability appreciably exceeds daphnid population biomass.

35. The unrealized grazing, growth, and reproductive potentials of D. pulex at dynamic population equilibrium allows these filter-feeding cladocerans to maintain the low phytoplankton abundance critical to biomanipulation of eutrophic lakes.

36. Maternally allocated energy reserves provided to the neonate as a function of food available to the adult was identified as the critical intrinsic physiological mechanism determining the viability of a filter-feeding cladoceran population when zooplanktivorous fish predation is reduced.

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