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Type-3 functional response in limnetic suspension-feeders, as demonstrated by *in situ* grazing rates

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Abstract

Field-measured grazing rates (ml/animal/d) of cladocerans (mostly daphniids) and diaptomids were assembled from various published studies and plotted as a function of corresponding phytoplankton concentration ($\mu g\,l^{-1}$ f.w.). Filtering rates of both zooplankton groups initially increased with seston concentration until maximal grazing rates were observed at approximately 4×10^2 and 1×10^2 $\mu g\,l^{-1}$ for cladocerans and copepods, respectively; at higher algal concentrations, filtering rates of both declined as a function of food concentration. The shape of these curves are most consistent with Holling's (1966) Type 3 functional response.

We found little support for the Type 3 functional response in published laboratory studies of *Daphnia*; most investigators report either a Type 1 or Type 2 response. The one study in which the Type 3 response was observed involved experiments where animals were acclimated at low food concentrations for 24 h, whereas those studies associated with response Types 1 or 2 had acclimation periods of only 1 to 3 h. We therefore assembled relevant data from the literature to examine the effect of acclimation period on the feeding rates of *Daphnia* at low food concentrations. In the absence of any acclimation, animals filtered at extremely low rates. After 2 h of acclimation, however, filtering rates increased 4 to 5-fold but declined again with longer durations; after > 70 h of pre-conditioning, filtering rates were almost as low as they had been with no acclimation.

We also found little support for the Type 3 functional response in published studies of copepods. The only study associated with a Type 3 response involved a marine copepod that had been subjected to a starvation period of 48 h; however, an analysis of the effects of acclimation period did not yield conclusive evidence that filtering rates of freshwater copepods (*Diaptomus* and *Eudiaptomus*) decrease significantly with acclimation duration.

The low filtering rates associated with long acclimation periods in laboratory experiments appears to be a direct result of animals becoming emaciated from prolonged exposure to low food concentrations, a situation which renders them incapable of high filtering rates. This may explain the Type 3 functional response for field cladocerans, since zooplankton in food-limiting situations are constantly exposed to low food concentrations, and would therefore have low body carbon and consequently less energy to filter-feed. We cannot, however, use this to explain the Type 3 response for field diaptomids, since copepods in the laboratory did not appear to lose body carbon even after 72 h of feeding at very low food levels, and there was inconclusive evidence that either *Diaptomus* or *Eudiaptomus* decrease their filtering rates with acclimation period.

Although Incipient Limiting Concentrations (ILC) for *Daphnia* ranged from 1 to $8.5 \times 10^3\ \mu g\,l^{-1}$, more than half of these fell between 1 and $3 \times 10^3\ \mu g\,l^{-1}$, bracketing the value of $2.7 \times 10^2\ \mu g\,l^{-1}$ for field cladocerans. There was, however, a great deal of variation in reported maximum ingestion rates (MIR), maximum filtering rates (MFR) and ILC values for *Daphnia magna*. ILC values from the few laboratory studies of freshwater copepods ranged between 0.5 to $2.8 \times 10^3\ \mu g\,l^{-1}$, and was higher than the ILC value of approximately $0.2 \times 10^3\ \mu g\,l^{-1}$ calculated for field populations of *D. minutus*. Generally, there was considerable agreement among laboratory studies regarding the shape of grazing-rate and ingestion-rate curves when data were converted to similar units and presented on standardized scales.

Introduction

The search for a unifying theory to explain the relationship between feeding rate of suspension-feeders and algal concentration can be traced back almost three decades. It began with Rigler's (1961) discovery of an incipient limiting concentration (ILC), a food concentration above which animals are assumed to ingest at maximal rates; below the ILC, McMahon & Rigler (1963; 1965) found that ingestion rates increased linearly with phytoplankton concentration. In Holling's (1965) survey of functional response types of invertebrate predators, he labelled this rectilinear increase of ingestion rates a Type 1 functional response (Fig. 1a). Later, other investigators confirmed the Type 1 response (Frost, 1972; Kersting & van der Leeuw, 1976), while others argued for a Type 2 response (Parsons *et al.*, 1967; Burns & Rigler, 1967; Porter *et al.*, 1982), which is characterized by a curvilinear increase of ingestion rates with food concentration (Fig. 1a). A Type 3 functional response, which describes a sigmoidal increase has also been reported (Frost, 1975; Buckingham, 1978), although this model has not been widely endorsed (Lampert, 1987).

Distinguishing among the three response types is important for several reasons. First, it is important from a behavioural perspective because different sets of assumptions regarding the combination of feeding components apply to each type of response. The feeding components of filter-feeders include the rate of successful search, feeding duration, and handling time of prey (Holling, 1966). For filter-feeding zooplankton, these components are incorporated into the term 'filtering rate', which is a measurement of the volume of water swept clear of algae per time unit. In the Type 1 response, search rate is constant while the handling time is negligible so that zooplankton graze at a constant rate below the ILC (Fig. 1b). In the Type 2 response, search rate is constant but handling time is neither negligible nor dependent on prey density; consequently filtering rate decreases continuously. In the Type 3 response, both search rate and handling time vary with algal concentration; since search rate is depressed at low prey densities, grazing rate initially increases and then declines with food concentration at a threshold concentration. In the past, some investigators (e.g. Burns & Rigler, 1967; Porter *et al.*, 1982; DeMott, 1982) have treated this threshold concentration as the ILC, even though there is perhaps no ILC in the sense of Rigler's (1961) study except for the Type 1 response. In this paper, we will refer to the ILC values regardless of response types whenever they have been identified by the investigators as such.

Designation of response types is also important from an ecological perspective because they vary with respect to their role in imparting stability to the plankton community. In both Type 1 and 2 responses, zooplankton are assumed to graze at maximal rates until their food supply is completely depleted; however, in the Type 3 response, a refugium is provided for the prey since grazing rates are reduced at low algal concentrations. Whereas the former two response types

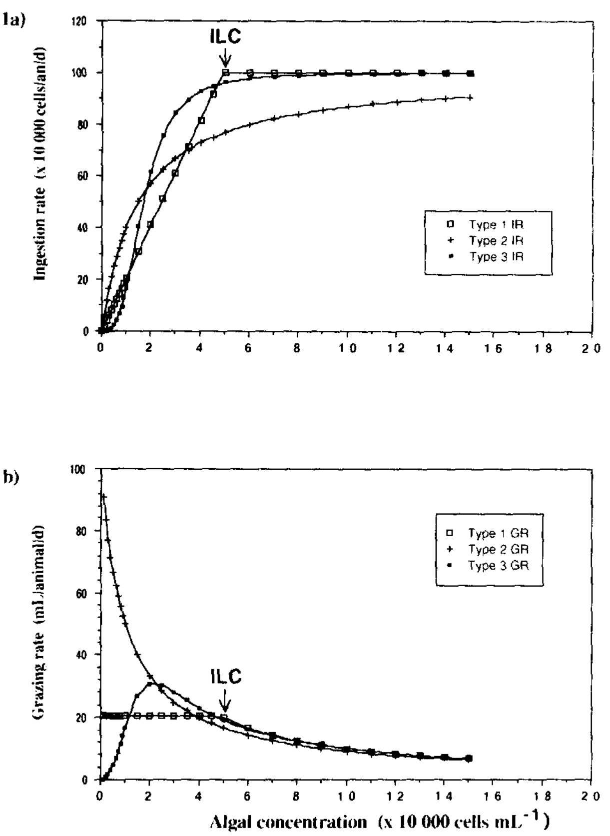

Fig. 1. (a) Theoretical ingestion rate curves based on mathematical equations that describe each of the three functional response types. ILC for the Type 1 response is 5×10^4 cells ml^{-1}; maximum ingestion rate (MIR) is 100×10^4 cells/animal/d in all cases. Equations that describe each functional response are as follows:

Type 1: for concentrations ≤ 5, $IR = 20.4\ x$, for concentrations > 5, $IR = 100$.

Type 2 (Holling's (1959) disc equation):

$$IR = MIR\ x/(k + x) = 100\ x/(1 + x)$$

Type 3 (Real's (1977) equation):

$$IR = MIR\ x^n/(G + x^n) = 100\ x^3/(5 + x^3)$$

where x = algal concentration (cells $\times 10^4$ ml^{-1}) and k is the concentration at which ingestion rate is half the maximal, and G is an affinity constant equal to the food concentration at which feeding rate is half its maximum value (Buckingham, 1978).

(b) Theoretical grazing rate curves back-calculated from above curves of ingestion rates for respective functional response types.

may lead to unstable oscillations or even extinction of both predator and prey, the Type 3 response is most consistent with a stable strategy of co-existence between zooplankton and phytoplankton (Steele, 1974). A theoretical basis also exists for expecting a Type 3 functional response. Lam & Frost (1976) and Lehman (1976) independently developed energy optimization models for two filter-feeders (*Daphnia* and *Calanus*, respectively), that assumed animals maximize their net energy intake within constraints imposed by external factors such as food concentration and internal factors such as gut fullness. These models predicted decreased grazing rates above and below a threshold algal concentration, and a sigmoidal increase in ingestion rates as a function of phytoplankton concentration.

Even though the Type 3 response is ecologically meaningful and theories have already been developed to explain it, it is rarely reported by investigators. Indeed, conventional wisdom almost dictates that herbivorous zooplankton do not feed with a Type 3 functional response (Lampert, 1987). One of the reason for the lack of support may be attributed to the convention of fitting mathematical curves to ingestion-rate data, which are often too variable or too few in the initial portion of the curve to unequivocally fit a linear, curvilinear or sigmoidal regression (Mullin *et al.*, 1975; Buckingham, 1978). Another factor may be due to use of inadequate acclimation periods in previous laboratory studies. These acclimation periods have been made necessary because investigators tend to culture or maintain zooplankton in high food concentrations, so that these well-fed animals must be acclimated to the experimental low food concentration prior to the grazing experiments.

Unfortunately, the length of the acclimation period, as well as length of time between zooplankton capture and measurement of feeding rate, and the food concentration to which animals are exposed during the withholding period, are all factors that may cause a change in the shape of the laboratory-measured functional response (Buckingham, 1978; Muck & Lampert, 1984). It is probably not a coincidence that experimental conditions associated with a Type 3 functional response have tended to involve lengthy acclimation periods (>24 h). Muck & Lampert (1980) have attributed the reduced filtering rates at the initial portion of the grazing curve to the fact that animals were starved and had become weakened with prolonged exposure to low food conditions during the 24-h acclimation. We argue that this type of pre-conditioning probably simulates the field situation more accurately than does a short acclimation period (<1 to 2 h) because animals in the field are more likely exposed to longer episodes of dilute concentrations from 12 to 24 h, even if they encounter algal-rich waters on a diel basis when they vertically migrate.

In this study, we propose to use published *in-situ* grazing rates from a number of studies to examine the functional response of two common filter-feeders in lakes, *Daphnia* and *Diaptomus*. In these studies, grazing rates are measured by the technique developed by Haney (1971) in which animals are captured in a plexiglas chamber within the water column and are allowed to graze on ambient algal concentrations during a short experimental period. Zooplankton in these experiments are not subjected to any acclimation period or any handling effects that accompany other 'field' methods in which animals are collected by townets and placed in grazing vessels either on board the boat or transported back to the laboratory for experimentation (Chow-Fraser, 1986a). Consequently, these *in-situ* data are free of any possible effects of inadequate acclimation periods, or variable food concentrations during transportation and withholding periods. Furthermore, results from these experiments are directly applicable to field situations without extrapolation and are therefore better than laboratory data for indicating how animals feed in nature.

The weaknesses of this field technique stem from several implicit assumptions. First, the radioactively labelled algae that are used as tracers are assumed to be a surrogate for all edible algae. Algae would be categorized as 'edible' based solely on size and morphology. This assumption may be upheld for many cladocerans but would be violated if animals selected food based on nutritional quality rather than on size, as is the case for some calanoid copepods (Vanderploeg *et al.*, 1990). Secondly, all edible algae are assumed to be equivalent in terms of filtration efficiency and/or elicit the same perceptual bias from grazers, and this assumption is difficult to uphold, especially for copepods; however, it is difficult to assess the extent to which this violation contributes to estimate errors. Thirdly, interference from non-edible algae on the grazing rate of suspension-feeders are not accounted for, although this would not be a problem except when blue-green or diatom blooms prevail. The final and perhaps major drawback is that contemporaneous grazing rates on more than three types of algae are difficult to obtain with this technique since it is exceedingly difficult to use more than three differential labels at a time. Consequently, data produced by this technique cannot be used for a comprehensive examination of algal selectivities, as is possible with the coulter-counter method (e.g. Vanderploeg, 1981). Although these problems do not in themselves invalidate the technique, they do however, limit the degree to which data can be automatically extrapolated without first applying appropriate 'edibility' criteria to individual grazer species.

Even though we are comparing published grazing data from several studies, we have included only investigations where a relatively narrow range of light and temperature conditions were involved to avoid possible confounding effects. We believe that this is a valid approach because Peters & Downing (1984) used information from more than thirty sources with little overlap in their dynamic range, to show that effects of food concentration on the feeding response of marine and freshwater suspension feeders were obvious in spite of non-standardized experimental conditions and inclusion of a variety of species. However, instead of using curve-fitting techniques on ingestion-rate data as is the conventional approach, we will examine the shape of the grazing-rate curve to determine the functional response. The advantage of this approach is that response Types 1 and 2 can be clearly distinguished from Type 3 even if there are extremely variable data in the initial portion of the curve. This is because grazing rates in the rectilinear and curvilinear models are maximal at concentrations below the ILC whereas in the sigmoidal model, grazing rate is initially low and then increases with particle concentration (see Fig. 1b). Thus, a significant positive correlation between grazing rate and food concentration below the ILC is unequivocal evidence for the Type 3 functional response.

We also compare laboratory data for several species of *Daphnia* and calanoid copepods. We will investigate the influence of acclimation duration on functional response type to determine whether or not differences in reported laboratory studies can be accounted for by differences in acclimation periods. We compare the composite functional response of field animals with those observed in laboratory studies. We also conduct a systematic comparison of response-curves among different species and different studies to comment on the extent of agreement among existing laboratory studies.

Methods and materials

Definitions and calculations

'Filtering rate' is used synonymously with 'grazing rate' and 'clearance rate' in the literature and we used it interchangeably in this paper. Unless otherwise indicated, 'edible algal concentration' is measured as μg/l f.w. and 'ingestion rate' has the units μg/animal/d. 'Filtering rate' is calculated as the quotient of ingestion rate and algal concentration and has the units ml/animal/d.

Description of field studies

The study sites in this paper include lakes and ponds of Ontario and Michigan. Particulars of the algal and animal species used in the assembled field studies are outlined in Tables 1 and 2. We obtained cladoceran filtering rates by using filtering-rate-length regression equations to interpolate the grazing rate of a 1 mm animal. These regression equations were either obtained from published studies (Chow-Fraser & Knoechel, 1985; Table 6; Haney, 1985; Table 4), or were generated from raw data provided by the authors of published studies (Knoechel & Holtby, 1986). The standardized size, 1 mm, was a convenient length to use because the corresponding grazing rate is simply the antilog of the intercept of the regression equations. We acknowledge that there is a variance associated with these values but ignoring this variance will not change the nature of our conclusions.

We assembled mean clearance rates of diap-

Table 1. Description of cladoceran field studies. All experiments were conducted between 10:00 and 17:00. Food concentration (FC; μg/l f.w.) corresponds to the concentration of 'edible' algae as defined by investigators (see Methods). (T = temperature; °C). n is the number of observations obtained from each source.

Investigators	Taxa	Incubation period	Tracer species (Longest linear dimension)	FC	Edible Algal size	T	n
Chow-Fraser & Knoechel (1985)	Cladocerans*	15–20 min	*Scenedesmus ovalis* & *Chlorella vulgaris* (4–8 μm)	6.4×10^1–2.1×10^{2a}	$<30\ \mu$m	17–20	9
Knoechel & Holtby (1986)	*Daphnia galeata*, *D. pulex*	5–10 min	*Rhodotorula* sp. (3–4 μm)	$4.4 \times 10^2 - 4.2 \times 10^{3a}$	$<30\ \mu$m	16–22	2
Haney (1985)	*D. catawba*	5–10 min	*Rhodotorula* sp. (3–4 μm)	1.0×10^4–8.0×10^{4b}	$<31\ \mu$m	22	4

[a] Includes contribution from tracer cells.

[b] Assumes a f.w.-d.w. ratio of 3.44 (see Methods).

* Cladoceran species include *Daphnia galeata*, *D. dubia*, *D. rosea*, *Diaphanosoma* sp., *Holopedium* sp., and *Ceriodaphnia* sp.

Table 2. Description of diaptomid field studies. Experiments other than those of Richman were conducted between 10:00 and 17:00; light conditions in Richman's experiments ranged from 600–1000 ft candles (time of day was not specified). See Table 1 for description of FC, *T* and *n*.

Investigators	Taxa	Incubation period	Tracer species (Longest linear dimension)	FC	Edible Algal size	*T*	*n*
Richman (1964)	*Diaptomus oregonensis* (adults)	1 h	Algae filtered through No. 25 plankton net	1.0×10^5–2.6×10^{5a}	$<64\ \mu m$	22–23	4
Knoechel & Holtby (1986)	*D. oregonensis* (1.2–1.4 mm total length)	5–10 min	*Rhodotorula* sp. (3–4 μm)	3.7×10^2–2.0×10^{3b}	$<10\ \mu m$	17–22	3
Chow-Fraser (1986b)	*D. oregonensis* (0.9–1.0 mm prosome length)	15–20 min	*Scenedesmus ovalis* (4–8 μm)	4.3×10^{1b}	$<10\ \mu m$	20	1
Chow-Fraser (1986a)	*D. minutus* (0.70–0.85 mm prosome length)	15–20 min	*Scenedesmus ovalis* & *Chlorella vulgaris* (4–8 μm)	2.7×10^1–5.8×10^{2b}	$<10\ \mu m$	18–22	8

[a] Assumes a f.w.-d.w. ratio of 3.44 (see Methods).

[b] Includes contribution from tracer cells.

tomids from Chow-Fraser (1986a, b; Fig. 3 and 2, respectively). The mean clearance rates from Knoechel & Holtby's (1986) study were calculated from raw data provided by them. Only measurements of adult copepods have been included in this paper; that investigators did not discrim-

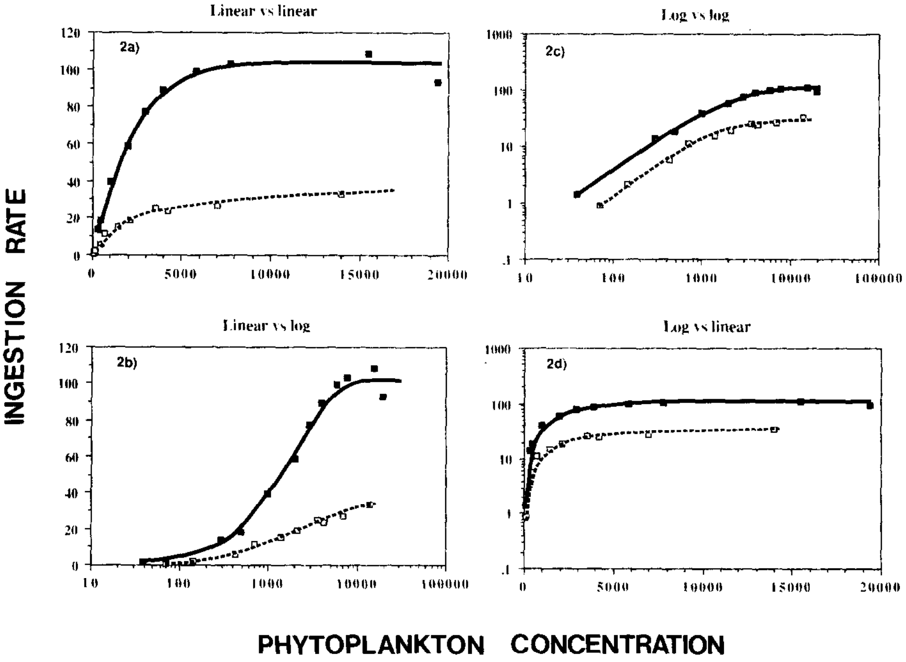

Fig. 2. Comparison of plots of ingestion rate (μg/animal/d) vs phytoplankton concentration (μg l^{-1}; f.w.) presented on: (a) linear axes (b) & (d) combination of linear and logarithmic axes and (c) log axes. Data correspond to ingestion rates of *D. rosea*, extrapolated from Burns & Rigler (1967; 1.7 mm, closed symbols) and DeMott (1982; 1.38–1.55 mm, open symbols).

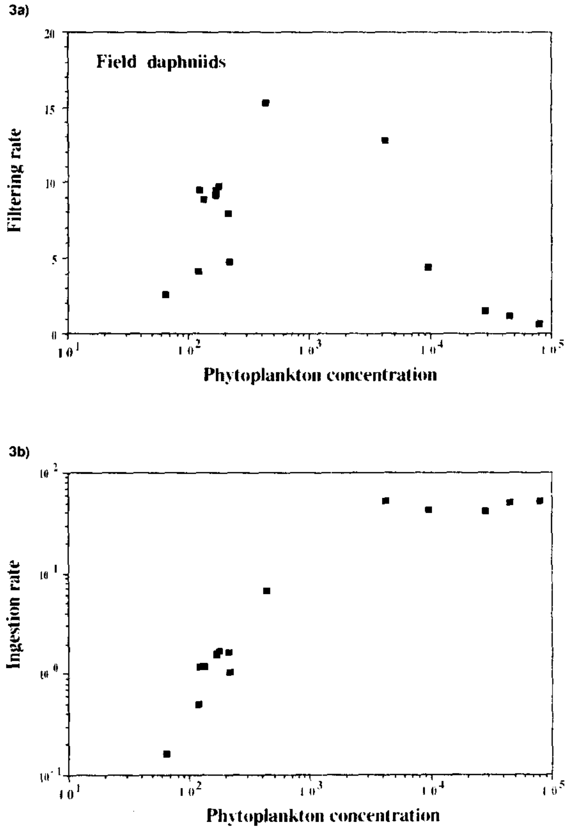

Fig. 3. Composite curves of a 1 mm cladoceran interpolated from field studies (see Methods). (a) Filtering rate (ml/animal/d) vs phytoplankton concentration $\mu g\, l^{-1}$; f.w.) (b) Ingestion rate (μg/animal/d) vs phytoplankton concentration ($\mu g\, l^{-1}$; f.w.).

inate between the grazing rates of male and female copepods may have contributed some unknown amount of variability to the data since copepods exhibit size dimorphism and copepods may graze as a function of size.

Size as a criterion of edibility

More than one size criterion was used to estimate the food concentration of 'edible' phytoplankton in the cited studies. For cladocerans, algal cell size appears to be a generally good preditor of edibility (Peters, 1984; Lehman & Sandgren, 1985; Vanni, 1987), and this is consistent with field and laboratory observations that daphniids tend to graze on food particles between 5 and 50 μm with relatively little selectivity (Burns, 1968; Gliwicz, 1969, 1977, 1980; DeMott, 1982, 1986; Muck & Lampert, 1984). While some investigators use <50 μm (Porter, 1973; Briand & McCauley, 1978), or <35 μm (Vanni, 1987) as the upper limit of edibility, investigators of the assembled studies in this paper have used a more conservative upper limit of edibility, but one which is still in line with the established size range. Both Chow-Fraser & Knoechel (1985) and Knoechel & Holtby (1986) used <30 μm in their studies, while Haney (1985) used <31 μm in his. For better comparison, we converted all reported concentrations to freshweights ($\mu g\, l^{-1}$) by applying a freshweight-to-dryweight (f.w.-d.w.) ratio of 3.44. This value is the mean ratio calculated from Nalewajko's (1966) list of 27 freshwater algal taxa.

By contrast, we recognize that the mechanism controlling food particle selection in calanoid copepods is very complex. It not only depends on algal size, but on nutritional quality, algal concentration and proximity to the scanning current of the copepod, as well as the feeding history of the animal (Vanderploeg *et al.*, 1988; Vanderploeg, 1990; DeMott, 1990). Since the tracers used in the studies had algal diameters between 4 and 8 μm, we applied an 'edibility' criterion of < 10 μm to more accurately reflect the size of the target algal group in these grazing experiments. Thus, the functional response of diaptomids that we are investigating in this paper will only apply to their feeding on small algal particles (< 10 μm).

Description of laboratory investigations

Investigations included in this paper had been carried out in laboratories from North American and western Europe (Tables 3 & 4). In most cases, investigators conducted grazing experiments at approximately 20 °C, in well-lit conditions. Although the list we have assembled is not comprehensive, we have tried to include as many taxa as possible.

Table 3. Description of laboratory grazing experiments with *Daphnia* sp. (mean body lengths; mm) on different algae (biovolume; μm^3). T = temperature (°C); AT = acclimation time (h); FRT = functional response type (after Holling, 1965); MIR = maximum ingestion rate (μg/animal/d); MFR = maximum filtering rate (ml/animal/d); ILC = Incipient Limiting Concentration ($\times 10^3$ μg/l). All investigators used the radiotracer method (Peters, 1984). * This study involved the use of coulter-counter.

Investigator	Species	Algal taxa	T	AT	FRT	MFR	MIR	ILC
McMahon (1965)	*magna* (3.54)	*Chlorella* sp. (34)	20	1	1	101	408	4.76
McMahon & Rigler (1965)	*magna* (2.8–3.3)	*Chlorella* sp. (34)	20	1	1	65	408	8.50
Porter *et al.* (1982)	*magna* (2.7)	*Chlamydomonas reinhardi* (150)[a]	20	1–2	2	100	85	1.50
Kersting & van der Leeuw (1976)*	*magna* (2.5–3.0)	*Chlorella vulgaris* (2–165)	18	2–3	1	77	221	2.90
Muck & Lampert (1984)	*longispina* (1.5–2.0)	*Scenedesmus acutus* (109)[b]	18	24	3	32	48	1.62
Burns & Rigler (1967)	*rosea* (1.7)	*Rhodotorula glutinis* (39)[c]	20	1–2	2	37	94	3.90
DeMott (1982)	*rosea* (1.47)	*Chlamydomonas reinhardi* (140)[d]	15	0.5–1	2	16	26	2.1–2.8
Geller (1975)	*pulex* (2.0)	*Scenedesmus* sp. (111)	15	1	1	41	43	1–5

[a] Assumes that each cell has a d.w. of 5.4×10^{-5} μg (Porter *et al.*, 1982) and a f.w.-d.w. ratio of 2.79 (*Chlamydomonas angulosa*; Nalewajko, 1966).

[b] Assumes that *S. acutus* is an ellipse (dimensions 13×4 μm; 109 μm^3) and 1.7544×10^{-5} μgC/cell (their Table 1).

[c] Assumes a that *R. glutinis* is a sphere with 4.2 μm diameter (Burns & Rigler 1967).

[d] Assumes that 0.25 μg d.w. = 5×10^3 cells (DeMott, 1982) and a f.w.-d.w. ratio of 2.79 (as indicated above).

Table 4. Description of laboratory grazing experiments with copepod species (mean body lengths; mm) on different algae (biovolume; μm^3). Table headings are same as those in Table 3. n/a = not available.

Investigator	Species	Algal taxa	T	AT	FRT	MFR	MIR	ILC
Richman (1966)	*Diaptomus oregonensis* females	*Chlorella vulgaris* (113)[a]	20	starved for 24 h	1	2.5	6.78	2.83
Horn (1981)	*Eudiaptomus gracilis* females (1.28–1.39)	*Scenedesmus quadricauda* (100)	20	12	2	12.0	30.0	2.50[b]
Muck & Lampert (1980)	*E. gracilis* females	*Scenedesmus acutus* (109)[c]	19	24	1	n/a	n/a	0.47

[a] Assumes that *Chlorella* is a sphere with 6 μm diameter.

[b] Calculated as MIR/MFR (after Kersting & van der Leeuw, 1976).

[c] Assumes that *S. acutus* is an ellipse (dimensions 13×4 μm; 109 μm^3) and 1.7544×10^{-5} μgC/cell (their Table 1).

Graphic presentation and interpretation of functional response type

In this paper, we advocate the use of the grazing-rate rather than ingestion-rate curve to discriminate between functional response types because of some inherent problems with regards to choice of scales used in graphical presentations of ingestion rates. For example, plots of grazing/ingestion rates vs algal concentration can be presented on either arithmetic or logarithmic scales. Most investigators have used linear scales for both axes (McMahon, 1965; Burns & Rigler, 1967; Frost, 1972, 1975; DeMott, 1982) while a few have used either a combination of linear and logarithmic scales (Porter *et al.*, 1982) or log-log scales (Richman, 1966). To demonstrate how the choice of scales has a dramatic effect on the shape of response curves, we have plotted rates of *D. rosea* from two independent studies (Burns & Rigler, 1967; DeMott, 1982; Fig. 2). In all but one case, the shape is monotonic curvilinear and resembles a Type 2 functional response (Fig. 2a,c & d); the exception is the linear-log plot which has a sigmoidal shape and resembles a Type 3 functional response (Fig. 1b). This comparison illustrates the need to standardize graphic presentations in cross-study analyses. In this paper, we will use log-scales for phytoplankton concentration and ingestion rate because of the large range in values, but will use a linear scale for the more restricted range of grazing rates.

Maximum ingestion rates (MIR), maximum filtering rates (MFR) and ILC

To allow us to compare field and laboratory data, we calculated some parameters of response curves typically calculated for laboratory studies such as maximum ingestion rate (MIR), maximum filtering rate (MFR) and ILC. Because the mathematics of the Type 2 response is relatively simple, and the shape of the ingestion-rate curve of field data resembled a Type 2 response, we used the Lineweaver-Burk transformation (after Horn 1981) to estimate MIR by regressing the reciprocal of ingestion rate against the reciprocal of algal concentration to obtain a y-intercept which represented 1/MIR (least-squares linear regressions were statistically significant ($P < 0.001$) for both cladocerans and *D. minutus*). The maximum filtering rate recorded in each case was used as the MFR value. The ILC was calculated by dividing MIR by MFR (after Kersting & van der Leeuw, 1976). This exercise was done solely for the purpose of comparing laboratory and field data, and was not intended to provide definitive parameters of the functional response for respective zooplankton groups.

Although the MIR, MFR and reported ILC values shown in Tables 3 and 4 are those identified by the investigators in the respective laboratory studies, we have converted them to standardized units (indicated earlier) to ease comparison. In all but one study, MFR values could be obtained directly from tables, regression equations, or gleaned from the text: in Porter *et al.*'s (1982) study, however, we had to extrapolate the maximum filtering rate from their Fig. 1.

We assembled filtering rates from several laboratory studies on *Daphnia* to compare the general shape of the grazing-rate curves. Since investigators reported algal concentrations in various units (μg d.w. ml^{-1}, cells mL^{-1} and μg C l^{-1}), we had to first convert these to standardized freshweights (μg l^{-1}) so they could be compared with the field grazing curve. The laboratory grazing data were not available in tables and could not be interpolated from regression equations: consequently, we had to extrapolate all of these from published figures. Description of the various experiments (i.e. tracers used, zooplankton species, food concentrations and experimental temperatures) and the published figures used to extrapolate laboratory grazing data are presented in Table 5. We do not use these to calculate maximum ingestion rates or ILC values (see above), but merely to indicate trends in the grazing data and to allow us to make cross-study comparisons. Whenever possible, we tried to estimate the actual data points used by the investigators in the plots; however, when the data are numerous or when axes are too compressed to permit resolution of individual values, we used the investigator's 'best-fit' line to extrapolate grazing rates from selected algal concentrations.

Results

Field investigations

The composite curve of grazing rates for the cladoceran field studies clearly possess both an ascending and a descending portion (Fig. 3a). Because of the great variability in grazing rates, however, we used a least-squares linear regression analysis to determine statistically the relationship between filtering rates and phytoplankton concentration. Since most published ILC values range between 10^3 and 10^4 μg l^{-1} (see Table 3) and filtering rates above the ILC are known to decrease as a function of algal concentration, we performed separate regressions on data below and above 10^3 μg l^{-1}. The analysis indicated that filtering rates below 10^3 μg l^{-1} increased linearly with log-phytoplankton concentration ($n = 10$; $r = 0.75$; $P < 0.02$), while those above 10^3 μg l^{-1} declined with log-phytoplankton concentration

Table 5. Description of *Daphnia* grazing rates extrapolated from published figures in laboratory studies. See Table 1 for description of FC and T.

Investigators	Taxa	Description of Tracer species (cell volume)	FC	T	Source
Porter *et al.* (1982)	*D. magna* (2.7 mm)	*Chlamydomonas*[a] *reinhardi* (150 μm^3)	1.5×10^2–1.7×10^5	20	Fig. 1
Burns&Rigler (1967)	*D. rosea* (1.7 mm)	*Rhodotorula*[b] *glutinis* (39 μm^3)	3.9×10^1–1.9×10^4	20	Fig. 2
DeMott (1982)	*D. rosea* (1.38–1.55 mm)	*Chlamydomonas*[c] (140 μm^3)	7.7×10^1–1.5×10^4	15	Fig. 2
Muck & Lampert (1980)	*D. longispina* (1.5–2.0 mm)	*Scenedesmus*[d] *acutus* (109 μm^3)	6.2×10^0–1.6×10^3	19	Fig. 4
Buckingham (1978)	*D. pulex* (1.28 mm)	Natural lake seston from Placid L.[e]	2.5×10^3–8.7×10^4[f]	20	Fig. 37

[a] Assumes that each cell has a d.w. of 5.4×10^{-5} μg (Porter *et al.*, 1982) and a f.w.–d.w. ratio of 2.79 (*Chlamydomonas angulosa*; Nalewajko, 1966).

[b] Assumes that *R. glutinis* is a sphere with 4.2 μm diameter (Burns & Rigler, 1967).

[c] Assumes that 0.25 μg d.w. = 5×10^3 cells (DeMott, 1982) and a f.w.–d.w. ratio of 2.79 (as indicated above).

[d] Assumes that *S. acutus* is an ellipse with dimensions 13×4 μm (109 μm^3) and 1.7544×10^{-5} μgC/cell (their Table 1).

[e] 80% of the seston had mean diameter ranging between 2–4 μm (Buckingham, 1978; p.56).

[f] Assumes a f.w.: d.w. ratio of 3.44.

($n = 5$; $r = -0.91$; $P < 0.05$). The shape of this curve thus conforms better to a Type 3 than to either a Type 1 or Type 2 functional response curve.

Corresponding ingestion rates appear to increase asymptotically with algal concentration (Fig. 3b). We regressed reciprocal-transformed ingestion rates on reciprocal-transformed phytoplankton concentration (see Methods) to calculate a maximum ingestion rate (MIR) of 40.65 μg/animal/d for field cladocerans. We divided this value by the maximum filtering rate (MFR) of 15.35 ml/animal/d to obtain an ILC value of 2.65×10^3 $\mu g\,l^{-1}$.

Since the composite curve of grazing rates for diaptomids (*D. minutus* and *D. oregonensis*) was incomplete because there were no available data at extremely high algal concentrations ($> 10^4$ $\mu g\,l^{-1}$), we included data from Richman's (1964) study. Instead of using the Haney chamber, Richman collected nanoplankton, labelled it with isotope in 65 ml glass bottles for 24 h, fed it to freshly caught copepods and replaced the animals at depths where they had been collected to run the grazing experiments. Owing to the adverse effects of handling mentioned earlier (collection and concentration; (Chow-Fraser, 1986a), Richman's data may have been artificially reduced and so are not directly comparable to the *in situ* data measured with Haney's technique. We include them in Fig. 4a and b only to flesh out the curve at high concentrations; their inclusion does not affect our designation of functional response types because the area of the curve in question correspond to concentrations below 10^3 $\mu g\,l^{-1}$. It is clear from Fig. 4a that diaptomid filtering rates initially increased with algal concentration up to 2×10^2 ($n = 8$; $r = 0.99$; $P < 0.001$), and then declined. The overall shape of this curve is therefore most consistent with a Type 3 functional response. Even without Richman's values at the high end of the curve, it is obvious that beyond concentrations of 5×10^2 $\mu g\,l^{-1}$, filtering rates became reduced with increasing algal availability.

The asymptotic effect of food concentration on ingestion rates became more obvious with addition of Richman's values (Fig. 4b). The complementarity of these data, despite the methodological and species differences suggest that the parameter defining the shape of the functional response curve is robust for diaptomids. Through regression analysis on reciprocal transformations of ingestion rates and phytoplankton concentrations, we determined and MIR value of 0.94 μg/animal/d (Fig. 4b). We divided this value by MFR of 4.9 ml/animal/d to obtain an ILC value of 0.19×10^3 $\mu g\,l^{-1}$.

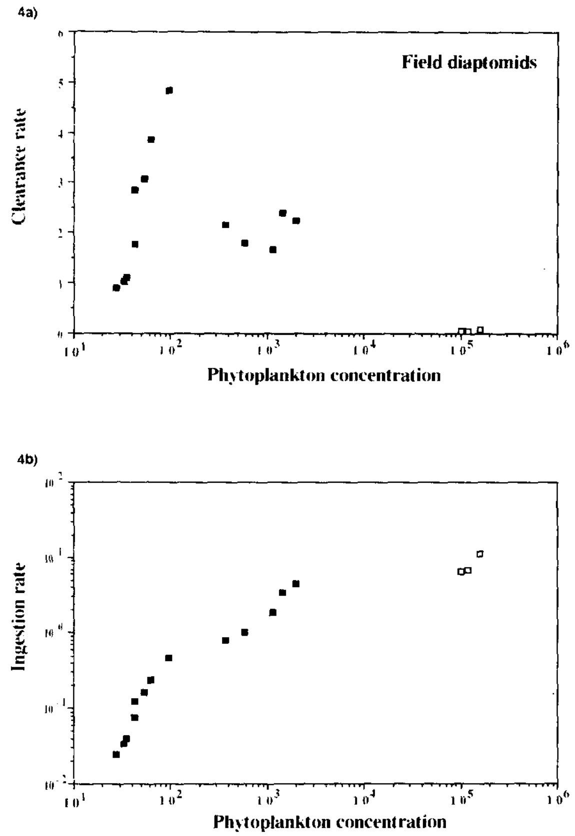

Fig. 4. Composite curves of adult diaptomids from field studies (see Methods). (a) Clearance rate (ml/animal/d) vs phytoplankton concentration ($\mu g\ l^{-1}$; f.w.) (b) Ingestion rate (μg/animal/d) vs phytoplankton concentration ($\mu g\ l^{-1}$; f.w.).

Laboratory investigations

Comparison of functional response types:

Daphnia species that were examined in the laboratory studies include *magna*, *rosea*, *longispina*, *hyalina*, and *pulex* (Tables 3). Most of the investigators reported either a Type 1 or 2 functional response. The only study in which a Type 3 functional response was observed involved experiments where animals were acclimated at low food concentrations for 24 h. In all others, experimentors employed acclimation periods ranging from less than 1 h to 3 h.

Buckingham (1978) conducted a detailed study of the effect of acclimation duration on the shape of functional response curves for *Daphnia pulex*. She noted that acclimation periods from 1 to 21 h had no appreciable effect on filtering rates at high food concentrations; however, at low food concentrations filtering rates declined by 30% after 4 h of acclimation, and by 40% after 21 h of acclimation. Animals acclimated for 21 h at the lowest food concentration did not appear to feed at all. The shape of respective grazing-rate curves corresponding to the 1 and 4 h acclimation periods were most consistent with a Type 2 functional response, whereas that for the 21 h acclimation was most consistent with a Type 3 functional response.

In an independent series of laboratory experiments with *D. longispina*, Muck & Lampert (1980) confirmed Buckingham's observation that *Daphnia* exhibited a Type 3 functional response when subjected to a 24 h acclimation period. They showed in another study that acclimation periods ranging from 0 to 72 h had a significant effect on filtering rates. In the absence of any acclimation, animals filtered at only 25% of the maximum rate which was achieved after a few hours of acclimation; after that, filtering rates declined linearly with acclimation duration.

A composite plot of data from both investigations show a remarkable degree of complementarity between studies (Fig. 5a). Despite differences in species and size range (Muck & Lampert used *D. longispina* (1.5–2.0 mm), while Buckingham used *D. pulex* (1.2–2.0 mm)), there was a significant negative correlation between filtering rates and acclimation period (from 1 to 72 h; $r = -0.83$; $P < 0.01$). Acclimation period appeared to have a very consistent effect on animals of this size range (i.e. between 1.0 and 2.0 mm) from other studies as well (see Table 3). MFR values from Burns & Rigler's (1967) and Geller's (1975) studies of 37 and 41 ml/animal/d, respectively (see Table 3) were close to 41.3 ml/animal/d, which is the predicted filtering rate of animals subjected to a 1 h acclimation period. By comparison, the much lower MFR values of 16 ml/animal/d corresponding to DeMott's (1982) study was also in line with that expected for a 30-min acclimation period, even though this may also have been attributed to the lower experimental temperature used.

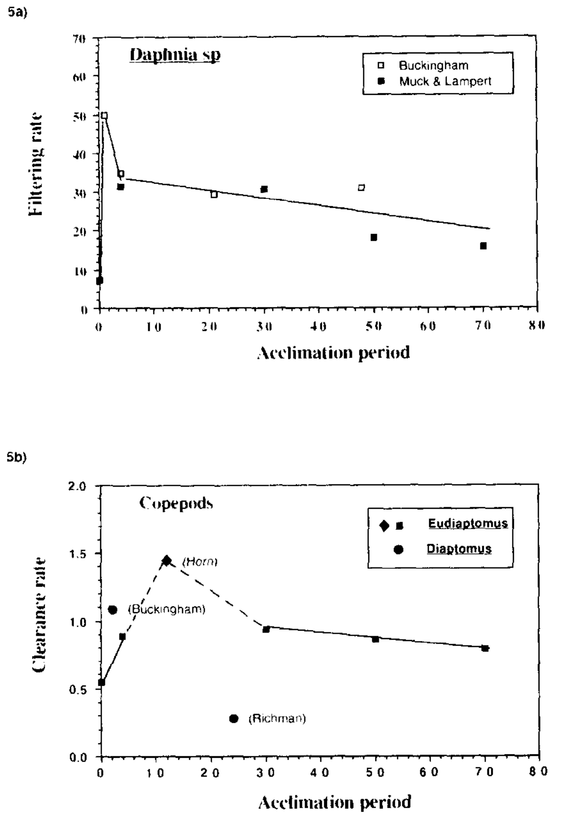

Fig. 5. (a) Effect of acclimation period (h) on filtering rates (ml/animal/d) of *Daphnia* at low experimental food concentrations. Solid line is fitted by eye through data from both studies to indicate the trend in reduced grazing rates with time.

(b) Effect of acclimation period (h) on clearance rates (ml/animal/d) of copepods at low experimental food concentrations. Solid line joins data from Muck & Lampert (1984) while the dotted line joins points from Muck & Lampert and Horn's (1981) studies.

Muck & Lampert (1984) noted that a decrease in individual body carbon paralleled the decrease in filtering rates over the 3 d acclimation period, even though average individual length did not change. They concluded that animals were unable to filter at high rates because of their starved and exhausted state after prolonged exposure to low food conditions. This may explain the Type 3 functional response for field cladocerans (Fig. 3a). Zooplankton from unproductive lakes (corresponding to data in the lower portion of the curve) may have less body carbon than animals of identical length from more productive environments (corresponding to data at the middle portion of the curve), and may thus be energetically incapable of high filtering rates.

There were comparatively few published laboratory studies on the functional response of freshwater copepods; the taxa examined only included *Diaptomus oregonensis* and *Eudiaptomus gracilis* (Table 4). All of the investigators observed either a Type 1 or 2 functional response. A 24 h acclimation period did not appear to produce a Type 3 functional response for *Eudiaptomus* and there was also no significant reduction in filtering rates or body carbon with length of acclimation (Fig. 5b; Muck & Lampert, 1984). There was also no evidence in support of a Type 3 response for *Diaptomus* after a 24 h acclimation (Vanderploeg *et al.*, 1984). Thus, the Type 3 functional response observed for field diaptomids cannot be explained in terms of metabolic requirements.

Nevertheless, a more detailed investigation of acclimation period should be carried out because the critical acclimation period may occur between 4 and 24 h, especially since Horn's (1981) 12 h acclimation produced an MFR which is substantially higher than those of Muck & Lampert's for the same copepod species. There was no obvious agreement between *Eudiaptomus* and *Diaptomus* with respect to acclimation effects since in the latter case, a longer acclimation period was associated with a greatly reduced filtering rate (Fig. 5b).

Despite a lack of support from laboratory studies of freshwater copepods, however, we found evidence of the Type 3 functional response in a study of a marine copepod, *Calanus pacificus* (Frost, 1975). Although his results may not be directly comparable to ours because of methodological differences (he used a cell-count method and he starved the animals for 48 h prior to grazing), there is at least the suggestion that calanoid copepods may exhibit a Type 3 functional response under laboratory conditions and this should be further examined for freshwater species.

Buckingham (1978) identified two other factors that had a significant effect on the type of functional response obtained in laboratory experiments for both daphniids and diaptomids. She found that the length of time between zooplankton capture and measurement of feeding rate, and the food concentration to which animals were exposed during this withholding period had an inconsistent effect on the animals' filtering rates at high and low experimental food concentrations. A combination of these two may have confounded any effect of acclimation period in the published studies, and may explain the discrepancies between field and laboratory data. Her study indicates that experimentors must be extremely vigilant in documenting the pre-feeding conditions of laboratory animals in order to permit meaningful cross-study comparisons.

Comparison of ILC values:

Despite differences in species, experimental temperatures and size of animals used, there is considerable agreement among laboratory studies with respect to ILC values for *Daphnia* (Table 5). The assembled ILC values range from approximately 1.0 to $8.5 \times 10^3\ \mu g\,l^{-1}$, with more than half of them between 1 and $3 \times 10^3\ \mu g\,l^{-1}$. The ILC of $2.7 \times 10^3\ \mu g\,l^{-1}$ for a 1 mm field cladoceran (Fig. 3) agrees well with $2.8 \times 10^3\ \mu g\,l^{-1}$, the ILC value for a 1.1 mm *D. hyalina* (Horn, 1981; Table 5). The results of this comparison suggest that laboratory data may be directly applicable to the field where high food concentrations are involved, although data corresponding to more dilute concentrations should not be extrapolated without scrutiny.

The three studies on freshwater copepods were associated with ILC values that ranged from 0.47 to $2.83 \times 10^3\ \mu g\,l^{-1}$ (Table 4). These values were all higher than the ILC value calculated for field data. The higher laboratory rates may reflect size difference between field and laboratory species, or perhaps differences in food composition in the various grazing experiments. Since diaptomids feed selectively on large particles, then grazing experiments conducted in the laboratory where only one size of alga is used would yield higher rates than in field experiments where animals are exposed to a choice of small and large algae and are therefore more likely to reduce their uptake of small, non-preferred cells.

Comparison of curve-shape:

When grazing rates and algal concentration were converted to standardized units and plotted on the same scales, we found consistency among daphniid species with respect to curve-shape (Fig. 6a). To make comparisons more meaningful, we have excluded data from DeMott's and Geller's studies (see Table 3) since their experiments had been conducted at 15 °C while all data

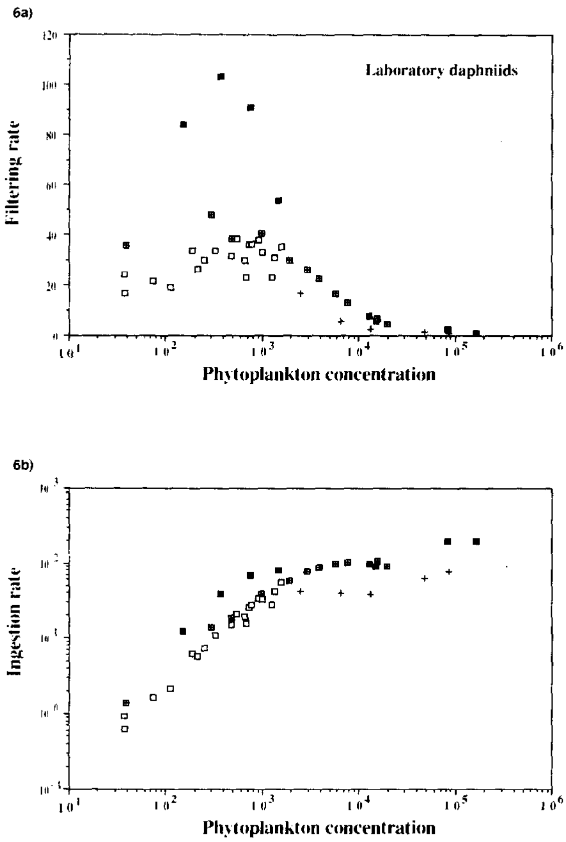

Fig. 6. Comparison of laboratory data measured at 20 °C for various size and species of *Daphnia*.

(a) filtering rate (ml/animal/d) vs phytoplankton concentration ($\mu g\,l^{-1}$; f.w.)

(b) ingestion rate (μg/animal/d) vs phytoplankton concentration ($\mu g\,l^{-1}$; f.w.).

Key to symbols: solid square = *D. magna* (2.7 mm); cross in open square = *D. rosea* (1.7 mm); open square = *D. longispina* (1.5–2.0 mm); cross = *D. pulex* (1.2 mm).

in Fig. 6 had been measured at 18° and 20 °C. Maximal filtering rates seemed to occur between an algal concentration of 4 and $5 \times 10^2\ \mu g\,l^{-1}$, although there were obvious differences in height of the curve and steepness of the slope on either side of the maximal grazing rates, which appeared to be a function of zooplankton size. *D. magna*, with a mean length of 2.7 mm had the highest MFR, and the steepest slopes, whereas *D. rosea*, with a mean size between 1.4 and 1.6 mm was associated with a flat curve and a low MFR value.

That large species graze at consistently higher rates compared with small species, even at low food concentration may explain why food thresholds increased with daphniid size (Gliwicz, 1990). The differential between grazing rates of large versus small animals is more pronounced at dilute concentrations $< 10^3\ \mu g\,l^{-1}$, but disappear at concentrations $> 10^4\ \mu g\,l^{-1}$ as the grazing curves of all animals converge regardless of body size. This is consistent with the hypothesis that large species lose their competitive advantage once ambient food concentration exceed the threshold of the smaller species, and explains why large daphniid species are competitively superior in oligotrophic waters where they are dominant (Gliwicz & Lampert, 1990).

Discussion

Conventional wisdom is that feeding curves of suspension-feeders are best described by either a Type 1 or Type 2 functional response; accordingly, zooplankton are assumed to graze at maximal rates from particle-free concentrations up to the ILC. Although a few exceptions have been published (most notably Frost, 1975), and a theoretical basis exists for expecting reduced grazing rates at low algal concentrations (Steele, 1974; Lam & Frost, 1976; Lehman, 1976), there is still a prevailing view that herbivorous zooplankton do not feed with a Type 3 functional response. We suggest that field populations of *Daphnia* and *Diaptomus* graze in a manner that is most consistent with Holling's (1965) Type 3 functional response. At concentrations below 4×10^2 and $1 \times 10^2\ \mu g\,l^{-1}$ for cladocerans and copepods, respectively, grazing rate increased with particle concentration and thereafter declined (Figs 3a and 4a).

We propose separate hypotheses to explain the Type 3 functional response for diaptomids and daphniids. The Type 3 response for *Daphnia* is probably directly related to low fitness that results from prolonged exposure to low food conditions in lakes. We speculate that this condition is best simulated in the laboratory when long acclimation periods are used prior to grazing experiments, and hypothesize that investigators failed to find a Type 3 response in previous laboratory studies because they used short acclimation periods. Even though filtering activity is reduced when either zero acclimation or a long acclimation period is used (Fig. 5a), the cause for each must be clearly distinguished. The tendency for *Daphnia* to reduce grazing activities or even stop grazing altogether after immediate exposure to low food concentration (Buckingham, 1978; Porter *et al.*, 1982; Muck & Lampert, 1984) is probably a short-term phenomenon that reflects the ability of the animal to discriminate between a high-food and low-food environment and to alter their feeding activities accordingly, while the latter reflects the inability of animals to filter-feed at high rates due to their starved condition.

Where calanoid copepods are concerned, reduced filtering rates at low food concentrations do not appear to be related to acclimation period or low body carbon. A more probably explanation is that animals can alter their feeding in response to short-term changes in food conditions (DeMott, 1990). *Diaptomus* does not feed with a single mode, but uses both a passive and an active mode (Vanderploeg, 1990). Very small particles (equivalent spherical diameter (ESD) $< 10\ \mu m$) are captured passively, carried in a double-shear scanning current, whereas larger particles (ESD $> 10\ \mu M$) are actively captured, that is, they are detected in the laminar double-shear scanning current and are brought into the mouth through coordinated motions of the mouthparts. Vanderploeg (1990) found that *Diaptomus* can used both an active and a passive feeding mode when they feed on particles in the size range of the tracer particles used in the *in-situ* grazing experiments concerned here. Perhaps the higher filtering rates at high concentrations reflects the use of both active and passive feeding modes, whereas the lower rates at low food concentrations reflect the use of the passive mode alone.

A fruitful avenue of research would be to examine how the functional response of diaptomids changes as a function of algal size and nutritional quality. High-speed cinematography (e.g. Vanderploeg & Paffenhöfer, 1985; Vanderploeg *et al.*, 1990) and laboratory feeding experiments (DeMott, 1990) have demonstrated that diaptomids will change their selection for algae, depending on food size or detectability and nutritional quality. Unfortunately, we cannot use grazing data from this study to speculate on the relative selectivity of *Diaptomus* for larger or small size particles since feeding rates on large algae had not been measured contemporaneously. There is as yet no clear relationship between functional response types and selectivity of diaptomids for preferred and non-preferred foods.

The extent of agreement among laboratory studies in regard to the shape of the ingestion-rate curves, maximum ingestion rates and ILC values indicate that filter-feeders respond in similar ways to changes in their food concentrations. We hope that freshweights will be used more consistently as a measure of phytoplankton biomass since the maximum volume of various foods eaten were similar (Table 3; McMahon & Rigler, 1965) despite differences in cell density. A standardized format for data presentation and data transformation should also be adopted so that curve shapes can be compared directly without tedious conversions (see Fig. 2).

The laboratory condition that best mimicks field situations is probably one in which animals have been acclimated for a 24 h period or longer. This is because animals in naturally dilute environments are not likely to encounter great changes in food concentrations, and should be constantly exposed to low food levels. Therefore, we recommend incorporation of long acclimation periods in future investigations of the functional response of animals in laboratory settings; however, we acknowledge that shorter time frames may be equally appropriate for zooplankton that live in patchy environments. But most of all, we encourage investigators to collect more field data so that our hypotheses can be tested. Other efforts should also be directed at fully understanding the effect of pre-conditioning duration on grazing rates of laboratory animals within a broad spectrum of algal concentrations, and to studying the relationship between grazing rate per unit body carbon and phytoplankton concentration in field populations.

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