

Factors Regulating in situ Filtering Rates of Cladocera

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Individual filtering rates of four species of *Daphnia*, as well as *Holopedium*, *Diaphanosoma*, *Ceriodaphnia*, and *Bosmina*, were measured in 10 lakes under various field conditions to identify important factors regulating in situ filter-feeding for these cladocerans. Linear regression analysis indicated that carapace length accounted for almost 60% of the total variance in individual filtering rates when data from all 10 lakes were pooled. We suggest that zooplankton in these lakes filter-feed in proportion to their volume, since the functional slope of this regression approximated 3. Taxonomic affiliation had generally little effect on filtering rates. Temperature, ranging from 12 to 22°C, had no statistically significant effect on filtering rate; there were also no significant differences between rates measured at dawn and dusk compared with midday rates for animals ranging in size between 0.30 and 1.30 mm. Addition of phytoplankton concentration as a second independent variable to the regression relating filtering rate to length further increased explained variance to 64%. Since the two main determinants of in situ filtering rates were zooplankton carapace length and concentration of edible phytoplankton, both of which are independent of taxonomic affiliation, investigators interested in assessing grazing losses should seriously consider measuring zooplankton in terms of size distribution rather than taxonomic affiliation.

On a quantifié, dans diverses conditions, les taux de filtration individuels chez quatre espèces de *Daphnia* et chez *Holopedium*, *Diaphanosoma*, *Ceriodaphnia* et *Bosmina* peuplant 10 lacs, afin de déterminer les principaux facteurs qui règlent la filtration *in situ* de ces cladocères. Selon une analyse de régression linéaire, la longueur de la carapace expliquait presque 60 % de la variance totale des taux de filtration individuels quand les données recueillies dans les 10 lacs étaient groupées. Les auteurs formulent l'hypothèse que ce zooplancton lacustre se nourrit par filtration en fonction de son volume, car la pente fonctionnelle de cette régression se rapprochait de 3. Les liens taxonomiques avaient généralement peu d'incidence sur les taux de filtration. La température, qui variait de 12 à 22°C, n'avait aucun effet statistiquement significatif sur ce taux; de plus, il n'y avait aucune différence significative entre les taux quantifiés à l'aube et au crépuscule par rapport à ceux qui étaient mesurés à midi chez les animaux dont la taille variait de 0,30 à 1,30 mm. L'ajout de la concentration du phytoplancton (comme seconde variable indépendante de la régression établissant un rapport entre le taux de filtration et la longueur) a fait passer la variance expliquée à 64 %. Comme les deux principaux facteurs déterminants des taux de filtration *in situ* étaient la longueur de la carapace du zooplancton et la concentration de phytoplancton comestible, deux facteurs indépendants des liens taxonomiques, les chercheurs qui s'intéressent à l'évaluation des pertes par broutage devraient sérieusement contempler la quantification de la taille du zooplancton au lieu des liens taxonomiques.

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Cladoceran zooplankton grazing imposes a basic loss on phytoplankton in pelagic ecosystems, and considerable effort has been channelled towards quantifying this loss (Gliwicz 1969, 1970; Porter 1972; Cushing 1976; Thompson et al. 1982). These attempts, however, have been hampered by an incomplete understanding of factors regulating filter-feeding in the field. Although many laboratory studies have been conducted they have limited predictive value for natural situations, because they are generally single-variate experiments involving at most a few zooplankton and phytoplankton species (McMahon and Rigler 1965; Burns 1969; Ivanova 1969; Buikema 1973; Geller 1975; Lampert 1977), or multivariate experiments that have been necessarily limited to

varying two variables at a few discrete levels (Schindler 1968; Hayward and Gallup 1976). There is a limit to the extent that laboratory studies can ever mimic lake conditions. Thus, while laboratory studies are useful in elucidating basic physiological mechanisms, field data must ultimately be used to evaluate the importance of factors regulating filter-feeding in natural populations. Our objective was to utilize field measurements of individual zooplankton filtering rates under natural conditions in a range of lakes to evaluate the relative importance of laboratory-identified factors in determining in situ filter-feeding activity.

In previous studies, filtering rates of *Daphnia* sp. have been found to vary as a function of simple morphological parameters

TABLE 1. Description of lakes in study area.

Lake	Township	Surface area (km ²)	Volume (Mm ³)	\bar{Z} (m)	Z_{\max} (m)	pH
Gull	Lutterworth	9.96	164.34	16.50	49.10	7.5
Moore	Lutterworth	1.83	13.80	7.56	21.60	6.0
Hall's	Stanhope	5.40	150.66	27.90	79.20	6.0
St. Nora	Stanhope	0.33	5.32	16.00	40.00	6.0
Head	Laxton/Digby	9.18	32.13	3.50	8.30	7.5
Mountain ^a	Minden	3.19	44.12	13.43	31.39	6.5
Plastic	Sherborne	0.33	2.64	8.10	16.76	5.6
Brady	Hindon	0.89	4.08	4.56	11.58	5.8
Blue Chalk	Ridout	0.50	4.70	9.37	21.95	6.0
Picard	Cavendish	0.76	7.69	10.15	35.05	7.4

^aMeasurements include A and B basins.

such as body weight (Richman 1958) and body length (McMahon 1965; Burns 1969). They were also found to be a function of biophysical parameters such as temperature (Burns 1969; Chisolm et al. 1975; Geller 1975), light (McMahon 1965; Buikema 1973) edible phytoplankton concentration (McMahon 1965; Geller 1975; Kersting and van der Leeuw 1976), and time of day in which rates were measured (Haney and Hall 1975; Starkweather 1975, 1983; Duval and Geen 1976). Blue-green filaments were also found to have inhibitory effects on feeding rates (Burns 1968; Webster and Peters 1978; Porter and Orcutt 1980; Gliwicz and Siedlar 1980). In this study, we examine the effect of some of these factors on in situ filtering rates. By evaluating the importance of these parameters, we are able to build an empirical model to predict filtering rates for a number of cladoceran species, and thereby free investigators of having to perform tedious and time-consuming grazing experiments in the field.

Materials and Methods

The 10 study lakes are in south central Ontario and vary considerably with respect to lake morphometry (Table 1). Mountain Lake has two distinct basins (A and B) that were sampled separately and treated as two water bodies. Total phosphorus in these lakes ranged from 5 to 12 mg·m⁻³, Chl *a* ranged from 0.8 to 4.0 mg·m⁻³, and pH ranged from 5.6 to 7.5.

Brady, Mountain A and B, Plastic, and Picard lakes were sampled in 1981; the remaining lakes were sampled in 1982. Each lake was visited once between June and September except for Mountain B and Plastic lakes, which were visited twice during the summer of 1981. Lakes were sampled at one station, usually at the deepest part of the basin.

We followed the procedure outlined in Holtby and Knoechel (1981) for labelling algae with ¹⁴C. The algal species used were *Chlorella vulgaris* (6–8 μm, longest dimension) and *Scenedesmus ovalis* (4–6 μm; Indiana Culture Collection) in 1981 and 1982, respectively. Sufficient radioactive cells to bring the specific activity in the grazing chamber to at least 1000 cpm·mL⁻¹ were added. Final concentration of labelled algae in grazing chambers ranged from 1000 to 5000 cells·mL⁻¹. This addition constitutes less than 10% of natural phytoplankton biomass in each lake.

Grazing Experiments

All of the grazing experiments were performed in situ using a 2-L Haney (1971) chamber, because filtering rates were

depressed when animals were first concentrated by vertical hauls with a plankton net and then placed into experimental beakers (P. Chow-Fraser, unpubl. data). Feeding experiments were conducted at various depths throughout the water column and the ambient water temperature corresponding to each experiment was monitored. Experiments were all conducted between 10:00 and 16:00, except for two sets of experiments comparing midday grazing rates with those measured at dawn (06:00) and at dusk (20:00).

Animals were allowed to feed at the depth of sampling for 10 or 15 min and were then collected on 64-μm-nitex screen. They were subsequently killed with hot water, rinsed with at least 1 L of filtered lakewater, and then stored frozen on dry ice until they were sorted. Replicate 5-mL aliquots of the labelled grazing-chamber water were also collected to determine available food radioactivity.

Edible Phytoplankton Concentration

Phytoplankton samples were collected to determine edible phytoplankton concentration in water strata corresponding to the depths at which grazing experiments were conducted. Integrated samples from 0–4 and from 4–8 m were collected with a tube sampler. The sampler consisted of two lengths of tygon tubing (inside diameter 1.5 cm) joined by a tubing connector. The upper portion was 4.5 m long, the lower 4.0 m; iron weights were attached to the lower end of the sampler. The apparatus was lowered slowly at right angles to the water surface. Water level inside the tubing was visually monitored during the descent to ensure that there was no more than a few centimetres difference between inside and outside water levels. Once 8 m of tubing had been submerged, the upper end was clamped shut and the lower end was retrieved by means of an attached string. In this manner, an 8-m column of water was obtained. The column was then split by carefully disconnecting the tubing connector, and the upper and lower portions were separately retained. After the procedure was repeated, upper and lower portions were respectively combined and subsamples were preserved with Lugol's iodine solution.

Samples from the 4-m column corresponding to the depths at which most of the grazing data were collected were then analyzed. Algal biomass was estimated from calculations of algal biovolumes. Phytoplankton freshweight (milligrams) was estimated to be equal to the calculated biovolumes on the basis that cell contents have a specific gravity of 1. Cell volumes were approximated by assigning simple geometric shapes to cells and using average cell dimensions in volume formulae. The edible

portion of the phytoplankton was operationally defined as algae whose maximum linear dimension were <30 μm .

Animals, stored in petri plates on dry ice, were sorted without addition of water or preservative. Zooplankton were identified using a dissecting microscope. *Daphnia* spp. were measured from the base of the tailspine to the anterior-most point of the carapace along the long axis of the body. Length of the body, excluding spines and setae, was measured for the remaining genera. For convenience, all of the length measurements will be referred to as "carapace length." Animals were stored individually in scintillation vials before they were prepared for scintillation counting.

Radioactivities of the available algae of replicate 5-mL samples of grazing-chamber (GC) water were determined by liquid scintillation counting in Aquasol II counting solution. Animals were individually digested in scintillation vials overnight at 50°C with 0.25 mL of NCS tissue solubilizer (Amersham). Radioactivities of the zooplankton were determined by liquid scintillation counting in OCS counting solution (Amersham; recommended for use with NCS). The procedure for scintillation counting for both algae and zooplankton is given in Holtby and Knoechel (1981). Zooplankton filtering rates were calculated as

$$\text{Filtering rate} = \frac{\text{dpm in animal}}{\text{dpm in 1 mL GC water}} \times \frac{1440 \text{ min} \cdot \text{d}^{-1}}{\text{time spent in GC}}$$

Statistical Analyses

A predictive slope is used to make predictions of y on x whereas a functional slope is a "measure of the central trend of a natural distribution" (Ricker 1973). For example, the predictive regression is appropriate for making predictions of filtering rate for animals sampled in study lakes and is not appropriate for cross-study comparisons. The functional slope, on the other hand, is appropriate for determining whether the power function of the relationship between filtering rate and length is 2, 3, or an intermediate value and is appropriate for cross-study comparisons. Under certain experimental conditions the predictive regression is a good estimate of the functional regression; however, when distributions of the data are open-ended and non-normal (see Table 2) the functional regression should be used routinely both for description and prediction (Ricker 1973). In past studies, investigators have tended to use the predictive regression indiscriminantly to estimate both functional and predictive slopes. Consequently, most reported values are actually estimates of the predictive regression, although they have been interpreted as functional regressions. To keep our values comparable with those in literature, we report both functional as well as predictive slopes, recognizing that predictive slopes from different studies should be compared cautiously.

Predictive regressions were estimated using Model I least-squares regression analyses (Ray 1982); functional regressions were estimated by Model II regression analyses (geometric mean regression) because both carapace length and filtering rate were subject to a combination of inherent variability and measurement error (Ricker 1973). At present, the standard error of the slope from a geometric mean regression is estimated by the standard error of the slope from Model I regression. Model I least-squares regression analyses were also used to compute a

TABLE 2. Summary of normality tests, using Kolmogorov-Smirnov D -statistic (SAS; Ray 1982). Values of $P < 0.05$ denote significant departure from normality (FR = filtering rate; L = length; $n = 845$).

Variable	D	P
FR	0.2104	<0.01
\log_{10} FR	0.0893	<0.01
L	0.0864	<0.01
\log_{10} L	0.1175	<0.01

multiple linear regression equation of filtering rate as a function of both carapace length and edible phytoplankton concentration, and to compare regression equations after the data were sorted by lake and species.

To test differences among zooplankton species with respect to filtering rates, we selected data obtained at approximately the same time, at the same depth, and within the same lake so that effects of temperature and diet composition were held constant. This procedure eliminated all but three lakes for the comparison. Small sample sizes for two lakes also necessitated a graphical rather than statistical analysis.

To determine if the high variance noted for small animals (*Bosmina*) was due to biological variability or due to Poisson variability in particle-encounter frequencies inherent in the experimental procedure, we investigated the effect of encounter rate of tracer cells on the variability of filtering rate. To test whether or not *Bosmina* ingested tracer cells randomly during the grazing period, a chi-square test of variance-to-mean ratio (Elliott 1979) was used.

Data distributions were tested for significant departures from normality with the Kolmogorov-Smirnov D -statistic for sample size >50 , and with the Shapiro-Wilk W -statistic for sample size <51 (Ray 1982). Variance-ratio test was used to test for homogeneity of variance (Zar 1984). We tested differences between midday rates and those measured at dawn and at dusk, and the effect of temperature on filtering rate in St. George Lake using two-way analysis of variance (Ray 1982). A nonparametric two-factor analysis of variance (Ray 1982) was used to test the effect of temperature on filtering rate in Plastic Lake because data distributions did not have homogeneous variances.

Results and Discussion

Our pooled dataset comprises 845 individual filtering rates measured in 10 lakes of different trophic over the course of two summer seasons. No attempt was made to regulate the percent contribution of any species to the dataset. In total, eight cladoceran species were sampled. Of the four *Daphnia* species identified, the dominant ones in the study were *D. galeata* ($n = 189$) and *D. dubia* ($n = 63$); *D. rosea* ($n = 35$) and *D. pulex* ($n = 21$) were present in only a few experiments. *Holopedium* ($n = 190$) and *Bosmina* sp. ($n = 251$) were collected mainly from Plastic Lake, although some measurements on these species were obtained in most of the other lakes. *Diaphanosoma* ($n = 12$) was present but rare in 6 of the 10 lakes. *Ceriodaphnia* ($n = 33$) was a dominant zooplankton in Head Lake and was seldom present in other study lakes. Fifty-one daphniids could not be identified and remained in the analysis as *Daphnia* sp. Experi-

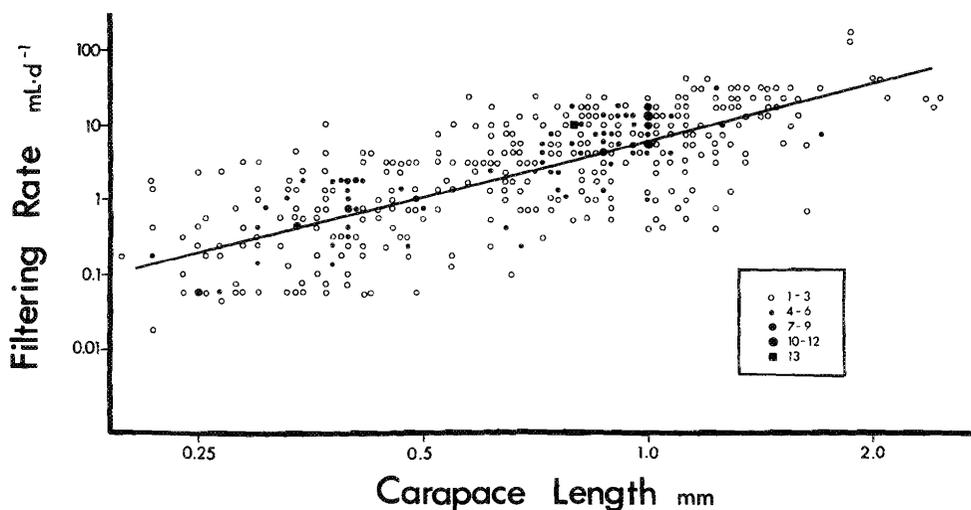


FIG. 1. Filtering rate vs. carapace length for data pooled from all lakes ($n = 845$). Solid line represents Model I least-squares regression (see Eq. 1). Each number corresponding to a symbol in the box represents number of overlapping points.

TABLE 3. Comparison of functions relating filtering rate to zooplankton body length ($FR = mL \cdot d^{-1}$).

Investigator	Zooplankton species	Relationship
McMahon 1965	<i>D. magna</i>	$\log_{10} FR = 2.20 \log_{10} L + 0.83$
Burns 1966	<i>D. rosea</i>	$\log_{10} FR = 3.02 \log_{10} L + 0.87$
Geller 1975	<i>D. pulex</i>	$\log_{10} FR = 2.42 \log_{10} L + 0.88$
DeMott 1982	<i>D. rosea</i>	$\log_{10} FR = 2.41 \log_{10} L + 0.81$

mental temperatures ranged between 10 and 22°C; in most cases, however, they were above 18°C.

Carapace Length

With the exception of a semi-log relationship reported by Hayward and Gallup (1976), filtering rate and zooplankton body length have generally been related in a log-log fashion (Table 3). Therefore, we first present a plot of filtering rate versus carapace length for the pooled data to examine the generality of the relationship.

A striking feature of the relationship between filtering rate and carapace length is the extreme variability in filtering rates (Fig. 1). Considering the heterogeneous composition of our dataset, however, this variability is not surprising. Since our measurements are of individual rates rather than group means, variability is probably due in large part to individual variability of ingestion rates. Narita and Ward (1972) found that filtering rates for an average 2.0-mm *D. similis* ranged from 1.3 to 32.3 $mL \cdot d^{-1}$, with a mean of 20.8 $mL \cdot d^{-1}$, despite the fact that their experiments were conducted under laboratory-controlled conditions. Thompson et al. (1982) also showed a 10-fold range in filtering rate of similar-sized animals in the field. There was high variation within a single grazing experiment. Replicate experiments at the same depth yielded equally variable results compared with data from experiments performed at the same temperature in different lakes (Table 4). The high coefficients of variation observed in Table 4 suggest that individual variation contributed substantially to overall variation in the pooled data. Besides individual variation, however, some variability may be

TABLE 4. Basic descriptive statistic of grazing data corresponding to single experiments, all conducted at 20–22°C. Only *D. galeata* (1–1.5 mm) are included in this analysis.

Lake	Depth (m)	n	Uncoded mean	Coefficient of variation (%)	
Brady	4	3	5.75	46.44	
	Gull Head	4	6	13.96	27.41
		1	17	3.91	109.59
Moore Mountain B	2	6	1.04	1929.60	
	3	5	1.51	302.11	
	3	6	3.01	106.36	
	5	3	11.75	45.28	
	2	10	1.85	85.74	
	3	8	6.16	17.21	
Mountain B	3	4	3.41	30.52	
	4	16	3.95	77.41	
	4	6	3.40	69.66	
	5	6	8.32	10.48	
	5	22	1.40	439.97	
	7.5	6	3.37	105.31	

associated with the insensitivity of the method to accurately measure individual rates of small animals such as *Bosmina*.

Variation in encounter rates of food particles becomes random when the amount of water filtered and hence number of particles ingested are low ($<1.0 mL \cdot d^{-1}$; <5 cells \cdot animal $^{-1}$). Because the ingestion rate of tracer cells for *Bosmina* is extremely low (rarely more than 15 cells during a grazing period), we speculate that the great individual variability in *Bosmina* filtering rate is due to random encounter probabilities. A chi-square test of variance-to-mean ratio for agreement with a Poisson distribution (Elliott 1979) indicates that *Bosmina* does in fact ingest tracer cells at random (Table 5). When ingestion rates are random, reliability of individual rates are severely reduced. Therefore, much of the variability associated with filtering rates of *Bosmina* is artifactual rather than natural. In order to increase reliability, we would have to greatly increase the encounter rate; however, since encounter rate cannot be further increased without altering the algal concentration in the

TABLE 5. Chi-square test of variance-mean ratio for agreement with a Poisson distribution (Elliott 1979) to determine if *Bosmina* sp. ingested tracer cells randomly. Values of $P > 0.05$ denote conformity with randomness.

Mean no. of cells ingested per grazing period	s^2	df	χ^2	P
1.66	0.45	9	2.43	>0.97
4.00	2.16	18	36.72	>0.25
7.51	4.58	27	35.23	>0.25
14.48	17.14	24	28.41	>0.25
16.33	16.65	23	23.45	>0.25
20.15	18.15	37	33.32	>0.25

grazing chamber, it seems impractical to assay individual variation in these animals using the Haney method.

Despite the large variability, carapace length was nevertheless an important predictor of filtering rate for the pooled dataset. A least-squares regression analysis produced a significant log-log relationship between filtering rate (FR; millilitres per day) and carapace length (L ; millimetres) (F -test; $P = 0.0001$), accounting for almost 60% of the variability in filtering rate ($r^2 = 0.589$):

$$(1) \log FR = 2.45 (\pm 0.071) \log L + 0.80 (\pm 0.020)$$

(numbers in parentheses are standard errors). The slope of the regression is equivalent to the exponent when filtering rate is expressed as a power function of body length. Our exponent of 2.45 compares well with those previously described in laboratory studies (Table 3) in which *Daphnia* filtering rate has been described as a function ranging between a square and a cube of zooplankton body length.

We employed Model II (geometric mean) regression to generate a functional slope for the pooled data, producing the following regression equation:

$$(2) \log FR = 3.19 \log L + 0.93.$$

Whereas slope of the predictive equation more nearly approximates a square of length, slope of the functional equation exceeds a cubic function of length. This comparison points out the inappropriateness in most cases of using the predictive slope to estimate the functional slope when both variables are subject to natural variability and measurement error. Only in cases where variance is very high (i.e. Blue Chalk and Hall's lakes in Table 6) does the predictive slope approximate the functional slope. The difference between the mean Model I slope of 2.45 and the mean Model II slope of 3.19 is not merely academic, because the value of the exponent indicates that animals in our lakes generally filter-feed in proportion to their volume rather than to surface area. However, this functional slope might be biased by lakes with large sample size, and might not be representative of all study lakes. This possible bias was examined by reorganizing the pooled data to yield regressions for individual lakes.

Functional slopes of the sorted data, representing the 11 water bodies, range from 2.67 to 3.95, the majority lying between 2.85 and 3.40 (Table 6). Mean value for these slopes, 3.22, is very similar to 3.19, slope of the pooled regression. Comparison of these regression coefficients (Tukey-Kramer method, Sokal and Rohlf 1981) indicates that they are statistically homogeneous ($P > 0.05$). Therefore, functional slopes for these lakes appear to approximate 3. Predictive slopes of the lake-specific regressions are also statistically homogeneous ($P >$

0.05); the mean value, 2.49, is again very similar to exponent value of the pooled regression, 2.45.

Statistical homogeneity in slopes for both these models indicates that the exponent in the filtering rate - length relationship is consistent from lake to lake despite the heterogeneous nature of the data. Mixed zooplankton assemblage, temperatures ranging from 10 to 22°C, and mixed phytoplankton communities all appear to have minimal effects on the exponent value. Since published observations indicate that zooplankton species (Burns 1969; Table 3), temperature (Burns 1969; Chisolm et al. 1975), and time of day (Starkweather 1983) can affect the exponent, a more detailed assessment of effects of these factors on filtering rates was conducted.

Zooplankton Species

A visual comparison of data corresponding to various cladoceran species in Brady and Mountain A lakes (Fig. 2) indicates that filtering rates are scattered about the regression line without any obvious pattern of species. Therefore, although no statistical comparisons can be made, these distributions do not appear to support the observation made by Burns (1969) that exponents associated with various *Daphnia* species are different.

The larger sample size of Head Lake facilitated a statistical comparison of filtering rates corresponding to *Ceriodaphnia*, *D. galeata*, and *D. dubia*. Linear regression analyses indicate that slope of the regression equation corresponding to *Ceriodaphnia* is significantly different from those of the two *Daphnia* species ($P = 0.0336$), although differences between *Daphnia* species are not statistically significant ($P = 0.3306$). Filtering rates associated with *Ceriodaphnia* are consistently higher than those of similar-sized *Daphnia* (Fig. 3). Although this comparison confirms observations made by Neill (1975) and Lynch (1978) that adult *Ceriodaphnia* are more efficient filterers than juvenile *Daphnia*, L. B. Holtby (unpubl. data) found that *Ceriodaphnia* did not consistently filter more efficiently than daphniids. The data again do not support observations made by Burns (1969) that different species of *Daphnia* require different regression equations.

DeMott (1982) reported differences between slopes for *Daphnia* and *Bosmina*, showing that filtering rate of *Daphnia* increased as a cube of length whereas that of *Bosmina* increased only as a square. In our study the data are too variable to resolve possible differences in regressions for the zooplankton species; the predictive and functional slopes corresponding to two species of *Daphnia* and *Bosmina* were homogeneous (Table 7) ($P > 0.05$). In all cases, the predictive slope approximated 2, whereas the functional slope approximated 3.

We also assessed the effect of zooplankton species on filtering rate by comparing lake-by-lake distributions of *D. galeata*. Filtering rates of *D. galeata* corresponding to seven study lakes are plotted together in Fig. 4 to illustrate the large intraspecies variation that existed across lakes. This large variation is in fact as great in magnitude as the interspecies variation in Head Lake (Fig. 3). Additionally, a comparison of lake-by-lake regressions reveals that the slopes are all homogeneous ($P = 0.9893$). Functional slope of the combined data is 3.07, compared with the predictive slope of 2.43. This disparity between functional and predictive slopes is again very similar to that for the pooled data described earlier.

Temperature

Filtering rates (corresponding to animals ranging from 0.30

TABLE 6. Regression statistics of filtering rate ($\text{mL} \cdot \text{d}^{-1}$) on carapace length (mm) for each lake; P represents the probability of obtaining observed slope if the true value is zero as determined by an F -test.

Lake	n	Regression model	Slope	SE	Intercept	SE	r^2	P
Brady	17	I	2.69	0.531	0.90	0.162	0.632	0.0001
		II	3.39		1.04			
Moore	24	I	3.15	0.507	0.98	0.193	0.638	0.0001
		II	3.95		1.19			
Picard	33	I	2.25	0.453	0.99	0.049	0.444	0.0001
		II	3.38		0.91			
Gull	17	I	2.14	0.410	0.99	0.044	0.640	0.0001
		II	2.67		1.00			
Mountain A	23	I	2.33	0.422	0.98	0.092	0.592	0.0001
		II	3.03		1.01			
Plastic	390	I	2.72	0.106	0.96	0.034	0.633	0.0001
		II	3.42		1.13			
Hall's	7	I	3.15	0.318	0.95	0.060	0.952	0.0002
		II	3.22		0.95			
Mountain B	170	I	2.15	0.173	0.62	0.039	0.481	0.0001
		II	3.11		0.72			
Head	121	I	2.52	0.220	0.68	0.069	0.523	0.0001
		II	3.48		0.88			
St. Nora	13	I	1.67	0.692	0.41	0.148	0.347	0.0342
		II	2.84		0.49			
Blue Chalk	24	I	2.60	0.389	0.48	0.095	0.818	0.0001
		II	2.88		0.44			

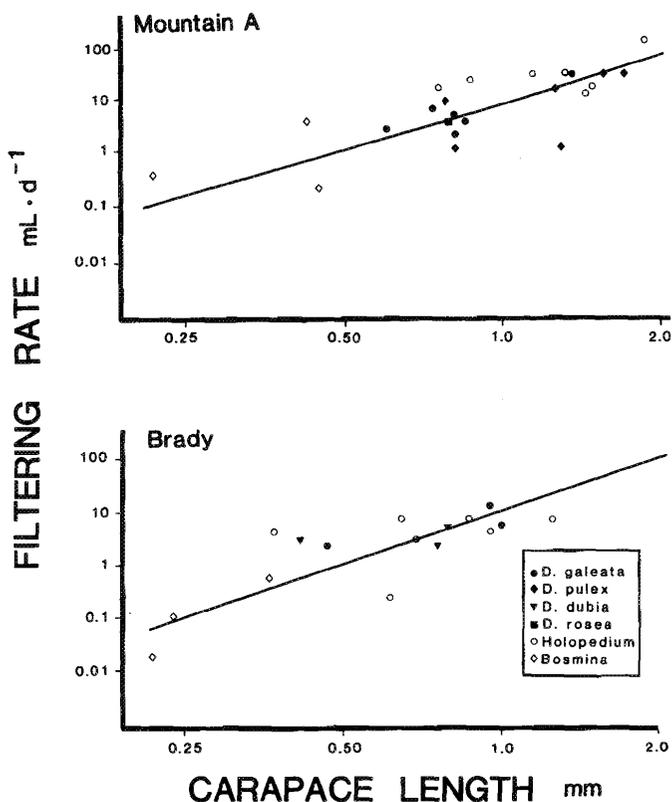


FIG. 2. Filtering rate vs. carapace length for Mountain A and Brady lakes. Solid lines indicate Model I least-squares regression through data.

to 1.20 mm) from Plastic Lake were grouped into five length intervals so that effect of temperature could be tested using two-way analysis of variance (Table 8). We found no statistically significant effect of temperature on filtering rates in the range of 10–20°C. Absence of a significant effect was not likely due to inclusion of many species in the analysis, since taxonomic affiliation did not appear to have had a noticeable effect on filtering rates in other lakes with this species-mix. Table 8 also included two analyses using single-species data from St. George Lake. (L. B. Holtby, unpubl. data). Data were grouped into appropriate length intervals and the effect of temperature was also tested using two-way analysis of variance. Again, we found no significant effect of temperature on filtering rates.

Haney (1973), Haney and Hall (1975), and Downing and Peters (1980) also failed to find a relationship between filtering rate and temperature in the field. By contrast, the effects of temperature on filtering rates in laboratory experiments have been somewhat varied. Whereas some investigators reported no significant effect (Schindler 1968; Buckingham 1978; Armitage and Lei 1979), others have reported a general trend towards higher filtering rate with increasing temperatures, although they do not concur on slope of the curve nor on optimum temperature (McMahon and Rigler 1965; Burns 1969; Kibby 1971; Geller 1975; Chisolm et al. 1975; Hayward and Gallup 1976; Kersting and van der Leeuw 1976). Armitage and Lei (1979) and Kibby (1971) have alluded to the possible role of temperature acclimatization in regulating filter-feeding in the field. Non-acclimatized animals apparently show little or no temperature effects. Kibby showed that within a range from 12 to 20°C, temperature optimum for filtering rate can be entirely a function

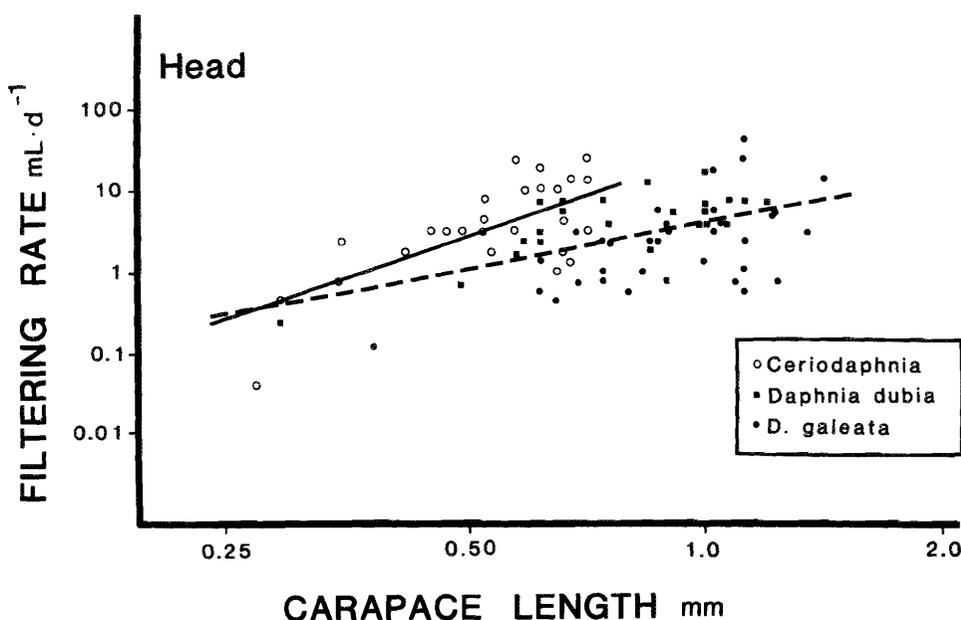


FIG. 3. Filtering rate vs. carapace length. Solid line represents Model I least-squares regression through *Ceriodaphnia* data; broken line represents regression through *Daphnia* data. Slopes of regressions corresponding to the two *Daphnia* species were homogeneous ($P = 0.3306$).

TABLE 7. Comparison of regression statistics of filtering rate ($\text{mL}\cdot\text{d}^{-1}$) on carapace length (mm) for *Bosmina* and *Daphnia* spp.; P represents the probability of obtaining observed slope if the true value is zero.

Zooplankton species	n	Regression model	Slope	SE	r^2	P
<i>D. galeata</i> ^a	56	I	2.32	0.235	0.644	0.0001
		II	2.89			
<i>D. pulex</i>	35	I	2.00	0.435	0.390	0.0001
		II	3.20			
<i>B. longirostris</i>	18 ^b	I	2.16	0.525	0.513	0.0008
		II	3.01			

^aExcluding data from Head, Mountain B, St. Nora, and Blue Chalk lakes. These lakes have significantly lower intercepts than other lakes in study.

^bThese represent means of animals grouped into 0.1-mm length intervals.

of the temperature at which animals are grown. In the current study, grazing experiments were conducted in situ at the depth and temperature of collection. Lack of a significant temperature effect might thus be interpreted as an indication that zooplankton under natural conditions are not acclimatized to a specific temperature.

Time of Day

Two sets of experiments were conducted to test the effect of time of day on filtering rate in Plastic and Mountain B lakes. Filtering rates were compared from experiments conducted at dawn (06:00) and at midday (13:00) in Plastic Lake and data from experiments conducted at dusk (20:00) and midday (14:00) in Mountain B Lake (Table 9). Results of the two-way analysis of variance indicate no significant diel differences in filtering rate for either *D. galeata* or *Bosmina* in our study. These results contrast findings of several field investigators who found increased rates at dawn and dusk compared with midday rates (Nauwerck 1959; Haney and Hall 1975; Duval and Geen

1976), and several laboratory experiments that have also indicated higher nighttime filtering rates (Starkweather 1975, 1983; Chisolm et al. 1975; Peterson et al. 1978). One reason for lack of a consistent effect in our study may be the relatively small size of animals in our samples (0.3–1.2 mm). Starkweather (1983) and Haney and Hall (1975) found that the largest size-classes generally underwent the greatest amplitude of daily change in feeding, while the smallest animals changed very little over the same period. However, Thompson et al. (1982) and L. B. Holtby (unpubl. data) found no nighttime increase in their field experiments that included large animals. Effect of time of day on field-measured filtering rates is obviously inconsistent and the reasons for this should receive further investigation.

Results of the preceding analyses indicate that zooplankton species, temperature, and time of day had no significant effect on filtering rates in our lakes, and therefore, these factors probably had no effect on the exponent of the functional relationship between filtering rate and carapace length. On the other hand, the intercepts vary considerably, from 0.44 to 1.19

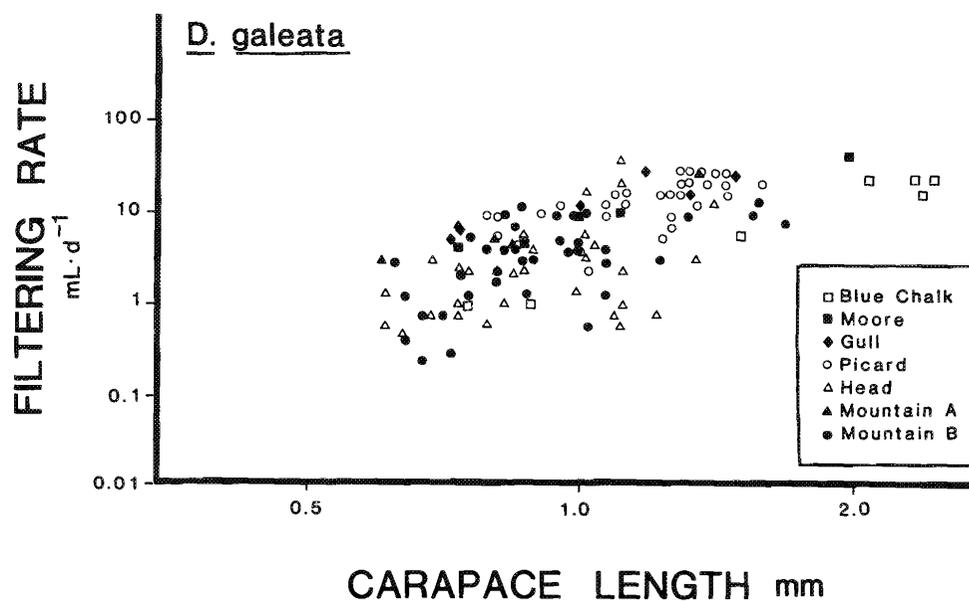


FIG. 4. Filtering rate vs. carapace length for *D. galeata*. Data were pooled from seven study lakes.

TABLE 8. Summary of two-way ANOVA's comparing cladoceran filtering rates at various temperatures. Values of $P < 0.05$ indicate a significant effect.

Temperatures tested (°C)	Lake	Experimental animal	<i>n</i>	Source of variation	<i>P</i>
10, 13, 20	Plastic	Cladocerans ^a (0.30–1.20 mm)	114	Temperature	0.9545
				Carapace length	0.0001
				Temperature × length	0.8331
12, 17	St. George	<i>Daphnia pulex</i> ^b (1.0–3.0 mm)	94	Temperature	0.9374
				Carapace length	0.0001
				Temperature × length	0.7118
17, 22	St. George	<i>Daphnia galeata</i> ^b (0.80–1.60 mm)	36	Temperature	0.2117
				Carapace length	0.0001
				Temperature × length	0.7867

^aInclude *Holopedium*, *Daphnia* spp., and *Bosmina* spp.

^bL. B. Holtby (unpubl. data).

(Table 6). Since the antilog of the intercept is equivalent to the predicted filtering rate of a 1-mm animal, the intercepts thus provide a means of comparing filtering-rate performance between lakes where regression slopes are similar. Although regression of intercepts on edible phytoplankton concentration was not significant ($P = 0.4860$), we added edible phytoplankton concentration to the general regression model because filtering rate has been found to vary inversely with food concentration beginning at a critical level referred to as the incipient limiting level (ILL) (McMahon and Rigler 1965).

Addition of edible phytoplankton concentration to the Model I regression increased the r^2 value from 0.589 to 0.636 ($P = 0.0001$) and yielded the following equation:

$$(3) \log FR = 2.74 (\pm 0.084) \log L - 0.63 (\pm 0.206) \log ED + 2.30 (\pm 0.454).$$

The negative value of the regression coefficient reflects the possible inhibitory effect of edible phytoplankton concentration on in situ filtering rate even at the low levels encountered in our lakes. Since the edible phytoplankton concentrations in the study lakes ranged from 40 to 400 $\text{mg} \cdot \text{m}^{-3}$, the negative coefficient

suggests that ILL in these lakes is lower than most published ILL values (Table 10). McMahon (1965) and Downing and Peters (1980) have suggested that ILL varies as a function of grazer body size. Since most animals in this study were small (1.2 mm) relative to those reported in Table 10, our lower ILL value may simply reflect the smaller zooplankton in our lakes. Another possible reason for this difference is that animals in laboratory experiments grazed on unialgal cultures, whereas animals in our lakes grazed on phytoplankton of diverse species and sizes in combination with detritus and inorganic particulate matter. Our data therefore indicate that the relationship between algal concentration and filtering rate in nature cannot be extrapolated from laboratory studies alone, since in situ filtering rate was detectably affected by phytoplankton concentration at levels lower than those examined in previous studies.

Empirical Model of Filter-Feeding

Carapace length emerged as the most important predictor of in situ filtering rate in our study. Together with edible phytoplankton concentration, it explained 64% of the variation in filtering rate (Eq. 3). Since this two-variable model was empirically derived from data that included *Daphnia* spp.,

TABLE 9. Summary of ANOVA's comparing diel differences in cladoceran filtering rates. Values of $P < 0.05$ indicate a significant effect.

Time of day tested	Lake	Experimental animal	n	Source of variation	P
Dusk and day (20:00 and 14:00)	Mountain B	<i>Daphnia galeata</i> (0.70–1.20 mm)	30	Time of day	0.3771
				Carapace length	0.0126
				Time × length	0.8204
Dawn and day (06:00 and 13:00)	Plastic	<i>Bosmina longirostris</i> (0.20–0.50 mm)	58	Time of day	0.4580
				Carapace length	0.0488
				Time × length	0.7025

TABLE 10. Summary of published incipient limiting level (ILL) values.

Investigators	Zooplankton species	Food species	ILL	
			cells · mL ⁻¹	g · m ⁻³
McMahon and Rigler 1965	<i>D. magna</i> (2.8–3.3 mm)	<i>Chlorella</i>	2.5×10^5	5 ^a
Porter et al. 1982	<i>D. magna</i> (2.7 mm)	<i>Chlamydomonas</i>	1.0×10^4	1.5 ^b
Chisolm et al. 1975	Arctic <i>Daphnia</i> (2.3–2.6 mm)	<i>Chlamydomonas</i>	2.6×10^4	11.0 ^c
Geller 1975	<i>D. pulex</i> (2.0 mm)	<i>Scenedesmus</i>	0.9×10^4 – 4.5×10^4 ^d	1–5
Hayward and Gallup 1976	<i>D. schoedleri</i> (1.5–2.0 mm)	<i>Chlamydomonas</i>	3×10^4	4.1–12.3 ^c
Burns and Rigler 1967	<i>D. rosea</i> (1.6 mm)	<i>Rhodotorula</i>	2.5×10^4	0.5 ^e

^aExtrapolated from fig. 1B (McMahon and Rigler 1965) and assuming a biovolume of $20 \mu\text{m}^3$ for *Chlorella* (Nalewajko 1966).

^bCalculated from the reported dry weight value of $0.54 \text{ g} \cdot \text{m}^{-3}$ and assuming that dry weight is 36.0% of the biovolume for *Chlamydomonas* (Nalewajko 1966).

^cUsing Nalewajko's (1966) biovolume for *Chlamydomonas* of $410 \mu\text{m}^3$.

^dCalculated on the basis that each cell has a biovolume of $111 \mu\text{m}^3$.

^eAssuming a biovolume of $20 \mu\text{m}^3$ (using published dimensions).

Holopedium, *Bosmina*, *Diaphanosoma*, and *Ceriodaphnia* that were collected under environmentally diverse conditions, it should be generally applicable. However, the model does not apply to calanoid copepod species (P. Chow-Fraser, unpubl. data; Chow-Fraser and Wong 1985) nor does it apply to lakes in which blue-green algal filaments are prevalent (P. Chow-Fraser, unpubl. data). Lakes ranging from oligotrophy to mesotrophy in which the species-mix is similar to that found in our lakes should be good candidates for testing the applicability of this model.

This empirical model for cladoceran filter-feeding will be particularly useful for generating large-scale estimates of community grazing rates in situations where grazing data are not available, or cannot be easily obtained. Since accurate sampling is a prerequisite to realistic models of energy transfer between phytoplankton and zooplankton, we hope that this model will permit investigators to concentrate on more accurate sampling rather than on sample processing.

Differences in nutritional status of animals could have contributed to the large individual variation associated with the relationship between filtering rate and length, since starvation can drastically influence the biomass–length relationship for

some cladocerans (Berg 1936; Tessier et al. 1983; Holtby 1981). Therefore, future studies should consider biomass as another useful determinant of filtering rate. Diel differences in field-measured filtering rates for large versus small animals should be given attention. Interference from inedible algal forms as well as usefulness of other “edibility” criteria in the model also need to be examined.

Our results indicate that filtering rates do not vary systematically among cladoceran species. Length alone was a good determinant of filtering rate. Different cladoceran species appear to respond to changing lake conditions homogeneously, and thus treatment of zooplankton based on size rather than on taxon would seem justified. Investigators interested in assessing the impact of losses on the phytoplankton should recognize that species data without corresponding length measurements are not appropriate for calculating grazing losses.

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