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## ALLOMETRIC THEORY: EXTRAPOLATIONS FROM INDIVIDUALS TO COMMUNITIES<sup>1</sup>

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**Abstract.** Physiological rates of individual organisms are well related to their body size. These allometric relationships suggest that ecological rates should also be related to the size structure of organisms in populations, communities, and ecosystems. We describe size distributions of zooplankton communities and explore the implications of such distributions on community grazing rates. Ninety zooplankton communities, varying in biomass and in size distributions, were sampled in 28 lakes in northeastern North America and their grazing rates were predicted with an allometric equation. Zooplankton size distributions vary in shape but, on average, can be described as bimodal. Predicted community mass-specific grazing rate decreases with increasing mean body size ( $r^2 = 0.92$ ) and is only slightly affected by the shape of community size distributions. Community biomass on the other hand increases with mean body size ( $r^2 = 0.39$ ). Total zooplankton grazing rate is expected to be higher in communities dominated by large zooplankton, but this relationship is obscured ( $r^2 = 0.15$ ) by temporal and spatial variability in zooplankton biomass. Although body size is a powerful predictor of individual physiological rates, its importance is expected to be largely masked at the level of communities.

**Key words:** allometry; community rate; community structure; ecological rate; grazing; size distribution; zooplankton.

### INTRODUCTION

Population, community, and ecosystem ecologists have long been interested in the patterns and implications of organism size distributions. Their efforts, however, have largely been independent. Population ecologists focus on the variability in size of individuals belonging to one species. They have extensively compared size distributions across types of environments (Huston and DeAngelis 1987,  $-3/2$  power law reviewed in Firbank and Watkinson 1990), and often use body size distributions as a surrogate or complement to age distributions in population dynamics studies (Ricker 1975, Hughes and Connell 1987). Community ecologists, on the other hand, often disregard size variability among individuals and use the mean size of species to describe patterns of community organization and infer their causes. For example, they have quantified the relationships among population density, species diversity, and mean body size (Lawton 1989). Ecosystem ecologists have focused on broad size distributions of organisms, usually without reference to taxonomic composition, to infer patterns of energy use, productivity, and nutrient or contaminant cycling (Sheldon et

al. 1977, Borgmann and Whittle 1983, Borgmann et al. 1984, Gerlach et al. 1985, Vézina 1986). Interestingly, distinctions among the three approaches to the study of size distributions also extend to the type of environments that have been studied. Population size distributions have been studied in a wide range of plant and animal species, but community size distributions have mostly been studied using terrestrial animals (e.g., Peters and Wassenberg 1983, Damuth 1987, Gaston and Lawton 1988, Maurer and Brown 1988, Blackburn et al. 1990), while the broad size distributions considered by ecosystem ecologists have been studied in the plankton and benthos of aquatic environments (e.g., Sheldon et al. 1972, Witek and Krajewska-Soltys 1989, Rodríguez et al. 1990, Tessier and Horwitz 1990, Sprules et al. 1991, Strayer 1991). Studies of size distributions at the level of populations, communities, and ecosystems are based on different ranges of body size and different levels of taxonomic resolution, and have focused on different questions in different types of environments.

Allometric theory provides a foundation for comparing the implications of size structure on rates of energy use, productivity, and nutrient cycling at the levels of populations, communities, and ecosystems. Allometric relationships describe the size dependence of biological characters and functions and are well established in the physiological and ecological literature (Peters 1983, Calder 1984). For example, small organ-

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isms have higher metabolic rates per unit mass than large organisms but, since they are smaller, they have lower rates per individual than large organisms. Physiological rates of organisms of different sizes cumulate to determine ecological rates of populations, communities, and ecosystems. We use the term ecological rate to represent any physiological rate applied to more than one organism, for example grazing rate of a population, excretion rate of a community, or whole-system respiration. Although physiological rates of individuals are well related to their body size, it remains unclear whether ecological rates can be predicted from characteristics of the size distributions of organisms.

Relationships between individual physiological rate and body size would be expected to apply directly at the population, community, or ecosystem level if all organisms were of equal size. The same relationships would then be found between ecological rates and the mean size of organisms as between physiological rates and individual body size. The size of organisms in populations, communities, or ecosystems, however, is not uniform. In populations, size distributions vary widely, both spatially and temporally. In communities and ecosystems, small organisms are generally more numerous than large organisms (e.g., Fuhrman 1981, Sprules and Munawar 1986, Nentwig 1989, Ahrens and Peters 1991a), both because species of small organisms can reach higher densities than large-bodied species (Peters and Wassenberg 1983, Brown and Maurer 1986, Damuth 1987, Lawton 1989) and because there are usually more species of small organisms than of large organisms (Warwick 1984, May 1988, Lawton 1989). The size structure of organisms should, therefore, affect ecological rates at all levels of study.

The link between allometric relationships, size distributions, and ecological rates at the level of populations, communities, and ecosystems has rarely been considered. Understanding this linkage, however, is crucial for developing models of ecological processes such as respiration or production, that can be extrapolated to different scales. Such flexible models would be particularly important to merge traditional physiological research, and current interests in modelling and predicting ecological processes at regional and global scales (Mooney 1991). This study addresses three questions about community size structure and energy usage based on size distributions of crustacean zooplankton in lakes. Our analysis concentrates on crustacean communities, but a similar approach could be applied to individual populations or to communities covering a much broader range of body sizes (e.g., bacteria to fish).

First, we ask whether zooplankton communities typically conform to simple patterns of size distribution. Log-linear relationships between density of organisms and body size have been found over large ranges in body size (Peters and Wassenberg 1983, Damuth 1987, but see Lawton 1990), but density peaks are often more

pronounced in communities where organisms cover a narrower range of body sizes (e.g., Griffiths 1986, Strayer 1991). If typical patterns of size distribution were found, empirical models describing these size distributions would facilitate comparisons among communities and testing of hypotheses concerning the impacts (e.g., nutrient regeneration, energy dissipation through respiration) of communities of differing size structure (Pace 1984, Poulet et al. 1986, Sprules and Munawar 1986).

We next address whether variation in community size structure affects ecological rates. From allometric theory, we know that mass-specific physiological rates of an organism decrease with increasing body size (Peters 1983). By simple analogy, we may expect community mass-specific rates (CSR) to decline with increasing mean body size ( $\bar{M}$ ) as:

$$CSR = a\bar{M}^b. \quad (1)$$

Since other characteristics of size distributions, for example the variance in body size or the skewness of a size distribution, may also affect community mass-specific rates, coefficients  $a$  and  $b$  in Eq. 1 are estimated empirically. We test the importance of mean body size and of the shape of size distributions in determining mass-specific grazing rates across zooplankton communities.

Finally, we evaluate the importance of variations in community biomass on ecological rates. Both the size and the abundance of organisms affect community rates. Individual body size is related to mass-specific rates, abundance and body size determine community biomass, and ecological rates are functions of mass-specific rates and community biomass. Communities with low biomass should have low ecological rates, but these rates may also be affected by the size of organisms found in different communities. Community biomass, however, may not vary independently of community size distribution. Population density ( $D$ ) usually decreases with mean body size ( $\bar{M}$ ; Peters and Wassenberg 1983, Brown and Maurer 1986, Damuth 1987, but see Lawton 1989) as:

$$D = c\bar{M}^d. \quad (2)$$

Population biomass ( $B$ ), which is the product of density and mean body size, is therefore expected to vary with mean body size as:

$$B = c\bar{M}^d \cdot \bar{M} = c\bar{M}^{d+1}, \quad (3)$$

where  $d$  is from Eq. 2. The magnitude of  $d$  varies among taxonomic groupings but is often  $> -1$  (e.g., for invertebrates  $d = -0.54$ , Peters and Wassenberg 1983; for birds  $d = -0.30$ , Brown and Maurer 1986; for mammals  $d = -0.78$ , for aquatic animals  $d = -0.87$ , Damuth 1987), suggesting that population biomass generally increases with mean body size ( $d + 1 \geq 0$ ). Relationships of the form of Eq. 2 are found for individual species and across a broad range of taxa (Peters and Wassenberg 1983, Brown and Maurer 1986,

Damuth 1987). We, therefore, pose the hypothesis that similar relationships can be found between biomass and mean body size at the level of communities. We test the relationship between zooplankton biomass and mean body size using data from a wide range of lakes.

Our analysis is based on measured zooplankton size distribution and on predicted grazing rates. We use size distributions from sampled communities to focus our analysis on communities that are found in nature. Grazing rates are predicted solely from zooplankton body size, without consideration of other important variables such as food concentration, food quality, or zooplankton taxonomic composition. The goal of this study is not to provide accurate predictions of the grazing rate of zooplankton communities (for such an analysis see Cyr and Pace 1992), but to explore the implications of allometric relationships at the level of communities, without the influence of other complicating variables.

## METHODS

### Zooplankton size distributions

Size distributions were measured on 90 zooplankton communities sampled in 28 lakes in Connecticut, New York, and Pennsylvania, USA, and southern Québec, Canada (latitude 41°15' N–45°30' N). Two data sets were used. The first data set ( $n = 60$ ) is based on monthly samples from 12 sites taken between May and September 1982. Integrated vertical samples of the water column were taken primarily with a bilge pump (see Pace 1984 for sampling details). The second data set ( $n = 30$ ) was collected between September–October 1988 and May–October 1989, and focused on nighttime surface (1–2 m depth) zooplankton (Cyr and Pace 1992). Crustaceans, including nauplii, were collected using a bilge pump and retained on a 73–80  $\mu\text{m}$  mesh net. For both sets of samples, invertebrates were anesthetized with carbonated water and preserved in 4% sucrose-formaldehyde.

Zooplankton biomass and size distribution were estimated from the density and the length of organisms. In 1982, a minimum of 400 individuals were counted per sample and densities were averaged from triplicate samples. The size of 20–25 organisms of the most abundant taxa and 10 organisms of the rarer taxa was measured in one pooled sample. In samples from 1988 to 1989, zooplankton densities were averaged from 3 to 8 replicates. All crustaceans were counted in samples containing <2000 organisms, or when counts did not conform to a Poisson distribution (Elliott 1977). Otherwise, subsamples were taken until at least 400 organisms of the most common taxon were counted. Thirty to fifty organisms per taxon were measured in each sample. Body lengths were converted to dry mass to determine community biomass and to make body size measurements comparable across taxa of different shapes. We converted body lengths to dry mass using the equations of Bottrell et al. (1976), Rosen (1981),

Persson and Ekbohm (1980), and Lawrence et al. (1987), correcting for detransformation (Bird and Prairie 1985).

Size distributions were expressed as the density of organisms in different size classes, regardless of their taxonomic affiliation (modified from the normalized size distribution of Sprules and Munawar [1986]). Densities are in  $\log_2$  units. Body size classes range from 0.016  $\mu\text{g}$  [ $\log_2(0.016) = -6.0$ ] to 64  $\mu\text{g}$  [ $\log_2(64) = 6.0$ ], increasing by 0.5  $\log_2$ (dry mass) units. For each community, we determined mean individual dry mass, the variance in individual body mass, and the number of modes of the size distribution. Troughs and peaks are defined as twofold changes [i.e., 1.0  $\log_2$ (density) units] found in two or more consecutive size classes.

### Grazing rate

The term grazing applied to zooplankton refers to a different mode of feeding than in the case of herbivorous insects or ungulates. Zooplankton usually act as "predators," eating and killing individual prey, rather than as "grazers," which remove only a part of each prey individual, rarely killing it (Begon et al. 1990).

We estimated zooplankton community grazing rates by calculating the contribution of each individual. Grazing rates, expressed as volume cleared of prey per unit time ( $\text{GR}_i$ , in millilitres per organism per day), were predicted for each individual measured using the general zooplankton model from Peters and Downing (1984: 769 [model 2]) parameterized for our communities. We chose this allometric equation because of its generality: it was developed using 350 laboratory grazing rate measurements on calanoids and cladocerans from marine and freshwater environments. We focussed our analysis on community size structure by allowing only body dry mass to vary, while other independent variables in the model were either assigned the average value from the communities we sampled (food concentration = 0.58  $\mu\text{g/g}$ ; converted from an average chlorophyll concentration of 7.55  $\mu\text{g/L}$  using the factors in Peters and Downing's [1984] Table 1), or were set to the median values of the model (food particle volume = 287  $\mu\text{m}^3$ , container volume = 425 mL, duration of the manipulation to measure grazing rate = 600 min; Peters and Downing 1984, Table 2). The resulting equation can be simplified to:

$$\log_{10}\text{GR}_i = 0.3915 + 0.546 \cdot \log_{10}M,$$

where  $M$  is body dry mass (in micrograms). Predictions were multiplied by a correction factor ( $e^{\text{RMS} \cdot 2.303/2}$ , where RMS is the model residual mean square) for detransformation from the logarithmic to the arithmetic scale (Sprugel 1983). Total community grazing rate (CGR, in litres per day) is calculated as:

$$\text{CGR} = \sum_j \sum_i [\text{GR}_{ij} \cdot (n_j/m_j)] / 1000,$$

where  $n_j$  is the number of invertebrates of taxon  $j$  present in a sample and  $m_j$  is the number of invertebrates

of taxon  $j$  sized. The mass-specific grazing rate of a community (in litres per milligram per day) is the quotient of total community grazing rate and community biomass (in milligrams). For comparisons among communities, total grazing rate is divided by sample volume and expressed as  $\text{day}^{-1}$ .

#### *Community biomass and mean body size*

Additional data on lacustrine zooplankton biomass, density, and/or mean body mass were extracted from published studies. We systematically reviewed all papers published in *Archiv für Hydrobiologie* (1984–1989), *Canadian Journal of Fisheries and Aquatic Sciences* (1980–1990), *Ecological Monographs* (1980–1990), *Ekologia Polska* (1974–1981), *Freshwater Biology* (1980–1990), *Journal of Plankton Research* (1987–1990), and *Limnology and Oceanography* (1980–1990). Inconsistency in the time periods reviewed for each journal reflect the content of our library at the time of the search. We limited our search to studies where crustacean biomass was estimated using length–mass relationships, a method comparable to the one we used.

#### *Statistical analyses*

All relationships were modeled using Model I linear regression analysis. The relationships between community mass-specific grazing rate and mean body size, and between community biomass and mean body size, are of enough ecological interest to warrant quantification, despite possible autocorrelation (Prairie and Bird 1989). We nevertheless verified, using randomization tests (two-tailed tests on  $r^2$  with  $\alpha = .05$ ; Sokal and Rohlf 1981, Jackson et al. 1990), that autocorrelation was not driving these relationships. Differences in community grazing rates associated with the shape of size distributions were sought by analysis of covariance, after testing for differences in slopes (Neter and Wasserman 1974).  $\log_{10}$  transformations were necessary to homogenize the variance of community biomass, mean body size, grazing rate, and chlorophyll concentration data. All analyses were performed on SAS for microcomputers (SAS 1988).

### RESULTS AND DISCUSSION

The crustaceans that we studied ranged in length from  $\approx 60 \mu\text{m}$  to 2.5 mm ( $\approx 0.01$ –75  $\mu\text{g}$  dry mass). Zooplankton were sampled between May and October (water temperature = 12°–26°C) in lakes that varied in trophic status (chlorophyll concentration in surface water = 0.6–71  $\mu\text{g/L}$ ). Zooplankton dry biomass ranged more than two orders of magnitude (0.007–1.232 mg/L) and was only weakly related to water temperature (ANOVA:  $P < .01$ , proportion of variance explained:  $r^2 = 0.10$ ) or to chlorophyll concentration (ANOVA:  $P < .001$ ,  $r^2 = 0.23$ ). The mean size of organisms ranged 20-fold (0.3–7.9  $\mu\text{g}$  dry mass) and was not related to chlorophyll concentration (ANOVA:  $P > .46$ ). Taxonomic composition varied from strong domination

(>90% biomass) by one taxon (*Daphnia* or cyclopoid copepods) to the presence (>1% biomass) of nine taxonomic groups.

#### *Are there patterns in zooplankton size distributions?*

Individual zooplankton were classified according to their dry mass into 25 size classes, in  $\log_2$  intervals, from 0.016 to 64  $\mu\text{g}$ . These classes were chosen to encompass the range of crustacean sizes we sampled and to obtain enough categories for statistical analyses of size distribution patterns. Other size class parameters could have been chosen. Wider size classes would raise the density of organisms found in each size class and reduce the number of size classes available. Narrower size classes would make classes for small organisms extremely narrow, resulting in many empty size classes. Changing size class width affects the level of resolution at which patterns of size distribution can be detected but, as will be seen, would not affect our results much.

The range of size distributions varied across communities. Size distributions covered between 12 and 22 size classes. The lower limit of size distributions ranged from 0.016 ( $=2^{-6}$ ) to 0.088 ( $=2^{-3.5}$ )  $\mu\text{g}$ , and the higher limit from 5.66 ( $=2^{2.5}$ ) to 64.0 ( $=2^6$ )  $\mu\text{g}$ .

The shape of zooplankton size distributions also varied among communities, both within a lake through time and among lakes (Fig. 1). Patterns of variation in size structure were sought using a principal components analysis on the covariance matrix in which size classes were used as variables, and  $\log_2$  density or percent  $\log_2$  density as responses. Variations in  $\log_2$  density across communities represent changes both in the shape of size distributions and in community biomass. Changes in percent  $\log_2$  density describe changes in the shape of size distributions only. A principal components analysis should identify which size classes vary the most in density among communities. The first three principal component axes, however, explained <50% of the variation in either  $\log_2$  density or percent  $\log_2$  density among communities. Eight or nine axes were necessary to explain 80% of the variation among size distributions. This suggests that differences among zooplankton size distributions, either in shape or in biomass do not hinge on variations from a simple combination of size classes.

Community size distributions varied in the number and position of density peaks (Fig. 1). Linear distributions mostly represent communities with high densities of small organisms and few large organisms (e.g., Fig. 1A, B), but one community (not presented in Fig. 1) showed the reverse pattern of having many large organisms (peak density at 16.0  $\mu\text{g}$ ). Unimodal distributions (e.g., Fig. 1C, D) have peaks in zooplankton density between 0.088 ( $=2^{-3.5}$ ) and 11.3 ( $=2^{3.5}$ )  $\mu\text{g}$ . Communities with bimodal size distributions (e.g., Fig. 1E, F) have peak densities of small crustaceans mostly

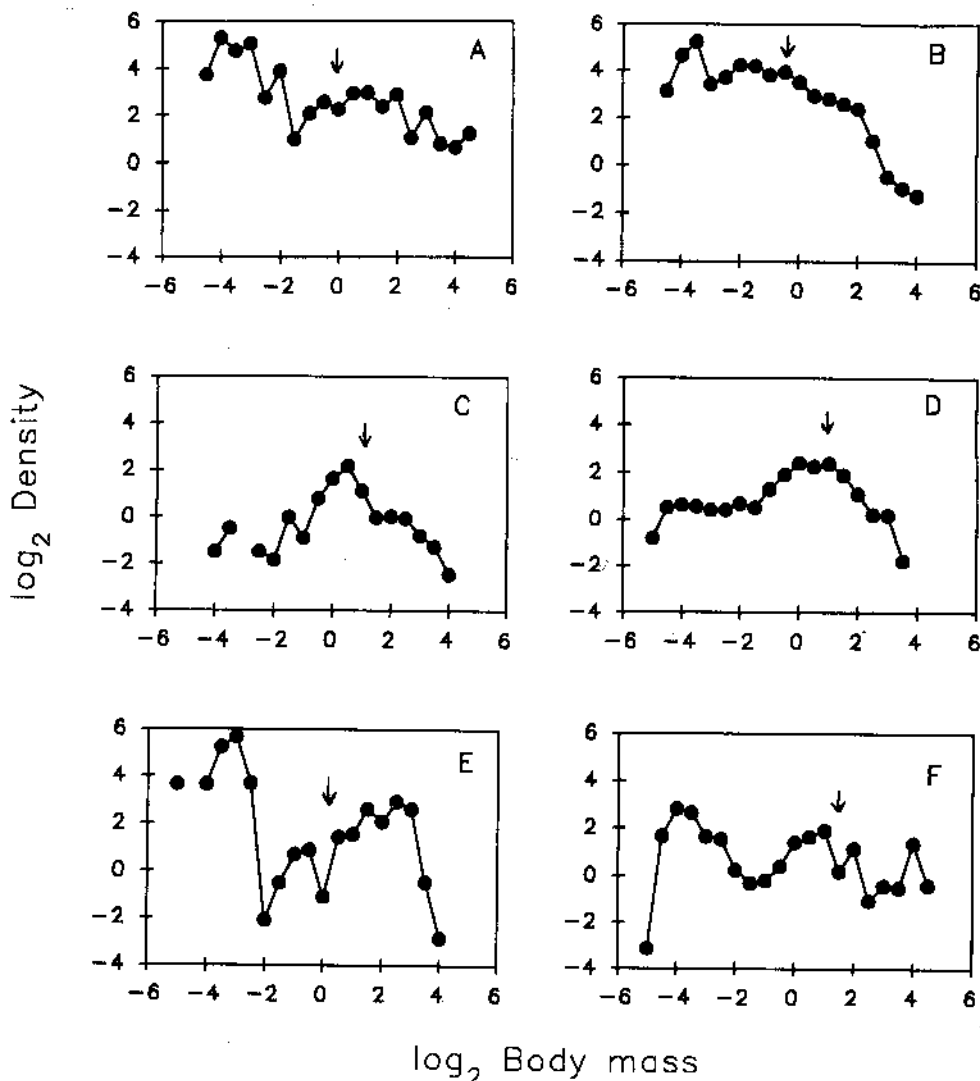


FIG. 1. Examples of linear (A, B), unimodal (C, D), and bimodal (E, F) community size distributions for zooplankton sampled from whole water columns (A, C, E) and from surface water at night (B, D, F). Density was measured as no./L, body mass as  $\mu\text{g}$ . Gaps in the size distributions indicate empty size classes.  $\downarrow$  indicate mean body mass. Zooplankton were collected in (A) Lake Memphremagog, Québec, in June, (B) Lake Tyrrel, New York, in September, (C) Lake Orford, Québec, in September, (D) Lake Popolopen, New York, in October, (E) Lake Massawippi, Québec, in July, and (F) Lake Lacawac, Pennsylvania, in June.

between  $0.044 (=2^{-4.5})$  and  $0.125 (=2^{-3}) \mu\text{g}$  (84% of communities), and peak densities of large organisms mostly between  $2.00 (=2^1)$  and  $11.3 (=2^{3.5}) \mu\text{g}$  (82% of the communities). More than half of the zooplankton communities we sampled classify as bimodal size distributions. Linear, unimodal, and trimodal distributions describe 19, 22, and 2% of the communities, respectively.

Size distributions of freshwater zooplankton, therefore, vary widely in shape across communities (Fig. 1) and are poorly described by log-linear models (77% of the communities with  $r^2 < 0.5$ ). This contrasts with large-scale size spectra found in freshwater and marine systems where, over large ranges in body size (volume or wet mass covering 6-11 orders of magnitude in pow-

ers of 10), small organisms are more abundant than large organisms (Sprules and Munawar 1986, Rodriguez et al. 1987, 1990, Ahrens and Peters 1991a). Abundance-body size relationships are usually described as log-linear (Sprules and Munawar 1986), but nonrandom residual variation is found in all communities (e.g., Griffiths 1986, Sprules and Munawar 1986, Hanson et al. 1989, Rodriguez et al. 1990). The variation in abundance-body size patterns we found among crustacean zooplankton communities (Fig. 1) reflects the moderate range in body size covered in our analysis (three orders of magnitude in dry mass).

The average size distribution summarizing the 90 zooplankton communities we sampled has a bimodal shape (Fig. 2). We find peaks of crustacean densities

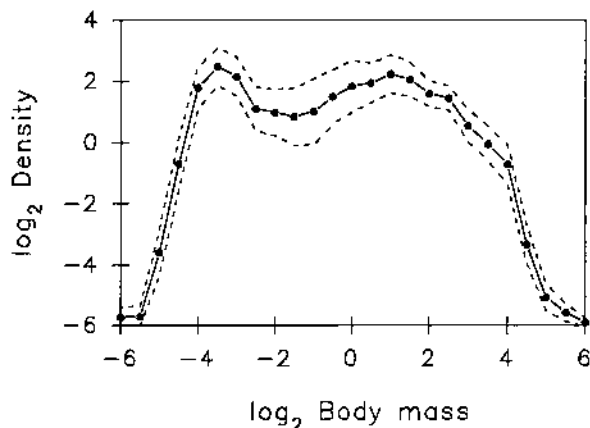


FIG. 2. Average zooplankton community size distribution. The density of organisms in each size class was averaged over 90 communities, sampled in 28 lakes. Densities were measured as no. animals/L; body masses are in micrograms. Dashed lines represent 95% confidence intervals around mean  $\log_2$  density in each size class. Size classes with no organisms were assigned a density of  $2^{-6}$  animals/L ( $\log_2$  density = -6) so they could be kept in the analysis.

in the  $0.09 (=2^{-3.5})$  and  $2 (=2^1)$   $\mu\text{g}$  size classes. The first peak represents naupliar copepods (size of nauplii ranges from 0.06 to 0.25  $\mu\text{g}$ ) while the second peak is formed by larger cladocerans and copepods. Small size classes ( $2^{-5}$ – $2^{-0.5}$ ) vary the most in  $\log_2$  density ( $s^2 = 7$ – $15.5$ ). The lowest variation in  $\log_2$  density ( $s^2 \leq 3$ ) is found in extreme size classes ( $2^{-5.5}$  and  $2^{-6}$   $\mu\text{g}$ ;  $2^{5.5}$  and  $2^6$   $\mu\text{g}$ ) which are empty in  $>85\%$  of the communities, and in size classes around  $2$ – $2.8$  ( $2^1$ – $2^{1.5}$ )  $\mu\text{g}$ . Low densities of crustaceans in small size classes, however, does not mean low density of small organisms since rotifers, algae, protozoans, and bacteria were not included in the analysis. The shape of the average size distribution illustrates the predominance of bimodal size distributions found in individual communities.

#### Does community size structure affect mass-specific grazing rates?

Predicted community mass-specific grazing rates vary from 3.3 to 14.9  $\text{L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$  for different communities (mean = 6.99  $\text{L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ ). Since physiological rates are well related to the size of individual organisms (Peters 1983), we expect community ecological rates to depend on community size distributions.

Predicted community mass-specific rates are closely related to mean body size (Fig. 3). Mass-specific rates in communities with equal mean body size varied, on average, by 7% of the mean, and, at most, by 27% of the mean (residual/predicted value). This residual variation could not be attributed to other simple parameters of zooplankton size structure (e.g., variance in body size, position of peak densities, relative height of peak densities), but was significantly, although weakly, affected by the general shape of the size distributions.

For a given mean body size, communities with unimodal size distributions tend to have slightly higher mass-specific grazing rates than communities with linear or bimodal distributions [intercepts of the  $\log_{10}$ (mass-specific grazing rate) vs.  $\log_{10}$ (mean body size) relationships are 0.97 for unimodal size distributions compared to 0.94 and 0.91 for bimodal and linear size distributions, respectively; ANCOVA,  $P < .001$ ]. For example, communities with a mean size of 0.5  $\mu\text{g}$  are predicted, on average, to graze 13  $\text{L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$  when their size distribution is unimodal and 10.6 or 11.9  $\text{L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$  when their size distribution is linear or bimodal, respectively. A difference of 10–20% in grazing rate, however, is small compared to differences among communities with different mean body size. Differences in predicted mass-specific grazing rates across zooplankton communities are mostly related to differences in mean body size and are only slightly affected by characteristics of community size distributions.

Allometric relationships cannot be extrapolated directly from an individual to the level of communities. The relationship between community mass-specific grazing rate and mean body mass has the same slope as the allometric model developed for individual organisms (slope = -0.45), but a lower elevation (Fig. 3, compare points with line). This suggests that community rates are overestimated when predicted from mean body size. Mass-specific grazing rates predicted from mean body size were, on average, 36% higher

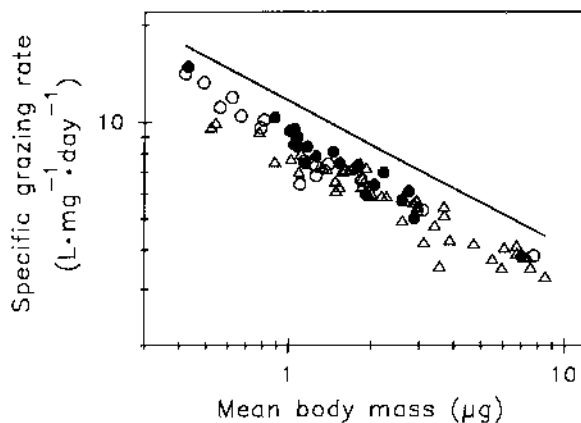


FIG. 3. Relationship between mass-specific grazing rates (SGR, in  $\text{L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ ) and mean body size (MEAN, in  $\mu\text{g}$ ) for communities with different shapes of size distributions ( $\log_{10}\text{SGR} = 0.94 - 0.45 \log_{10}\text{MEAN}$ ,  $r^2 = 0.92$ ). Each point represents a community.  $\circ$  represent communities with linear size distributions ( $n = 17$ ),  $\bullet$  those with unimodal size distributions ( $n = 20$ ),  $\Delta$  those with bimodal size distributions ( $n = 51$ ), and  $\blacksquare$  those with polymodal size distributions ( $n = 2$ ). Mass-specific grazing rates are predicted using an allometric equation developed for freshwater and marine zooplankton (Peters and Downing 1984). The line represents predictions for individual organisms or, in terms of communities, a community where all individuals have the same size.

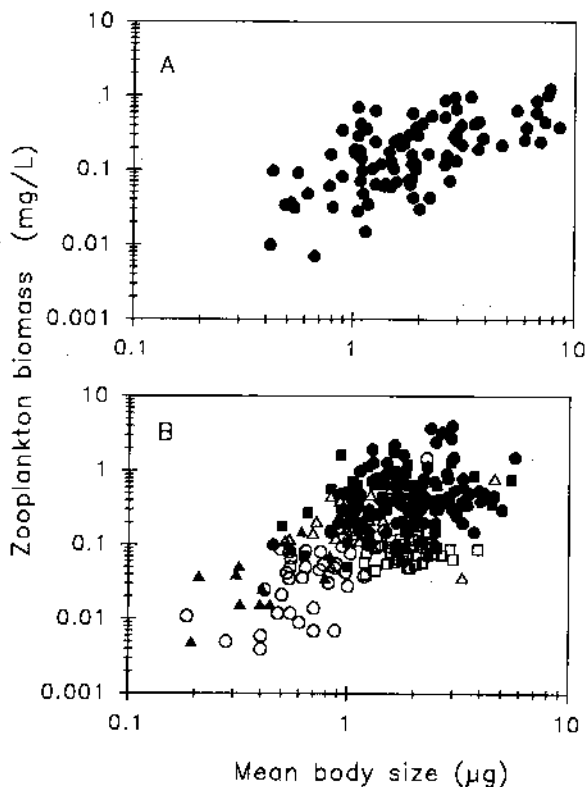


FIG. 4. Relationship between crustacean community biomass and mean body size. (A) Sampled communities ( $r^2 = 0.39$ ,  $P < .0001$ ,  $n = 90$ ). (B) Literature data; ● Esjmont-Karabin et al. 1980; ■ Węgleńska et al. 1983; ▲ Orcutt and Pace 1984; □ Patalas and Salki 1984; ○ Esjmont-Karabin and Węgleńska 1988; △ McQueen et al. 1989. Characteristics of the literature data are listed in Table 1. Pooling all data ( $n = 393$ ), crustacean community biomass (ZB, in mg/L) is related to mean body size (MEAN, in  $\mu\text{g}$ ) as:  $\log_{10}\text{ZB} = -0.88 + 0.88 \log_{10}\text{MEAN}$  ( $r^2 = 0.50$ ).

than the mass-specific rates predicted from community size distributions. The largest deviation was  $6.1 \text{ L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ , while the average difference was  $2.4 \text{ L} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ . Median and geometric mean body sizes are smaller than arithmetic mean body sizes and would lead to even more severe overestimations of mass-specific grazing rates. The discrepancy between the grazing rates predicted from mean body size and from individual body sizes is due to the nonlinearity of the relationship between grazing rate and body size. In a hypothetical community where all organisms were of equal size, we would predict that they all graze at the same rate. In this community, mass-specific grazing rate would be well related to mean body size. In another community with equal mean size but with variability in individual body size, a high density of small organisms would have to be present to balance the few large organisms. This high density, however, would not necessarily compensate for the disproportionately low grazing rate of small organisms.

The discrepancy between predictions for individuals and for communities must be related, by mathematical necessity, to the variability in individual body size found within each community. This variability, however, cannot be easily quantified because community size distributions do not follow normal distributions. To avoid overestimations, community mass-specific grazing rates should be predicted by adding the contribution of organisms of different sizes rather than from mean body size alone.

#### How does community biomass affect community grazing rate?

Community grazing rates depend on the magnitude of both mass-specific rates and community biomass. Mass-specific grazing rate decreases with increasing mean body size (Fig. 3), but in the zooplankton communities we sampled, community biomass increases with mean body size (ANOVA:  $P < .001$ ,  $r^2 = 0.39$ , Fig. 4A). Higher zooplankton biomass partly compensates for lower mass-specific grazing rate as mean body size increases (Fig. 3), but introduces a lot of variability into the relationship between predicted total community grazing rate and mean body size (Fig. 5).

Additional data on zooplankton biomass, density, and mean body mass were found for 303 communities in six published studies (Table 1). The zooplankton were collected in 14 lakes and reservoirs with surface area of  $0.05\text{--}2372 \text{ km}^2$ , maximum depth of  $3.6\text{--}40 \text{ m}$  and Secchi depth, a measure of water clarity, of  $0.6\text{--}3.7 \text{ m}$ . Zooplankton biomass ranged between  $0.004$  and  $4.01 \text{ mg/L}$  and mean crustacean body mass between  $0.2$  and  $5.7 \mu\text{g}$  dry mass. A positive relationship between zooplankton biomass and mean body size was also found using the literature data (Fig. 4B), corroborating the pattern we found (Fig. 4A). As in the communities we sampled, however, the relationship was poor.

The large variability in zooplankton biomass across lakes and time periods is partly related to environ-

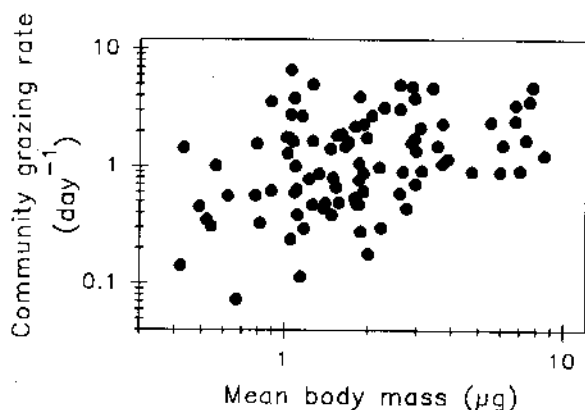


FIG. 5. Relationship between zooplankton community grazing rate and mean body size ( $r^2 = 0.15$ ;  $P < .001$ ;  $n = 90$ ).

TABLE 1. Characteristics of the published data used to test the relationship between total crustacean biomass and mean body mass. In all studies, zooplankton were collected from the whole water column.

Study	Number of lakes	Total no. samples	Sampling period (mo)	Sampler*	Mesh size ( $\mu\text{m}$ )	Length-mass equation†
Esjmont-Karabin et al. 1980	4	115	03-12	B	60	1
Węgleńska et al. 1983	5	50	03-10	B	60	1
Orcutt and Pace 1984	1	13	01-12	N, J, V	64	2
Patalas and Salki 1984	1	48	midsummer	N	77	3
Esjmont-Karabin and Węgleńska 1988	2	39	04-07	B	30	1
McQueen et al. 1989	1	38	04-10	SP	80	4

\* B is a 5-L Bernatowicz sampler, J is Juday trap, N is a net, SP is a 35-L Schindler-Patalas trap, V is a Van Dorn bottle.

† Length-mass equations used to convert lengths into biomass are, as cited in each paper: (1) Hillbricht-Ilkowska and Patalas 1967, (2) Persson and Ekbohm 1980, Pace and Orcutt 1981; nauplii biomass estimated from volume: (3) Edmondson 1971, (4) Sprules 1984. We assumed a dry mass: wet mass ratio of 0.1.

mental conditions. Differences in zooplankton biomass among the communities we sampled were related to differences in chlorophyll concentration, a measure of lake trophic, and in water temperature. The best model describing zooplankton dry biomass (ZB, in milligrams per litre) in the communities we sampled is:

$$\log_{10}ZB = -2.06 + 0.75 \log_{10}M + 0.47 \log_{10}C + 0.04T, \quad (4)$$

where  $M$  is mean body mass (in micrograms),  $C$  is chlorophyll concentration (in micrograms per litre), and  $T$  is water temperature (in degrees Celsius) (ANOVA:  $P < .001$ ,  $r^2 = 0.63$ ,  $n = 85$ ). Zooplankton biomass is known to vary widely, both across and within lakes, and to be difficult to predict (Sommer et al. 1986, Yan 1986, Ivanova 1987, Patalas 1990). It is, therefore, not surprising to find large unexplained variation in zooplankton biomass across the communities we sampled.

The relationship between zooplankton biomass and mean crustacean size, although never previously documented, could be expected (Sterner 1989). Mass-specific grazing rate decreases with the size of organisms (Fig. 3). Therefore, if all communities were to have, on average, equal biomass, we would expect communities dominated by small zooplankton to graze more than communities dominated by large zooplankton. Communities dominated by large zooplankton, however, are usually associated with more intensive grazing, both within lakes and among lakes. In mesotrophic to eutrophic lakes, large increases in the density of *Daphnia* during the spring reduce algae to very low densities, creating clear-water phases (Lampert et al. 1986, Sommer et al. 1986). More generally, lake bio-manipulation and the concept of trophic cascade are based on the premise that the manipulation of zooplankton community structure towards large crustaceans, especially *Daphnia*, can help suppress phytoplankton biomass (Shapiro 1980, Carpenter et al. 1985). The importance of grazing by large zooplankton is also found when comparing different lakes, where ratios of algal biomass (measured as chlorophyll concentration) to phosphorus concentration, a major limiting nutrient

for algae in lakes, tend to be lower in lakes with large zooplankton (Hrbáček et al. 1978, Pace 1984). To account for these observations, communities dominated by large zooplankton must either reach higher biomass than communities dominated by small zooplankton or graze more per unit biomass than is predicted by allometric equations. Allometric equations may tend to underestimate the grazing rate of large crustaceans since they do not consider the wider range in food particle sizes that can be used by large individuals (Burns 1968, Kobayashi 1991). Our analysis shows that larger zooplankton reach higher biomass but does not eliminate the possibility that they could also have higher mass-specific grazing rates than is predicted by allometric equations.

*Are ecological rates related to size structure at the level of communities?*

Total community grazing rate is the product of opposing trends in mass-specific grazing rate and biomass with mean body size. On average, zooplankton community grazing rate is higher in communities dominated by large organisms (slope of regression model = 0.52, ANOVA:  $P < .001$ ; Fig. 5), but the relationship is weak ( $r^2 = 0.15$ ). The relationship would have been even weaker had we considered the errors associated with the prediction of grazing rate and of body mass. A large part of the scatter in community grazing rate is propagated from the variability in biomass among zooplankton communities (Fig. 4A).

Several factors not considered in the allometric equation we used are expected to further obscure the relationship between community grazing rate and mean body size in natural communities. Our analysis assumes that zooplankton grazing rate varies only with individual body size. Grazing rates, however, differ among zooplankton taxa. Cladocerans graze more than copepods of the same size (Petersen and Downing 1984, Knoechel and Holtby 1986) and mass-specific grazing rates decrease more slowly with body size in cladocerans than in copepods [slope of allometric relationships: cladoceran median  $b = -0.21$ ,  $n = 20$ ; copepod

median  $b = -0.48$ ,  $n = 4$ ; Chow-Fraser and Knoechel 1985, Haney 1985, Chow-Fraser and Sprules 1986, Knoechel and Holtby 1986, Jarvis et al. 1988, Mour-elatos et al. 1989, Pinto-Coelho 1991; assuming (dry mass) = (body length)<sup>2.65</sup>, Bottrell et al. 1976]. We expect, therefore, variation in taxonomic composition of natural zooplankton communities to introduce variability in community grazing rates. Environmental conditions, for example, food concentration, temperature, or turbidity, also affect zooplankton grazing rates (Gulati et al. 1982, Hart 1986, 1988, Cyr and Pace 1992). Moreover, predictions of grazing rates using allometric equations are appropriate for highly edible algal species but tend to overestimate grazing rates on algal assemblages (Gliwicz 1969, Lampert 1988, Cyr and Pace 1992). These factors are expected to increase the variation in community grazing rate independently of mean crustacean size, thereby reducing our power to detect a trend in grazing rate with mean body size. Relationships between ecological rates and characteristics of size distributions may be impossible to detect in natural communities.

#### GENERAL DISCUSSION

Zooplankton community size distributions vary among communities but, in north temperate lakes can be described, on average, as bimodal. Predicted community mass-specific grazing rates decline with increasing mean body size and are only slightly affected by other characteristics of the size distributions. Community biomass, on the other hand, increases with mean body size. Combining these two relationships suggests that communities dominated by large zooplankton should tend, on average, to graze more than communities dominated by small zooplankton. We expect, however, large variability around this relationship, making it difficult to detect in situ. Allometric relationships applied to individual organisms are useful to predict community grazing rate, but we do not expect simple parameters of community size distributions, such as mean body size, to be good predictors of community rates. Although body size is a powerful predictor of individual physiological rates, its importance may be largely masked at the level of communities.

Our results can be extrapolated to other ecological rates. Production, respiration, and phosphorus and nitrogen excretion rates are related to individual crustacean body size (Banse 1982, Ejsmont-Karabin 1984, Ikeda 1985). As in the case of grazing rate (Fig. 3), community mass-specific rates should decrease with mean zooplankton body size. Because zooplankton community biomass increases with mean body size (Fig. 4), community rates of production, respiration, and excretion are expected to increase with mean body size. The strength of the relationship, however, will depend on the magnitude of the slope relating mass-specific physiological rates to individual body size. A shallower negative slope for individual rates should

result in a steeper slope relating total community metabolic rate to mean body size and should, consequently, be easier to discern from background variability. The relative magnitude of the slopes relating mass-specific rates and community biomass to mean body size should affect the strength of the relationship between total community rates and mean body size.

We expect simple parameters of size distributions, such as mean or median body size, to also be poor predictors of ecological rates at the levels studied by population and ecosystem ecologists. Populations vary both in patterns of size distribution and in biomass. We expect that, similar to the results from zooplankton communities, ecological rates at the level of populations will not be clearly related to simple characteristics of size distributions because of variation in population biomass. Broad ranges of sizes and taxa, on the other hand, appear to have a more regular pattern of size distribution than taxonomically restricted populations or communities (Sprules and Munawar 1986, Witek and Krajewska-Soltys 1989, Ahrens and Peters 1991a). Over a large range of body sizes, an overwhelming number of organisms are very small. As a result, mean or median body size are insensitive measures of community size structure. The slopes of normalized size distributions vary in different ecosystems (Sprules and Munawar 1986, Rodríguez et al. 1987), but are insensitive to the shape and the residual variation associated with different distributions (Sprules and Munawar 1986, Ahrens and Peters 1991a). The usefulness of different size distribution parameters in predicting process rates over large ranges of body sizes remains to be tested.

The regularity of body size distributions at large scales can reduce the biomass information necessary for predicting ecological rates in planktonic environments (reviewed in Borgmann 1987, Boudreau et al. 1991). Models based on allometric relationships and on the assumption of constant energy transfer among size classes, have been used to predict fish biomass, fish productivity, and contaminant transport from phytoplankton or zooplankton biomass (e.g., Borgmann and Whittle 1983, Borgmann et al. 1984, Minns et al. 1987, Sprules et al. 1991). Predictions of ecological rates, however, may be affected by the observed departures from log-linear body size distributions (e.g., Rodríguez et al. 1990, Ahrens and Peters 1991a, Sprules et al. 1991) and by differences in allometric equations among groups of organisms (Dickie et al. 1987, Boudreau and Dickie 1989). Our study suggests that the shape of body size distributions over small ranges of body size should not affect the prediction of ecological rates.

Community rates may also be estimated by adding the predicted contribution of each organism present (e.g., Kasprzak 1985, Leavitt and Carpenter 1990, Vanni and Findlay 1990). One important application of allometric models is to predict the magnitude of ecological rates, such as herbivory, production, respiration, or nutrient regeneration, over large spatial and

temporal scales. The technology to measure individual body size is developing rapidly, especially for small organisms (e.g., Robertson and Botton 1989, Sprules et al. 1992). The accuracy and precision of predicted ecological rates, however, can only be as good as the allometric relationships themselves. Respiration rates are well predicted from available allometric equations (Ahrens and Peters 1991b). Allometric relationships also accurately predict grazing rates on single algal species (e.g., Knoechel and Holby 1986, Cyr and Pace 1992), but overestimate grazing rates on natural phytoplankton assemblages (Cyr and Pace 1992). Phytoplankton growth rates are predicted assuming optimal light conditions and tend to overestimate primary production in variable light environments (Joint and Pomroy 1988). Allometric equations have mostly been developed from laboratory measurements of physiological rates. They should be rigorously tested on assemblages of organisms in situ before they can be used to make large-scale predictions.

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