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Plankton community respiration: relationships with size distribution and lake trophy

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Abstract

Allometric interpretations of community size structure often assume that laboratory relations between physiological rates and body size apply in the field, but this assumption is rarely examined critically. We therefore tested the hypothesis that limnoplankton community respiration rates are predictable functions of mean body size, and compared these functions to laboratory relations. Over a broad range of trophic conditions ($6.5 \leq [TP] \leq 130\ \mu g\ l^{-1}$; $1.2 \leq [chl\text{-}a] \leq 29\ \mu g\ l^{-1}$), the mean respiration rate per organism for picoplankton, nannoplankton, and net plankton assemblages was a power function of mean organism size, with an exponent of 0.73. When respiration (R) and biovolume (B) are standardized to equivalent carbon units, the R/B ratio was a power function of mean organism size, with an exponent of -0.30. These results provide empirical support for the contention that size distributions may be used to construct comprehensive models of community physiology. The total epilimnetic phosphorus concentration was correlated with both the biovolume and respiration rate of the plankton community, as well as with the respiration rates of the three plankton size classes; so these aspects of community function may also be predictable functions of lake trophic state.

Introduction

The rate of respiration is correlated with most other physiological rates. Because long-term production is proportional to respiration for a wide range of populations (Humphreys, 1979), the respiration rate of an entire community provides an easily measured index of production in that community. Rates of growth (Banse, 1976) and nutrient excretion (Ikeda, 1985) also vary with rates of respiration. Furthermore, the bioaccumulation of contaminants by aquatic organisms is affected by the rate of oxygen consumption (Neely, 1979), and the allometry of contaminant fluxes suggests a similar dependency (Jorgensen, 1979). In short, respiration rate is a fundamental measure of biological activity.

Plankton community respiration rates must be measured in situ or very soon after removal of the sample from the lake (Lampert, 1984). Even then, the choice of procedure may bias the measurements, because not all procedures measure the same thing. Measurement of the activity of the electron transport system (ETS) represents the maximum potential oxygen demand of the community, but measurement of oxygen uptake repre-

sents the extent to which aerobic organisms realize this potential (Packard, 1971, 1985; Devol, 1975). In spite of such methodological difficulties, some general trends have been identified. For example, plankton community respiration rates tend to increase with biomass, and assemblages of larger organisms respire at a lower rate than similar biomasses of smaller organisms (Williams, 1984).

At present, no models have been shown to predict the respiration rate of planktonic communities, but two approaches hold promise. One approach would extend the existing knowledge of community responses to lake trophic status. Existing relationships describe both static and dynamic properties of plankton communities as functions of the total phosphorus concentration (reviewed in Peters, 1986). For example, phosphorus concentration has been related to primary production (Smith, 1979; Gelin & Ripl, 1978; Elser *et al.*, 1986), zooplankton abundance (Pace, 1986), and relative abundances of net plankton and nannoplankton (Kalff & Knoechel, 1978). If an analogous relation were available for respiration rate, one could predict total community respiration from the phosphorus concentration. The second approach extends the size-dependence of respiration rates of individual taxa, observed in laboratory studies. Rather than concentrating on the allometric response of individual organisms, one could seek size-based trends within whole communities. Thus one could measure the respiration rate of plankton assemblages delimited by size (rather than by taxon) and so determine the size dependence of the community rate. Since the exponents of taxonomically-specific relationships tend to be similar (Lavigne, 1982; Banse, 1979), one might hypothesize that community regressions would follow a similar trend. Such an extension would provide a test of the assumption (e.g. Griesbach *et al.*, 1982) that relationships observed on isolated taxa also apply to whole size classes containing many taxa in the field.

In this paper, we develop models of community physiology based upon lake trophic status and community size structure and so assess the hypotheses that respiration rates are predictable functions of the total epilimnetic phosphorus concentration and of the abundance and size of the plankton.

Materials and methods

Sampling

Samples were collected during July and August, 1987 from 12 lake sites in southern Quebec, representing a broad range of trophic conditions (Table 1). Integrated epilimnetic samples were collected during the day through a 2.5 cm diameter tube connected to a piston pump. This apparatus has been shown to collect both phytoplankton and zooplankton effectively (Pace, 1986). Water samples were stored in dark brown Nalgene bottles in a cooler containing ice packs during transit to the laboratory (maximum duration = 1 h).

Oxygen uptake

For oxygen uptake experiments, samples were divided upon arrival at the lakeside laboratory into picoplankton ($<5\ \mu$m), nannoplankton (5–40 μm), and net plankton ($>40\ \mu$m), using 40 μm square mesh stainless steel screens and 5 μm Nuclepore filters. In order to obtain measurable, reliable, and significant differences between cumulative size fractions, the size-fractionated subsamples were then concentrated on glass fibre filters (0.45 μm nominal porosity). Cornett & Rigler (1986) have shown that this concentration procedure does not significantly alter the rate of oxygen consumption by seston. For each subsample except one, a total of 1 l of size fractionated water was used (895 ml filtered through the glass fibre filter and 105 ml added to the incubation bottle). The remaining sample, from a highly eutrophic lake, received only 400 ml of source water. The fractionated subsamples and samples of the whole community were then incubated in the dark for 24 h at in situ temperatures (18–22 °C). The whole community sample, similarly concentrated on a glass fibre filter and immersed in whole lake water, provided

Table 1. Concentrations of phosphorus (mg m^{-3}) and chlorophyll (mg m^{-3}) in integrated epilimnetic samples used for respiration observations. The tabulated concentrations are those measured in the filtrate from a filter of the indicated porosity (in μm) and include particles that would pass through smaller filters. Newport, North, Central, and South are basins of Lake Memphremagog.

Lake		<0.4 μm	<5 μm		<40 μm		Total	
		P	P	Chl	P	Chl	P	Chl
Orford	Aug. 24	3.7	5.3	0.6	5.3	1.3	6.5	1.6
Stukely	Aug. 17	4.1	5.4	0.3	5.7	1.4	6.6	2.2
Orford	July 22	3.7	5.7	–	6.6	–	7.9	–
Lyster	Aug. 14	4.4	8.4	0.3	7.6	1.1	9.1	1.6
North	Aug. 13	7.9	9.7	0.5	10.3	0.8	12.2	1.6
Baldwin	Aug. 12	7.2	10.8	0.7	12.0	1.0	13.1	2.0
Central	Aug. 15	7.8	10.3	0.0	11.7	0.2	13.5	1.2
Cerises	Aug. 23	8.0	12.2	–	15.5	4.2	16.6	6.3
South	Aug. 22	6.9	11.9	1.0	12.8	1.8	18.6	3.5
Newport	July 23	11.7	16.5	–	17.9	–	22.7	4.1
Pond	Aug. 11	15.8	20.1	1.4	21.8	1.6	22.9	3.8
Magog	Aug. 10	14.5	24.1	0.8	29.5	5.5	39.3	9.0
Waterloo	Aug. 16	19.7	34.6	4.5	57.3	16.2	130.1	28.9

a check on the accuracy and effects of the fractionation procedure. Initial and final oxygen concentrations were determined using the sodium azide modification of the Winkler technique (APHA, 1971).

Size composition

The size distribution of plankton biomass over the range from 0.2 to 1500 μm equivalent spherical diameter (ESD) was determined by direct microscopic examination. The abundance and approximate diameters of bacteria were determined by epifluorescence microscopy with DAPI stain (Porter & Feig, 1980) of samples preserved in 2% formaldehyde. Larger organisms in the picoplankton fraction were measured at 1250 × on an inverted microscope, using samples preserved in Lugol's iodine solution. Nannoplankton were measured at 1000 × and 400 × (Lund *et al.*, 1958). Net plankton and zooplankton were measured at 100 × on the inverted microscope and at 40 × under a dissecting microscope, using both samples in Lugol's and others preserved in 2% formalin. Individual volumes of organisms larger than 5 μm greatest axial linear dimension (GALD) were estimated by measuring length and width and taking the volume of similar regular geometric shapes as approximations. Smaller organisms were counted in nine diameter intervals between 0.2 and 5 μm. At least 400 organisms were counted and measured in each of the three size fractions. No attempt was made to identify the organisms systematically to taxon, but the three size classes correspond roughly to picoplankton (bacteria, minute eucaryotes), nannoplankton (e.g. zooflagellates, phytoflagellates, smaller algae), and a mixture of algal net plankton and zooplankton.

Chemical analyses

Epilimnetic phosphorus concentrations were measured as an indicator of lake trophic state. The total phosphorus concentrations in each size fraction and in the total sample were determined in triplicate, using the ascorbic acid modification of the molybdenum blue technique (Strickland & Parsons, 1968) after digestion with potassium persulfate under pressure (Menzel & Corwin, 1965). As further confirmation of trophic differences between lakes, chlorophyll a concentrations were also measured in triplicate (Strickland & Parsons, 1968) and corrected for phaeophytin.

Data analyses

The biovolume (ppm) in each size class was defined as the sum of the volumes of all organisms in the size interval (1 ppm = 10^9 μm^3 l^{-1}), and individual organism volumes are expressed in μm^3. When conversions among units were required, all organisms were assumed to have a density of 1 g cm^{-3}, implying that 10^6 μm^3 of biovolume is equivalent to 1 μg of biomass; 1 μg of oxygen respired was taken as equivalent to 0.375 μg of carbon (Parsons *et al.*, 1984); picoplankton were assumed to contain 0.0963 pg μm^{-3} of carbon (Simon, 1987); nanoplankton and net plankton volumes were converted to carbon equivalents using the empirical formula for phytoplankton from Mullin *et al.* (1966): $\log_{10} C = -0.29 + 0.76 \log_{10} V$. In these samples, both size classes were dominated by algae (Ahrens, 1989), so the application of this equation to rotifers, and crustaceans would not greatly affect what are necessarily crude estimates of the carbon content for the whole class.

Results and discussion

Respiration rates ranged from 94 to 1300 mg O_2 m^{-3} d^{-1} (Table 2). The highest rate is similar to the 1200 mg O_2 m^{-3} d^{-1} measured in natural *Anabaena* collections (Gessner & Pannier, 1958), but lower than the 6800 mg O_2 m^{-3} d^{-1} found in a fertilized Georgia pond (Welch, 1968). In mesotrophic Lake Washington (summer chlorophyll 5 mg m^{-3}), Devol & Packard (1978) found a summer average respiration rate of 180 mg O_2 m^{-3} d^{-1}, similar to our intermediate values. In Findlay Lake (Devol, 1979), the depth-averaged maximum annual respiration rate of 20 mg O_2 m^{-3} d^{-1} was lower than our measurements. But this lake appears more oligotrophic (summer PO_4-P = 1 mg m^{-3}) than any of ours (Table 1). Hence our respiration measurements are consistent with previous results.

Relationships with phosphorus

Over 85% of the variation in the log transformed total epilimnetic respiration rate is explained by variation in the total phosphorus concentration (Fig. 1). Potential bias due to the high value for Lake Waterloo was examined by calculating a separate relationship for the remaining points. The resulting parameters (intercept = 3.0, slope = 0.82) were not significantly different ($P < 0.01$) from those for all thirteen points (Fig. 1). Total phosphorus also predicts a significant portion of the variation in individual size class respiration rates (Fig. 2).

Table 2. Mean rates of oxygen uptake (mg O_2 m^{-3} d^{-1} ± SE, n = 3) in samples incubated in dark-bottles. The order of the samples is that in Table 1.

Lake	Picoplankton <5 μm	Nanoplankton 5-40 μm	Netplankton >40 μm	Sum of fractions	Measured total
Orford	74 ± 5.3	1 ± 0.5	20 ± 2.0	95	109 ± 5.1
Stukely	18 ± 3.5	88 ± 21.5	1 ± 0.9	106	94 ± 9.4
Orford	42 ± 12.2	1 ± 0.5	7 ± 1.6	50	59 ± 5.8
Lyster	105 ± 8.6	7 ± 2.6	70 ± 4.4	182	157 ± 13.0
North	126 ± 10.8	21 ± 5.2	32 ± 3.0	179	194 ± 8.4
Baldwin	60 ± 13.8	14 ± 7.0	126 ± 8.6	200	187 ± 6.3
Central	207 ± 13.8	14 ± 3.5	60 ± 4.7	280	295 ± 24.4
Cerises	130 ± 5.6	53 ± 15.7	11 ± 1.6	193	183 ± 15.0
South	47 ± 9.8	40 ± 7.7	42 ± 13.8	130	155 ± 12.2
Newport	182 ± 9.3	70 ± 11.1	14 ± 3.2	266	234 ± 10.4
Pond	228 ± 13.4	35 ± 16.1	98 ± 9.7	361	320 ± 20.8
Magog	123 ± 3.9	70 ± 6.8	189 ± 10.8	382	408 ± 16.9
Waterloo	819 ± 19.2	459 ± 37.7	158 ± 10.1	1435	1287 ± 124.7

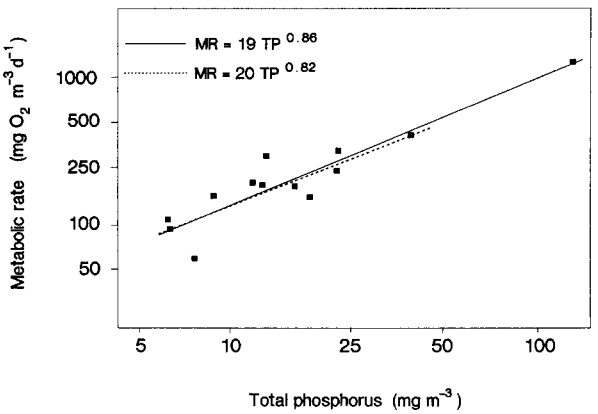

Fig. 1. The relationship between total epilimnetic phosphorus concentration and the metabolic rate of the plankton community. The regression lines (for n = 12 and 13) are not statistically different from one another (P > 0.05).

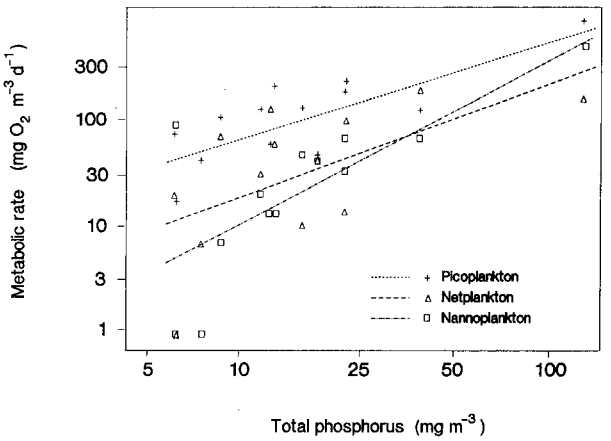

Fig. 2. The relationships between the total epilimnetic phosphorus concentration and the respiration rates of three plankton size classes. In each case, n = 13.

Table 3. Parameters of the Model I predictive regressions between logarithms of the variables measured. Natural logs were used in every case, except no. 4, where base 2 was used. In every case $P < 0.005$, except no. 10, where $P < 0.05$. Abbreviations of the variables (X, Y) used in the regressions are defined in the footnotes.

	Y	X	Intercept	(SE)	Slope	(SE)	S_{xy}	R^2	F	n
1.	SR	TR	−0.31	(0.242)	1.059	(0.045)	0.119	0.980	551	13
2.	MR	MV	−16.50	(0.324)	0.728	(0.041)	1.37	0.894	313	39
3.	TR	SV	3.34	(0.529)	0.754	(0.194)	0.515	0.579	15	13
4.	N	MV	5.756	(0.058)	−0.793	(0.005)	1.900	0.937	24624	1647
5.	R/B	MC	−1.871	(0.262)	−0.295	(0.041)	1.364	0.589	53	39
6.	TR	TP	2.932	(0.310)	0.858	(0.107)	0.304	0.854	64	13
7.	SV	TP	0.700	(0.553)	0.692	(0.191)	0.541	0.544	13	13
8.	R_s	TP	2.133	(0.629)	0.909	(0.217)	0.616	0.614	18	13
9.	R_m	TP	−1.278	(1.230)	1.579	(0.425)	1.204	0.557	14	13
10.	R_l	TP	0.423	(1.260)	1.095	(0.435)	1.233	0.365	6	13
11.	MP	MC	−4.269	(0.194)	0.795	(0.030)	1.010	0.950	703	39
12.	CH	TP	−1.650	(0.447)	1.003	(0.151)	0.171	0.815	44	12
13.	PR	TP	−0.729	(0.287)	1.694	(0.084)	0.665	0.863	410	67
14.	PR	TR	−2.687	(1.196)	1.537	(0.222)	0.626	0.810	48	13

SR = summed respiration rate of all three size classes (mg O_2 m^{-3} d^{-1})
TR = total community respiration rate (mg O_2 m^{-3} d^{-1})
R_s, R_m, R_l = respiration rates of small, medium, and large size classes (mg O_2 m^{-3} d^{-1})
SV = summed volume or biomass of all three size classes (ppm)
MR = mean respiration rate of an individual organism (μg O_2 d^{-1})
MV = mean volume of an individual organism (μm^3)
TP = total epilimnetic phosphorus concentration (mg m^{-3})
N = density of organisms in a size class (ml^{-1})
MP = mean phosphorus content per organism (pg)
MC = mean carbon content per organism (pg)
R/B = ratio between size class respiration and size class biomass (d^{-1})
CH = epilimnetic chlorophyll-a concentration (mg m^{-3})
PR = estimated primary production (mg C m^{-3} d^{-1})

The general applicability of this respiration – phosphorus relation cannot be established because of the unavailability of similar data from other systems. Instead, the biomass-phosphorus responses were examined (Table 3) to see if these lakes were similar to others in that respect at least.

Phosphorus is strongly correlated with the chlorophyll concentration, an indicator of algal biomass (Table 3). The parameters of this relationship (-0.72, 1.00) describe a line intermediate between those for Florida lakes (-0.15, 0.74; Canfield, 1983) and for spring turnover phosphorus versus summer mean chlorophyll (-1.14, 1.45; Dillon & Rigler, 1974). Our parameters are individually not significantly different from those calculated for many of the same lakes by Pace (-0.53, 1.05; 1984), although their joint distribution is significantly different ($P < 0.01$). The total phosphorus concentration and the total biovolume are also highly significantly correlated, as are total respiration and total biovolume (Table 3). Some coefficients of determination in Table 3 are lower than those reported elsewhere for similar relationships (e.g. Peters, 1986) because they are based on point values rather than seasonal means.

A further check on the validity of our estimate of the trophic response of total respiration may be made by comparing respiration with total production. Primary production is higher in lakes with higher phosphorus concentrations (e.g. Gelin & Ripl, 1978; Smith, 1979; Elser *et al.*, 1986). To compare our respiration rates to an estimate of average primary production (PROD, mg C m^{-3} d^{-1}), we developed a power relationship between mean production and total phosphorus concentration using the data in Smith (1979):

$$\ln \text{PROD} = -0.73 + 1.69 \ln \text{TP} .$$

The parameters of this relationship may be compared with those (intercept = 2.93; slope = 0.86) for the trophic response of respiration (mg C m^{-3} d^{-1}). At the lowest observed level of phosphorus (4 mg m^{-3}), production is 5 mg C m^{-3} d^{-1}, whereas the predicted respiration rate is 23 mg C m^{-3} d^{-1}. As phosphorus increases, production increases faster than respiration, until production equals respiration at about 25 mg TP m^{-3}. Beyond this point, i.e., in eutrophic systems, production exceeds respiration. Only 3 of our 12 lakes exceeded this threshold.

Because these comparisons involve average trends from quite different water bodies, the discrepancy between production and respiration cannot be interpreted very closely. Nevertheless, the magnitude of the P : R ratio in oligotrophy (0.22) requires some explanation. Many are possible. Because the respiration rates are consistent with other estimates for plankton respiration and with allometric estimates of respiration for the different size classes (see below), one cannot easily dismiss the low P : R ratios as an artefact of high respiration rates. There is a possibility that the regression based on Smith's (1979) data does not apply to Southern Quebec lakes, but these lakes have been shown representative of many other general patterns in lake trophy (Peters, 1986). It is also possible that the 13 estimates of respiration from midsummer have over-estimated average respiration over the growing season and that this average value would be similar to that for average primary production. However, this implies greater synchronicity in respiration in oligotrophic lakes than in eutrophic lakes whereas synchronicity seems less in oligotrophic lakes (Marshall & Peters, 1989), so the chances of bias may be smaller in oligotrophy. Conceivably Smith's (1979) primary production rates are too low, although these were measured by many different scientists, using the best available technology. We cannot exclude these explanations, but find them less interesting than a final possibility, that planktonic respiration rates actually exceed rates of primary production in oligotrophic and mesotrophic lakes.

The low P : R ratio suggests some source of fixed carbon other than primary production. In oligotrophic Lake Almind, Denmark, bacterial uptake of dissolved organic carbon (DOC) accounted for 75% of daily carbon fixation (Sondergaard *et al.*, 1988). A similar supplement

would restore the carbon balance in our oligotrophic lakes. The DOC pool in these lakes, calculated from lake colour, varies between 2 and 4 mg C l^{-1} (Rasmussen *et al.*, 1989). These levels are larger than those estimated for Lake Almind, and if similar mechanisms are at work, they would be sufficient to explain the excess of respiration over production in some of our lakes. If we are correct in suggesting that DOC plays so important a role in oxygen metabolism in the surface waters of oligotrophic lakes, then these lakes are dependent upon energy subsidies from the watershed. As lakes become progressively more eutrophic, this subsidy becomes less important. As a result, metabolism rises more slowly than primary production with eutrophy until, in eutrophic lakes, production exceeds respiration.

Allometric relationships

To test the applicability of allometric relationships based upon laboratory studies to our field samples, we needed to estimate mean organism size and corresponding mean individual respiration rates. The mean organism size in each size fraction was estimated by dividing the class biovolume by the number of organisms (Table 4).

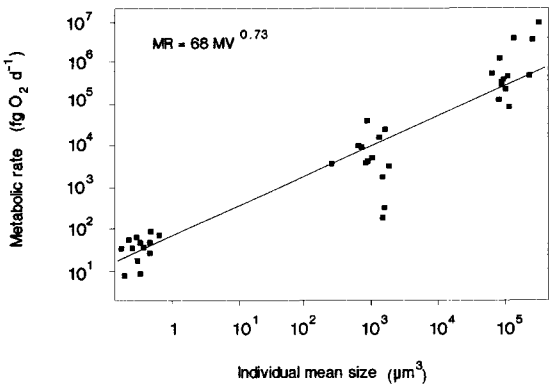

Fig. 3. The relationship between the mean size of plankton in screen-separated assemblages and the mean metabolic rate per organism.

The individual respiration rates were similarly calculated by dividing the respiration rate of the size class by the number of organisms in the class. This procedure is valid only if the sum of the size class rates approximates the observed community total. Table 2 shows that this is so. A regression between the mean sizes and the mean respiration rates per organism measures the allometric response of respiration to body size in mixed natural plankton communities. This relationship (Fig. 3) is highly significant ($R^2 = 0.89$, $P < 0.005$), and has a slope of 0.73.

Table 4. Numbers (N, in thousands ml^{-1}), mean sizes (MV = mean volume in μm^3), and total volumes (in ppm = $\mu m^3 \times 10^{-6}$ ml^{-1}) of organisms in the three size classes. Sample order is that in Table 1.

Lake	<0.5 µm ESD			5–40 µm ESD			>40 µm ESD			Total volume
	N	*MV*	Volume	*N*	*MV*	Volume	*N*	*MV*	Volume	
Orford	1522	0.46	0.70	5220	1460	7.62	70	89282	6.25	14.6
Stukely	2030	0.33	0.66	5520	1295	7.15	12	115737	1.39	9.2
Orford	1516	0.46	0.70	3000	1550	4.65	18	95544	1.72	7.1
Lyster	1434	0.64	0.91	3840	1456	5.59	57	84006	4.79	11.3
North	2615	0.33	0.85	5350	813	4.35	60	64145	3.85	9.1
Baldwin	3302	0.30	0.97	2710	1022	2.77	15	324450	4.87	8.6
Central	5858	0.17	1.00	4260	1822	7.76	129	110870	14.31	23.1
Cerises	3474	0.37	1.30	5680	711	4.04	49	103040	5.05	10.4
South	5794	0.19	1.08	9300	887	8.25	125	89884	11.24	20.6
Newport	2764	0.29	0.81	1780	860	1.53	29	234445	6.82	9.2
Pond	4063	0.22	0.89	9360	255	2.39	29	258342	7.51	10.8
Magog	3438	0.25	0.87	7000	641	4.49	52	136687	7.12	12.5
Waterloo	9143	0.48	4.43	18890	1589	30.02	1259	81541	102.66	137.1

Table 5. Parameters of linear regressions between the natural logarithms of metabolic rate (pg O_2 d^{-1}) of individual organisms and body size (μm^3). Most relationships had to be transformed to these common units. The unknown precision of these transformations precludes the setting of confidence limits on the intercept. The intercepts shown have been backtransformed to an arithmetic scale.

Organisms	Size range (ESD, μm)	Intercept	Slope	95% CI of Slope	Source
Algae	3–40	0.242	0.90	0.79–1.02	Banse (1976)
Unicells	0.6–60	0.045	0.83	0.72–0.94	Robinson *et al.* (1983)
Unicells	1.2–125	0.507	0.76	0.72–0.80	Hemmingsen (1960)
Protozoa	12–270	6.596	0.68	– –	Klekowski (1981)
Euk. unicells	130–250	0.628	0.74	0.66–0.82	Banse (1982)
Rotifers	100–230	19.936	0.52	0.21–0.82	Banse (1982)
Zooplankton	300–14,400	0.979	0.84	0.82–0.85	Ikeda (1985)
Crustaceans	250–17,000	2.943	0.78	0.77–0.80	Ivleva (1980)
Poikilotherms	780–570,000	1.623	0.74	0.72–0.76	Hemmingsen (1960)
Plankton	0.7–85	0.068	0.73	0.65–0.81	This study

Many relationships between metabolic rate and body size have been determined for planktonic organisms. Some of the most general of these were reported in Peters (1983) and are shown in Table 5 and Fig. 4. These relationships differ methodologically from the regression calculated in this paper in that cultured organisms from specific taxa were used, whereas we used natural communities divided into three size classes.

We are able to compute 95% confidence limits for our own parameters and compare these confidence regions with values reported previously. Five of the nine slope estimates in Table 5 are not significantly different from ours. Furthermore, the intercepts (at an individual size of 1 μm^3) from those three regressions which include organisms as small as the picoplankton are similar to ours. Finally, our predicted respiration rates for picoplankton are only about 50% higher than those predicted by the unicell regression of Robinson *et al.* (1983), and about 50% lower in the upper size range of their data set. Given the variability even among laboratory estimates, this 50% disparity is not large. The similarity of our field relation to those reported for unicells likely reflects dominance by algae in these samples (Ahrens, 1989), although it is possible that the depressed metabolic rates of rotifers and minute crustaceans (Banse, 1979) is also reflected in the low rates we measured for our largest size class.

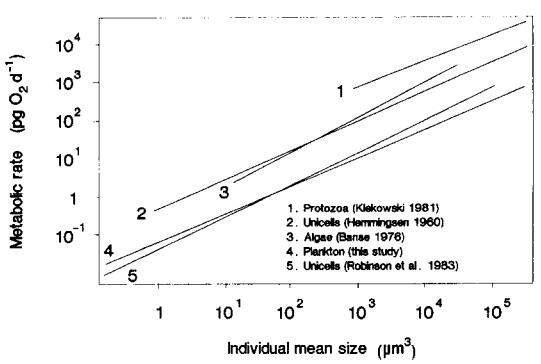

Fig. 4. A comparison of five regressions between body size and metabolic rate for planktonic organisms. Only regression 4 (this study) is based on natural community samples separated by size alone.

The consistency of our field estimates with previous results is also apparent when size specific rates are considered. The mean ratios of respiration : biomass (R : B) for picoplankton, nannoplankton, and net plankton respectively were 0.727, 0.038, and 0.027 per day and declined as a power function of mean organism size, with an exponent of – 0.30 (Fig. 5). The slopes of the relationships between either P : B or R : B and body size tend to decrease with increasing ranges of body sizes in taxonomically homogeneous laboratory samples (Banse & Mosher, 1980;

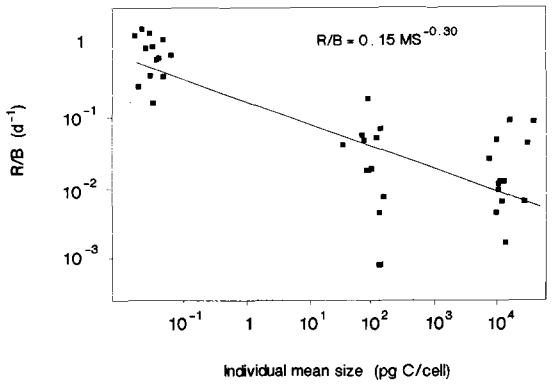

Fig. 5. The relationship between the respiration/biomass ratio and the mean size of plankton in screen-separated assemblages from natural plankton communities.

Dickie *et al.*, 1987). This is also true for at least some field samples from mixed communities: for example, Schwinghamer *et al.* (1986) fitted slopes of −0.304 and −0.337 to the relationships between R : B and size of marine benthic meiofauna and macrofauna respectively, whereas the slope of the regression for both size groups combined was only −0.21. Both Banse & Mosher (1980) and Dickie *et al.* (1987) speculated that the steeper slope within more homogeneous groups (e.g. meiofauna, fish) reflects an ecological scaling factor, confounding the overall general power relationship between metabolic rate and body mass.

Our R : B versus body size regression has a slope (−0.30) which is intermediate between the two extremes (−0.21 for the large scale regression, −0.37 for more homogeneous groups). This might be expected, since our size range is relatively small (compared to the range from bacteria to whales), yet we have a mixture of taxonomic and ecological types (prokaryotes and eukaryotes; autotrophs and heterotrophs; unicells and small metazoans, etc.). An alternate possibility is that the proposed ecological scaling factor is in part a statistical artefact, since the probability of obtaining a steeper regression slope increases as the range of the independent variable decreases (Peters, 1988).

Dickie *et al.* (1987) argued that the ecologically-realized respiration rate for individual organisms, termed an 'ecological food requirement', should be proportional to the 0.67 power of body size. Platt and Silvert (1981) have proposed that the respiration rate exponents are 0.67 for aquatic organisms and 0.75 for terrestrial organisms. Our exponent of 0.73 is not significantly different from 0.67 nor from the average (0.73) of laboratory studies with both terrestrial and aquatic organisms (Peters, 1983). Dickie *et al.* (1987) based their conclusion on parameter estimates for herbivorous mammals; they also noted that mammalian density is proportional to the −0.75 power of body mass, and that the ratio B : R is proportional to the 0.33 power of size. We found similar patterns in the plankton. Using a large set of size distribution data (n = 1647) collected in our lakes throughout the summer of 1987, plankton density was proportional to the −0.79 power of body mass (Fig. 6), which does not differ significantly from the mammalian result; B : R was proportional to the 0.30 power of body mass, which is not significantly different from 0.33. Our results confirm that the mean respiration rate per organism in lakes, as well as in fields, scales to the $^2/_3$ to $^3/_4$ power of body size, but are too crude to show if the scaling is 'ecological' or simply 'physiological'. Of course, even if some particular data set were to yield values sig-

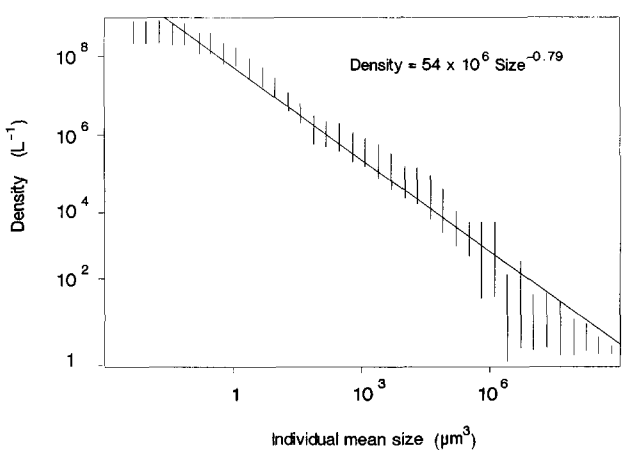

Fig. 6. The relationship between body size and density in natural plankton communities. Estimated densities were based on microscopic counting of abundance in as many as 39 size intervals in 58 plankton samples collected.

nificantly different from one extreme or the other, this statistical observation in itself could not establish the conclusion that specific ecological or physiological mechanisms are at work.

The main significance of our allometric relation for field metabolism lies in its demonstration that laboratory-based respiration rates and allometric relations can be extrapolated to the field. This is often assumed in limnological and ecological allometry (Peters, 1983; Calder, 1984), but rarely demonstrated. It has often been noted (Hemmingsen, 1960; Banse, 1976) that the common size dependence of growth, respiration, and photosynthesis suggests that numerous underlying physiological processes are similarly size-dependent; and new data and analyses have borne this out (e.g. Blueweiss *et al.*, 1978; Schlesinger *et al.*, 1981; Knoechel & Holtby, 1986; Ikeda, 1985; Ivleva, 1980; Fenchel, 1974; Peters, 1983; Calder, 1984). The exponents of the allometric dependencies of production, growth, and turnover rates on body size may therefore be predicted from the exponent of the equation for respiration rate (e.g. Dickie *et al.*, 1987). For example, if growth and respiration rate are related to body size by a common exponent of 0.75, then the instantaneous rate of increase (r) is predicted to be a power function of body size with an exponent of -0.25. Perhaps more remarkable than the question of whether a particular rate has an exponent closer to 0.67 or to 0.75 is the observation that many studies using different methodologies, different organisms, and different environments yield fairly similar results. We have shown that the relationship between metabolic rate and body size in field communities is not different from that which would be predicted from more restricted laboratory relationships. Parallel relations presumably exist for other rates and processes.

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