

Verh. Internat. Verein. Limnol.	27	2996-3000	Stuttgart, December 2000
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## Correlations and seasonal patterns in grazing and potential phytoplankton growth

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### Introduction

Planktonic herbivory has been studied from a variety of perspectives (e.g. LEHMAN & SANDGREN 1985, STERNER 1989, CARPENTER et al. 1991, 1998, STERNER & HESSEN 1994). It is a focal trophic interaction in biomanipulation and a key process for us to understand. However, despite its obvious role in trophic interactions and nutrient cycling, there is no clear way to predict the level of planktonic herbivory in lakes (e.g. CYR & PACE 1992, 1993, CYR 1998). This study had two objectives: to obtain a community-level estimate of grazing in a variety of lakes; and to relate estimates of grazing to various physical, chemical and biological characteristics of the lakes.

### Methods and analysis

Experiments were conducted from June to August 1997, using seven lakes at the Experimental Lakes Area (ELA) in western Ontario (49° 40' N, 93° 45' W). Six of the lakes (Lakes 110, 239, 240, 305, 470, and 625) are oligotrophic, which is typical of the Pre-Cambrian Shield region. Lake 470 is shallow

and has high concentrations of dissolved and particulate organic carbon. The seventh lake (Lake 227) has been artificially fertilized for several decades and is eutrophic (HECKY et al. 1994). Some aspects of lake morphometry, water chemistry and biological communities are described in Table 1.

In the dilution gradient technique (LANDRY & HASSETT 1982), samples of lake water and associated organisms are diluted with various proportions of filtered water and incubated in the presence of excess nutrients. Simultaneous estimates of overall phytoplankton growth and losses to grazing can be determined with minimal handling of plankton. This method makes several assumptions about the phytoplankton and zooplankton. Phytoplankton growth is assumed to be exponential, density-independent, and not limited by nutrients:

$$N_t = N_0 e^{(k-g)t}$$

where  $k$  is the nutrient-saturated phytoplankton growth rate in the absence of grazers, and  $g$  is the loss rate due to grazing ( $\text{time}^{-1}$ ). Grazing is assumed to follow a simple linear functional response based on

Table 1. Characteristics of seven study lakes at the Experimental Lakes Area, Ontario.

Lake	110	227	240	470	625	305	239
Area (ha)	5	5	44	6	75	52	56
$Z_{\text{max}}$ (m)	13	10	13	2	35	33	30
TDP ( $\mu\text{g/L}$ )	1	2	2	1	1	1	2
TDN ( $\mu\text{g/L}$ )	255	510	320	375	220	175	220
Secchi depth (m)	7.0	0.5	3.0	1.4	4.5	6.5	4.0
Chl $a$ ( $\mu\text{g/L}$ )	0.316	70.3	2.27	3.86	1.43	0.706	1.39
Dominant macrozooplankton	<i>Daphnia</i> , Calanoida	Rotifera, <i>Daphnia</i>	<i>Holopedium</i> , Cyclopoida	Rotifera, Calanoida	<i>Holopedium</i> , Calanoida	<i>Daphnia</i> , Cyclopoida	Calanoida, <i>Holopedium</i>
Mean length (mm)	0.41	0.12	0.25	0.15	0.36	0.50	0.38
Cladocerans $\text{L}^{-1}$	3.0	0.6	3.7	6.0	7.4	4.8	7.6
Adult Copepods $\text{L}^{-1}$	19.2	11.5	5.7	14.9	14.9	6.3	7.9
Fish present	planktivores, piscivores	none	planktivores, piscivores	planktivores	planktivores, piscivores	planktivores, piscivores	planktivores, piscivores

the phytoplankton-zooplankton encounter rate. If these assumptions are met, increasing the concentration of grazers should cause a linear decrease in apparent phytoplankton growth rate.

One incubation was conducted per lake. Water was collected at the deepest point in the lake, from five depths evenly spaced above the thermocline, and filtered through an 80- $\mu\text{m}$  Nitex mesh screen. Zooplankton were sampled from the same depths using a 15-L Schindler-Patalas trap with 80- $\mu\text{m}$  Nitex mesh. Zooplankton collections were a combination of equal volumes sampled the night before and on the morning of each start date. Twelve bottles were filled with 2.32 L total volume of zooplankton, lake water and 0.2- $\mu\text{m}$  filtered lake water to provide two replicates of six dilutions (1.0, 0.9, 0.7, 0.5, 0.3, and 0.1 $\times$ ). Nutrients were added to provide an additional 100 M  $\text{NH}_4\text{Cl}$ , 2  $\mu\text{M}$   $\text{NaH}_2\text{PO}_4$ , 40  $\mu\text{M}$   $\text{Na}_2\text{SiO}_3$ , and trace metals (GUILLARD & LORENZEN 1972) to prevent nutrient limitation. Bottles were incubated for 3 days in a wire rack placed in Lake 240 at a depth of 1.5 m. Temperatures at this depth in Lake 240 varied little during the summer (19–23 °C).

The zooplankton community was characterized according to species composition and mean body length (Table 1). Omnivory and bacterivory, while they could not be excluded from the experiments, were not assessed. Chlorophyll was used to estimate phytoplankton biomass. Water samples were filtered onto Whatman GF/F filters, frozen, extracted in 90% alkaline acetone, and read on a calibrated Turner 10-AU fluorometer with adjustments to correct for pheopigments (WETZEL & LIKENS 1991, WELSCHMEYER 1994). Lake chlorophyll concentrations were estimated from the average of four samples (Table 1), and initial concentrations in the incubation bottles were assumed to be equal to the appropriate dilution times this initial concentration. Three replicate final chlorophyll samples were taken per bottle.

Apparent phytoplankton growth rates were calculated based on exponential growth:

$$\mu = \ln(\text{chl}_f / \text{chl}_i) / t$$

where  $\mu$  is apparent growth rate ( $\text{day}^{-1}$ ),  $\text{chl}_f$  is final chlorophyll ( $\mu\text{g/L}$ ),  $\text{chl}_i$  is initial chlorophyll ( $\mu\text{g/L}$ ), and  $t$  is the incubation time (days). Linear regression of  $\mu$  as a function of dilution provides two coefficients: the y-intercept, which corresponds to nutrient-saturated phytoplankton growth in the absence of grazers ( $k$ ), and the slope, corresponding to the grazing impact ( $-g$ ). From these coefficients, the amount of chlorophyll grazed per day as a fraction of

standing biomass was calculated as:

$$\frac{N_o - N_o e^{-g}}{N_o} = 1 - e^{-g}$$

and the fraction of daily potential production lost to grazing is:

$$\frac{N_o(e^k - 1) - N_o(e^{k-g} - 1)}{N_o(e^k - 1)} = \frac{e^k - e^{k-g}}{e^k - 1}$$

(LANDRY & HASSETT 1982).

The use of chlorophyll as an estimator of phytoplankton biomass could introduce various types of error into the calculations of phytoplankton growth and zooplankton grazing rates. Chlorophyll from phytoplankton cells which are dead but intact, or incompletely digested by zooplankton (HEAD & HARRIS 1992), could affect biomass estimates. Additionally, the relative chlorophyll content of phytoplankton cells may vary according to physiological condition or taxonomic composition (RIEMANN et al. 1989).

## Results and discussion

Estimates of  $k$ , the nutrient-saturated growth rate of the phytoplankton, ranged from  $-0.036$  (a net loss) to  $1.046$  (Table 2). Estimates of  $g$ , the grazing impact, ranged from  $0.098$  to  $0.873$  (Table 2). All seven regressions had a negative slope, which would indicate grazing activity. The Lake 625 regression, however, was not statistically significant ( $P = 0.212$ ). This data set had one missing data point and several high leverage points. The remaining regressions were marginally to strongly significant ( $P < 0.10$ , Fig. 1, Table 2). Only one regression, for Lake 240, failed a linear lack of fit test using pure error. The regression of Lake 239 had the only extreme outlier (externally studentized residual of  $-8.376$ ) which was removed for subsequent analyses (Fig. 1). Grazing as a fraction of biomass ranged from 9 to 58% and consumed 69 to 402% of potential production (Table 2).

One of the principal goals of this study was to correlate estimates of grazing with physical, chemical and biological characteristics of the various lakes. With only seven experiments, it is difficult to assess the effects of a large number of lake characteristics on grazing parameters.

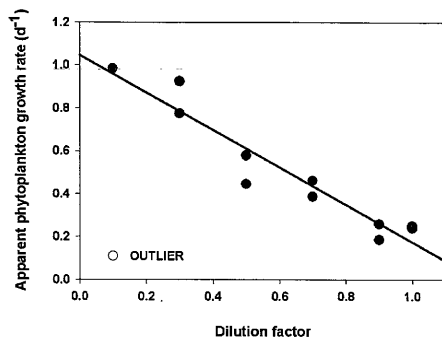


Fig. 1. Results of dilution experiment for Lake 239. A dilution factor of 1× contains ambient lake concentrations of organisms. A dilution factor of 0.5× contains half the ambient concentration of organisms. The hollow circle indicates the only outlier excluded from further data analysis. The line is from least squares regression.

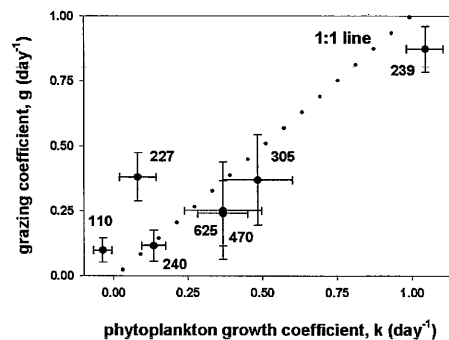


Fig. 2. Correlation of estimates of potential, nutrient-saturated phytoplankton growth,  $k$ , and loss rate to grazing,  $g$ , for the seven lakes. Error bars are  $\pm$  one standard error. The 1:1 line indicates where  $k = g$ . Numbers by the data points are the identification numbers of the lakes.

Experiments conducted later in the summer generally had both higher potential growth rates and higher grazing rates than those earlier in the summer. The results fall into three scenarios. Lake 227, the fertilized lake with a very high concentration of chlorophyll, was the only lake for which grazing was much higher than phytoplankton growth. Phytoplankton from Lake 110 had a negative growth rate. Lake 110 is one of the most oligotrophic lakes, with the lowest chlorophyll concentration in the survey, although nutrients should not have been limiting in the experimental bottles. Phytoplankton from the other five oligotrophic lakes had growth rates slightly higher than grazing rates. Despite a wide range of lake characteristics, including the zooplankton community structure, estimates of grazing ( $g$ ) were highly correlated with the estimates of potential, nutrient-saturated phytoplankton growth ( $k$ ) (Table 2, Fig. 2,  $n = 7$ ,  $r^2 = 0.599$ ,  $P = 0.041$ ). CYR (1998) also found little variation in grazing rates across low-productivity lakes with very different zooplankton communities. The artificially fertilized, eutrophic lake (Lake 227) deviates most strongly from this correlation (without it,  $n = 6$ ,  $r^2 = 0.951$ ,  $P = 0.001$ ). Results from lakes 239, 240, 305, 470 and 625 fall just

below the 1:1 line along which  $g = k$  and grazing would remove 100% of production (Fig. 2); actually, about 80% of potential production was consumed by grazing (Table 2). Therefore, the nutrient-saturated growth rates slightly exceeded zooplankton grazing. If growth rates in the lakes are actually lower than in the nutrient-saturated incubation, then grazing might exceed production. Trials with and without excess nutrients would be useful to test this possibility.

Such a consistent relationship between  $k$  (potential growth rate) and  $g$  (rate of herbivory) (Fig. 2) is initially surprising, although it is consistent with several other recent studies (LANDRY et al. 1997, LATASA et al. 1997, central equatorial Pacific; BURKHILL et al. 1987, coastal north Atlantic). If the estimates of potential phytoplankton growth do capture some of the characteristics of phytoplankton growth rates in the actual lakes, the correlation between  $k$  and  $g$  (with  $k$  slightly higher than  $g$ ) has implications for phytoplankton and zooplankton dynamics. The seasonal pattern may indicate that both phytoplankton growth and zooplankton grazing increase during the summer season from June to August. Zooplankton grazing pressure may be tracking increases in phytoplankton

Table 2. Regression statistics, herbivory calculations, and date of experiment. See methods for formulas for percent of standing biomass grazed per day and percent of potential production grazed per day.

Lake	110	227	240	470	625	305	239
k	-0.036	0.082	0.135	0.368	0.368	0.485	1.046
g	0.098	0.380	0.116	0.240	0.251	0.369	0.873
p	0.063	0.002	0.081	0.087	0.212	0.061	0.000
r <sup>2</sup>	0.305	0.630	0.274	0.265	0.167	0.307	0.916
% biomass grazed	9.3	31.6	11.0	21.3	22.2	30.9	58.2
% production grazed	(k < 0)	402	87	69	72	80	90
Date	172	179	195	213	205	199	219

biomass and growth rate, or phytoplankton growth rate may indirectly increase as a result of zooplankton grazing pressure, or both. The similarity of k and g may also indicate a balance between grazers and phytoplankton, characteristic of nutrient-limited systems with tight coupling of nutrients, phytoplankton, and zooplankton (LANDRY et al. 1997). This may have long-term implications for phytoplankton-zooplankton interactions and population dynamics if phytoplankton communities capable of high growth support zooplankton communities that exert intense grazing pressure. If growth and grazing are correlated, a wide range of grazing rates may have the same net effect on phytoplankton standing biomass. Algal potential growth rate appears to be one of the most accurate predictors of herbivory rate in these lakes, perhaps indicating a trade-off in algae between characteristics which control maximal growth rate in the phytoplankton and those that provide defense against herbivory. Such a trade-off is thought to be fundamental in terrestrial plants (HERMS & MATTSON 1992), and the same may be true for phytoplankton in some lakes.

### Acknowledgments

We thank ROBIN M. STERNBERG for technical assistance, JOHN H. SCHAMPEL and KIMBERLY L. SCHULZ for helpful discussions and comments on the manuscript, and the ELA staff for field support. Financial support provided by NSF Ecology Program Grant to R. W. S., NSF REU Grant to R. W. S. and R. M. S., and NSF Graduate Research Fellowship to A. E. G.

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