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# Species-specific rates of growth and grazing loss among freshwater algae[1]

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*Abstract*

Recent investigations into the population dynamics of phytoplankton communities have emphasized the variabilities of loss rates rather than growth rates in governing the changes that occur. Many freshwater phytoplankton, however, grow at rates that are measurably less than their maximum physiological capability because of nutrient limitation. At any moment the nutrient most limiting in situ division rates varies from species to species within an assemblage and the extents of limitation change with time. Rates of mortality inflicted by herbivorous zooplankton are likewise species-specific, but the size of algal particles is a good predictor of whether the particle will be grazed at all. We manipulated grazer abundances and nutrient concentrations in enclosures to examine the effects on algal net growth rates. Grazed species were usually unicellular organisms. Some colonial species showed increased growth rates in the presence of grazers; in all cases these species were limited by N or P in situ. The variability of algal growth rates was much greater than that of measured loss rates due to grazing. Alternate loss rates, primarily sinking, seem to exhibit variability similar to growth rates in comparisons among all species in the assemblage.

Two premises about the dynamics of phytoplankton have been advocated in recent years. Some workers have claimed that oceanic species grow at rates not restrained by nutrient stress, because of rapid nutrient cycling, so that all dynamics observed in nature can be ascribed to physical factors and grazing losses (Goldman et al. 1979). Even when the precise mechanism is disputed this premise has been accepted as a guide for calculations about nutrient uptake in the ocean (Jackson 1980). The second claim is that the sizes of phytoplankton particles are of paramount importance in determining relative growth rates and relative grazing stress among coexisting species of phytoplankton (O'Brien 1974; Laws 1975; Steele and Frost 1977; Margalef 1978; Smith and Kalff 1983).

These subjects bear directly on the mechanisms responsible for seasonal succession of plankton species in nature. Freshwater ecologists have long suspected that individual species of algae succeed through their relative abilities to use nutrients (Pearsall 1932; Hutchinson 1944). Observations that changes in ambient concentrations of nutrients correspond with changes in species composition in predictable ways are taken as strong evidence for that view (Tilman et al. 1982). However, several experimental studies show dominant control of the population dynamics of individual algal species by loss rates due to sinking and grazing (Knoechel and Kalff 1975, 1978; Crumpton and Wetzel 1982; Reynolds et al. 1982). It may be simply that the variability of ambient growth rates in nature is slight compared to the range of possible loss rates.

Growth rates in nature cannot be evaluated from laboratory studies alone; even continuous algal cultures are useful but inadequate analogs of nature because of the restrictions they impose on population dynamics. Loss rates from grazing and other processes in nature are neither necessarily equal among co-occurring species nor completely balanced by nutrient inputs as is the case in the cultures. Unless the experiments include the complete species assemblage of interest any conclusions require substantial extrapolation. Most routine field measurements are likewise unsatisfactory. It is difficult to draw inferences from measure-

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ments of primary productivity or C:N:P ratios in situ because, among other reasons, those gross properties reflect the status of only the dominant species and not that of the species that may soon become dominant. They are moreover divorced by several steps from the actual division rates they are presumed to reveal. In his provocative review of phytoplankton periodicity, Reynolds (1984) argued that there is no single factor ultimately determining seasonality in activity and dominance of the phytoplankton. He argued that the periodicity is the outcome of responses to environmental variability mediated by physiology and behavior.

We regard three measurements as prerequisite to adequate interpretation of algal dynamics: species-specific division rates, species-specific loss rates, and the character and extent of nutrient limitation. We believe that the measurements can be obtained from natural plankton communities and have used in situ perturbations of nutrient and grazer abundance to evaluate the magnitude of the effects. By combining experiments with field observations we have tried to decipher the causes for changes in freshwater phytoplankton communities.

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## *Methods*

We combined close-interval measurements of physical, chemical, and biological properties in Egg Lake and Sportsmans Lake, Washington, with series of experiments using enclosures of lake water in situ. Egg Lake is a 5-m monomictic basin on San Juan Island (Lehman and Sandgren 1978; Lehman 1979). Sportsmans Lake is a 2.5-m basin about 100 m downstream from Egg Lake through marshland. The lakes share similar species compositions in the spring. Owing to its extreme shallowness, Sportsmans Lake develops extensive stands of *Ceratophyllum* by mid-May and we consequently restricted most of our work to the open waters of Egg Lake. We measured temperature with a Whitney TC-5C thermistor and light penetration with a Li-Cor quantum radiometer, Whitney photometer, and a Secchi disk. We measured dissolved P, SRP, $NH_4^+$, $NO_3^-$, $O_2$, alkalinity, pH, total P, and particulate C, N, and Si by techniques described by Lehman (1979). In the experiments the natural plankton community was subjected to nutrient additions and to alterations of the abundance of the dominant herbivore, *Daphnia pulex*. The enclosures were transparent plastic bags holding 18 liters of lake water suspended at 1.5-m depth. Their volume and design permitted them to be thoroughly mixed before samples were removed in the field. The bags were filled by three successive casts of a 6-liter Van Dorn sampler from 1.5 m, the depth of midepilimnion during our work from April to June 1976. In some treatments crustacean macrozooplankton were sieved from the water through a plankton net of 130-$\mu$m aperture; large algal colonies or filaments were never common during our work, so the material retained by the nets was almost exclusively *D. pulex*, *Diaptomus oregonensis*, and cyclopoid copepodids. In other treatments, the animals retained by sieving 18 liters of water were added to those present in an enclosure, doubling the ambient abundances of macrozooplankton. Some enclosures served as control treatments and the enclosed water was not sieved or manipulated. In other treatments, we added nutrients to final concentrations of 1 $\mu$M $NaH_2PO_4$ or 7.5 $\mu$M $NH_4NO_3$, either singly (designated "P" or "N" treatments) or in combination (designated "*"). In a few cases we also added the trace metal solution of the Guillard (1975) WC culture medium, at a tenth the recommended final concentrations. Since these treatments never yielded significant deviations from the controls, either in bulk chemical assays or species counts, they have been combined with control treatments in our analyses. The experiments lasted for 3 or 4 days depending on the rates at which algal populations and added nutrients changed inside the enclosures.

The net rates of growth of individual species of phytoplankton inside the enclosures were based on cell counts. For abun-

dance and dry weight of zooplankton we collected (63-$\mu$m aperture net) and counted the entire assemblage in each enclosure at the end of an experiment. Abundances of the plankton in situ were assessed from vertical series of samples taken with a Van Dorn sampler (phytoplankton) and a transparent plankton trap of 30-liter capacity (zooplankton). Diel sampling studies quantified daily vertical migratory behavior and patchiness of the animal populations. Phytoplankton were preserved with acid Lugol's and counted in settling chambers by inverted microscope.

*Results*

Biomass of algae and zooplankton in Egg Lake during spring 1976 is plotted in Fig. 1. Values are mean epilimnetic abundances based on averages of samples from 0.5, 1.5, and 2.5 m. The phytoplankton was dominated by a bloom of *Asterionella formosa* that reached peak abundance during May. Volumes for individual taxa were determined from volumetric displacements by clay scale models. Other than *Asterionella,* the main components of the phytoplankton were cryptomonads and chrysophytes. The zooplankton was dominated by *D. pulex*; taxa other than *Daphnia* and *Diaptomus,* including rotifers, contributed little additional mass to the dry weight estimates shown.

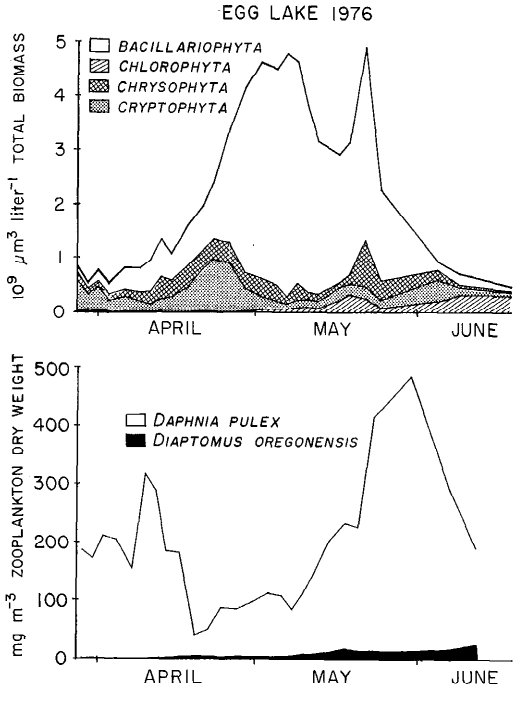


Fig. 1. Biomass composition of phytoplankton and zooplankton in Egg Lake.

Four experiments were done in Egg Lake: 19–23 April during the period of increasing abundance of *Asterionella*; 9–13 May, during its first decline; 19–22 May during a temporary recovery by the population; and 7–10 June at the end of its abundance. Figure 2 illustrates the combined effects of nutrient additions and grazer abundances on four species of algae from an enclosure experiment in May. For each phytoplankton species present in numbers sufficient for reliable counts we computed *net* observed growth rates ($r$) for each enclosure from

$$r = \ln(N_t/N_0)/\Delta t \qquad (1)$$

where $N_0$ is initial cells ml$^{-1}$, $N_t$ is final cells ml$^{-1}$, and $\Delta t$ is the duration of the experiment (days). Time-course checks showed that the assumption of exponential changes was reasonable in our brief experiments. We cannot reject the possibility that some growth rates are underestimated owing to environmental constraints imposed by the enclosure scheme and duration. However, the practical consideration we faced was the need to permit species-specific differences in net growth rates to become translated into species-specific differences in population abundance that we could measure with precision. The experimental designs represent our judgment about the minimum finite intervals needed for meaningful rewards for the substantial labor of species-level plankton counting. Computed net growth rates are plotted in Fig. 2 against zooplankton biomass determined from direct counts, size-frequency measurements, and length-to-dry-weight conversions (Bottrell et al. 1976).

Some of the enclosures, usually six or eight per experiment, were treated by addition or removal of zooplankton but did not receive nutrient additions. These treatments were used to compute a linear regression relating net growth ($r$) to zooplankton biomass ($Z$).

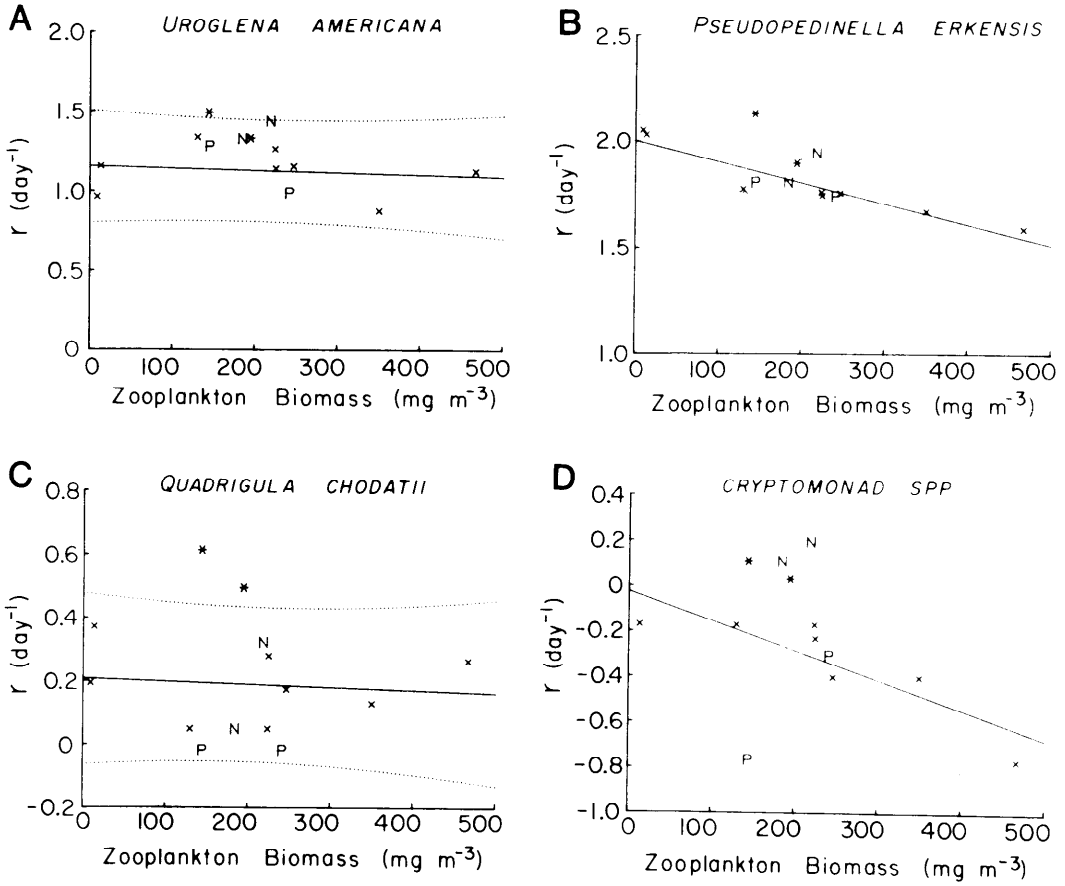


Fig. 2. Responses shown by species coexisting and experiencing the same experimental manipulations in Egg Lake, 19–22 May 1976. Slopes and confidence intervals are computed from treatments with no nutrient addition. A. *Uroglena americana* was not grazed and not stimulated by nutrients. B. *Pseudopedinella erkensis* was grazed but not stimulated by nutrients. C. *Quadrigula chodatii* was not grazed but simultaneous addition of N and P increased its growth. D. An approximately equal mixture of *Cryptomonas marsonii* and *Chroomonas nordstedii*: both were grazed and both responded to nutrient addition.

The slope of the empirical relationship has units of $m^3$ (mg zooplankton biomass)$^{-1}$ $d^{-1}$ and is an estimate of the species-specific filtering rate of *Daphnia* on the algal species (Lehman 1980). The intercept ($d^{-1}$) is an estimate of in situ algal growth rate in the absence of grazers. A confidence envelope around the regression line computed by

$$Y_{\text{conf}} = Y \pm t_{90} \times s\left[1 + 1/n + \frac{(x_i - \bar{x})^2}{\Sigma(x_i - \bar{x})^2}\right] \quad (2)$$

represents the region within which we regard it likely that individual departures from the regression line are the result of chance. Against this scheme we plot net growth rates computed for the algal species from treatments that received additions of $NH_4NO_3$ (N), $NaH_2PO_4$ (P), or both nutrients simultaneously (*). The nutrient treatments were done in pairs. We regard nutrient addition to be effective at increasing species-specific growth rate if computed growth rates fall outside the confidence envelope for both members of the pair, a conservative esti-

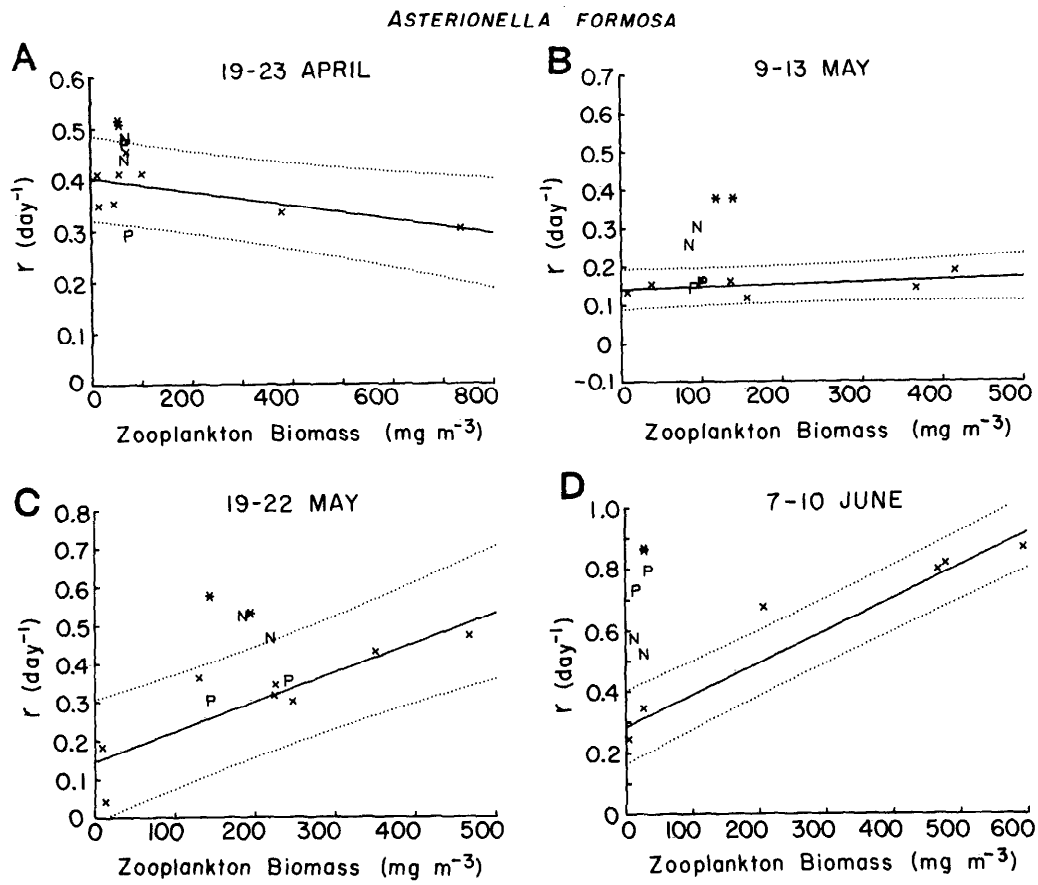


Fig. 3. Responses of *Asterionella formosa* in experiments repeated at four times during its presence in Egg Lake. Nutrient additions were made to ambient (control) levels of zooplankton in all except the 7–10 June experiment, in which the water was sieved before addition of nutrients. The point at 200 mg $m^{-3}$ was omitted from linear regression because the true relationship is probably hyperbolic in the case of enhancement.

mate of nutrient effects. The probability that both replicates of a nutrient treatment would deviate simultaneously (both above or both below) by chance alone is <0.5%. We adopted the conservatism because practical considerations restricted our replicate number to two for each nutrient treatment, and because between 10 and 15 species were analyzed in each experiment.

We found this to be a particularly effective technique for diagnosing species-specific responses to grazing and to nutrients within a natural plankton community. Field logistics were kept manageable and the experiments integrated into the regular sampling regime for the lake plankton. Within a single experiment we could identify species that were *not* being grazed and were *not* stimulated by our nutrient enrichments (Fig. 2A), species that were grazed but not affected by nutrient additions (Fig. 2B), species not grazed but stimulated by nutrients (Fig. 2C), and species that were both grazed and stimulated by nutrient addition (Fig. 2D). We identified the species being grazed as those for which the slopes of the fitted regression lines relating net growth rates to zooplankton abundance were significantly less than zero (e.g. Fig. 2B,D). Other species either were not grazed (slope of regression

line equals zero), or they at times actually profitted from the presence of grazers (Fig. 3).

The responses by individual species to the experimental manipulations often changed from one experiment to the next, as illustrated by data for *A. formosa* (Fig. 3). When the zooplankton population was dominated by large-bodied adult *Daphnia* in April, *Asterionella* was grazed (Fig. 3A). As the proportion of juvenile *Daphnia* increased later in the season, no grazing on that colonial diatom could be measured. In most cases we added nutrients to an otherwise unaltered plankton assemblage. In the 7–10 June experiment, however, we removed grazers from enclosures before adding nutrients in order to investigate the effects of nutrient additions in the near-absence of herbivores. The increased growth of *A. formosa* (Fig. 3D) that resulted from nutrient addition could also be obtained at elevated abundances of animals, implying that *Asterionella* was poorly grazed and that it used nutrients released into the water by the zooplankton. At the same time that *Asterionella* was responding positively to the zooplankton, smaller cells like *Pseudopedinella* (Fig. 2B) were clearly being grazed.

There was a tendency for small particles to be grazed more readily than large ones (Fig. 4). One-way ANOVA confirmed that particle size (the maximum linear dimension of an algal "unit," free cell or colony), but not volume of individual cells, was a major factor in determining whether species were grazed ($P < 0.0001$). Aside from this generalization, however, grazing rates (slopes of the regression lines) for grazed species were not size-dependent. Using cell length for unicells and colony diameter as a measure of phytoplankton particle size we found no significant correlations between phytoplankton size and zooplankton grazing rates in any single experiment or in data from all four Egg Lake experiments and two Sportsmans Lake experiments considered together ($|R| < 0.1$). The magnitudes of grazing rates were influenced somewhat by temperature ($P < 0.02$, one-way ANOVA) so that the first experiment in Egg Lake (epilimnion temperature = 9.6°C) yielded grazing rate slopes lower than in the other five

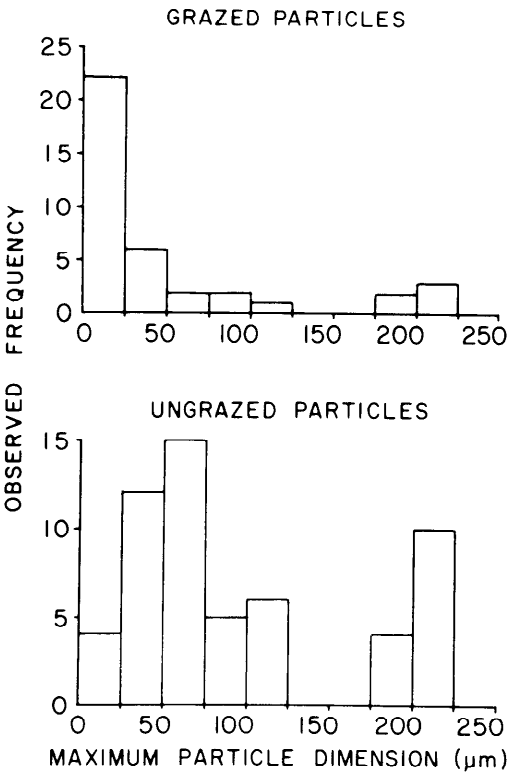


Fig. 4. Frequency distributions of particle size for species that were grazed and for all ungrazed species in all experiments. Evidence for grazing is taken to be those cases in which regressions of $r$ vs. biomass of zooplankton yield slopes significantly $<0$.

experiments at temperatures from 11.6° to 16.0°C. Even by accounting for the apparent effect of temperature, however, grazing rates were species-specific and independent of particle size.

Our analysis of the species-specific effects of nutrient additions on phytoplankton growth in Egg Lake confirms a general shift from P to N limitation during spring previously documented on a community-wide basis (Lehman and Sandgren 1978). We found frequent instances where nutrient additions increased growth rates beyond the confidence interval constructed around the regression line for grazing (Fig. 2A,B). Some species responded to a specific nutrient (e.g. N or P: Fig. 2D) while others responded only to simultaneous additions (P + N: Fig. 2C). Furthermore, nutrient stimulation was

Table 1. Summary of growth responses of algal species to grazing and nutrient additions. Response is scored on the basis of the slope of regression lines in the case of grazing and on the basis of two growth rate assays simultaneously exceeding rates enclosed by the 90% C.I. of the regression in the case of nutrient limitation. We analyzed 98 total responses in six independent experiments in Egg and Sportsmans Lakes, April to June 1976.

| Nutrient limitation present | Net growth response to zooplankton | | |
|---|---|---|---|
| | Grazed | No effect | Enhanced |
| No | 27 | 41 | 0 |
| Yes | 9 | 16 | 5 |

not correlated to phytoplankton particle size as measured by either mean cell volume or by colony or cell diameter based on binomial run tests (Sokal and Rohlf 1981).

The results from the 19–22 May experiment (Fig. 3C) illustrate the diverse responses of phytoplankton to manipulations of nutrients and zooplankton. At this time in the lake *Asterionella* appeared to be dependent on recycled nutrients obtained from other species as a result of grazing by zooplankton, while coexisting phytoplankton species were either unaffected by grazing or were actively being grazed (Fig. 2). Some of the species unaffected by grazing were stimulated by nutrient additions, as were some of the actively grazed species. The responses of individual phytoplankton species to manipulations of nutrients and grazers in all experiments are summarized in Table 1. The most common responses were species grazed but not stimulated by nutrients, species not significantly affected by either grazing or nutrient additions, and species stimulated by nutrients but not grazed. No species at any time exhibited a stimulation of growth rate in the presence of grazers unless it was also nutrient-limited, an observation that is very

Table 2. Species-specific grazing effects by experiment. E1 to E4 are experiments in Egg Lake and S1 to S2 those in Sportsmans Lake. Symbols indicate if a species was grazed (−: regression slope significantly <0), there was no grazing response (0: slope not significantly different from zero), or growth rates increased with animal abundances (+: slope significantly >0). Species not present in countable numbers—×.

| | Cell vol ($\mu m^3$) | E1 | E2 | E3 | E4 | S1 | S2 |
|---|---|---|---|---|---|---|---|
| Species grazed in one or more experiments | | | | | | | |
| *Ankyra ancora* (G. M. Smith) Fott | 345 | 0 | 0 | − | 0 | 0 | × |
| *Ankyra lanceolata* (Korsch.) Fott | 19 | 0 | 0 | − | 0 | 0 | 0 |
| *Asterionella formosa* Hassal | 514 | − | 0 | + | + | 0 | − |
| *Chroomonas minuta* (Skuja) Bourrelly | 86 | − | 0 | × | − | − | − |
| *Chroomonas nordstedii* Hansgirg | 935 | − | − | − | × | 0 | − |
| *Cryptomonas marsonii* Skuja | 570 | × | × | − | − | × | × |
| *Cryptomonas rostrata* Skuja | 5,300 | 0 | − | − | − | 0 | − |
| *Dinobryon divergens* Imhof | 138 | 0 | 0 | 0 | + | − | − |
| *Eudorina elegans* Ehr. | 627 | × | 0 | 0 | 0 | − | 0 |
| *Hillea* sp. | 54 | × | × | 0 | − | × | − |
| *Mallomonas akrokomonas* Rutt. | 157 | 0 | 0 | 0 | − | 0 | 0 |
| *Pseudopedinella erkensis* Skuja | 121 | − | 0 | − | − | − | 0 |
| *Stephanodiscus subtilis* Cleve | 397 | × | × | × | × | − | − |
| *Synura spinosa* Korsch. | 505 | 0 | − | + | 0 | 0 | × |
| *Uroglena americana* Calkins | 35 | 0 | 0 | 0 | − | 0 | 0 |
| Minute flagellates and coccoid cells | 14 | − | − | − | − | − | − |
| Species not grazed in any experiment | | | | | | | |
| *Anabaena flos-aquae* (Lyng.) Breb. | 34 | × | × | × | × | × | 0 |
| *Aphanizomenon flos-aquae* (L.) Ralfs | 10 | × | × | × | × | 0 | 0 |
| *Chrysosphaerella longispina* Lauterb. | 339 | 0 | × | × | × | × | × |
| *Dinobryon cylindricum* Imhof | 94 | × | × | 0 | × | × | × |
| *Mallomonas caudata* Iwanhoff | 3,171 | × | × | 0 | 0 | × | × |
| *Mallomonas crassisquama* (Asmund) Fott | 603 | 0 | 0 | × | × | 0 | × |
| *Quadrigula chodatii* (Tan.-Ful.) G. M. Smith | 103 | 0 | 0 | 0 | 0 | 0 | + |
| *Sphaerocystis schroteri* Chodat | 133 | 0 | 0 | 0 | 0 | × | × |

Table 3. Species-specific instances of nutrient limitation by experiment. Species stimulated by nutrient additions in one or more experiments were identified as explained in the text. Significant increases in net growth rates resulted from addition of $NH_4NO_3$ alone (N), $NaH_2PO_4$ alone (P), or only by simultaneous addition of both nutrients (*). Experiments are identified as in Table 2.

| | E1 | E2 | E3 | E4 | S1 | S2 |
|---|---|---|---|---|---|---|
| *Ankyra ancora* | N | 0 | 0 | 0 | 0 | × |
| *Ankyra lanceolata* | * | * | 0 | 0 | 0 | 0 |
| *Asterionella formosa* | * | N | N | P, N | 0 | 0 |
| *Chroomonas minuta* | 0 | 0 | × | 0 | 0 | * |
| *Chroomonas nordstedii* | 0 | 0 | N | × | * | * |
| *Cryptomonas marsonii* | × | × | N | 0 | × | × |
| *Cryptomonas rostrata* | 0 | * | 0 | 0 | 0 | 0 |
| *Dinobryon divergens* | 0 | 0 | 0 | N | 0 | 0 |
| *Eudorina elegans* | × | * | 0 | 0 | × | 0 |
| *Hillea* sp. | × | × | 0 | * | × | * |
| *Mallomonas akrokomonas* | 0 | 0 | N | P, N | 0 | 0 |
| *Mallomonas caudata* | × | × | N | 0 | × | × |
| *Quadrigula chodatii* | 0 | * | * | P | 0 | * |
| *Sphaerocystis schroteri* | 0 | * | N | * | × | × |
| *Stephanodiscus subtilis* | × | × | × | · | 0 | P |
| *Synura spinosa* | 0 | * | * | 0 | 0 | × |
| Minute flagellates and coccoid cells | 0 | * | 0 | 0 | 0 | 0 |

unlikely to be caused by chance alone ($P < 0.01$, $\chi^2 = 12.0$, 2 df). Most likely it was nutrients released from *Daphnia* that increased the growth rates of these nutrient-limited populations.

Responses of individual species to grazing and nutrient additions are listed for all six experiments in Tables 1 and 2. Grazed species were typically unicellular organisms like *Pseudopedinella, Ankyra,* and the cryptomonads. The species that responded positively to grazer additions were colonial forms like *Asterionella, Dinobryon, Synura,* and *Quadrigula.* Nitrogen limitation was a transient phenomenon in Egg Lake during May owing to release of P from emerging macrophytes (Lehman and Sandgren 1978; Lehman 1979), and the limitation affected diatoms, chrysophytes, cryptomonads, and chlorophytes alike (Table 3).

## *Discussion*

The novel feature of the analysis that we used is its ability to decipher individual process rates at the species level within a natural plankton assemblage. Other workers have used enclosures to examine species-specific effects of grazing (e.g. Porter 1972, 1973; Gliwicz 1975; Weers and Zaret 1975; McCauley and Briand 1979), but the emphasis has usually been on identifying the taxa that are grazed rather than the rates per se. Our findings are generally in agreement with those of previous workers in regard to the types of response shown: some algae are depressed by grazers, others are unaffected, and still others are stimulated. The stimulation is almost certainly a response to nutrient release by the grazers.

Porter (1973, 1975, 1976, 1977) has argued that the enhancement shown by colonial species in response to the herbivore *Daphnia* results from viable passage of cells through the guts of the animals. The species she used for her examples, *Sphaerocystis schroteri* Chodat, was present in four of our experiments and was never affected by the grazers. It was usually limited by N or P, and thus its lack of response might be ascribed to compensatory effects of grazing and nutrient release. Three of the four taxa for which we observed growth enhancement by grazers, *Asterionella, Synura,* and *Dinobryon,* do not have the durable cell walls and gelatinous sheaths that Porter (1977) claimed requisite for gut passage. One volvocalean species, *Eudorina elegans,* was grazed in one experiment (Table 2) when the population was dominated by gonidia rather than the larger parent colonies. We

believe that larger colonies are often spared from ingestion at the expense of unicells and that if those species are simultaneously nutrient-limited, they can profit from recycled N and P. It is possible that if we had added crustaceans to many times natural levels extreme changes in ingestion behavior might have occurred. In fact, the gut contents of our animals were little more than an amorphous mush presumably derived from cryptomonads, small chrysophytes, and minute unicells. Our data lend no support to the notion that viable gut passage is quantitatively important to phytoplankton community structure.

The diversity of species-specific responses to nutrients and grazers among coexisting species at a given time, and for a single species during the persistence of its population in the lake, is an important feature of phytoplankton assemblages. Nonspecific indicators of phytoplankton community response, such as particulate carbon, respiration rates, Chl *a*, and particle abundance, may reflect the conditions influencing the population dynamics of only one or a few dominant species. The dynamics of the whole plankton community and the dynamics of minor species that may become dominants in the future would be uninterpretable by such community-wide indicators. A large percentage (56%) of the species responding to nutrient additions in our study did so only when P and N were added simultaneously. This suggests that near colimitation of growth by more than one nutrient could be common and underscores the balances that define resource competition for these species.

A large proportion of species in our experiments (42%) did not respond to either grazing manipulations or the addition of nutrients often considered to be growth-limiting in lakes. We added trace metals in some of our enclosure experiments but never found any significant response. Perhaps our limits of precision based on cell counts prevented us from quantifying weak differences, or perhaps there was genuinely no response. Alternatively we can imagine cases in which nutrient regeneration by grazers sufficiently compensated for grazing mortality so that the *net* apparent effect of increased grazing pressure was zero. To exclude the possibility that such compensatory effects biased our conclusions about grazing rates and particle size, we omitted from analysis those instances where grazed species were simultaneously nutrient-limited. Nonetheless the reduced set of grazing rates remained dependent only on temperature, not on individual cell size, cell volume, or algal "unit" dimensions. The possibility certainly exists that grazers select their prey by criteria other than that of size alone (Poulet and Marsot 1978; Alcaraz et al. 1980; Paffenhöfer 1984), and our data suggest that they do so in nature.

Because our interpretations rely on rates calculated from measurements of enclosed populations, we necessarily have to test the data skeptically for evidence of inconsistency or aberrant behavior. The most secure way of doing so is to determine if enclosure-based rates are consistent with field dynamics of populations. A direct test is possible with *A. formosa*, the biomass dominant and the only substantial source of biogenic silica during April and May in Egg Lake. Lehman (1979) showed that sinking losses estimated from enclosures were identical to those calculated from the mass balance of Si in the epilimnion [0.176 $d^{-1}$ (SE = 0.014) vs. 0.177 $d^{-1}$ (SE = 0.017)] during mid-May. Analogous comparisons are not possible for other species owing to the difficulty of obtaining reliable independent estimates of permanent sinking loss rates (cf. Walsby and Reynolds 1980; Sommer 1984). We were able, nonetheless, to identify a few instances of probable enclosure effects on individual species. The regression lines of net growth rates on zooplankton biomass did not always intersect the growth rate axis at positive values; in 20 of 98 cases the intercept was significantly less than zero. That means that taxa were declining inside the enclosures exclusive of the effects of any metazoan zooplankton. The observation itself is not necessarily aberrant because physiological death (e.g. Jassby and Goldman 1974) and heterotrophic flagellates (Fenchel 1982; Landry and Hassett 1982) are sometimes implicated as important loss vectors and could not be excluded from our experiments. However, in 17 of these cases, the

enclosure-based growth rates were lower than simultaneous net growth rates of the same species in situ. That means that on balance these species were growing faster in the lake than in the enclosures. The most obvious enclosure effects were on *Synura spinosa,* which exhibited negative net growth rates in every enclosure experiment. Other algae which showed the phenomenon only occasionally were *Cryptomonas rostrata* (three cases), *Chroomonas minuta* (two cases), *Mallomonas akrokomonas* (two cases), *Mallomonas crassisquama* (two cases), and *Mallomonas caudata, Uroglena americana,* and *Chrysosphaerella longispina* (one case each). There were some instances in each experiment and in both lakes.

Because many of these species are chrysophytes that can form cysts, some of the discrepancy between enclosures and lake might be explained by increased rates of cyst formation by enclosed populations or, alternatively, by recruitment of excysting cells into the lake plankton. The abundance of *Synura* cysts in fact increased markedly inside enclosures, and so the apparent loss of vegetative cells is really a demographic consequence. We are faced, nonetheless, with the conclusion that some enclosure-based growth rates cannot be extrapolated securely to field populations and 17 suspect cases are thus excluded from the following analyses.

The nutrient responses we recorded in our experiments represented direct increases in growth rates made possible by nutrient additions. Nutrient levels were not returned to ambient background levels before experiments were terminated so that second-order effects like competition for exhausted supplies could not obscure the results. We cannot resist asking from our data whether nutrient limitation or grazing by herbivores is more important in regulating plankton populations in nature. To address the problem we combine our experimental results with the dynamics of species populations in the lakes. We identified those taxa for which net population changes in the lake were significantly greater or less than zero during each experiment and tabulated the data according to whether the species were simultaneously grazed or nutrient-limited (Table 4). Although the data hint that increasing populations are less likely to be grazed than are decreasing populations, overall they provide no statistical reassurance that either nutrient limitation or grazing is a *dominant* control of population dynamics in most cases. Populations rise or fall in relation to the balances struck between growth rates and loss rates at the species level. Because of species-specific differences in physiology and susceptibility to grazing, identical environmental circumstances lead to different balances for every species present. Population dynamics of the phytoplankton can be deciphered mechanistically, but that is probably best done at the species level. Reynolds (1984) drew almost the same conclusion about the balances between growth and loss rates, but he favored grouping the phytoplankton species among 19 assemblages based on common empirical periodicities. Particle morphology, especially the segregation by axial dimension and surface: volume ratio advocated by Lewis (1976), is a central part of his scheme. Our results are concordant with his theory in the sense that small round forms are more susceptible to grazing than are large or elongate ones, but inspection of Table 3 shows that nutrient limitation can afflict taxa of very diverse sizes and shapes.

Table 4. Comparison between populations of phytoplankton that were either decreasing or increasing in abundance in the lake while enclosure experiments were underway.

| | Net change in lake population | |
|---|---|---|
| | Decrease | Increase |
| Nutrient-limited? | | |
| No | 21 | 25 |
| Yes | 6 | 10 |
| Grazed? | | |
| No | 15 | 23 |
| Yes | 12 | 12 |

We examined our data to evaluate the magnitudes of growth and loss rates attributed to different causes and to assess the variabilities of these rates among species. We chose to incorporate in our analysis the uncertainty of our determinations, because the individual growth and filtering rates are

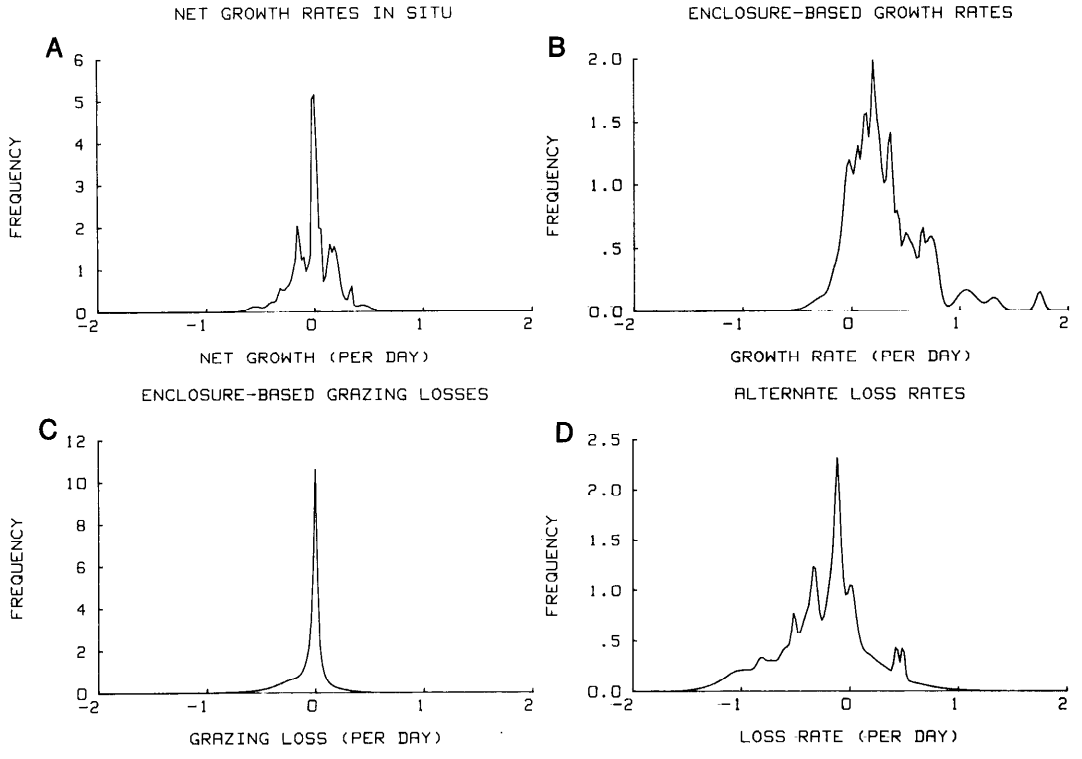


Fig. 5. Probability density functions constructed by Eq. 4. The area under each distribution = 1.0 and thus the curves represent the likelihood that particular growth or loss rates existed for species in our plankton assemblages. The panels represent the terms in Eq. 3: $r_{\text{lake}}$ (A); $\mu$ (B); $F \times Z$ (C); and $A$ (D).

subject to variable uncertainties of estimation. We propose the simple model

$$r_{\text{lake}} = \mu + F \times Z + A \qquad (3)$$

where $r_{\text{lake}}$ is the net rate of population growth in the lake ($d^{-1}$), $\mu$ is cell division rate ($d^{-1}$), $F$ is the alga-specific clearance rate ($m^3\ mg^{-1}\ d^{-1}$) by zooplankton ($Z$, mg $m^{-3}$), and $A$ is alternate loss or gain processes (sinking, dilution, excystment, etc). This model conforms to our empirical data and thus we can use it to separate net growth rates into several components, though not necessarily into the most elementary dynamic processes.

We estimate each $\mu$ and its standard error by species from the intercepts of the regression plots (Figs. 2, 3); we get each $F$ and its standard error from the slopes. Mean daily biomass of zooplankton in the epilimnion is estimated from lake plankton counts during each experiment and from measured diel variabilities in epilimnetic abundance. Net growth rates of algae are estimated from linear regressions of the logarithms of cell abundances in the lake vs. time over periods that include each experiment. Alternate loss rates, $A$, are calculated by difference. Estimates of the error of each calculated rate (i.e. $F \times Z$ and $A$) are obtained by first-order error propagation (Meyer 1975).

We combine the individual estimates for all species into a single probability density function $P(z)$, where $z$ is the random variable of interest (growth or loss rate, $d^{-1}$):

$$P(z) = (1/n) \sum_{i}^{n} [1/s_i(2\pi)^{1/2}] \cdot \exp[-(z - \bar{x}_i)^2/2s_i^2]; \qquad (4)$$

$\bar{x}_i$ and $s_i$ are the individual means and their estimation errors. Resulting frequency distributions are shown in Fig. 5. Enclosure-based growth rates (Fig. 5B) are quite variable among all species (distribution mean = 0.307 $d^{-1}$, SD = 0.357). In contrast, grazing losses (Fig. 5C) are not nearly as variable (mean = −0.053, SD = 0.159). Losses other than grazing (Fig. 5D) are required to reconcile enclosure-based growth with net changes in situ, but the rates are little more variable than the growth rates themselves (mean = −0.230 $d^{-1}$, SD = 0.406).

We draw several conclusions from these findings. First of all, our "enclosure-based growth rates" are imperfect estimates of cell division rates because all loss processes cannot be excluded from the terms. The main losses omitted are sinking and grazing by metazoa. It appears that the grazing losses are relatively small in general. This is because mortality rates inflicted by the zooplankton are products of both filtering rates and animal abundance; even when individual filtering rates are large, the loss rate experienced by an algal population will be small if animals are not abundant. Figure 5C implies that for most species in our study most of the time the effect of grazers was insignificant.

Many of the discrepancies between enclosure-based growth rates and net growth in situ must consequently be caused by forces other than grazing. It is possible, also, that for some species growth rates in enclosures are elevated over actual rates in situ. The light climate at 1.5 m inside the enclosures might have been more favorable for some species than conditions in the ca. 2.5-m-deep epilimnia. We think this unlikely, however, because enclosures are more often indicted for their detrimental effects than for their favorable ones. Much of the alternate "loss" rate in Fig. 5D is probably sinking, but other processes are in evidence also. Occasional increases of *Dinobryon* species much faster than would seem possible from their growth rates were almost surely the result of excysting cells entering the plankton.

The central result of this analysis with relevance to theories of plankton dynamics is that the variance of loss rates is little different from that of growth rates in these natural communities.

The hypothesis that phytoplankton in natural systems grow at rates not restrained by nutrient stress is not supported by our data. Thirty-one percent of the total number of individual species' responses to nutrient additions resulted in increased growth rates that could not be ascribed to zooplankton effects or physical factors. The importance of phytoplankton "unit" size in determining susceptibility to zooplankton grazing is supported by our work, but its influence on the relative competence of species engaged in competition for nutrients is downplayed by our data. Phytoplankton are species-specific in the rates at which they respond to grazing and nutrient stress. Cell size and cell shape are evolutionary responses to many selective forces operating simultaneously. The phenotypic responses to these factors could be as varied as the genotypic diversity present. General trends in cell morphology can be expected among phylogenetically diverse assemblages of species like those that compose phytoplankton communities, and those trends have been neatly elaborated by others, but understanding the dynamics of the plankton requires attention to the biological entities themselves.

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