References and Notes

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2. J. P. Kennett, *ibid.* **14**, 305 (1968).
3. S. W. Stone, *ibid.* **2**, 361 (1956); A. D. Hecht, *J. Paleontol.* **48**, 1217 (1974).
4. Bergmann's rule states that among living organisms, maximum size generally occurs in colder waters. This rule, in theory, applies to warm-blooded animals, but it is usually applicable to cold-blooded animals as well. While some species may show a size increase with decreasing temperature, it seems more reasonable to suggest that the maximum average size of a species should occur in its optimum regions, where such regions are defined in terms of several environmental factors. While in some areas temperature may be a dominant factor in controlling size, it is not necessarily the only variable of importance. See for example, H. B. Moore, *Marine Ecology* (Wiley, New York, 1966), pp. 24–30; D. V. Ager, *Principles of Paleoecology of the Marine Biosphere* (Prentice-Hall, Englewood Cliffs, N.J., 1973), pp. 119–125.
5. Data are reported only for samples where more than ten individuals could be measured, and where the samples are unbiased by solution effects. Morphologic gradients were determined for populations in size fractions 125 to 250 μm and > 250 μm. Similar environmental trends were observed for both size groups. Data are reported here for the size fraction > 250 μm. The curves drawn in Fig. 1A represent, for each temperature, the observed maximum average size for each species. The data from which these curves were drawn show a large variation in size within a population at any one temperature; this is probably due to factors, other than temperature, which affect a population's average size. The detailed geographic distribution of each species is given in (*6*).
6. A. D. Hecht, *J. Foraminiferal Res.*, in press.
7. *Globigerinoides ruber* pink, white, normalform, and kummerform populations have been differentiated. In normalform populations the final chamber of the last whorl is larger than previous chambers; in kummerform ones the final chamber is smaller than previous chambers. Pink populations are larger in test size than white ones, and kummerform populations are larger than normalform ones (*6*). The pattern size variations for *O. universa* in the Atlantic Ocean is similar to that reported by Bé *et al.* (*1*) for populations in the Indian Ocean.
8. Data given in Fig. 1B are replotted from data given in Kennett (*2*). Right-coiling populations of *G. pachyderma* are recognized as a separate species by R. Cifelli [*J. Foraminiferal Res.* **3**, 157 (1973)] and is called *Globigerina incompta*.
9. In the absence of experimental studies of test growth, optimum regions of a species' niche are usually defined by its relative abundances [J. S. Bradshaw, *Contrib. Cushman Found. Foraminiferal Res.* **10**, 25 (1959); A. W. H. Bé and D. S. Tolderlund, in *Micropaleontology of the Oceans*, B. M. Funnell and W. R. Riedel, Eds. (Cambridge Univ. Press, New York, 1970), p. 105]. Abundance data used in this study are based on a study of 191 core-top samples in the Atlantic Ocean as reported by Kipp (*10*). I plotted these data against winter surface temperatures and salinities, and from such curves defined the temperature-salinity ranges where abundances were in the upper 10 percent of the range. Temperature-salinity regions for maximum test sizes are from Fig. 1.
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11. J. S. Bradshaw, *Contrib. Cushman Found. Foraminiferal Res.* **12**, 87 (1961).
12. W. V. Sliter, *ibid.* **21**, 87 (1970).
13. J. Imbrie and N. Kipp, in *The Late Cenozoic Glacial Ages*, K. K. Turekian, Ed. (Yale Univ. Press, New Haven, Conn., 1970), p. 11.
14. C. Emiliani [*J. Geol.* **74**, 109 (1969)] indicates that size variations in Pleistocene populations of *G. ruber* are directly related to temperature in cores outside the tropics. Size variations in populations from Caribbean cores, however, are not related to changes in temperature.
15. Unpublished data of A. D. Hecht and C. Emiliani show that abundances and test size changes in populations of *G. truncatulinoides* are clearly related and vary inversely with paleotemperatures.
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17. I thank M. Bohn and K. Roddenberry for research assistance. C. Emiliani provided unpublished data and reviewed the manuscript. Supported by NSF grant GA 43244 (Geological Oceanography).

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Enhancement of Algal Growth and Productivity by Grazing Zooplankton

Abstract. *Colonies of the common planktonic green alga,* Sphaerocystis schroeteri, *are only partially disrupted and assimilated by* Daphnia magna, *a natural predator. The* Daphnia *break up the outer protective gelatinous sheath that surrounds* Sphaerocystis *colonies, but most of the algal cells emerge from* Daphnia *guts intact and in viable condition. During gut passage, these viable cells take up nutrients, such as phosphorus, both from algal remains and from* Daphnia *metabolites. This nutrient supply stimulates algal carbon fixation and cell division. Enhanced algal growth, observed after gut passage, can compensate for the minor losses to the population caused by grazing. Nutrients regenerated by grazers may produce the summer bloom of gelatinous green algae during the seasonal succession of lake phytoplankton.*

Herbivorous zooplankton are traditionally considered to reduce the abundance of algae during grazing (*1*). However, recent studies show that primary productivity and the numbers of certain algal species increase in the presence of grazers (*2–4*). Nutrients, such as phosphorus, that are excreted by zooplankton (*5*) may stimulate the growth of algae not cropped during grazing. In this study, the uptake of excreted phosphorus and carbon by algae known to survive grazing (*4*) is documented and the contribution of this nutrient source to algal primary productivity and population growth is determined.

Cells of the colonial green alga, *Sphaerocystis schroeteri*, increase in number when the number of grazers is experimentally increased (*3*). Colonies consist of cells embedded in a complex polysaccharide sheath. They are ingested by *Daphnia magna*, *D. galeata mendotae*, and other natural predators, but more than 90 percent of the *S. schroeteri* cells are undamaged by gut passage through the grazers (*4*). Large colonies are broken into smaller clusters of cells with the loss of a few cells and sheath material. They are fed on by *D. magna* at a lower rate and are assimilated less efficiently than unsheathed unicellular green algae, such as *Chlamydomonas reinhardi* (Table 1) (*6*).

During gut passage, the intact cells of *S. schroeteri* take up nutrients from the remains of edible algae and from *Daphnia* metabolites. Light-dependent uptake and incorporation of phosphorus and carbon from algal remains were examined by allowing *D. magna* to fill their guts with a mixture of unlabeled *S. schroeteri* and *Ankistrodesmus falcatus* that was saturation-labeled with either $NaH^{14}CO_3$ or $K_2H^{33}PO_4$ (*7*). The spindle-shaped single cells of *A. falcatus* are easily assimilated by *Daphnia* and are easily distinguished from the palmelloid gelatinous colonies of *S. schroeteri* (Fig. 1a). After 1 hour of feeding in either the light or the dark, animals were anesthetized, fixed, dehydrated, embedded, sectioned, and examined for the distribution of radioactivity by using microautoradiography (*8*).

The heavy grain density over ingested *S. schroeteri* cells (Fig. 1, b and c) documents their uptake and incorporation of ^{33}P from *A. falcatus* remains in both the light and the dark. Carbon-14 is taken up and incorporated more in the light than in the dark. No incorporation of label by control *S. schroeteri* from *A. falcatus* cells in the feeding suspension was detected. The autoradiographs give a conservative indication of uptake since soluble label is removed during washing and dehydration and only label incorporated into fixed, insoluble cell components remains. Phosphorus uptake in both the light and the dark is expected since uptake and storage of phosphorus is independent of light (*9*). The predominance of light-dependent carbon uptake, however, suggests that it is primarily the result of autotrophic and not heterotrophic processes. The accumulated phosphorus and carbon may be taken up in both organic and inorganic forms.

Uptake of phosphorus from the metabolites of *Daphnia* was documented by feeding unlabeled *S. schroeteri* to *D. magna* that were saturation-labeled with ^{33}P and had empty guts (*10*). Feces containing intact *S. schroeteri* were collected and were examined for the distribution of radioactivity by using microautoradiography (*8*). Uptake and incorporation of ^{33}P from the metabolites of *Daphnia* were detected in the cells of *S. schroeteri* (Fig. 1d).

The effect of gut passage on algal

growth was determined by direct observation of algal cells that survived gut passage through *D. magna* and cells, from the same culture, that were not ingested by *Daphnia* (*11*). The number of living cells increased significantly ($P < .01$ as determined by an analysis of variance) from 100 ± 8 at the beginning to 164 ± 15 at the end of the first 24 hours after gut passage. No significant change occurred in the noningested algal cells. These numbered 106 ± 10 immediately after gut passage and 107 ± 9 after 24 hours. Therefore, the algae ingested by *D. magna* increased in number by 63 ± 6 percent (mean ± standard deviation) during the first 24 hours after gut passage. Primary productivity, measured as the rate of carbon fixation, also increased in *S. schroeteri* cultures enriched with *Daphnia* excretia (*12*). Nutrients excreted by *Daphnia* as algal remains and animal metabolites can, therefore, stimulate primary productivity. These nutrients are presumably available in high concentrations in the *Daphnia* gut. They are taken up and stimulate the division of algae that survive gut passage.

Differential digestion and nutrient enrichment of gelatinous green algae may be important factors determining the growth and seasonal succession of algae in lakes (*3*, *13*). In in situ grazing experiments, *S. schroeteri* numbers increase when the number of grazers is increased (*3*). The *S. schroeteri* are ingested by the dominant grazers, but more than 90 percent of the cells emerge from the grazers' guts intact and in viable condition (*4*). As shown in this study, there can be a 63 percent increase in the number of *S. schroeteri* cells in 24 hours due to gut passage. During the summer when these algae are abundant, they are likely to be ingested one to four times daily (*14*). Under these grazing conditions, the nutrient enrichment during gut passage can more than compensate for the losses of cells and sheath material during grazing and can result in algal population growth.

In many lakes, the spring phytoplankton bloom consists of nongelatinous unicellular algae such as cryptomonads, diatoms, naked green algae, and nannoplankton. These algae have rapid growth rates and bloom by utilizing nutrients supplied during spring turnover. They are easily ingested and assimilated by grazers. As nutrients are depleted and grazer populations increase, these algae decline in number and are replaced by colonial gelatinous green algae, such as *S. schroeteri*, which bloom in the summer when nutrients such as phosphorus and nitrogen are in limiting supply in the water column (*15*). Presumably, these algae rely on grazers as rich localized sources of nutrients. Their loss of some sheath material and cells to the grazers is more than compensated for by the nutrients gained during gut passage. One can easily conceive of this as a nascent symbiosis between aquatic plants and animals. These gelatinous algae are poorly assimilated and are probably of low nutritional value to the grazers, which ultimately decline in numbers. The phytoplankton then shifts to a community dominated by slow-growing inedible forms, such as blue-green algae, which survive under the nutrient-deplete conditions of late summer and early autumn.

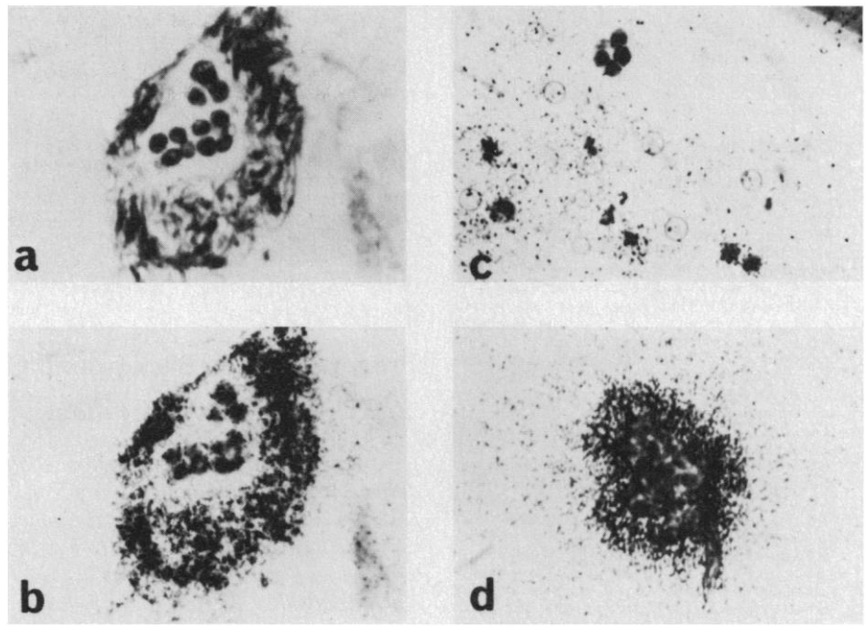

Fig. 1. Microautoradiographs showing uptake and incorporation of ^{33}P by *Sphaerocystis schroeteri* during gut passage through *Daphnia magna*. Sources of phosphorus are digested algal cell remains (a to c) and *Daphnia* metabolites (d). (a) Food bolus in the mandibles of *D. magna* contains gelatinous colonies of spherical *S. schroeteri* cells surrounded by numerous, smaller, spindle-shaped cells of the digestible alga *Ankistrodesmus falcatus* (×200). *Ankistrodesmus falcatus* was labeled with $K_2H^{33}PO_4$ before feeding. (b) Grain density in the emulsion overlying (a) documents the presence of ^{33}P in *A. falcatus* and its uptake by previously unlabeled cells of *S. schroeteri* (×200). (c) Section through the rectum of *D. magna* showing accumulation of ^{33}P in intact *S. schroeteri* cells. The *A. falcatus* cells have been broken up and dispersed. Clear circles are 12-μm plastic beads (×250). (d) Heavy accumulation of ^{33}P by a colony of *S. schroeteri* collected from the feces of a saturation-labeled *D. magna* (×300).

Table 1. Feeding rates (F), assimilation rates (A), and assimilation efficiencies (100 × A/F) of *Daphnia magna* fed *Sphaerocystis schroeteri* and *Chlamydomonas reinhardi*. Rates are expressed as micrograms of algae (dry weight) per animal per hour. *Sphaerocystis schroeteri* is a gelatinous green alga that survives gut passage through *Daphnia* with the loss of some of its cells and sheath. The naked, single cells of the green alga *C. reinhardi* are easily broken up and assimilated by *Daphnia*. Abbreviations: $\bar{X}$, mean; S.E., standard error; and N, number of experiments.

Feeding rate			Assimilation rate			Assimilation efficiency
$\bar{X}$	S.E.	N	$\bar{X}$	S.E.	N	(%)
Sphaerocystis schroeteri						
5.32	0.87	10	1.78	0.21	9	33
Chlamydomonas reinhardi						
13.13	1.99	9	7.90	1.20	7	60

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J. P. Barlow and J. W. Bishop, *Limnol. Oceanogr.* **10** (Suppl.), R15 (19 R. H. Peters and D. R. S. Lean, *ibid.* **18**, 270 (19 R. H. Peters and F. H. Rigler, *ibid.*, p. J. W. Bishop and J. P. Barlow, *ibid.* **20**, 148 (1975); R. H. Peters, *Verh. Int. Ver. Theor. Angew. Limnol.* **19**, 273 (1975); D. R. S. Lean and M. N. Charlton, in *Environmental Biogeochemistry*, J. O. Nriagu, Ed. (Ann Arbor Science Publishers, Ann Arbor, Mich., 1976), pp. 283–294.
6. *Daphnia magna* were cultured in aerated, aged

tap water and fed *Chlamydomonas reinhardi* and *Ankistrodesmus falcatus*, easily assimilated green algae that are natural, high-quality foods of *Daphnia* [D. W. Schindler, *J. Anim. Ecol.* **37**, 369 (19 ➡ F. B. Taub and A. M. Dollar, *Limnol. Oceanogr.* **13**, 607 (19 ➡ D. Arnold, *ibid.* **16**, 906 (1971)]. Algae were cultured axenically in Woods Hole medium [J. Stein, Ed., *Phycological Methods* (Plenum, New York, 1973)] with glycylglycine buffer and without silicate. They were saturation-labeled by adding 20 μc of $NaH^{14}CO_3$ in 1 ml of sterile distilled water to 50 ml of log growth phase culture 2 days before use. Algae were saturation-labeled in the same way with $K_2H^{33}PO_4$ for autoradiographic studies. Experimental feeding suspensions were prepared by centrifuging, washing, and resuspending algae in the appropriate experimental feeding medium at the desired algal concentration. Concentrations were determined as cell counts and dry weight. Feeding and assimilation rate determinations were made adapting procedures of D. W. Schindler (cited above), J. E. Schindler [*J. Anim. Ecol.* **40**, 589 (1971)], and D. Arnold (cited above). Adult *D. magna* were sorted and equivalent-sized animals were acclimated to experimental conditions for 2 hours before use. Samples of *D. magna* (20 to 30) were pipetted into 300-ml bottles filled with aquarium water that had been filtered through 0.45-μm HA Millipore filters; the concentration of ^{14}C-labeled algae was at least 0.1 mg (dry weight) per milliliter. This is well above the incipient limiting concentration at which feeding rates are maximal and are independent of food concentration. Bottles were rotated at 1 rev/min to keep animals and food in suspension. Feeding rates were determined by removing animals after 10 minutes, rinsing for 1 minute in unlabeled algae, and immobilizing them in boiling water. Feeding periods of up to 1 hour, used by previous workers, exceed the gut passage time for most *Daphnia* species. This experimental error yields erroneous, low feeding rates and excessively high calculated assimilation efficiencies. Radioactivity ingested per animal and activity per milliliter of feeding suspension were determined by liquid scintillation (D. Heisey and K. G. Porter, in preparation). Assimilation rates were determined by removing animals after 1 hour and allowing them to clear their guts of radioactive algae for 1 hour in a suspension of unlabeled algae. Radioactivity incorporated and retained in the animals was determined by liquid scintillation. The relation between this net value and absolute assimilation measurements is discussed by W. Lampert [*Verh. Int. Ver. Theor. Angew. Limnol.* **19**, 2913 (1975)]. Assimilation efficiencies were calculated as 100 × (dpm incorporated per animal per hour)/(dpm ingested per animal per hour), where dpm is disintegrations per minute.

7. *Daphnia magna* were fed a suspension of 5×10^3 (12-μm) plastic beads per milliliter for 1 hour to flush their guts. They were then pipetted into 300-ml light or dark bottles of feeding suspension containing 2.5×10^3 cells per milliliter each of labeled *A. falcatus* and unlabeled *S. schroeteri*. One hour of feeding on a rotating plankton wheel (1 rev/min) allowed animals to fill their guts but not produce or reingest significant amounts of feces.
8. Methods were adapted f ➡ G. W. Fuhs and E. Canelli, *Limnol. Oceanogr.* **15**, 962 (1970); M. L. Brock and L. D. Brock, *Mitt. Int. Ver. Theor. Angew. Limnol.* **15**, 1 (1968); H. Rogers, *Techniques of Autoradiography* (Elsevier, Amsterdam, ed. 2, 1973). Kodak NTB-3 emulsion was used. Incubation times for ^{14}C and ^{33}P slides were 32 and 59 days, respectively.
9. B. H. Ketchum, *J. Cell Comp. Physiol.* **13**, 373 (1939); G. P. Fitzgerald, *J. Phycol.* **6**, 239 (1970).
10. *Daphnia magna* were fed saturation-labeled *A. falcatus* for 1 week before use. Their guts were flushed of algal remains (*7*) and they were fed unlabeled, log growth phase *S. schroeteri* (5×10^3 colonies per milliliter) for 1 hour. Animals were then transferred to a suspension of plastic beads to aid in gut evacuation.
11. *Daphnia magna* were fed a suspension of *S. schroeteri*. Feces were collected and streaked onto five sterile plates of 2 percent agar (Difco-Bacto) in distilled water. Five plates of algae from the same culture, but which had not been fed to *D. magna*, were also made. Cells were visually monitored at ×400. Values in the text are the means ± standard deviations for five replicate plates and represent an increase over 24 hours, not the population parameter *r*.
12. Equivalent amounts of *S. schroeteri* in stationary growth phase were placed in five tubes with 10 ml of algal culture medium (*6*) deficient in nitrogen, phosphorus, and vitamins and in five tubes with 10 ml of deficient medium in which *D. magna* swam (two animals per milliliter) for 2 hours before use. To each tube 0.5 μc of $NaH^{14}CO_3$ was added and all the tubes were incubated at 20°C for 2 hours in cool white fluorescent lighting (100 microeinstein m^{-2} sec^{-1}). Carbon-14 fixation rates in deficient and *Daphnia*-enriched medium were 554 ± 124 dpm/ml and 12,596 ± 982 dpm/ml, respectively.
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Properties of the Background Global Aerosol and Their Effects on Climate

Abstract. *Properties of the aerosols above Hawaii, Alaska, and the South Pole are derived from sun photometry at several wavelengths. The mass loading of aerosol material is several milligrams per square meter. At the South Pole the mean particle radius is 0.04 micrometer; at Hawaii in March 1975 there was a thin volcanic layer with a mean particle radius of 0.1 micrometer. The aerosols cause heating of the earth-atmosphere system at the poles and cooling at low latitudes.*

Minute particles suspended in the earth's atmosphere (the atmospheric aerosols) interact with the atmospheric radiation field and potentially can affect climate by increasing or decreasing the radiation that passes into or out of the earth-atmosphere system (*1*). The aerosol influence on the heat balance interests scientists mainly because of the possibility that fluctuations in the aerosol concentrations may be responsible for climatic changes. For instance, there is evidence of a correlation between dust layers found in ice cores and the temperature (as determined from oxygen isotopic analyses) at the time the layers were deposited, with dusty periods corresponding to lower temperatures (*2*).

The earth's aerosol load is known to undergo natural variations due to occasional injections of ash and gas into the stratosphere by volcanic eruptions (*3*) and to variations in surface sources, such as changes in vegetation or changes in the size of desert areas. Of particular interest, however, is the possibility that the global aerosol load is also significantly altered by human activity, with effects ranging from pollution of the stratosphere by supersonic transports to industrial process pollution. In view of this, it is important to establish a quantitative measure of so-called baseline data on aerosols to use as a reference against which future changes can be gauged.

In this report I discuss the background aerosol parameters at the Mauna Loa Observatory (MLO), Hawaii, and the South Pole, as derived from precision multiwavelength measurements of the total vertical optical atmospheric transmission made by using the sun as a standard source of irradiance over the wavelength interval $400 < \lambda < 1000$ nm. The measurements were made at the South Pole in December 1974 and at MLO in March 1975. In addition, selected data acquired in Alaska are discussed.

The total vertical optical extinction of sunlight in the earth's atmosphere is conveniently expressed in terms of an optical depth, τ_T, and is due to molecular or Rayleigh scattering, τ_R; gaseous absorption, τ_G, and scattering and absorption by the atmospheric aerosols, τ_A. The latter term is of interest here and was derived by subtracting tabulated values of τ_R and values of $\tau_G = \tau O_3 + \tau NO_2$ (*4*, *5*).

The aerosol optical depth curves (aerosol extinction spectra) as a function of wavelength were used to derive aerosol parameters by referring to curves calculated from Mie theory, assuming that the aerosols (i) are spherical with an index of refraction $n = 1.5 + i0.002$ and (ii) are distributed by size according to a modified gamma size distribution function defined by the relationship $dn/dr = a\,r^2e^{-br}$, where dn/dr is the number density of aerosol particles and r is the particle radius (*6*). With appropriate values chosen for the coefficients a and b, the modified gamma size distribution function defined by the relationship $dn/dr = a\,r^2e^{-br}$, where dn/dr is the number density of aerosol particles and r is the particle radius (*6*). With appropriate values chosen for the coefficients a and b, the modified gamma distribution function can closely simulate actual tropospheric or stratospheric aerosol size distributions derived from direct sampling techniques. Although the fit of the modified gamma distribution function may not always be perfect, when a and b are properly cho-