10. T. M. Donahue, personal communication.
11. V. A. Krasnopolsky and V. A. Parshev, *Kosm. Issled.* **17**, 763 (1979).
12. V. L. Barsukov, I. L. Khodakovsky, V. P. Volkov, K. P. Florensky, *Space Res.* **20**, 197 (1980).
13. R. G. Knollenberg and D. M. Hunten, *J. Geophys. Res.* **85**, 8039 (1980).
14. P. Connes, J. Connes, W. S. Benedict, L. D. Kaplan, *Astrophys. J.* **147**, 1230 (1967); L. D. G. Young, *Icarus* **17**, 632 (1972).
15. V. I. Oyama, G. C. Carle, F. Woeller, *Science* **208**, 399 (1980).
16. J. S. Lewis and F. A. Kreimendahl, *Icarus* **42**, 330 (1980).
17. I. L. Khodakovsky, V. P. Volkov, Yu. I. Sidorov, V. A. Dorofeeva, M. V. Borisov, *Geokhimiya* **1979** (No. 12), 1747 (1979).
18. A. P. Vinogradov, Yu. A. Surkov, F. F. Kirnozov, *Icarus* **20**, 253 (1973); Yu. A. Surkov, F. F. Kirnozov, V. M. Glazov, G. A. Feodoseyev, *Space Res.* **17**, 659 (1976).
19. S. Nozette and J. S. Lewis, *Science* **216**, 181 (1982).
20. The calculations follow the method of Lewis and Kreimendahl (*16*). Thermodynamic data are from *JANAF Thermochemical Tables* (National Bureau of Standards, Washington, D.C., 1971); R. Robie, B. S. Hemingway, J. R. Fisher, *U.S. Geol. Surv. Bull. 1452* (1979); K. C. Mills, *Thermodynamic Data for Inorganic Sulphides, Selenides and Tellurides* (Butterworth, London, 1974); G. K. Johnson, G. N. Papatheodorou, C. E. Johnson, *J. Chem. Thermodyn.* **13**, 745 (1981); *ibid.* **12**, 545 (1980); D. D. Wagman, W. H. Evans, V. B. Parker, R. H. Schumm, R. L. Nuttall, *Natl. Bur. Stand. (U.S.) Tech. Note 270-8* (1981); and references listed in B. Fegley and J. S. Lewis, *Icarus* **38**, 166 (1979).
21. The pressure, temperature, composition conditions assumed in these calculations are 95 bars total pressure, 750 K surface temperature, $P_{O_2} = 10^{-22.5}$ bar, $P_{HCl} = 10^{-4.0}$ bar, $P_{S_2} = 10^{-4.0}$ bar, and $P_{HF} = 10^{-5.2}$ bar.
22. Other As- and Sb-bearing gases included in the calculations but not abundant enough to be graphed are As, AsO, AsH_3, AsF, AsF_2, AsF_3, AsF_5, AsCl, $AsCl_2$, $AsCl_3$, Sb, SbO, SbH_3, SbN, and SbF_3. The solid and liquid arsenic oxides As_2O_4, As_2O_5, and As_4O_6 are unstable and do not precipitate as pure condensates on the surface of Venus. Formation of more complex minerals, such as As-bearing apatites and complex Sb oxides, for which thermodynamic data are unavailable, may result in lower gas phase abundances for As and Sb. Thus our results are firm upper limits.
23. We thank the Planetary Atmospheres and Planetary Geophysics and Geochemistry (NGR-22-007-269 to A. G. W. Cameron) program offices of NASA for support of this work through grants to J. S. Lewis Associates, Inc., and to A. G. W. Cameron, Harvard College Observatory. We thank G. K. Johnson for providing his Sb_2S_3 data before publication. B.F. also thanks A. G. W. Cameron for support and facilities.

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The Role of Surface Chemistry in Filter Feeding by Zooplankton

Abstract. *Surface chemistry of both particles and animals is important in filter feeding at low Reynolds number.* Daphnia magna, *fed mixtures of three sizes of polystyrene particles, retained particles that were smaller than the mesh size of the animals (1.0 micrometer) at greater efficiencies than predicted by a sieving model. Retention efficiency of the smallest particles (0.5 micrometer) was increased when negative surface charge on the particles was neutralized, and retention was decreased when a nonionic surfactant was added to reduce wettability.*

Filter feeding is the dominant process of primary consumption in freshwater and marine environments. It is often described as sieving, in which particles too large to pass through an animal's filtering mesh are captured. Capture efficiency of various sized particles is thought to be related to the array of mesh sizes on the filtering appendages (*1*); however, it appears that sieving is not the mechanism by which fine particles are captured by small filter feeders. Films of copepod feeding show little or no movement of water through the filtering meshes (*2*). Brittle stars are able to catch particles smaller than the spaces between their mucus-covered tube feet, and the surface charge on particles determines their affinity for retention (*3*). Our observations of *Daphnia* indicate that the majority of water movement is over, not through, the meshes of the filtering combs. Also, there is no evidence of mucus enhancement of filtering in *Daphnia* (*4*).

We report that particle capture in these animals occurs at low Reynolds number (Re), is not a sieving process, and is strongly influenced by surface chemistry, such as surface charge and wettability of the particles. The findings suggest that differential or selective feeding on natural particles may occur on the basis of surface properties of the particles, as well as on their size and shape. This can explain the ability of filter feeders to capture ultrafine particles such as bacteria, clays, and colloids that are much smaller than the minimum mesh size of the filtering appendages.

Filter feeding by small invertebrates occurs at low Re, where fluid flow is slow and laminar and all motion is dominated by viscous rather than inertial forces (*2*, *5*). The Re for the filtering combs on the third and fourth appendages of *Daphnia magna* (Fig. 1, A to C) is in the range 0.4 to 2.0; for a single seta it is 10^{-2} to 10^{-3}; and for a single setule it is 10^{-3} to 10^{-4} (*6*). The boundary layer, or the region of reduced flow around a single setule, extends approximately 10 μm under these conditions, which is far beyond the next setule (*7*). Therefore, little or no flow occurs between setules, and the appendage functions as a solid wall, analogous to the hirsute wings of small insects (*8*). Observations of a scaled-up model of a *Daphnia* appendage, made with 110-μm mesh plankton netting oscillated in glycerin, support this since no fluid was observed to pass through the mesh of the model (*9*).

A capture mechanism that may function under these conditions is electrostatic or ionic attraction. It operates over shorter distances in water than in air but nevertheless can be important in particle capture and retention, especially in slow laminar flow regimes (*10*). We expand and redefine this mechanism to include all surface chemical interactions between particle and filter, such as ionic or hydrophobic-hydrophilic interactions.

We tested the sieving model and the role of surface chemistry in filtering by feeding suspensions of polystyrene

Table 1. Relative ingestion of three particle sizes of unmodified polystyrene by *Daphnia magna*. Particles were presented at equal densities by volume, with total densities similar to those found in nature (10^4 cm^{-3} for alga-sized particles and 10^6 to 10^7 cm^{-3} for bacteria-sized particles). Data reported are proportions transformed with an arcsin–square root transformation, and are thus shown as degrees. Numbers in parentheses are percent feeding efficiencies expressed as the ratio of observed to expected proportions of the 0.5-μm particles. Relative ingestion of all three particle sizes were compared by *t*-tests adjusted for multiple comparisons (*12*). Expected proportions, based on concentrations in feeding suspensions (*11*), were compared with the control test (treatment 1). Deionized (0.5-μm particles) and surfactant treatments (treatments 2 and 3, respectively) were compared to the control treatment. In all treatments where *t* was significant, 0.5-μm particles were ingested in a significantly lower proportion than expected. When 0.5-μm particles were dropped from the analysis and proportions of the larger particles were recalculated, no statistically significant differences were observed in the relative ingestion of 1.1- and 5.7-μm particles, indicating that both of the larger particles were collected in the same proportions at which they were present in suspension.

Particle size (μm)	Concentration in suspension (No./cm^3)	Expected proportion (degrees)	Proportion in gut (degrees)		
			Treatment 1 (*N* = 9)	Treatment 2 (*N* = 9)	Treatment 3 (*N* = 9)
5.7	10^4	8.6	18.0*	16.8	20.4
1.1	1.4×10^6	16.8	34.6†	39.6	43.4†
0.5	1.5×10^7	71.0	49.2† (64)	45.4 (51)	39.1* (44)

*$P < .05$. †$P < .005$.

0036-8075/82/0611-1225$01.00/0

Table 2. Relative ingestion of three particle sizes by *Daphnia magna*, with 0.5-μm particles amide modified. Data reported are as described in the legend to Table 1. Treatment 4 is the control, and treatment 5 has surfactant added.

Particle size (μm)	Concentration in suspension (No./cm^3)	Expected proportion (degrees)	Proportion in gut (degrees)	
			Treatment 4 (N = 8)	Treatment 5 (N = 10)
5.7	10^4	9.4	9.7	19.8
1.1	1.4×10^6	18.4	18.4	28.5*
0.5	1.2×10^7	69.2	68.9 (100)	51.8† (71)

*$P < .05$. †$P < .01$.

spheres to *D. magna*. The sieving model predicts that all particles smaller than the mesh size of 1.0 μm (range 0.85 to 1.25 μm) will pass through the filter. Other interception models predict that some small particles will be captured. Three sizes of polystyrene spheres [0.5, 1.1, and 5.7 μm in diameter (Fig. 1D)] were used, the diameter of the smallest being about one-half the average intersetular opening. Animals were allowed to feed for 30 minutes, killed, and the ingested particles in their guts were counted (*11*). Equal volume (and weight) concentrations of particles were used at total abundances similar to those of alga- and bacteria-sized particles in nature (Table 1). The abundance of each size class of particle in the gut was compared with that in the feeding suspension (treatment 1, Table 1) (*12*). Results show that the 0.5-μm particles were collected in a lower proportion (64 percent) than that present in suspension and, therefore, at a lower efficiency than either of the larger particles. When the smallest size class was dropped from analysis, the two larger size classes were shown to be ingested in the same proportions at which they were present in suspension.

These results confirm what we know from other feeding studies (*13*). Natural bacteria, usually 0.1 to 1.0 μm in diameter, are collected by *Daphnia* at about 30 to 60 percent of the efficiency of algae that are 2 to 5 μm or larger, and colloidal organic matter can be collected and used as food if it is present in high concentrations.

These results allow us to reject the sieving model and consider the other filtration mechanisms. Since there was no detectable difference in the animals' capture efficiency on the two larger particle sizes (1.1 and 5.7 μm), we changed the surface characteristics of only the smallest particles. The polystyrene spheres we used have a net negative charge due to attached SO_4^- groups and adsorbed SO_4^{2-} ions on the surfaces (*14*). Adsorbed SO_4^{2-} ions were removed with ion exchange resins (treatment 2, Table 1), and attached SO_4^- groups were replaced with amide groups to neutralize the charge (treatments 4 and 5, Table 2) (*14*). In treatments 3 and 5 we added small amounts of a nonionic surfactant to the feeding suspension (*15*).

Removal of adsorbed SO_4^{2-} ions by ion exchange (treatment 2, Table 1) did not significantly change uptake efficiency (51 percent) of the 0.5-μm particles, probably because the charge density was not sufficiently reduced owing to the

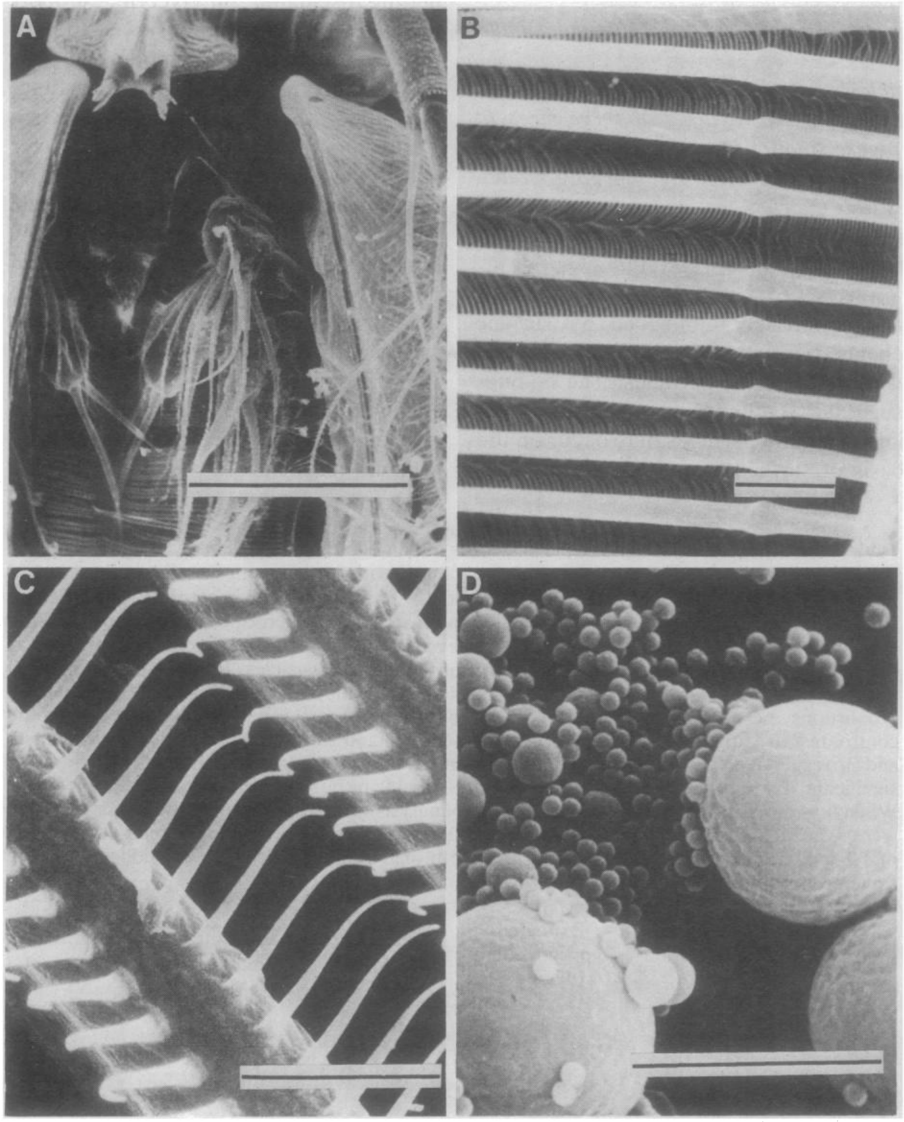

Fig. 1. The filtering chamber of *Daphnia magna* (A) showing the rostrum, labrum, first and second thoracic limbs, and filtering combs on the third limb (scale bar, 100 μm). (B) A view from behind the comb on the third appendage showing knuckle-like reinforcements near the base of the setae and the continuous and even distribution of setules (scale bar, 10 μm). Setules are arranged at angles on the setae (C) so that no gaps occur on the inward stroke of the filtering comb (scale bar, 5 μm). Setules have an average diameter of 0.4 μm, and intersetular openings range from 0.85 μm near the base to 1.25 μm at the tip. These dimensions are constant over the filtering comb. On the basis of Re, the boundary layer around a single setule was estimated to extend beyond the next six setules, suggesting that the appendage is effectively a solid wall allowing little or no flow of water through the comb. (D) A mixture of polystyrene beads (5.7, 1.1, and 0.5 μm) used in feeding efficiency experiments (scale bar, 5 μm). Beads are clumped in the micrograph because of drying for scanning electron microscopy but are dispersed and separate during the feeding experiments. [Micrographs by Y. Feig]

remaining, bound SO_4^- groups. Amide-modified 0.5-μm particles were ingested in the same proportion (100 percent efficiency) at which they were in suspension (treatment 4, Table 2), in contrast to the 0.5-μm unmodified polystyrene particles (treatment 1, Table 1). Addition of a surfactant caused a statistically significant reduction in capture efficiency of 0.5-μm unmodified particles (treatment 3, Table 1) to 44 percent and of amide-modified particles (treatment 5, Table 2) to 71 percent. These experiments indicate that capture efficiencies of the smallest particles can be affected by changing surface charge of the particles and by changing wettability. Neutral particles were captured more readily than particles with a net negative charge, and addition of a surfactant, which increases the wettability of both particles and animals, caused more particles to escape the filtering apparatus of the *Daphnia*.

Differential particle capture on the basis of charge and wettability has general significance for freshwater and marine filter feeding. Natural particles have a range of surface properties that affect their adsorption to surfaces and movement through fluids (*16*). Anomalous selective feeding by zooplankton may be explained on the basis of surface chemistry, in that the animals' filtering appendages may have had greater affinities for some particles than for others (*17*). Selective filter feeding by copepods (*18*) may in fact be due to surface chemistry interactions rather than size selection or taste selection. Surface charge is affected by *p*H (*16*), so we may expect that environments with extreme *p*H values will affect filter-feeding capabilities of small invertebrates. The elimination of certain zooplankton species from systems with elevated *p*H due to high rates of photosynthesis, or lowered *p*H due to dissolved humic substances or acid rain (*19*), may be due to a reduced ability of certain species to capture food as well as other effects mediated by *p*H. Finally, we may expect surface adaptations of filter-feeding animals and their prey to enhance or reduce particle capture. An example of this might be the nonwettability of the exoskeleton of cladocerans, which frequently imprison small individuals in the surface tension of the water, but may aid in particle capture. The interactions between surface chemistry and feeding may change some of our models in aquatic ecology.

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References and Notes

1. M. Anraku and M. Omori, *Limnol. Oceanogr.* **8**, 116 (1963); P. Nival and S. Nival, *ibid.* **21**, 24 (1976); C. Boyd, *ibid.*, p. 175.
2. M. A. R. Koehl and J. R. Strickler, *ibid.* **26**, 1062 (1981).
3. M. LaBarbera, *Science* **201**, 1147 (1978).
4. Films of *D. magna* feeding show that particles flow across the surface of the third filtering appendage and are intercepted in the distal region of the filtering comb near the body wall. Particles then begin to move with the filtering appendages. Examination by scanning electron microscopy showed no evidence of mucus or mucus pores on the appendages or in the region of the food groove.
5. E. M. Purcell, *Am. J. Phys.* **45**, 3 (1977); R. E. Zaret, in *Ecology and Evolution of Zooplankton Communities*, W. C. Kerfoot, Ed. (University Press of New England, Hanover, N.H., 1980), p. 3. $\mathrm{Re} = \rho(ua/\mu)$, where ρ is fluid density, μ is viscosity, u is speed of flow, and a is the length of the object [G. K. Batchelor, *An Introduction to Fluid Dynamics* (Cambridge Univ. Press, Cambridge, 1970)].
6. Re's were calculated from appendage beat rates of 3 to 6 Hz (K. G. Porter, J. Gerritsen, J. D. Orcutt, Jr., *Limnol. Oceanogr.*, in press), appendage length 0.5 mm, width 0.25 mm, setal diameter 3.5 μm, and setular diameter 0.4 μm, with distance of appendage movement equal to an arc of 60°.
7. At low Re the magnitude of the boundary layer is $d/\sqrt{\mathrm{Re}}$ (*8*), where d is the diameter of the setule.
8. C. P. Ellington, in *Swimming and Flying in Nature*, T. Y. T. Wu, C. J. Brokaw, C. Brennan, Eds. (Plenum, New York, 1975), p. 783.
9. The model was oscillated with dye on one side to observe the flow. Re of both model and *Daphnia* appendage were approximately the same, allowing comparison under the principle of dynamic similarity (*5*).
10. L. A. Spielman, *Annu. Rev. Fluid Mech.* **9**, 297 (1977); D. I. Rubenstein and M. A. R. Koehl, *Am. Nat.* **111**, 981 (1977). Sieving is a special case of direct interception, where particles impinge on two adjacent fibers. Inertial impaction of particles on the fibers can be ruled out for fine particle feeding because of the negligible inertia of small particles at low Re. Brownian (random) diffusion and gravitational deposition result in a longer path length of a particle through a filter, thus increasing the probability of encountering a fiber. To be effective, these mechanisms require a long transit time in the filter apparatus and are therefore probably negligible in zooplankton filter feeding.
11. Healthy adult animals (> 2 mm) were starved in particle-free water for 24 hours before the experiments. Particle suspensions were in equal concentrations by particle volume (Tables 1 and 2). Concentrations were verified by microscopical counts of stock suspensions followed by dilution to the required concentration. Animals ($N = 25$) were placed in 125 ml of feeding suspension on a revolving plankton wheel (1 rev/min) to prevent settling. Animals were sieved, washed in particle-free water, anesthetized in CO_2, and preserved in formaldehyde. Guts of eight to ten animals were dissected on slides and relative abundances of particles determined from at least ten nested subsamples, where 5.7-μm particles were counted at 160× magnification, and smaller particles were counted at 1000× with Nomarski interference contrast. Accuracy was verified with a focal-plane micrometer. Expected proportions of particles were calculated from the known concentrations in suspension and the known relative magnification.
12. Proportions of each size class present in the gut of each animal were transformed (arcsin–square root) to degrees for comparison to expected proportions. The probability levels for the multiple comparisons by *t*-tests, were controlled at the α level by use of α/k, where k is the number of comparisons. In Tables 1 and Table 2 $k = 3$. The 0.5-μm size class was then dropped from analysis, proportions of the larger particles were recalculated, retransformed, and analyzed with a *t*-test to determine if there was any difference in relative ingestion, independent of the smallest particles.
13. B. J. Peterson, J. E. Hobbie, J. F. Haney, *Limnol. Oceanogr.* **23**, 1039 (1978); S. S. Gellis and G. L. Clark, *Physiol. Zool.* **8**, 127 (1935).
14. H. J. van der Hul and J. W. Vanderhoff, *Br. Polym. J.* **2**, 121 (1970). All particles were from Dow Diagnostics.
15. Tween-20 (Fisher Chemical).
16. K. C. Marshall, *Interfaces in Microbial Ecology* (Harvard Univ. Press, Cambridge, Mass., 1976); R. R. P. Chase, *Limnol. Oceanogr.* **24**, 417 (1979).
17. *Daphnia* ingest more algae than equivalent-sized glass beads [A. M. Gliwicz, *Ekol. Pol. Ser. A* **17**, 663 (1969)]. Glass is wettable and may have less affinity for the filtering appendages. Bimodal feeding selectivity of *Daphnia* [M. S. Berman and S. Richman, *Limnol. Oceanogr.* **19**, 105 (1974)] is unlikely given our observations of *Daphnia* behavior [see (*6*)] but may be due to low affinity for intermediate-sized particles in the experiment.
18. S. A. Poulet and P. Marsot, *Science* **200**, 1403 (1978).
19. R. L. Kring and W. J. O'Brien, *Limnol. Oceanogr.* **21**, 313 (1976); W. G. Sprules, in *Ecology and Evolution of Zooplankton Communities*, W. C. Kerfoot, Ed. (University Press of New England, Hanover, N.H., 1980), p. 657.
20. We thank Y. Feig and A. Hooten for valuable assistance. J. Reeves and an anonymous referee provided statistical advice. Supported by NSF grants DEB 80-05582 and DEB 79-22633. Publication No. 9 of the Lake Oglethorpe Limnological Association.

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Deep Oxygenated Ground Water: Anomaly or Common Occurrence?

Abstract. *Contrary to the prevailing notion that oxygen-depleting reactions in the soil zone and in the aquifer rapidly reduce the dissolved oxygen content of recharge water to detection limits, 2 to 8 milligrams per liter of dissolved oxygen is present in water from a variety of deep (100 to 1000 meters) aquifers in Nevada, Arizona, and the hot springs of the folded Appalachians and Arkansas. Most of the waters sampled are several thousand to more than 10,000 years old, and some are 80 kilometers from their point of recharge.*

The geochemical and hydrogeologic literature provides a broad spectrum of notions regarding the occurrence of dissolved oxygen (DO) in ground water. The views range from the idea that DO is absent below the water table (*1*, *2*) to the idea that DO is purportedly generated by the radiolysis of water at depths of 2 to 3 km (*3*). The prevailing opinion (*1*, *4*, *5*) is that the bulk of DO in recharge water is consumed in the soil and unsaturated (or vadose) zones by microbial respiration and the decomposition of organic matter, or rapidly thereafter in the aquifer by various mineral-water and organic oxidative reactions. Despite the multitude of studies of ground-water geochemistry in the last decade, measurements of DO in