Microscale Patchiness of Nutrients in Plankton Communities

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Abstract. Autoradiography was used to identify the presence of nutrient patches produced by zooplankton. Algal cells which encounter patches of phosphorus-33 released by swimming animals accumulate more label than cells that do not enter the patches. Differential labeling of algae does not occur when turbulence in the fluid is increased by stirring. Nutrient patchiness at the scale of millimeters or less in nature probably influences the course of competition and coexistence among the phytoplankton.

Phytoplankton in lakes and oceans probably experience nutrient environments that are variable at small scales. Differences in competitive success among species of algae may depend in part on their relative abilities to profit from brief encounters with nutrient-rich patches produced by zooplankton. This view complements those about species structure and population dynamics of phytoplankton communities that have been extrapolated from results of continuous algal culture (1). Suggestions that competition in nature is mimicked in culture systems (2) rely on the assumption that environmental concentrations are homogeneous, like those of well-mixed cultures.

Because inorganic phosphorus in fresh waters and inorganic nitrogen in ocean waters are often undetectable by conventional means (3), it may seem reasonable that populations succeed through their relative abilities to obtain limiting nutrients from constant near-zero concentrations as they do in continuous algal cultures. Heterogeneity in supplies of limiting nutrients, however, can theoretically lead to changes in the biotic fabric of plankton communities, and some laboratory studies have shown this (4).

A crucial question is whether or not the requisite patchiness occurs in nature. The answer depends in part on the identification and importance of patch-generating processes. That swimming zooplankton might create nutrient micropatches of crucial importance to oceanic phytoplankton has been suggested (5) and subsequently attacked on the ground that dispersion is too rapid at small scales for the proposed mechanisms to work (6). Some investigators state that microzones could not supply the nutrient requirements of phytoplankton (7). Our work on lakes Washington and Ontario has shown that nutrients released from crustacean zooplankton through eggestion and excretion provide the major share of those used by phytoplankton during summer months (8). We now report that phytoplankton obtain some nutrients from micropatches.

To determine whether algal benefit from zones of nutrient enrichment near animals, we prepared adult females (2 mm long) of the freshwater cladoceran *Daphnia pulex* by feeding them heavily labeled cells of the green alga *Ankistrodesmus falcatus* for 2 days to achieve body burdens of about 5 μCi of 32P. The animals were well rinsed in cell-free nonradioactive medium, and groups of ten were transferred by pipette to two experimental vessels, each of which contained 10^5 cells per milliliter of *Chlamydomonas reinhardtii* in 300 ml. The *Chlamydomonas* had been suspended for 2 days before the experiments in culture medium free of added phosphorus so that their cellular reserves of phosphorus were reduced (9).

One experimental vessel was mixed with a magnetic stirring bar (300 rev/min) separated from the animals by Nitek netting to avoid injury to them. The second vessel was not stirred. Although they were not injured, the animals that were stirred released phosphorus somewhat faster than those in the unstirred treatment, as judged by liquid scintillation counts and autoradiographic analyses. In low light (0.169 μE m⁻² sec⁻¹, 400 to 700 nm) the animals swam throughout the volume of both vessels.

A third vessel containing algae but no animals was mixed vigorously (670 rev/min), and at intervals of 2 minutes we injected 10 μl of sterile water containing 0.01 μCi of 32P and 0.1 n mole of PO₄. We calculated these additions to match expected release rates from the animals, which were determined from preliminary experiments. Dye studies had shown that the mixing was sufficient to disperse added substances almost instantly.

After 30 minutes the contents of the vessels were poured through Nitex sieves, which retained the animals, into beakers containing 1 ml of acid Lugol's preservative. The duration of the experiment was set to ensure, on the basis of theoretical expectations and preliminary experiments, that fewer than 20 percent of the algal cells in the unstirred vessel would encounter nutrient patches produced by the animals. The interval was also short enough so that no eggestion of intact cells of *Chlamydomonas* could be detected. Samples of 1 ml were drawn immediately through 0.45-μm Millipore filters which were then prepared for track autoradiography. We used Kodak NTB-3 emulsion and recorded tracks as five or more silver grains along a trajectory. The tracks record the paths taken by individual β particles emitted from decaying 32P nuclei.

Frequency distributions of observed β tracks per cell (Table 1) suggest that all cells were equally labeled in the two mixed vessels (treatments 1 and 3) and that the amount of 32P per cell was variable in the unstirred vessel (treatment 2).
ment 2). Because the tracks represent individual events of radionuclide decay, a Poisson distribution of tracks per cell is expected if all the cells contain an identical amount of radioisotope. Treatments 1 and 3 follow the Poisson model. The observed distribution of β tracks in treatment 2, however, differs indisputably from a Poisson distribution (P = 10⁻⁷). There are more cells with no tracks as well as with two or three tracks than can be matched by a Poisson distribution (1). This finding suggests that the algal cells became labeled differentially while they were in the presence of the radioactive animals. Most cells were weakly labeled but a few apparently encountered patches enriched with 32P were released by the swimming animals. Without artificial stirring the patches persisted long enough for the algal cells to exploit them. When the solution was stirred, all cells were labeled equally, indicating that the patches can be dispersed fast enough by artificial stirring to make the isotope equally available to all cells.

The results from the track autoradiography were corroborated by independent experiments in which a thin emulsion layer of Kodak NTB-2 nuclear emulsion was used and grain distributions constructed. In this case the model distribution tested was not Poisson but Neyman's type A (11). The distribution of tracks or grains matched that of the respective model for stirred treatments but was more skewed than the model in unstirred treatments.

The unstirred treatments we used are more representative of natural communities than the stirred treatments. When turbulent energy spectra, length scales of diffusivity, and the characteristics of fluid flow around microzooplankton are considered the prominent mechanism of dispersion in lakes and the open ocean at scales of a millimeter or less arises from molecular processes (12). Microcinematography has shown that the fluid environment around feeding Daphnia and both marine and freshwater copepods is viscous (13). Our results show that nutrient patches produced by zooplankton exist long enough for algae which encounter them to absorb more nutrient than do algae outside the patches. Using estimates of swimming speed and phosphorus release for Daphnia (14), we calculated characteristics of the nutrient micropatches produced by the animals. As judged by their uptake physiology, the Chlamydomonas can augment their cell quota by as much as 12 percent per encounter. Such circumstances place a premium on the maximal rates at which


9. At the end of 2 days in phosphorus-deficient medium the Chlamydomonas contained 3.4 × 10⁻¹³ mol of phosphorus per cell and maximum uptake rates had increased to 9.5 × 10⁻¹² mol of phosphorus per cell per minute. The cells were 6 mm in diameter.

10. Chemical standards of the species were used to detect our observed frequencies against the Poisson distribution with a mean equal to that estimated from the observations and 3 degrees of freedom. The difficulty of discerning many individual 32P tracks derived from a single cell of Chlamydomonas required that exposure times be kept short enough so that probabilities of finding more than four tracks per cell would be negligible.

11. N. L. Johnson and S. Kotz, Discrete Distributions (Houghton Mifflin, Boston, 1969), p. 216. Stirred treatments conformed to Neyman's distribution (P < 0.05), but the unstirred treatment did not (P < 0.01).

12. Observed power spectra for physical and biological properties demonstrate that the effects of large-scale physical forces dissipate effectively during the cascade to scales on the order of meters (T. M. Power, P. J. Richardson, T. M. Dillon, B. A. Agee, B. J. Doiner, D. A. Godden, L. O. Myrup, Science 189, 1088 (1975); R. L. Desman and T. Platt, J. Mar. Res. 34, 295 (1976)). Temperature microstructure in open waters suggests that diffusive fluxes at scales of centimeters are low (M. C. Gregg, C. S. Cox, P. W. Hackett, J. Phys. Oceanogr. 3, 458 (1973)). Microstructure at large scales is not expected to result in turbulence on scales of millimeters. Turbulence is also not likely to be generated at that scale by swimming microzooplankton because flow will be laminar, as suggested by the low Reynolds numbers (C. Kerfoot, D. C. Kelly, J. R. Strickler, in Evolution and Ecology of Zooplankton Communities, W. C. Kerfoot, Ed. (University Press of New England, Hanover, N.H., 1980), p. 10) and by drag characteristics (J. T. Lehman, Limnol. Oceanogr. 23, 170 (1977)).


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