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## Measuring the ecological significance of microscale nutrient patches

Now that we know algae can exploit miniature patches of nutrients produced by zooplankton (Lehman and Scavia 1982a,b), the next, even more interesting challenge is to measure the ecological significance of the phenomenon in nature. Is it an important addition to the known suite of factors that governs population dynamics and community structure? As Lehman (in press) has argued: "Empirical approaches are needed because present theoretical models are unsatisfactory. It is inappropriate to calculate encounters between algae and animals strictly from swimming velocities," as Strickler (1982) has also shown so clearly.

Most of our work will be described in print elsewhere but we can report here what is already published or in preparation. The

first communications have evidently aroused some interest (Currie 1984). Our original inquiries about presence or absence of microscale nutrient patches were motivated by straightforward calculations of mass balance. We recognized that during summer months in both Lake Ontario and Lake Washington most of the P and N used by phytoplankton was regenerated in situ by zooplankton (Scavia 1979; Lehman 1980). The observation is obviously a general one for marine and freshwater alike (Harrison 1980; Perry and Eppley 1981). Zooplankton can be a major source of nutrition, but the mechanism of supply is something else. McCarthy and Goldman (1979) asserted that small nutrient patches *might* exist, but they were greeted with much

skepticism (Jackson 1980; Williams and Muir 1981). When skepticism arises from calculations using models that stand on many untried assumptions it potentially confuses more than enlightens. The problem developed some appeal for us when we heard from proponents and detractors alike that determining the existence or exploitation of ephemeral micropatches would be "impossible," but happily that position never reached the presses.

We presented what we called a "nutrient plume model" as a first step in conceptual development and interpretation of data (Lehman and Scavia 1982*b*). However we pointed out (p. 5004) that "Although the model . . . is appealing because of its mechanistic details, it ignores important features of zooplankton behavior." That reservation is important and has been echoed repeatedly (Lehman 1982, in press). Simplistic models like that one are principally heuristic, because they can enlighten readers about basic principles. The problem with them is that uncritical or incomplete reading can lead to misunderstanding and ill-founded exercises (e.g. Currie 1984).

On the basis of swimming speeds, animal abundances, experiment duration, treatment volumes, and our initial guesses about plume cross sections, we figured that about 5% of the algae would have (and survive) encounters in our experiments. Currie's (1984) calculations do not carry the reasoning as far, but they are on the track to the same results. Data later showed that the proportion was closer to 40%. The difference is precisely the reason for our (better) "simple encounter model" (Lehman and Scavia 1982*b*) and for an interesting avenue of research pursued subsequently by J. Davis, a student at the University of Michigan. Using a long-focal-length, dark-field filming technique designed for us by J. R. Strickler, Scavia and Davis (in prep.) quantified encounters of *Chlamydomonas* with feeding *Daphnia*. Many algal cells are directed inside the carapace, only to be shunted along the body surface to the posterior. Strickler in fact called our attention to the phenomenon, which occurs both above and below the incipient limiting concentration for ingestion by the animals. On the basis of particle-balance measurements, about 40%

of the *Chlamydomonas* cells entrained in the feeding currents are released again.

The concentration regimes experienced by these cells and the actual encounter scenario are outside our biologically naive "nutrient plume model" but are congruent with our "simple encounter model." The results render Currie's (1984) approach irrelevant and confirm the suspicions that led us beyond that line of reasoning in our original work. It is evidently possible to make measurements of the nutrients acquired by these cells. This way the nutritional benefit from an encounter can be measured rather than guessed.

Another concern about the relevance of nutrient patches in nature, which is still sometimes argued (e.g. Currie 1984), is the notion that even at 5 nM or less algae can always get plenty of  $\text{PO}_4^{3-}$ . When investigators cite a background phosphate concentration determined by Rigler's (1966) bioassay technique, they cite the value which by the nature of the analysis is a steady state one. Net uptake is zero. The arguments are published elsewhere (Lehman and Sandgren 1982; Lehman in press; Lean and White 1983). Only increases above the equilibrium value provide nutrients for growth. This is important ecologically because the difference between *some* net uptake of limiting nutrient and *no* net uptake is easy to comprehend.

As Tilman (1980) and Lehman (1982) have argued, effects of nutrient patches are most likely to be measured in terms of species composition. When nutrients are supplied artificially in patches, rather than uniformly, the application technique controls the species composition of Lake Michigan plankton assemblages (Scavia et al. in prep.). Moreover, when continuous and semicontinuous unialgal cultures were maintained on patchy and uniform nutrient regimes at the same dilution rate, the steady state patch-driven populations had, on average, less P per cell than their nonpatchy controls. Thus, the effect on individuals demonstrated by Lehman and Scavia (1982*a*) carries over to the physiology of the population. Algae that inhabit lakes where nutrients released from zooplankton are their mainstay exhibit extraordinary kinetic abilities. The *Chlamydomonas* we used in

our patch experiments could double its cell quota of P in about 30 min. But Lehman and Sandgren (1982) found algae in Third Sister Lake, Michigan, that could double their quotas in <2 min when given a pulse of phosphate.

Measuring patch effects is admittedly harder in nature than in the laboratory. But thoughtful experiments and interpretations must still provide the metric. One promising line of inquiry at present is the characteristic spectra of X-rays emitted from radiated individual algal cells. Frequency distributions of P·cell<sup>-1</sup> in natural populations have been measured by this method (Lehman in prep.). To evaluate the significance of microscale patchiness it is necessary to choose times when mass balance studies show that most algal P comes from zooplankton. The matter is moot otherwise because unless algae rely on those nutrient sources, searching for the significance of micropatches would be silly.

We emphasize that just because patches exist, it does not follow that algae grow rapidly (as urged by Goldman et al. 1979). Productivity could in fact be less in patchy than in uniform conditions (Lehman 1982). The environmental circumstances are not a matter of choice, but rather of fact for the algae. Our aim is to measure and decipher those circumstances as a way to learn more about community structure and species interactions in the plankton.

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