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3. Grazing, Nutrient Release, and Their Impacts on the Structure of Phytoplankton Communities

Abstract

Part of the problem in deciphering the causes for changes in algal species abundance and productivity is that the observed dynamics could be generated by unlimited numbers of combinations of gains and losses. The rates of individual contributing processes are often much greater than the resultant net rates and thus relatively small changes in any one process can lead to rapid changes in population abundance. The influences created by herbivorous zooplankton are particularly important because the animals exert selective mortality on some algal species and they simultaneously regenerate vital inorganic nutrients to available pools. Owing to production of refractory material and animal biomass the nutrients are released in different proportions than they were consumed, thus altering the ratios of supply rates of nutrients to the phytoplankton and influencing the outcome of competition between species for limiting resources.

Introduction

Because of their influence on species composition and population dynamics in aquatic communities the interactions among planktonic algae and herbivorous zooplankton are central to discussions of trophic dynamics. The principal elements at work are differential mortalities, differential nutrient release and differing importance of planktonic cycling of nutrients compared to both ambient pools and allochthonous supplies. Operating at the species level these factors are ultimately responsible for the differing degrees of success with which algal species attain dominance or persistence in the plankton. Part of the intrigue of this subject is that the several mechanisms involved are conceptually distinct but are inseparable in practice.

Because grazers do not convert all or even a major share of their consumed prey into sustained consumer biomass, mortalities inflicted by them are necessarily coupled to releases of nutrients in one form or other. This nutrient cycling is never perfect and, of course, nutrients are persistently lost from the systems; but then neither are the systems divorced from nutrient inputs. Sometimes we envisage space or time scales at which the gains and losses are in approximate balance, but it is important to remember that episodic perturbations punctuate the monotony of even these imagined steady states. Fortunately the emphasis here is on the dynamics rather than the statics of aquatic systems. The changes we see, be they large or small, represent the differences among processes which are all proceeding simultaneously at rapid rates. Individual species of algae can divide swiftly when nutrients and physical conditions are favorable, but it is the differences in the gains and losses experienced by each species which cause us to note its prominence or absence in the water.

Planktonic productivity may often be limited by the supply rates of nutrients, which in turn are often subject to rapid biotic cycling. Swift turnover of algal biomass by grazers and subsequent release of biologically reactive nutrients to the water can fuel rapid and sustained biological production. Obviously the biomass thus produced does not accumulate; the standing crop is constrained by the total mass of nutrient present. There is likewise no increase in externally harvestable yields for the same reason. What is affected is the component structure of the community. When all rates are fast, meaning that individual gain and loss terms are uniformly large in magnitude, it is then that imbalances in these rates can lead to wholesale alterations in the biotic fabric of communities, simply because differences between very rapid rates can be much greater than differences between very slow rates. What this means is that a pelagic system with rapid cycling fluxes can respond quickly when perturbations alter the imbalances that always exist.

Nutrient Exchange and Cycling

Because dissolved forms of nitrogen and phosphorus include the immediate sources of elements vital to primary biological production, substantial efforts have been undertaken to quantify fluxes between dissolved pools and the biota. Particular interest has been focused on reactions involving the phytoplankton, which are the base of the trophic pyramid in pelagic communities. Most of our knowledge about the interactions and the kinetics of processes in these has required perturbing the systems in some way and measuring

the results. This may be through massive additions of nutrients to lakes (Einsele 1941; Nelson and Edmondson 1955; Schindler 1975, 1977) or through the use of bioassays or tracer techniques. The latter methodology was pioneered at the whole lake level by Hutchinson and Bowen (1950), Hayes et al. (1952) and Rigler (1956), from whose work and through subsequent re-interpretations (Rigler 1973) it became very clear that exchanges between dissolved and particulate phases for P, at least, occurred on the scale of minutes. Intense interest in the rapid removal of tracer-PO_4 from solution spawned the Rigler bioassay (Rigler 1964, 1966, 1968) in an effort to quantify true concentrations of dissolved orthophosphate in lake water, and led ultimately to the elaborate model by Lean (1973) of P-exchange among several functional pools. Because the results show that the dissolved tracer turns over so rapidly primarily as a result of biological mechanisms (e.g., Lean 1976; Lean and Nalewajko 1976; Nalewajko and Lean 1978) there is a tendency to regard this behavior as the fundamental process controlling the concentration of phosphate and perhaps sometimes that of other nutrients. Whereas this may indeed prove to be the case, it provides no insight to the flux rates responsible for biological production in lakes and oceans. What is measured in these experiments is isotope equilibrium only, not mass flux associated with de novo synthesis of biomass. The measurements quantify the unidirectional movement of molecules across a cell membrane, even though an almost equal number are moving simultaneously in the opposite direction. The isotope technique consequently helps identify a freely exchangeable pool of nutrient that is associated with living cells, and sometimes permits the size of the pool to be estimated. To identify processes and rates that are responsible for accrual of phytoplankton biomass, net rates of flux must be measured. Organisms that divide once per day must have the means to augment their cellular nutrient contents at that rate at least. The issue moves therefore to time scales and to nutrient concentrations for which it is possible to measure rates of influx that substantially exceed efflux from the cells.

Responses to Added Substrate

Mechanisms of transport-mediated nutrient uptake and nutrient-controlled cell growth have been reviewed by Button (1978). Uptake of a nutrient and its incorporation in cell biomass must be viewed as a several stage process involving external concentrations of the nutrient substrate (S_{out}), a transport component (T), a labile internal pool (S_{pool}), and structural cellular constituents (S_{cell}).

Reversible formation of a substrate-transport complex is the intermediate step between equilibration of the internal and external substrate pools:

$$S_{out} + T \rightleftarrows TS_{out} \rightleftarrows TS_{pool} \rightleftarrows T + S_{pool} \quad (1).$$

The internal pool comes into dynamic equilibrium with both S_{out} and S_{cell}, and sets the rate of cellular synthesis:

$$S_{pool} \rightleftarrows S_{cell} \quad (2).$$

These two pools each consist of components that vary somewhat independently of each other (Rhee 1973, 1974), but this generalized scheme is an adequate description of events. It makes clear the point that rates of uptake of nutrient from solution do not directly control growth rate. When cells are at steady state with constant ambient concentrations such as in a chemostat, rates of uptake can indeed be calculated from growth rates and cell quotas of nutrients (e.g., Rhee 1973, 1974, 1978), but when external concentrations are changing that approach is unsatisfactory (e.g., Burmaster 1978, 1979b). The cell quota, the amount of nutrient per cell or per unit biomass, changes in response to environmental conditions, and it is closely linked to growth rates (Droop 1968, 1973, 1974, 1977; Fuhs et al. 1972; Brown and Harris 1978).

Droop (1973) avoided the issue of identifying separate cellular nutrient compartments when he advanced the cell quota as the determinant of nutrient-limited algal growth and illustrated the empirical validity of the relationship:

$$\mu = \mu_m(1 - k_Q/Q) \quad (3)$$

for growth of algae limited by P, Fe or vitamin B_{12}. The μ is cellular growth rate (per day), μ_m is the theoretical maximum rate, Q is the cell quota (μmol per cell or per unit biomass) and k_Q is the minimal amount of nutrient necessary for cell division. Other authors have discounted the general validity of this approach by demonstrating that for other nutrients, particularly C, N, and sometimes Si, Eq. 3 is a poor description (Caperon and Meyer 1972; Goldman et al. 1974; Goldman and McCarthy 1978). The discrepancies arise because cell quotas are not only determinants of growth rates, they are products of them, too, and because some nutrients are subject to much greater variability in the cell than are others (Goldman and McCarthy 1978).

Button (1978) solved the relevant equations for the kinetics implicit in Eq. 1. Active transport, molecular diffusion and product inhibition are all involved to some extent. Growth rates are controlled by rates of supply of nutrients from the water only to the point at which intracellular conversion of available nutrient into structural

components becomes the rate-limiting step. Maximal rates at which nutrients can be transported into the cell may be many times faster than they can be utilized once they get there. This means that concentrations at which growth rates become saturated will be much lower than concentrations required to saturate the uptake mechanisms (Lehman et al. 1975; Button 1978; Burmaster 1979a).

Those uptake mechanisms are usually evaluated by Michaelis-Menten kinetics:

$$u = u_m \cdot S_{out}/(K_S + S_{out}) \qquad (4),$$

where u is uptake rate (maximum $u = u_m$) and K_S is the half saturation constant for uptake. The model in Eq. 1 implies that flux rates may deviate from these simple kinetics under some circumstances (Button 1978). Brown et al. (1978) in fact demonstrated empirically that rates of uptake proceed faster at low concentrations of phosphate than would be expected by fitting Eq. 4 to data obtained at higher concentrations and extrapolating down to the low values. The effect does not seem to be caused by the rapid exchange fluxes discussed earlier, and it may imply the existence of more than one transport system in algal cells, each with a different affinity for a single nutrient. The rapid exchange between external and internal pools does suggest, however, that there could be a finite concentration at which net uptake is zero, as has occasionally been discovered for P (Brown and Button 1979) and for Si (Kilham 1975). The threshold values will almost certainly be species-specific. A crucial ecological question may thus be how ambient concentrations compare to these values.

More deviations from simple uptake kinetics can come from diffusion limitation at low nutrient concentrations (Harvey 1937b; Munk and Riley 1952; Pasciak and Gavis 1974; Gavis 1976). Molecular diffusion in the boundary region around a cell might not be rapid enough to maintain high flux rates regardless of the affinity of the transport system. These effects can be very important when ambient concentrations are low, in which case sizable concentration gradients needed to maintain rapid diffusive flux cannot be established well.

Although there are good reasons to suspect that simple and traditional kinetic analyses do not give an adequate description of uptake rates at low concentrations, the half saturation constant obtained from those analyses is still of interest. Ranges of K_S have been documented for many species and nutrients (see summaries by Healey 1973; Lehman et al. 1975), and they raise some important questions. For instance

in all cases the half saturation constant is much greater than the concentrations usually encountered on average in solution. Does this mean that the uptake system is always far undersaturated? If so, what is the adaptive advantage of possessing a system with so much unused capacity? A key consideration is that the maximum possible rate of uptake is usually far greater than necessary to support the maximum possible rate of cell division. It follows that uptake and storage of nutrients beyond immediate cellular needs could be a common occurrence.

Nutrient Release

Although there are times when ambient pools of nutrients or the supply rates of nutrients from outside the system are adequate to account for observed rates of planktonic production (e.g., Lehman 1979), there are other times when cells utilize inorganic nutrients much faster than the substances are supplied from external sources or from ambient dissolved pools, both in lakes (Barlow and Bishop 1965; Ganf and Blazka 1975; Lehman 1980b; Richey 1979) and oceans (Eppley et al. 1973; Dugdale 1976). Some of the demand must be sated by nutrients cycling within the water column. Two alternative mechanisms are often proposed to account for the requisite fluxes. Some authors claim that physiological death of phytoplankton (Jassby and Goldman 1974) and autolysis aided by microbial attack on moribund cells account for most of the recycling (Golterman 1973). Rates of physiological death among the phytoplankton are very hard to ascertain, however (Kilham and Kilham, this volume), so their importance in nature remains unknown. When they occur and whatever their cause, cell death and lysis release phosphate rapidly because of the labile nature of phosphate-ester bonds and the autolytic enzymes present in cells. The rapid efflux from living cells detected during isotope equilibrium experiments probably represents diffusion of molecules from high concentrations inside the cell membrane. It is not included here because as mentioned earlier it represents only one part of a two-way flux whose net value may be close to zero for living cells.

An alternative source for the nutrients is regeneration from the algae indirectly through the grazing activities of herbivorous zooplankton. Excretion and breakdown of incompletely digested remains of egested algal cells liberate nutrients that are very reactive biologically, and which are available not only to the prey of the herbivores, but also to their competitors. To illustrate the effect that nutrient release from zooplankton can have on nutrient cycles in aquatic systems, it is useful to review first what is known about the mechanisms and rates of feeding and metabolism.

Feeding by Zooplankton

Empirical investigations have shown that grazers can influence the composition and abundance of algal communities (Cushing 1963; Haney 1973; Kerfoot and DeMott, this volume), particularly after the spring bloom. Also documented is the fact that grazers are very selective about the types of particles they ingest (Harvey 1937a; Arnold 1971; Nival and Nival 1973; Berman and Richman 1974; Richman et al. 1977; Gilbert and Bogdan, this volume). Some of the selection may be dictated by the mechanical properties of the filtering apparatus (Nival and Nival 1976; Boyd 1976; Barlow and Monteiro 1979), but there may also be a high degree of chemosensation and decision-making involved (Friedmann and Strickler 1975; Poulet and Marsot 1978; Donaghay and Small 1979; Strickler, this volume; Koehl, this volume). The favorite procedures for measuring feeding rates rely either on direct quantification of changes in abundance of the food particles (e.g., Reeve 1963; Coughlan 1969; Frost 1972), or on incorporation by the animals of a radioactively labelled food (e.g., Rigler 1961b; Geller 1975). Early workers suggested that filter-feeding zooplankton were completely automatic, in the sense that each animal would always filter a constant volume of water (Fleming 1939; Harvey 1942). Studies by Ryther (1954) and Marshall and Orr (1955), however, soon made it clear that at high concentrations of food particles the rate of ingestion levels off to some maximum value. Subsequent work showed that the observation held for both field and laboratory populations (Rigler 1961b; Reeve 1963; Burns 1966; Parsons et al. 1967). Several different formulations were advanced to describe the empirical results mathematically, but the choice of which equation an author used to represent his data appears to have been completely subjective. In the hope of finding a single "best" equation, Mullin, Stewart and Fuglister (1975) used Frost's (1972) extensive data on feeding rates of Calanus pacificus to try to distinguish the best empirical model by statistical means. They found that the data fit the three different models they examined almost equally well.

Some authors have taken a less empirical approach to the issue and have tried to justify grazing models from basic assumptions about feeding behavior. Cushing (1959, 1968) and Crowley (1973) derived formulations for grazing zooplankton from the same constructs that Holling (1959) used to erect a scheme for predation rates among animals in general. An alternative approach advanced by Lam and Frost (1976) and Lehman (1976) treated grazing as an optimization process for the grazer in which effort is expended to gather food, and nutritional reward results from its digestion. Frost (1975)

showed that the feeding behavior of Calanus is consistent with the optimization hypothesis but not with the other models commonly in use. Paffenhöfer (this volume) provides important caveats to this approach particularly relevant to comparisons of species that differ in ability to store lipids and wax esters. These life history considerations plus detailed cinemagraphic analyses of feeding behavior now in hand (Strickler, this volume) open the way to more realistic versions of these early models.

Beyond the matter of feeding rates on a single food type and their mathematical representation is the issue of selectivity exhibited by zooplankton when they are presented with the array of possible food species in nature. Many authors (e.g., O'Neill 1969; Bloomfield et al. 1973; Park et al. 1974; Vanderploeg and Scavia 1979) have proposed that simple coefficients applied to each food source can represent both the mechanical biases of the food-gathering mechanism (passive selection, in the sense of Frost 1977), and the more active selection/rejection process based perhaps on taste (Poulet and Marsot 1978). The approach is basically sound, but the models used to represent the behavior are incomplete for a variety of reasons. First, the animals can change their selectivity in response to the nutritional quality and abundance of available prey. Wilson (1973) and Richman et al. (1977), for instance, showed that some copepods change their selectivity in response to changes in the available particle spectrum. Sometimes the previous feeding history of the animals is important, too (Donaghay and Small 1979). Furthermore, maximal feeding rates are dependent on the food species. To some extent this is because the volume ingested plays a role in regulating feeding rates (McMahon and Rigler 1965; Geller 1975) and because different food species have distinctly different carbon (or nutrient) to volume ratios. Also, there are considerable differences among food species in the degree to which they are compressed inside the gut (Geller 1975). Combining these factors with the potential handling and interference problems presented by some algae the search for invariant coefficients of "feeding efficiency" on different food types seems unjustified.

Once food is ingested by a zooplankter, only a fraction of it is assimilated; the rest is egested. Rates of assimilation and egestion will influence not just secondary production in situ, but rates of nutrient cycling as well. Strong experimental support exists for the claim that digestion efficiencies are specific to individual food types (Lefévre 1942; Marshall and Orr 1955; Arnold 1971; Porter 1973; Korstad 1980). Rates and efficiencies of assimilation may

sometimes be identical for taxonomically dissimilar organisms like Scenedesmus, a green alga, and Asterionella, a diatom, but very different for more similar organisms like the green algae Scenedesmus, Stichococcus, and Staurastrum (computed from data of Geller 1975 and Lampert 1977b). Some authors have reported instances of "superfluous feeding" (Beklemishev 1962) at high food abundances. That is, much more material is ingested than the animals can possibly assimilate. Conover (1966a) and Lampert (1977b) have disclaimed the occurrence of superfluous feeding among herbivorous zooplankton, but one should not conclude that assimilation efficiency is independent of food concentration. Schindler (1968) demonstrated that the ratio of assimilated energy to ingested energy decreases by approximately a factor of 2 when Daphnia magna is fed on progressively more concentrated diets. In other words, when food is very abundant and processing rates are rapid, digestion is less complete than when food is rare. This corresponds to Geller's (1975) observations about variable gut passage times. At low food abundances ingested material may be retained for more than an hour inside the gut of Daphnia pulex, but when external concentrations are high, food is egested within ten minutes. Other workers similarly find differences in assimilation efficiencies with different feeding rates (Gaudy 1974; Corner et al. 1976).

Most experiments suggest that large differences in assimilation efficiency as a function of food concentrations are unlikely. Differences of a factor of 2 (Schindler 1968) or less (Lampert 1977b) are probably the full range that occur in natural populations. The picture is a little different when considering the fate of materials that are ingested but not assimilated by the animals. The fact that Schindler (1968) reported assimilation efficiencies between 90% and a little more than 40% means that between 10% and 60% of the ingested material may be returned to the water unassimilated. Regarded in this way the variability of the egested portion is much greater than the variability of the assimilated portion an a relative basis. The nutrients associated with this egested material are either released to inorganic pools immediately or are subsequently remineralized by microbial decomposers. Another consequence of inefficient feeding was described by Lampert (1978) who showed that uningested cells that are broken or damaged during filtering activities of the animal may leak dissolved organic carbon to the water; it can be assumed that nutrients like P and N are released as well. Other investigators have reached the same conclusion (e.g., Cushing 1955; Conover 1966b; Martin 1970; O'Conners et al. 1976; Bowers and Grossnickle 1978). Among

carnivorous cyclopoid (Brandl and Fernando 1975a, 1975b) and calanoid (Anderson 1970; Bowers and Warren 1978; Kerfoot 1978; Landry 1978) copepods, which leave partially eaten prey and fragments after an attack, release rates may be even higher. These various fluxes associated with imperfect feeding efficiencies can be important to nutrient recycling at times. Their magnitudes must be added to those of nutrients that are excreted or selectively egested. It follows that the nutrient ratios in the egested material may be substantially different from the ratios that are ingested.

The point is important because metabolic excretion of N and P from zooplankton has often been estimated from measured respiration rates (e.g., Conover and Corner 1968; Satomi and Pomeroy 1965; Ganf and Blazka 1974; Devol 1979). The published O:P and O:N ratios are subject to considerable variability, which may reflect the nutritional condition of the animals (Mayzaud 1973; Ikeda 1977). Lampert (1975) showed that much of the carbon assimilated by Daphnia pulex is metabolized almost immediately, this because the metabolic demands of herbivorous zooplankton are met largely by the immediate use of newly digested food, rather than by catabolism of body constituents (Lampert 1977a). Radiotracer techniques confirm that notion (Peters and Rigler 1973; Peters 1975). This means that the nutrient content of excreted material may not bear any simple relation to the elemental composition of the animal tissue.

Ketchum (1962) first identified the possible significance of differential excretion of N and P by zooplankton in relation to the composition of their food. Butler et al. (1969) seized on that importance and documented the mechanisms responsible for differential nutrient release. They first illustrated that the N:P ratio of the fecal pellets of Calanus always exceeded the ratio of the animals' diet by 29% to 70%. Then, recalling the work of Marshall and Orr (1955) and Corner et al. (1967) they showed that Calanus extracts N and P from its food with differing efficiencies. Nitrogen was less readily assimilated than was phosphorus and thus the fecal pellets reflected the differences in digestion. The N:P ratio of soluble excreted material, however, was lower than the N:P of the diet. Fecal pellets sink swiftly, removing their enclosed nutrients from immediate consumption, but the excreted products are soluble and directly available to algae.

In light of these observations the most secure method for determining nutrient release from zooplankton is to measure the nutrients directly. There are problems with interpreting the results, nonetheless. Measured concentra-

tions represent a balance between rates of nutrient remineralization by the zooplankton and the simultaneous uptake of the nutrients by phytoplankton. First removing the algae from the water is not satisfactory, because animals without food behave differently from well-fed ones (Conover and Corner 1968; Takahashi and Ikeda 1975; Mayzaud 1976; Ikeda 1977; Lampert 1978). Similarly, concentrating the zooplankton to obtain unambiguous measurements of nutrient excretion can mean that food supplies may be rapidly exhausted, the animals may be damaged, or their physiology, including the rates and forms of excreted substances, may change (Mullin, Perry, Renger and Evans 1975). As an example, Johannes and Webb (1965) indicated that release of organic N was substantial for natural plankton, and others working with concentrated natural collections have sometimes found the same (Le Borgne 1973). Corner and Newell (1967), on the other hand, reported that Calanus helgolandicus consistently released about 75% of its N as ammonia, and that release of organic N was only substantial when the animals were crowded. In general, the most cautious studies demonstrate that most of the N is released to the water as NH_3 (e.g., Butler et al. 1969; Jawed 1969; Jacobsen and Comita 1976; Gardner and Scavia 1981), but a measureable fraction, usually less than 25%, consists of other compounds (e.g. Mayzaud 1973; Mayzaud and Dallot 1973). A similar disagreement exists over the relative rates of release of inorganic and organic P. Although concentrated net plankton may release as much as half of the P in organic form (Pomeroy et al. 1963; Satomi and Pomeroy 1965; LeBorgne 1973), careful laboratory studies with undamaged animals find that most of the release in short-term assays is PO_4 (Rigler 1961a; Butler et al. 1969; Peters and Lean 1973; Ferrante 1976).

What this means is that most of the N and P released by zooplankton is in precisely the chemical forms most immediately useful to phytoplankton, NH_3 and PO_4. Efforts to quantify these release rates in nature are thus complicated by the necessary presence of algae in the water. In fact the presence of algae probably has introduced biases in most traditional measurements of nutrient regeneration in situ (cf. Lehman 1980b) but the problems can be overcome and rates can be measured for intact assemblages (Lehman 1980a, 1980b).

Tight Biotic Coupling of Released Nutrients

The new analyses show that nutrient turnover by zooplankton can be large compared to all other sources and that it alone can supply most of the algal demands for N and P.

Despite these potentially rapid rates of nutrient remineralization, however, the ambient concentrations of dissolved nutrients usually remain very low during the seasons of highest productivity (see McCarthy and Altabet, this volume). The reason is that released nutrients do not accumulate in the water, they are swiftly removed by the algae and used to enhance their growth. Cycling fluxes intensify and less algal biomass is needed to maintain a given level of productivity; new biomass is generated just as quickly as the old biomass is consumed or lysed and the nutrients are regenerated. Despite low average concentrations of dissolved nutrients, algal production is fueled by rapid biotic cycling of P and N where the emphasis this time is on net fluxes, not the two-way fluxes that isotope equilibrium experiments show. There are basically two mechanisms by which this can happen. On the one hand, uptake rates at low concentrations of P may be much greater than would be expected by extrapolating down from high concentrations, a possibility that has already been discussed. This notion is countered somewhat, however, by the possible existence of threshold concentrations necessary for positive net uptake (e.g. Brown and Button 1979). On the other hand, the scheme might be analogous to the one that McCarthy and Goldman (1979) envisage, with algae encountering very heterogeneous microenvironments, some of which are severely enriched with nutrients owing to remineralization events. If nutrients are rapidly sequestered by the cells in these episodic and disjoint patches and then subsequently used for growth, the large uptake and luxury storage capacities of algal cells that were discussed earlier can be seen to have great significance. This scheme in contrast to the last one relies on concavity of the uptake function or a threshold value for uptake. Otherwise the convex asymptotic behavior of a simple Michaelis-Menten model would guarantee that constant low levels of nutrients would allow more net accumulation than would sporadic saturating pulses, given the same total mass of nutrients (Scavia and Lehman, unpublished). Because zooplankton are dominant agents of nutrient release at some times and places, this scheme merits attention (e.g., Turpin and Harrison 1979) despite arguments against it (Jackson 1980).

Experiments show that algae can exploit nutrient patches produced by individual zooplankters (Lehman and Scavia 1982a, 1982b). Evaluating the ecological significance of such microscale patchiness of nutrients in nature is a new challenge. 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) shows so clearly. Furthermore, algae in nature can exhibit extraordinarily

rapid transient rates of nutrient uptake, much faster even than those of the laboratory cultures used by Lehman and Scavia in their experiments (Lehman and Sandgren 1982; McCarthy and Altabet, this volume). Finally, strict interpretation of the isotope exchange method for assessing turnover of PO_4 in nature presumes, as described earlier, that influx and efflux from cells are in close balance during unperturbed conditions.

If empirical approaches do show that small scale patchiness of nutrients is a recurring feature of natural communities, its importance is likely to be expressed in terms of species interactions, rather than community productivity per se (Lehman, in press). An example of this may be the discovery (D. Scavia, unpublished) that algae grown in a patchy nutrient regime can maintain fixed growth rates with on average less limiting nutrient per cell than they need in uniform regimes.

Nutrient release from the zooplankton is tied ultimately to their feeding rates. Some of the nutrients assimilated by the herbivores and used for growth and reproduction contribute to fluxes through higher trophic levels, but most of the assimilated nutrients are returned to solution one way or other during the season. Activities of the grazers cause selective mortality on the one hand, and fertilization on the other. The effects of the animals on rates of competitive displacement of algal species by influencing differential growth rates are potentially much greater than those caused by grazing losses alone. Nutrients released to the water as a consequence of the activities of the animals are available to all the algae, not just to the preferred prey of the grazers. This means that herbivores can be depressing the abundances of some algal species through selective grazing, and enhancing productivity of others by nutrient release.

Moreover, the effects of nutrient release can be expressed differentially through the community. I have already mentioned the differential rates at which N and P are ingested, egested and excreted. There are bound to be differences among other nutrients, too. An element like Si is certain to be refractory to digestion by zooplankton and thus it will be selectively egested. When egested material is concentrated in fecal pellets as in copepods it is practically assured swift transit from the euphotic zone. Recycling by zooplankton is thus biased against Si in the same way that there are differences in the ratios at which N and P are cycled. This may lead to progressive biases in supply rates that can affect community structure through mechanisms discussed by Kilham and Kilham (this volume). It is the

interplay of these cycling rates with allochthonous nutrient inputs and differential mortalities that shapes the community.

Depending on the relative rates and magnitudes of nutrients supplied from autochthonous and allochthonous sources the plankton are subjected to a spectrum of resource availabilities. In Lake Washington, for instance, N and P were supplied to the epilimnion from external sources in ratios of 26:1 to 36:1 by atoms during the summer months, 1970 to 1977 (Lehman 1980b). In September, 1977, herbivorous zooplankton in that lake regenerated N and P at about 15:1 by atoms; simultaneous measurements of nutrient uptake suggested that the lake phytoplankton removed added nutrients in the ratio 10:1. Because magnitudes of nutrient supply from the watershed, from eddy diffusion, and from internal cycling change seasonally, the realized rates of supply to the phytoplankton change also, as do their proportions. When only a single algal species is present, ratios of N:P measured in algal uptake and in zooplankton regeneration may be identical, whether the algae are nutrient deficient or not (Lehman 1980a, table 4) but the presence of many species in natural assemblages, each with different optimal nutrient supply ratios (Rhee and Gotham 1980) creates an opportunity for differential growth and community change.

Conclusion

Processes responsible for biotic cycling of nutrients in the water column deserve increased attention in light of discoveries that external sources of nutrients are sometimes insufficient to explain observed rates of biological production in lakes and oceans. The chief difficulties slowing rapid and complete analyses of the systems are primarily technical ones that arise because fluxes associated with production and with losses are intimately connected.

Only the outline of the focal processes in nutrient cycling is known at present with great assurance, but that outline provides a guide for future work. A detailed kinetic description of nutrient uptake by assemblages of natural phytoplankton at concentrations slightly above ambient is one vital need. So are measurements of nutrient release in situ by the zooplankton, including not just juvenile and adult crustaceans but rotifers and protozoa as well. Particularly important are effects of age-structure, size and species composition on the flux rates anticipated through seasons, and from year to year. The contributions of the microzooplankton have been poorly studied in proportion to their likely importance. Needed, too, are renewed evaluations of

mechanisms and determinants of selective grazing by herbivorous zooplankton. That line of inquiry will probably prove central to a description of events in the open water, because that singularly behavioral process potentially limits the standing crop of phytoplankton and thus their overall nutrient uptake capacity, and also it represents the first step in a sequence by which nutrients are remineralized back to biologically-reactive dissolved form by herbivores.

The issue rests no longer on identifying these pathways, or even on asserting their general importance, but rather on determining the magnitudes of nutrient and biotic fluxes in nature and integrating them into a coherent, internally consistent, and dynamic exposition of the structure and productivity of pelagic ecosystems.

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