

RAPID RESPONSE PAPER

Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals

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(Received 14 July 1988; in revised form 23 November 1988; accepted 30 November 1988)

Abstract—A new extension of digestion theory and re-interpretation of published empirical evidence suggest that the principal pathway of dissolved organic carbon (DOC) from phytoplankton to bacteria is through the byproducts of animal ingestion and digestion rather than via excretion of DOC directly from intact phytoplankton. Simple model calculations reveal that for a substance with diffusion coefficient equalling $10^{-5} \text{ cm}^2 \text{ s}^{-1}$, excess (over ambient) concentrations of solute in a fecal pellet of typical size (diam. $\leq 1 \text{ mm}$) are lost rapidly; $\geq 50\%$ of any excess is diffused out of the pellet within 5 min—even in a stagnant water column and without particle sinking. Reasons for rapid loss and its insensitivity to fluid dynamic conditions are small size of the pelletal reservoir and the sharp concentration gradient between pelletal and ambient concentrations upon pellet release. As a consequence, most solutes initially contained in fecal pellets of zooplankton generally will remain in the 10–100 m thick water layer within which the pellets initially are deposited. Focus on animal-caused organic release over these very short time scales may help to resolve some of the growing paradoxes of DOC standing stocks and fluxes in the upper ocean.

INTRODUCTION

THE importance of the microbial loop in aquatic food webs today is little disputed. Recent measurements based on nucleotide radiolabeling and protozoan grazing rates show that heterotrophic bacterial production demands a substantial rate of supply of dissolved organic carbon (DOC), often amounting to 20–40% of the mean carbon fixation rate (AZAM and FUHRMAN, 1984; HAGSTRÖM, 1984; LANCELET and BILLEN, 1985). While there still is room for debate about the sink for this bacterial production (DUCKLOW *et al.*, 1986), scaling arguments (FENCHEL, 1984) and experiments (SHERR and SHERR, 1984) provide convincing evidence that zooflagellates can be effective grazers of free-living planktonic bacteria, and the list of other effective grazers is growing (KING, 1982; BIRD and KALFF, 1987; SHERR and SHERR, 1987).

Recent measurements show that the feedback from bacterial production to primary production is indirect, i.e. that heterotrophic bacteria are competitors with photoautotrophs for inorganic nutrients that limit primary production (typically nitrogen in the

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ocean and phosphorus in fresh waters (WHEELER and KIRCHMAN, 1986; GOLDMAN *et al.*, 1987; VADSTEIN *et al.*, 1988). Inorganic nutrients are returned to phytoplankton and made available to other bacteria as secretions and excretions by bacteriovores.

Consequently, in addition to the energetic costs of replacing lost molecules, competition with bacteria also produces selective pressures on phytoplankton to avoid leakage. Further, the DOC flux implied by bacterial growth estimates based on incorporation of radiolabeled nucleotides, on frequency of dividing cells, or on uptake rates of small, radiolabeled, organic substrates is large. Its sheer magnitude severely strains the presumed principal pathway of DOC that flows from primary producers to heterotrophic bacteria and thereby closes the microbial loop. Extant models of organic carbon flux in upper ocean waters (e.g. FASHAM, 1984; PETERSON, 1984) identify the dominant DOC flux to heterotrophic bacteria as direct leakage of soluble photosynthate from primary producers; these models generally require 10% or more of primary production to be lost to the phytoplankton cell in this form. Data to support such high leakage rates are difficult to find, most of the recent direct measurements on isolated (from the rest of the community) phytoplankton cells indicating less than 10% leakage (LANCELET and BILLEN, 1985).

We provide an alternative analysis of the problem based on the recent derivation of a theory of mass balance for animal digestion (PENRY and JUMARS, 1986, 1987; JUMARS and PENRY, 1989) that appears to relieve the inconsistencies arising from the assumption that phytoplankton leak at high rates. A much more consistent picture of carbon flow in aquatic systems emerges if heterotrophic bacteria obtain DOC as a byproduct of animal feeding and do so at a rate equivalent to 10–50% of carbon fixation by phytoplankton. Our analysis, together with recent results from direct observations of particles through a range of ocean depths (CHO and AZAM, 1988; KARL *et al.*, 1988) drive increasing attention to the early stages of particle degradation, i.e. during ingestion and immediately after pellet release.

THEORY

Reasons for incomplete digestion

Reactor theory applied to animal digestion entails a simple mass balance. A full derivation of such a mass balance for several types of material processing seen in animal guts is provided by PENRY and JUMARS (1987), but we extract only one type for treatment here as an example. The most common arrangement is for all or part of an animal's gut to behave as a plug-flow reactor, with limited axial mixing relative to radial mixing; particles in this kind of tubular flow are egested in the same sequence that they are ingested. For this case the general solution of the mass balance equation is (PENRY and JUMARS, 1987)

$$\tau = C_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A} \quad (1)$$

For Michaelis–Menten digestive kinetics, the solution becomes (JUMARS and PENRY, 1989)

$$\tau = \frac{K_m}{V_{\max}} \left[-\ln(1 - X_{Af}) + \frac{C_{A0} X_{Af}}{K_m} \right], \quad (2)$$

where $-r_A$ is the digestive disappearance rate of diet component A ($\text{mol vol}^{-1} \text{time}^{-1}$), τ is

the residence time for a food item in the gut or alternatively the time required to process one gut volume of food material (time), C_{A0} is the initial concentration of limiting component A in the food (mol volume^{-1}), X_A is the conversion of component A into products (dimensionless fraction), X_{Af} is the final conversion after residence time T in the gut, V_{\max} is the maximal conversion rate of component A into product ($\text{mol volume}^{-1} \text{time}^{-1}$), and K_m is the concentration of component A at which conversion rate of component A is one-half of its maximal rate (mol volume^{-1}).

This expression is purely kinetic and descriptive. To provide ecological predictions from this mass balance, one must impose ecological constraints. We adopt the common one that organisms act to maximize their individual fitnesses by maximizing their individual rates of material or energy gain. If digestion were the rate-limiting step in its acquisition of nutrients, one would expect an animal to process food in such a way as to maximize the rate of digestive conversion. In terms of the model variables, the animal would act (cf. JUMARS and PENRY, 1989) to maximize

$$\frac{X_{Af}C_{A0}v}{\tau}, \quad (3)$$

where v is the volume of the animal's gut. If V_{\max} , K_m and C_{A0} are held constant, then rate of gain rises with decreasing τ and decreasing τ translates into decreased X_{Af} . Given Michaelis-Menten kinetics, the longer a volume of gut contents is held, the lower the conversion rate, because substrate concentration drops as conversion proceeds. It is a common misconception, particularly among non-biologists, that it always is in an animal's best interests to maximize digestive efficiency. The value of our explicit analysis is its focus on the variable of most relevance to the animal in terms of survival and reproduction, i.e. rate of gain, rather than on the variable most commonly used in models, i.e. efficiency of conversion. The same qualitative results are found with guts modeled more accurately as stirred-tank and batch reactors, though the respective solutions differ in quantitative detail (PENRY and JUMARS, 1987; JUMARS and PENRY, 1989).

Much water-column herbivory is by protozoans that do not possess true guts. Nonetheless they can be treated by reactor theory equations, for the feeding rate saturates at a given volume of material contained in digestive vacuoles (FENCHEL, 1987), analogous with a full gut. In the protozoan homologue of plug flow, the wastes from digestive vacuoles would be egested in the same sequence that the vacuoles were formed. In the reactor theory terminology of PENRY and JUMARS (1987), random order of expulsion of digestive vacuolar contents after ingestion would correspond with a stirred tank reaction, while processing of a single vacuole could be treated as a batch reaction.

For a given food cell type, the empirical pattern of ingestion by suspension feeders as a function of food abundance is well established (PETERS and DOWNING, 1984) and is in accord with these predictions. As encounter rate with food increases and allows ingestion rate to increase, τ drops. Ingestion rate reaches a plateau at which some step other than digestive reaction (e.g. ingestion itself as a mechanical process, absorption of digestive products through the gut wall, subsequent internal transport, or biosynthesis) becomes rate limiting, and further increases in ingestion rate are either impossible or costs of them outweigh potential gains. If Michaelis-Menten kinetics prevail, then an inescapable consequence (equation 2) is that digestive efficiency (X_{Af}) drops when τ falls. When food

abundance is not limiting, it thus is in the animal's best interests (mol product produced time^{-1}) to have lower conversion efficiency and faster throughput than when food is scarce.

An important point regarding the principal source of organic carbon for bacterial production is that the generally observed assimilation efficiencies of 70–90% organic carbon from phytoplankton (TANDE and SLAGSTAD, 1985, and references therein) are consistent with egestion of roughly 10–30% of ingested plant material. It may be in the form of either unconverted substrate ($1 - X_{Af}$) or in the form of unabsorbed digestive products [$C_{A0}(1 - X_{Af})$]. For any fixed absorption kinetics, the greater the rate of digestive production, the greater will be the rate of egestion of converted but unabsorbed products. Even the unconverted digesta, however, are likely to be in a physical form more available to microbial attack than would be the contents of a healthy plant cell, for animal digestion obviously entails "breaking down the prey's defenses" (SIBLEY, 1981). Further, particularly with rapid throughput, digestive enzymes will be expelled with the feces and may continue to produce products or may themselves be digested by bacteria.

PENRY and JUMARS (1987) review the empirical support for application of reactor theory to deposit feeders and to herbivores that utilize fermentation. For suspension feeders, there are data to support the two important assertions that assimilation efficiency drops with increasing food abundance (decreasing T and X_{Af}) and that labile digesta are egested and available to bacteria. In copepods (DAGG and WALSER, 1986) as well as tunicates (ROBBINS, 1985) fecal pellets become more robust and have higher Stokes settling velocity when food is abundant than when it is scarce. SMERDA *et al.* (1971) observed live passage of bacteria through the guts of nematodes at high feeding rates but not at low ones. Release of solutes by zooplanktonic fecal pellets has been noted (e.g. LAMPERT, 1978), but has not been incorporated into any general theoretical framework or mass balance. All of these pieces of information can be combined in a consistent carbon-flow model (Fig. 1) that does not violate intuition, measurements or foraging theory.

The fate of particulate byproducts of digestion is the subject of much recent study, and the provisional conclusion seems to be that despite the dominance of large particles in vertical fluxes (McCAYE, 1975) and the lability of those particles that do succeed in running the vertical gantlet (LOCHTE and TURLEY, 1988), most organic particulate material does not find its way out of the upper few hundred meters of the water column (CHO and AZAM, 1988; KARL *et al.*, 1988). By comparison, the dissolved component of unabsorbed material passing through animal digestive systems has received very little attention. Thus we examine in a preliminary model the fate of such solutes, much in the spirit of McCAYE's (1975) initial analysis of particulate fluxes. We also note that the distinction between particulate and dissolved fraction is a difficult one semantically, because the physical breaking or chemical degradation of a cyanobacterial or plant cell wall during ingestion and digestion makes a large percentage of material change categories operationally. A bag of solutes is a particle; a punctured bag is a particle with twice the surface area exposed to seawater, but its contents are no longer particulate.

Fate of solutes ejected in fecal pellets

To explore the potential fates of solutes contained in ejected fecal pellets, we resort to advection–diffusion models. We consider an ambient external solute concentration and a pelletal solute concentration of the same substance. Specifically, we assume that the pellet retains its cylindrical or spherical shape, that its outer boundary is completely

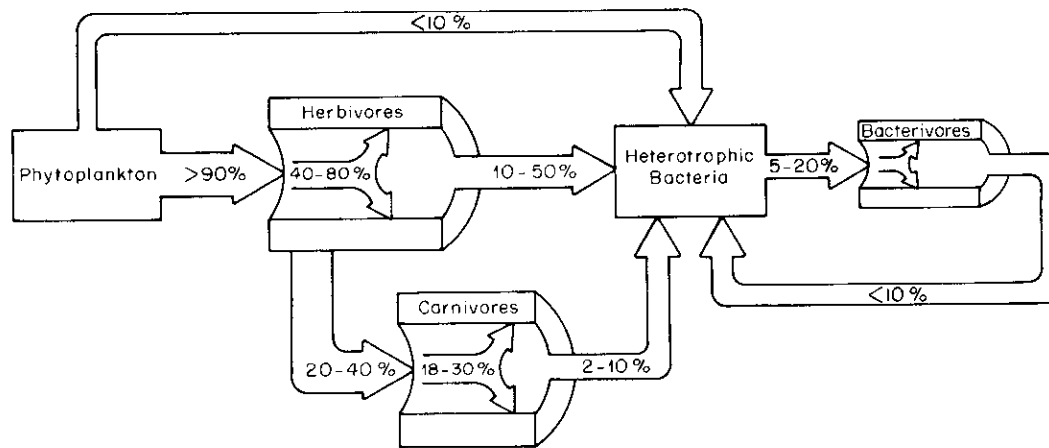


Fig. 1. Suggested paths of carbon flow through the food web of a pelagic community in steady state. Herbivores explicitly include protozoans. Divergences within half-cylinders represent absorption. Magnitudes of flows are indicated as percentages of primary production and for simplicity do not include losses due either to creation of refractory dissolved organics or to sinking of particles. Also for simplicity (and because the two have not in general been separated in experiments) the magnitudes of our outflows from animal guts include leakage from prey during handling and ingestion. In this view byproducts of feeding by animals clearly dominate the sources of organic matter to heterotrophic bacteria.

permeable to the molecule or ion in question, and that the solute concentration within the pellet is uniform upon defecation. We make no corrections for tortuosity in internal diffusion paths (because such small corrections are not in the spirit of our order-of-magnitude analysis), and we take the internal and external diffusion coefficients to be identical ($D = 10^{-5} \text{ cm}^2 \text{ s}^{-1}$), without any impedence due to ion exchange or absorption. We consider a range of pelletal diameters from $10 \mu\text{m}$ to 1 cm and a range of excess densities ($\rho_s - \rho$, or pelletal density minus seawater density) of 0.01 to 0.5 (KOMAR *et al.*, 1981). To represent the two extremes of general fecal pellet morphology, we model diffusion from both spheres and infinite cylinders.

Pellets can be egested into a range of fluid dynamic conditions. If they emerge into stagnant water and have no excess density (and thus no settling velocity), solute transfer will be by molecular diffusion alone, characterized by a minimal Sherwood number (Sh). The Sherwood number, the ratio of mass transfer rate due to advection relative to that due to molecular diffusion, is not a very familiar one in oceanography, and so a brief digression is in order. An easy mnemonic for our application is that it increases with the rate of transfer of solute from the rich environment of a fecal pellet to the poor one of the ambient ocean. The slightly more familiar heat-transfer analog is the Nusselt number (Nu).

The Sherwood number is calculated (e.g. LIH, 1975) as $Sh = kd/D$, where k is the coefficient of mass transfer (cm s^{-1}) and d is the diameter of the particle or structure. Sh increases with the more familiar Reynolds number ($Re = \text{ratio of inertial to viscous forces}$), with the slightly less familiar Schmidt number ($Sc = \text{ratio of momentum diffusivity to mass diffusivity}$), and thus with the Peclet number ($Pe = ReSc$). Applications of these latter nondimensionalizations to mass transfer from slowly dissolving, settling particles are well treated by CSANADY (1986).

We make use of the heat-transfer analogy and integrate under the curves presented by CRANK (1956, Figs 3.1 and 3.2, p. 29) to find that 50% of the volumetrically integrated concentration difference between inside and outside a spherical pellet will be eliminated when $(Dt/r^2)^{0.5} = 0.4$. Here t is time and r is the radius of the pellet. For a cylinder, equivalent loss occurs for $(Dt/r^2)^{0.5} = 0.5$. To eliminate 90% of the difference, $(Dt/r^2)^{0.5}$ would have to equal roughly 1.0 and 1.5, respectively, for the sphere and cylinder. The opposite bound is that fluid dynamics are sufficient to maintain the pelletal boundary constantly at the original ambient concentration of solute. This situation in nature can occur either through mixing produced by some external (to the particle) forcing such as wind or through high excess density and large size of the pellet yielding a high settling velocity. The associated Sherwood number is large, indicating that advection grossly dominates diffusion in the mass transfer. To lose one-half of the volumetrically integrated initial concentration difference [calculated from CRANK (1956) by graphical integration of Fig. 6.1, p. 86, for the sphere and of Fig. 5.3, p. 67, for the cylinder] would then require $(Dt/r^2) = 0.09$ and 0.11 for the sphere and cylinder, respectively. For 90% loss, those figures would change to 0.24 and 0.39. [For applications requiring greater precision, CRANK (1956) also provides the relevant formulae for analytic or numerical solution.] For any of these cases, diffusion times and diffusion coefficients are inversely proportional; halving D would double t for a pellet of fixed r .

Rapid diffusion insensitive to fluid dynamic conditions (Fig. 2) arises because of the combination of a relatively small reservoir of material in the pellet and the steepness of the initial concentration gradient. By the time the gradient becomes weak enough for appreciable slowing of the equilibration between pelletal and ambient concentrations, adjustment of the pelletal solute concentration to the ambient is 90% complete. Fluid dynamics, specifically those embodied in the Sherwood number, become important only in this last minor adjustment or at unrealistically large (for dominant planktonic herbivores) pellet sizes. Here advective removal (fast settling velocity of the

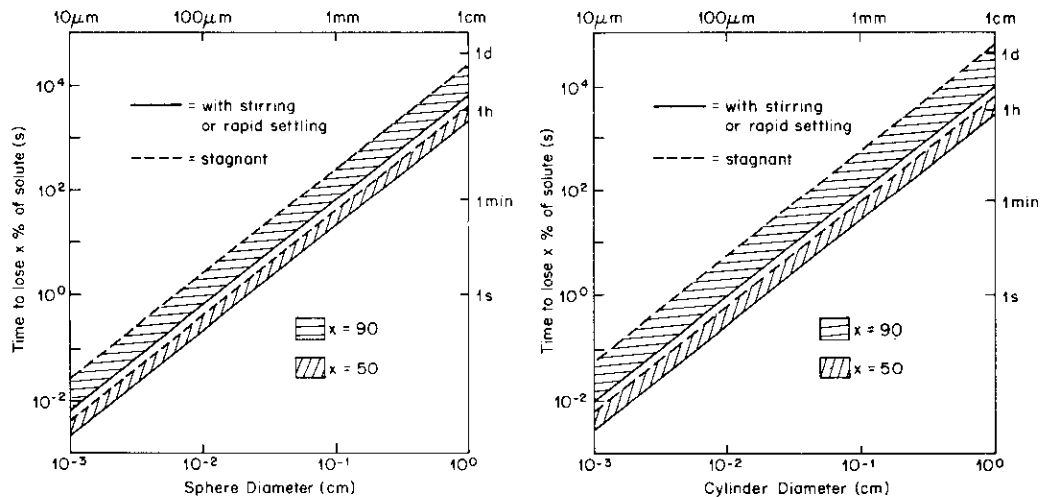


Fig. 2. Time required for elimination of 50 or 90% of the volumetrically integrated (within the pellet) concentration difference between a fecal pellet of a given shape and diameter and ambient seawater under varying conditions of fluid motion. Values outside the shaded areas are impossible under the assumptions specified in the text.

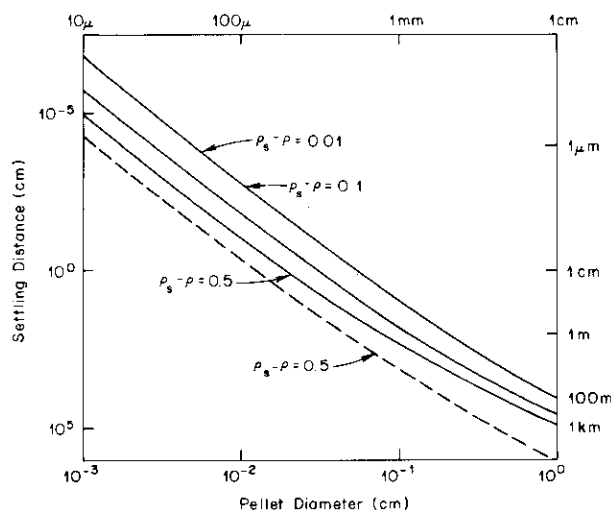


Fig. 3. Distance through which a pellet permeable to molecular diffusion would settle before losing either 50% (solid line) or 90% (dashed line) of the volumetrically integrated concentration difference in its solutes from the surrounding seawater. Settling velocities are calculated from the formulae of DIETRICH (1982) for smooth spheres. Settling of more cylindrical objects would be slightly slower (DIETRICH, 1982), but this difference would be offset by the slightly slower diffusion out of a cylinder vs a sphere.

pellet or high shear about the pellet) serve to keep the diffusional gradient steep. Figure 2 also displays a remarkable insensitivity to particle shape. Despite the fact that the geometry and hence diffusion of excess solute away from the pellet is fully three-dimensional in the spherical case and only two-dimensional in the modeled cylindrical case, diffusion kinetics are dominated by the shortest path to the ambient fluid, i.e. by the radius of the pellet. Thus they are slowed in cylinders vs spheres only to a small degree unless the water is stagnant and the last small fraction of equilibration is of concern (Fig. 2). The important consequence of rapid diffusion from pellets to issues of material cycling is that the great majority of excess solutes in freshly egested fecal pellets will remain in the water layer where egestion occurs (Fig. 3).

DISCUSSION

Intuition from the more familiar steady-state or quasi-steady-state models of diffusion (e.g. CSANADY, 1986) is misleading for this unsteady case, which has closer analogy with the excretory plumes of nitrogenous wastes treated by JACKSON (1980). The formula provided by JACKSON (1980, his equation 2) in fact could be integrated to give results similar to those of Fig. 2 under the constraints of square cross-section for the fecal pellet and of stagnant water (transport by molecular diffusion alone). Irrespective of fluid dynamic conditions, adjustment of the pelletal concentration toward ambient concentrations is remarkably fast (Fig. 2). For a pelletal diameter <1 mm, 50% of the concentration difference integrated over the volume of the pellet will be eliminated in <5 min, even in stagnant water (Fig. 2). It thus is no great wonder that the contribution of solutes from this source has not yet been resolved in laboratory and shipboard experiments. Diffusion of solutes from pellets thus also could explain the enigmatic short-term

“leakage (in soluble form) of ingested carbon” observed by PECHENIK (1979) and may be a major source of newly resolved amounts of DOC (SUGIMURA and SUZUKI, 1988). To examine the importance of this diffusional process, future experiments will have to be tailored to its inherently extremely short time scale.

It would be relatively easy to modify the calculations for Figs 2 and 3 to represent specific pelletal geometries. The settling velocity formulae of DIETRICH (1982) can be applied to more realistic shapes of pellets. Diffusion into and out of such bodies can be modeled by decomposing them into component shapes and using transfer coefficients appropriate to the resulting Sherwood numbers (e.g. KREITH, 1973; LIH, 1975). We forego these procedures for our crude analysis because of the shape and fluid-dynamic insensitivity demonstrated in Fig. 2. Further, there is a paucity of data verifying heat or mass transfer models at the larger end of the pelletal size scale (low end of the turbulent particle Reynolds number range). For the latter reason we have elected to be conservative in producing Fig. 3. For 10- and 100- μm particles, the calculations represent the lower bound of Sherwood numbers, because the particles are clearly in the Stokes range and Sherwood numbers never exceed 5.1, with 2 being the theoretical minimum for a sphere. For both 1- and 10-mm particles, we took a diffusion time that is the simple mean of the two fluid dynamic extremes of Fig. 2, although the true values are closer to the shorter extremes. The concave upward curvature in Fig. 3 and the convergence of lines for particles of differing specific gravities above 100 μm are due to the added turbulent drag on a sphere when the Stokes range is exceeded. Divergence of the dashed line for 90% loss is due to the slowed rate of diffusion over large radii and across flattened gradients.

Thus, the overwhelming portion of labile solutes will remain in the upper mixed layer rather than be lost to deeper water—even if originally enclosed in rapidly sinking pellets. Until pelletal diameters of order 1 cm and greater are attained, it is difficult to transport pelletal solutes out of the 10–100 m layer in which pellets are released (Fig. 3). Physical disintegration of pellets would further accelerate the loss. The same particles in the 250- to 500- μm diameter range, that are so effective in vertical particulate flux (MCCAVE, 1975), are ineffectual in carrying their solute loads. This result is all the more surprising since settling distance during loss of a given percentage of solute scales as the fourth power of pelletal diameter—because settling velocity and time to diffuse a given distance each scale with the square of pelletal diameter. Again, it would be difficult from purely observational approaches in mixed communities to separate diffusion of partially digested phytoplankton remains in pellets from phytoplankton leakage.

We suggest that a major reason why this otherwise obvious source of bacterial nutrition—solute diffusing from fecal pellets—has not received more attention is because it requires the connection of a functional response in animals with a population response in bacteria. Theory for crossing levels in the ecological hierarchy is poorly developed, with theories of interactions tightly centered on population–population effects. Further, there are many empirical studies that show good correlation between abundances of bacteria and phytoplankton (e.g. Fuhrman *et al.*, 1980; BIRD and KALFF, 1984), tempting one to infer direct phytoplankton leakage as the mechanism. What is easily forgotten is that grazers are ubiquitous in these systems and have gut residence times that readily can account for such correlations. When phytoplankton cell concentrations are higher, herbivores will egest a greater proportion of the food value in what they ingest (TANDE and SLAGSTAD, 1985, and references therein). Residence times of phyto-

plankton in guts or food vacuoles (minutes to tens of hours) fall in the appropriate range to be coupled to population responses in bacteria. A seasonal pattern with high bacterial growth at the end of a bloom—without more direct evidence in favor of one mechanism or the other—is no better evidence for direct phytoplankton leakage than for grazing release of DOC.

A second major reason why the animal feeding pathway to bacteria has been overlooked is that food-web models generally do not treat it. The focus in terrestrial food-web models has been on transfer in herbivore–carnivore–higher carnivore series, with detrital pathways generally treated separately. On the time scales considered by most terrestrial food-web models, appreciable fecal material of herbivores or carnivores does not re-enter the dominant herbivore–carnivore pathways of material flow. The predominance of microphagy among animals, the short generation times of plants, and the ability of water to transport (via advection and diffusion) both solutes and particles make this terrestrial mindset undesirable for aquatic applications.

Our analysis suggests that direct leakage from primary producers need not be the dominant DOC supply to bacteria. There are other reasons to believe that many published estimates of such leakage are inflated. Virtually any of the usual methods for separating solutes from solids can produce artifacts when applied to living organisms. Excessive pressure drops during filtration will release cell contents, but no methodology has yet provided unambiguous evidence that mild filtration is entirely free from such artifacts. We must concur with SHARP'S (1977) analysis that (p. 381), "Evidence of extensive excretion by phytoplankton is not good." A more recent analysis (BJØRNSSEN, 1988) concludes similarly that high percentages of excretion (relative to carbon fixation) and high absolute rates of excretion are unlikely to coincide, for there is little reason for a healthy (rapidly producing) cell to have a high percentage of excretion. Laboratory studies of unstressed, healthy cells generally do not show high percentages of excretion (LANCELET and BILLEN, 1985), and high percentages of *apparent* phytoplankton excretion reported from the field have not separated the contribution of the byproducts of animal digestion.

A telling fact is that contributions from both leakage during ingestion and diffusion from pellets repeatedly have been shown in combination to exceed 10% and reach as much as 30% of ingested carbon (CONOVER, 1966; JOHANNES and SATOMI, 1967; LAMPERT, 1978). Leakage during ingestion (sloppy feeding) could be well treated via the equations of JACKSON (1980), so we have not elaborated upon it here. We suggest that these earlier observations of high, feeding-induced DOC production have been ignored largely because, unlike the fate of the assimilated portion of carbon, there has been no theoretical framework for treating the fate of this material. We hope that theoretical approaches like JACKSON'S (1980) and ours can help to fill this void.

AZAM *et al.*'s (1983) classic synopsis of the microbial loop is frequently cited in support of high direct phytoplankton leakage rates and closure of the microbial loop by them. The data AZAM *et al.* (1983) give in their Fig. 1 come from JOIRIS *et al.* (1982), using the methods of LANCELET (1979). They were produced by straining whole seawater samples through the mesh (size not specified) of a zooplankton net prior to incubation with ^{14}C -labeled bicarbonate. We assume from the methods in similar experiments by LANCELET (1983) that the mesh size used was consistently 200 μm . Thus small metazoan grazers, not to mention Protozoa and phagotrophic algae, were certainly included. In any case this simple correlation based on field data is weak evidence for any particular mechanism of release of DOC from phytoplankton. Besides these data, perhaps the most frequently

cited evidence of apparent leakage comes from Hagström and coworkers (e.g. LARSSON and HAGSTRÖM, 1982), who used no prefiltration. Although their estimates of leakage are less excessive (10–16% of primary production), their measurements thus do not distinguish between direct leakage and digestive products.

Other evidence that sometimes is cited to indicate high direct leakage by phytoplankton is even less capable of identifying mechanisms of DOC transfer from phytoplankton to bacteria; it focuses on the heterotrophic bacterial demand (e.g. COLE *et al.*, 1982) rather than the DOC supply. Thus, contrary to the case for leakage during ingestion and diffusion from fecal pellets and to invocations in the titles of the above-referenced papers, we know of no published data that show convincing evidence of *direct* leakage rates in excess of 10% of primary production for any healthy marine phytoplankton population under natural conditions or well-simulated natural conditions. Such high leakage rates seem unlikely both on optimal foraging (by phytoplankton) grounds and because primary production is, by definition, an anabolic process in which the sizes of molecules are increased and their passive transport rates reduced.

The byproducts of ingestion and digestion are the natural targets of further research on the sources of organic matter for bacterial production. In some regions, macrozooplankton grazing can process over 60% of annual primary production (WELSCHMEYER and LORENZEN, 1985). In others (MARRA *et al.*, 1987) primary production and microzooplankton grazing have been shown to be equal on the time scale of a few days. To a first approximation (Fig. 1), all primary production is grazed, and so digestive production seems the only likely source of organic matter to fuel a level of bacterial production in excess of 10% of primary production. The need to find a single source of large magnitude has been eased somewhat by the re-analyses of STRAYER (1988) and SCAVIA (1988), who show that secondary production even at steady state can exceed primary production; but we believe that we have identified and given some of the peculiar kinetic characteristics of the dominant source. These peculiar kinetics of sloppy feeding and fecal leaching provide an alternative to rapid variation in phytoplankton physiology for explaining the time-varying kinetics of DOC appearance in incubations (LANCELET, 1979).

Our application of reactor theory coupled with diffusion from pellets thus in many ways directs attention toward unsteady conditions. Where and when would one expect especially large fluxes of carbon to become available to heterotrophic bacteria via the pathway of incomplete digestion and absorption by animals? In an animal operating to maximize rate of digestive production, feeding rate will be highest and assimilation efficiency lowest when food availability is greatest. Thus one would expect to see high fluxes along this pathway during bloom conditions, while food available per individual herbivore as well as abundance of herbivores remains high. Large fluxes of organic matter to bacteria via this route can be expected to occur while phytoplankton specific growth rate is still high and high percentages of direct excretion (relative to the magnitude of carbon fixation) would not be expected. If food abundance changes gradually, one can anticipate (HASSETT and LANDRY, 1983) selective pressure for changes in enzyme kinetics (i.e. in V_{max} and K_m of equation 2, with consequent changes in τ).

If our analysis is correct in identifying digestive byproducts as the dominant source of nutrition to heterotrophic bacteria, a consequence should be intense selective pressure on bacteria to approach this rapidly diffusing source of labile organic matter (cf. arguments of JACKSON, 1987). Paradoxically, the kinetics of diffusion of small molecules are so rapid, however, that the time for bacteria to find and attach (e.g. RIMES and

GOULDER, 1985) may be too long to offer much advantage as a point source. The advantage may accrue instead as a diffuse source (many distributed fecal pellets) to unattached bacteria. Alternatively, bacteria in the hindgut, either attached or in passage, may reap the major benefits of digestive byproducts. Digestion theory would suggest that a large portion of the variability observed in degree of bacterial colonization of guts and pellets (summarized in NAGASAWA and NEMOTO, 1988) as well as of exterior body surfaces (NAGASAWA, 1988) of marine animals may be due to varying lability of the food source. One would expect production of labile byproducts to be most striking in animals feeding on rich foods in times of plenty, i.e. under conditions of superfluous feeding. SEIDERER *et al.* (1987), for example, found that bacteria in guts benefited from the rich plant foods ingested by anchovies. Our early data for a benthic deposit feeder from intertidal sediments seasonally rich in diatoms are consistent with this suggestion (PLANTE *et al.*, in press). Conversely, it is not surprising to find thorough digestion and little regrowth of bacteria on substrates of poor food value (BOYLE and MITCHELL, 1978).

We conclude that there is ample reason for a clearer focus on dissolved organic byproducts of ingestion and digestion and suggest that the equations provided by JACKSON (1980) and the information of our Fig. 2 be used to set bounds on suitable time scales for experiments. We gladly concede that our estimates of diffusion times (Fig. 2) and settling distances (Fig. 3) may be radically wrong if diffusion is severely hindered by adsorption, ion exchange or impermeability of fecal membranes; but such an error would not endanger our primary conclusion that digestive byproducts are major sources of bacterial nutrition. It would simply alter the ratio of those byproducts that were effectively particulate at the point of pellet ejection and at various settling depths. With the digestion-theory formalism and an awareness of the short inherent time scales of unhindered solute release from fecal pellets, these issues can now be explored systematically.

Acknowledgements—The writing of this analysis was supported by ONR Contract N00014-87-C-0160 and NSF Grant OCE-8608157. Our thoughts and writings were clarified by K. Banse, B. Dade, J. Deming, A. Nowell, and an anonymous reviewer.

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