Limnol. Oceanogr., 42(2), 1997, 398–404

Accumulation of degradable DOC in surface waters: Is it caused by a malfunctioning microbial loop?

Abstract—Recent literature indicates that dissolved organic carbon (DOC) may accumulate in productive surface waters. Such accumulation will allow export of DOC to the aphotic zone by diffusion and downwelling. As an alternative to models based on low degradability, we here propose a mechanism where bacterial carbon consumption is restricted due to food web mechanisms controlling both growth and biomass of the bacteria: growth rate is kept low by bacteria–phytoplankton competition for mineral nutrients, and biomass is kept low by bacterial predators. With such a mechanism, otherwise degradable material may accumulate and become subject both to chemical transformation and vertical transport. The steady-states of a model describing the interactions between heterotrophic bacteria, phytoplankton, and bacterivorous protozoa is used to explore how the balance between DOC production and consumption shifts along a gradient from oligotrophy to eutrophy.

Recently obtained data (Copin-Montégut and Avril 1993; Carlson et al. 1994) and reexamination of old data (Williams 1995) suggest that dissolved organic carbon (DOC) may accumulate in the photic zone of the ocean during the productive season. Such accumulation will allow export of carbon to the aphotic zone through vertical mixing processes in the water column, and the process is, at least in oligotrophic areas, potentially more important than the transport via sinking particles (Copin-Montégut and Avril 1993; Carlson et al. 1994). Because the accumulation of DOC in surface waters is not stoichiometrically locked to the Redfield carbon : mineral nutrient ratio, because its export does not require import of new nutrients, and because the transport mechanism is by diffusion and advection rather than by sinking, such a biological dissolved C pump would function fundamentally different from the classical particle pump (Thingstad 1995). Accumulation can be explained if the DOC is assumed to be refractory (Legendre and Le Févre 1995). Such slowly degradable material may either originate from particular nondegradable components of biologic material (Brophy and Carlson 1989; Tanoue et al. 1995) or there may be processes in seawater converting material into chemically refractory forms (Keil and Kirchman 1994). As a variation on this theme, a slow hydrolyzing step from polymers to monomers may be the delaying mechanism (Billen 1990).

We here want to draw attention to the fact that such accumulation can also be explained within the framework of models assuming the material to be easily degradable. In such a model, the microbial loop may be malfunctioning in the restricted sense that it cannot consume all the degradable DOC released from the food web. This model can be combined with models linking food web structure with trophic status (Thingstad and Sakshaug 1990). Such a combination would give a model suggesting a shift from microbially dominated food webs exporting DOC in oligotrophic or semi-oligotrophic areas to systems dominated by classical food chains exporting carbon also via sinking particles in eutrophic areas.

With a ^{14}C age of deep-water DOC of ~4,000–6,000 yr (Druffel et al. 1992), the traditional view has been that oceanic DOC is essentially a nondynamic refractive pool. For the surface water, the view of extreme recalcitrance of nearly the whole DOC pool has, however, been challenged by increasing evidence that release and consumption of DOC in the oceans' photic zone may not be tightly coupled (Carlson et al. 1994; Williams 1995; Zweifel et al. 1995). Around 10–15% to as much as 40–50% of the DOC has been found to be biologically degradable (Ogura 1972; Servais et al. 1987; Kirchman et al. 1991), with 19% found as a mean in a recent review (Søndergaard and Middelboe 1995). For samples taken during the spring bloom on Georges Bank, before the depletion of nitrate, only a small fraction was found to be labile (Chen et al. 1996). After blooms of diatoms (Ittekot 1982) and *Phaeocystis* (Billen and Fontigny 1987), DOC has been found to increase temporarily by as much as ~280 and ~380 μM C. Several studies of the vertical distribution of DOC have also demonstrated a gradient in DOC between surface waters and the deep aphotic zone (Table 1). The existence of such a gradient indicates that, given sufficient time, the accumulated DOC must be degradable in the chemical and physical environment of the aphotic zone. The concentration difference between the top layer and deep waters can be taken as an estimate of the concentration of such potentially degradable DOC. Such estimations give very variable results (Table 1). Levels of at least 50 μM C seem, however, obtainable even in fairly oligotrophic regions. An example is the northwest Mediterranean (Copin-Montégut and Avril 1993). In these waters the DOC accumulated may seem very large when compared to total microbial biomass, which is typically ~4–5 μM C (Rassoulzadegan et al. 1988), but similar numbers for DOC and particulate organic carbon are also cited by Williams (table 2 of Williams 1995) based on data from other areas.

Reviewing older data from the coasts of the Netherlands, California, and western Canada, Williams (1995) concluded that there is a clear seasonal pattern in DOC accumulation. Newer data based on high-temperature catalytic oxidation confirm a seasonality in other areas such as the Baltic Sea (Zweifel et al. 1995), the northwestern Mediterranean (Copin-Montégut and Avril 1993), and the Sargasso Sea (Carlson et al. 1994). Both in the Mediterranean (Copin-Montégut and Avril 1993) and in the Sargasso Sea (Carlson et al. 1994), the pattern of change indicates that DOC still remaining in the photic zone at the time of winter mixing of the water column may be transported down by the deep mixing processes.

Closely related to the balance between release and con-

Table 1. Surface and deep water concentrations of DOC in different areas.

Area	DOC surface (μM C)	DOC deep water (μM C)	Depth (m)	Reference
Baltic Sea	300	280	200	Zweifel et al. 1995
Mediterranean Sea	92	50	2,000	Copin-Montégut and Avril 1993
North Atlantic	71	50	5,000	Pakulski and Benner 1994
Sargasso Sea	110	92	4,500	Druffel et al. 1992
Sargasso Sea	90	55	250	Carlson et al. 1994
S. California Bight	60	50	900	Williams 1986
Gulf of Mexico	118	70	500	Pakulski and Benner 1994
North-central Pacific	72	34	6,000	Druffel et al. 1992
Equatorial Pacific	64	60	4,000	Pakulski and Benner 1994
Georges Bank	72–85	54–56	200–1,500	Chen et al. 1996

sumption of DOC is the concept of the microbial loop (Azam et al. 1983). In a generalized version this may be seen as the consortium of mechanisms whereby organic carbon is diverted as DOC from the upward flux of particulate organic carbon toward higher trophic levels, and recycled to the bottom of the food chain. There it may (or perhaps may not) be reincorporated into particulate form by uptake into heterotrophic bacteria. A multitude of these diverting mechanisms have been suggested in the literature, including passive (Bjørnsen 1988) and active (Williams 1990) excretion by phytoplankton, sloppy feeding and excretion by protozoan and by metazoan grazers (Eppley et al. 1981; Jumars et al. 1989), and viral lysis (Bratbak et al. 1992). The latter may in principle occur at all trophic levels. As events of presumably large local significance one could also include in such a scheme higher trophic level processes such as fish spawning (Dundas 1985).

All explanations of accumulation based on low degradability imply that bacterial growth rate is carbon limited. There are, however, indications in the literature suggesting that this is not always the case; examples include stimulation of bacterial growth by addition of phosphate to water samples from the northwestern Mediterranean (Zweifel et al. 1993; Thingstad et al. unpubl.) and the Gulf of Mexico (Pomeroy et al. 1995), and large luxury consumption of phosphate by the bacterial size fraction during short-time incubation of samples from the brackish layer of Norwegian fjords (Thingstad et al. 1993). Whether bacterial mineral nutrient limitation is a feature particular to P-deficient environments is so far not known. The relatively high P content of bacterial biomass (Norland et al. 1995) would be expected to contribute to such a difference.

The simple assumption that autochthonously produced degradable DOC accumulates due to mineral nutrient limitation of bacteria creates, however, a variation of Hutchinson's paradox (Hutchinson 1961). If, as is usually assumed, bacteria are better competitors for mineral nutrients than are phytoplankton, why do they not outcompete phytoplankton, thereby reducing the release of organic carbon in the system until the bacteria become C limited? Such an argument might (incorrectly) seem to suggest that mineral nutrient limitation of heterotrophic bacteria is an unstable situation without the potential to explain long-term accumulation of degradable DOC.

Further complications to this situation are introduced if one considers the potential effects of oligotrophy and eutrophy. A eutrophic community, rich in mineral nutrients to be shared among the different compartments of the food chain, might be expected to have a high rate of DOC release due to contribution from abundant populations at numerous trophic levels. On the other hand, carbohydrate release from nutrient-limited phytoplankton might be speculated to be a feature of oligotrophic systems, although oligotrophy is not always thought to imply severe mineral nutrient limitation of phytoplankton growth rate (Goldman et al. 1979). Whether the bacterial consumption rate can adjust to such changes in release is, however, not immediately obvious.

We here explore an idealized model of microbial trophic interactions containing what we think is close to the minimum number of elements required to qualitatively explain the principles regulating the balance between release of degradable DOC and its consumption by bacteria. The model is deliberately kept simple to emphasize such principles, rather than involving all biological and physical detail suspected to interfere. The flow structure of the limiting element in our model includes (Fig. 1) phytoplankton (A) and bacteria (B) competing for the mineral nutrient (N), and protozoa (P) preying on bacteria. N, A, B, and P denote the concentration of the limiting element in the pools of free nutrients, phytoplankton, bacteria, and protozoa, respectively.

Additionally, we make the following assumptions: The phytoplankton-specific growth rate μ_A is limited by the mineral nutrient concentration N so that $\mu_A = \alpha_A N$, where α_A is the algal affinity for the dissolved mineral nutrient N. The bacteria are either mineral nutrient or carbon limited, so that either the specific bacterial growth rate is $\mu_B = \alpha_B N$ (mineral nutrient limitation) or bacterial production is $Y_B \psi$ (C limitation). Y_B is here the yield of bacteria on organic material assumed to be autochthonously produced in the system at rate ψ. The bacterial predator is assumed to be food limited so that the specific growth rate of the bacterivorous protozoa can be described by the simple product $Y_P \alpha_P B$, where Y_P is the yield of protozoa on their bacterial prey and α_P is their affinity (i.e. clearance rate) for bacterial prey. Loss due to higher predators, viruses, or other mechanisms is represented by specific death rates δ_B, δ_A, and δ_P for bacteria, phytoplankton and protozoa, respectively. We also assume that these loss processes instantaneously return the mineral nutrient to

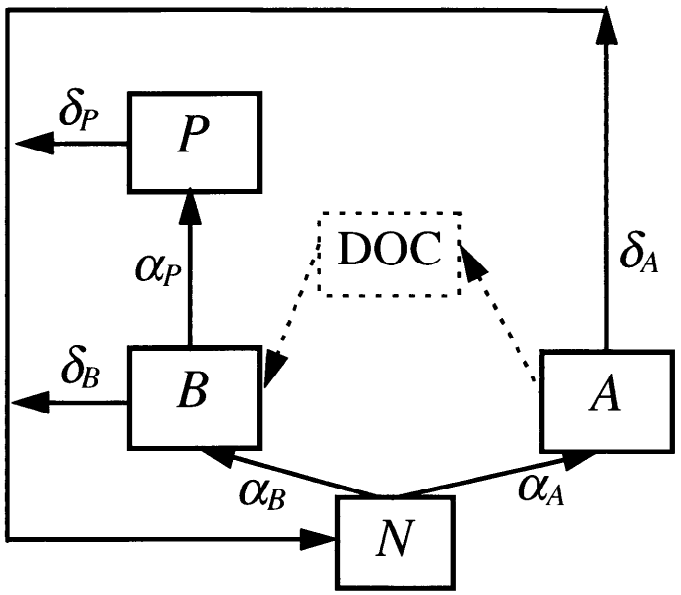

Fig. 1. Flow structure of the model. N, A, B, and P denote concentration of the limiting element in free mineral nutrients, phytoplankton, bacteria, and bacterivorous protozoa, respectively. Solid arrows denote the flows of the mineral nutrient, dotted arrows the flows of DOC. Mineral nutrients lost from any population by processes (e.g. predation, viral lysis) are assumed to be instantaneously returned to the pool N of free mineral nutrients. δ values are specific loss rates from the populations; α values are affinities for nutrient uptake. The effects of more complicated models for production of DOC and of variable loss rates from A, B, and P are discussed in the text.

the pool of dissolved mineral nutrient (arrows from B, A, and P back to N in Fig. 1). Initially we assume all δ values to be constants. The system is assumed to be closed with respect to the limiting element so that there is a given total concentration N_T, to be shared among the pools N, A, B, and P. N_T will be termed enrichment of the system and is a measure of the degree of oligotrophy/eutrophy. For the sake of illustration of the principles behind the balance between release and consumption of DOC, we initially make the simplifying assumption that DOC release rate ψ is proportional to phytoplankton biomass (Bjørnsen 1988), i.e. $\psi = kA$.

By expressing all of N, A, B, and P in nutrient units, Y_P becomes the fraction of nutrient in the prey incorporated into predator biomass, while Y_B can be expressed as $(1 - r)f_B$, where r is the fraction of the organic substrate respired and f_B is the nutrient : carbon ratio of bacterial biomass.

The differential equations describing the changes in populations as growth minus sum of losses are given in Table 2. Equilibrium solutions for N^*, B^*, P^*, and A^* (the asterix is used throughout to denote equilibrium values) will in general be functions of N_T. The requirement that all variables must have non-negative solutions gives four different regions for N_T with qualitatively different solutions (Table 3). The case of main interest here is region Ω_4 where all three populations are present and bacteria are mineral nutrient limited. The three other regions are briefly characterized as follows. For N_T in Ω_1, there is not enough nutrients for phytoplankton to balance loss with growth; all of the limiting element exist as free mineral nutrients (N^*). For N_T in Ω_2, phytoplankton must have a constant growth rate balancing their loss rate. Concentration of free mineral nutrients therefore remain constant. Phytoplankton (A^*) increase linearly with N_T, and bacteria (B^*) increase proportionally to phytoplankton. Bacteria are C limited and consume as much mineral nutrients as they need to consume all the DOC produced. For N_T in Ω_3, the concentration of bacteria (B^*) has reached the level where predator growth balances loss. Bacterial biomass (B^*) remains constant at this level, while phytoplankton and protozoa increase with N_T. Because bacteria are still C limited, their growth rate increase with the increasing rate of supply of DOC. In this situation, concentration of free mineral nutrients (N^*) remains constant and bac-

Table 2. Equations describing the flow of limiting elements within the food web of Fig. 1.

The differential equation describing changes in populations as the difference between growth and losses are:

Phytoplankton:
$$\frac{dA}{dt} = \alpha_A NA - \delta_A A \qquad (1)$$

Bacterial predators:
$$\frac{dP}{dt} = Y_P \alpha_P BP - \delta_P P \qquad (2)$$

Bacteria:

When mineral nutrient limited
$$\frac{dB}{dt} = \alpha_B NB - \alpha_P BP - \delta_B B \qquad (3a)$$

When C limited
$$\frac{dB}{dt} = Y_B \psi - \alpha_P BP - \delta_B B \qquad (3b)$$

Additionally, there is the mass balance requirement that the sum of the different pools equals the system nutrient richness N_T:
$$N_T = N + A + B + P. \qquad (4)$$

By using the equilibrium condition that all three differentials must equal zero, this gives four algebraic equations that can be solved for the four variables. N, A, B, and P as functions of enrichment N_T. With the additional requirement that all variables must be greater than or equal to zero, this gives the solutions listed in Table 3 and shown graphically in Fig. 2.

Table 3. Equilibrium solutions for the model in Table 2. Solutions shown graphically in Fig. 2 are functions of enrichment N_T. Mineral nutrient limitation of bacteria and accumulation of degradable DOC occurs when N_T is in region Ω_4. Other characteristics of the four regions (Ω_1–Ω_4) for N_T are given in the text.

Region containing N_T	N^*	A^*	B^*	P^*
Ω_1	N_T	0	0	0
Ω_2	$\frac{\delta_A}{\alpha_A}$	$\frac{N_T - N^*}{1 + Y_B k/\delta_B}$	$\frac{Y_B k/\delta_B (N_T - N^*)}{1 + Y_B k/\delta_B}$	0
Ω_3	$\frac{\delta_A}{\alpha_A}$	$N_T - N^* - B^* - P^*$	$\frac{\delta_P}{Y_P \alpha_P}$	$\frac{N_T - N^* - (1 + \delta_B/kY_B)B^*}{1 + \alpha_P B^*/kY_B}$
Ω_4	$\frac{\delta_A}{\alpha_A}$	$N_T - N^* - B^* - P^*$	$\frac{\delta_P}{Y_P \alpha_P}$	$\alpha_P^{-1}\left(\frac{\alpha_B}{\alpha_A}\delta_A - \delta_B\right)$

terial growth rate cannot increase beyond what is possible for this value of N^*. When this growth rate is reached (for $N_T = N_T^C$ in Fig. 2), the system shifts into region Ω_4 and mineral nutrient limitation of bacteria. In Ω_4, N^*, B^*, and P^* remain independent of N_T (Table 3). As long as the loss rates (δ_A, δ_B, and δ_P) are assumed constant and bacteria are mineral nutrient limited, the degree of eutrophication will only affect the phytoplankton biomass A^*. Interestingly, this pattern is similar to the observation of Cho and Azam (1990) of bacteria becoming increasingly dominant relative to phytoplankton along a gradient toward oligotrophic systems.

Bacterial consumption (ϕ) of DOC is (by definition) given as bacterial production ($\mu_B B$) divided by the yield (Y_B):

$$\phi = Y_B^{-1}\mu_B B, \tag{5}$$

which upon insertion gives the consumption rate at equilibrium:

$$\phi = (1 - r)^{-1} f_B^{-1} Y_P^{-1} \frac{\alpha_B}{\alpha_A \alpha_P} \delta_A \delta_P. \tag{6}$$

In Ω_4 where equilibrium release rate ψ^* for DOC exceeds consumption rate ϕ^*, there will be a net accumulation of autochthonously released DOC (at rate $\psi^* - \phi^*$) as shown in Fig. 2. Accumulation will continue until a level where loss through other processes, such as export by turbulent vertical diffusion, balances the excess release. The reason for the inability of bacteria to consume all DOC produced in region Ω_4 is the combination of top-down control (from predation) of biomass and bottom-up control (from competition) of growth rate. Low biomass can thus not be compensated by high growth rate or vice versa.

In Ω_4, algal biomass is the only equilibrium value changing with N_T (as long as the δ values are assumed constant). Increased N_T will thus lead to increased DOC release, while

Table 4. Symbols used. Suggested numerical values for a P limited system used to compute the steady-state solutions shown in Fig. 2.

Enrichment (sum of limiting element in all pools)	N_T	
Free mineral nutrients	N	
Phytoplankton biomass (in nutrient units)	A	
Bacterial biomass	B	
Biomass of predators on B	P	
Biomass of common predator on A and P	C	
Algal affinity for mineral nutrient	α_A	5 liters (μmol P)$^{-1}$ h^{-1}
Bacterial affinity for mineral nutrient	α_B	10 liters (μmol P)$^{-1}$ h^{-1}
Clearance rate (affinity) of predator on B	α_P	4 liters (μmol P)$^{-1}$ h^{-1}
Clearance rate (affinity) of predator on A and P	α_C	
Specific algal loss rate	δ_A	0.01 h^{-1}
Specific bacterial loss rate (apart from predation)	δ_B	0.01 h^{-1}
Specific loss rate of bacterial predator	δ_P	0.01 h^{-1}
Fraction of bacterial nutrient incorporated into predator	Y_P	0.5
Fraction of consumed DOC respired by bacteria	r	0.7
P:C ratio of bacterial biomass	f_B	0.02 mol P (mol C)$^{-1}$
DOC release rate by phytoplankton	k	5 mol C (mol P)$^{-1}$ h^{-1}
Bacterial consumption rate for DOC	ϕ	
Rate of production of DOC from the food web	ψ	
Specific growth rate of phytoplankton	μ_A	
Specific growth rate of bacteria	μ_B	
ith range for N_T, corresponding to one type of solution to the model in Table 2	Ω_i	

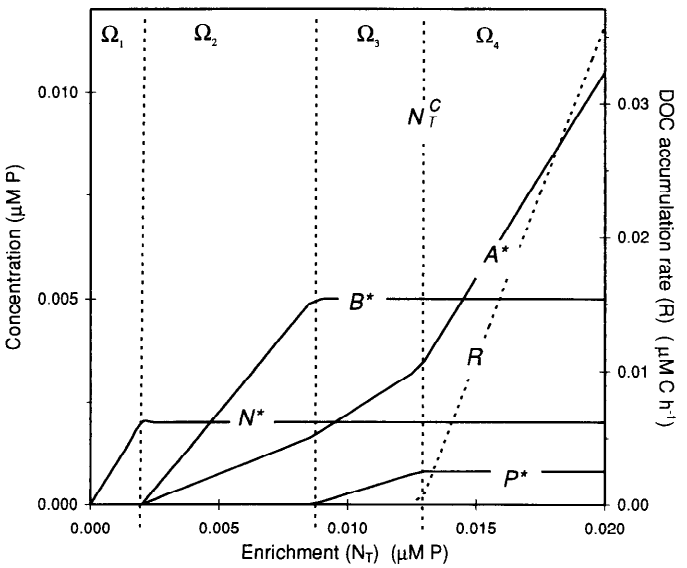

Fig. 2. Steady-state solutions N^*, B^*, A^*, and P^* to the model in Table 2 drawn as functions of system enrichment N_T (formulas given in Table 3). Dotted vertical lines indicate transition between regions Ω_1–Ω_4 where there is a qualitative change in the steady-state solution. For region Ω_4 ($N_T > N_T^C$), there is a net rate of DOC accumulation (dotted line marked R). Parameter values used to compute the curves are given in Table 2.

consumption will remain constant. An analytical expression for N_T^C, the critical enrichment defining the left border of region Ω_4 (*see Fig.* 2), can be found from the requirement that DOC release by phytoplankton balance consumption by mineral nutrient limited bacteria, i.e. that $\psi^* = \phi^*$. By using Eq. 6 and expressions in Table 3, this gives:

$$N_T^C = \alpha_A^{-1}\delta_A + Y_P^{-1}\alpha_P^{-1}\delta_P - \alpha_P^{-1}\delta_B + \frac{\alpha_B}{\alpha_A\alpha_P} \times \delta_A[1 + k^{-1}(1 - r)^{-1}f_B^{-1}Y_P^{-1}\delta_P]. \quad (7)$$

The position of this point on the N_T scale is thus a feature of the total system and involves all parameters of the model. Although these parameters have straightforward biological interpretations, there is considerable freedom in estimating their values. The value of N_T^C is sensitive to the three loss rates (δ values) as well as to the relative and absolute magnitudes of the three affinities (α values). As an illustration for a P-limited system, the parameters suggested in Table 3 are used in drawing Fig. 2 and give a change to P-limited bacteria as N_T increases beyond ~12 nM P, i.e. corresponding to somewhere in the order of 1 μM C in microbial biomass. Both the release mechanism for DOC and the parameter values chosen can be questioned, but adding more release mechanisms (e.g. viral lysis and sloppy feeding) would extend the Ω_4 region toward lower N_T. The region giving DOC accumulation would thus extend farther into the oligotrophic region. At some sufficiently low value for N_T, however, bacterial growth rate must become C limited due to lack of primary production of organic material.

In Fig. 2, the eutrophic end of the N_T scale will always correspond to mineral nutrient-limited bacteria and DOC accumulation. This result may, however, be a function of our assumption that the specific loss rates of phytoplankton and bacterial predators (δ_A and δ_P) are constants. If we modify our model and assume that these loss rates are dominated by a ciliate-type predator that can feed on both phytoplankton and the bacterial predator with the same clearance rate α_C, we can replace $\delta_A = \delta_P = \alpha_C C$, where C is ciliate biomass. This gives bacterial carbon consumption (by insertion into Eq. 6):

$$\phi^* = (1 - r)^{-1}f_B^{-1}Y_P^{-1}\frac{\alpha_B}{\alpha_A\alpha_P}\alpha_C^2C^2. \quad (8)$$

Increasing system enrichment N_T in the type of models used here will lead to increases in the population sizes of higher predators (Thingstad and Sakshaug 1990). Eq. 8 thus implies that bacterial consumption will increase with N_T. Whether there will be a shift back to C-limited bacteria at higher N_T (i.e. whether there is a right border to Ω_4) thus depends upon what processes increase most with N_T—production ψ^* or bacterial consumption ϕ^*. It is possible to make such models where DOC accumulation is a phenomenon only for intermediary values of enrichment N_T (results not shown). A realistic model describing this would be fairly complex since it would require both a food web model describing how new phytoplankton and new predators establish as a function of N_T, as well as physiological models describing how these populations release DOC.

The experimental indications of P-limited bacterial growth rates in environments as diverse as the northwestern Mediterranean (Thingstad and Rassoulzadegan 1995), the Gulf of Mexico (Pomeroy et al. 1995), and Norwegian fjords (Thingstad et al. 1993) suggest that Ω_4 may cover a fairly broad range of N_T values in P-limited systems. Support for the idea that Ω_4 may extend to high values of N_T is also found in the recent review of Søndergaard and Middelboe (1995) where they conclude that there is more labile DOC in eutrophic than in oligotrophic areas. In the context of the model suggested here, this would be explained as the sum of release processes increasing faster than the degradation process with increasing eutrophication, rather than by a low half-saturation constant for bacterial consumption as suggested by Søndergaard and Middelboe.

Billen et al. (1990) have explored a model essentially analogous to the DOC/bacteria/bacterial predator subsystem of the model used here; they assumed bacteria to be C limited and predator death rate (δ_P) to be constant. From their experimental data, which showed a large increase in B and a relatively smaller increase in μ_B with increasing bacterial production ($=\mu_B B$), they concluded that bacteria are to a larger extent bottom-up (substrate) rather than top-down (predator) controlled. In the more generalized framework of the model presented here, a large change in B could be interpreted as a large increase in the predatory pressure on bacterial predators (an increase in δ_P). A relatively small change in N^*, and thus in μ_B for mineral nutrient-limited bacteria, could be interpreted as a relatively smaller increase in phytoplankton predation (i.e. in δ_A). In a more elaborate model allowing increased eutrophication to lead to establishment of competing phytoplankton species of larger cells, N^* would also be kept low (Thingstad and Sakshaug 1990).

The theory also suggests the need for testing in experimental model systems since a food web containing phytoplankton, bacteria, and bacterial predators should result in little degradation of allochthonosly added DOC, and at the same time allow algal–bacterial coexistence. This corresponds exactly to the result found by Pengerud et al. (1987).

Competition–predation models including different size classes of phytoplankton and predators (Thingstad and Sakshaug 1990; Armstrong 1994) describe how higher predators and larger species of competing algae establish as a response to increasing N_T. The result of increasing enrichment is thus a shift toward systems dominated by a classical food chain that exports carbon as sinking POC. Combination of such models with the model discussed here thus gives a consistent framework within which we can explain a shift from communities dominated by small microbial organisms with a potential for DOC export in oligotrophic (low N_T) areas to communities dominated by a classical food chain and particle export in eutrophic (high N_T) areas.

An aspect of region Ω_4 of additional interest is that viral lysis of bacteria (represented here by δ_B) has no effect, neither on bacterial biomass nor on bacterial growth rates (*see* expressions for N^* and B^* in Table 3). The consumption rate for DOC thus remains independent of whether viral lysis of bacteria is assumed or not. In region Ω_4, bacterial viruses will act essentially as competitors to bacterial predators, reducing the biomass of these (*see* expression for P^* in Table 3) and allow more of the available nutrient to accumulate in phytoplankton biomass.

Another point of interest is that this model suggests a solution to the apparent paradox of nutrient-limited phytoplankton stimulating their bacterial competitors by DOC excretion (Bratbak and Thingstad 1985); if region Ω_4 is large (i.e. if mineral nutrient limitation of bacteria is the rule rather than the exception), bacteria will simply not be stimulated by increased DOC supply.

In nature, the combined competition/predation-based explanation for DOC accumulation suggested above would probably not function in isolation. With increased concentrations and turnover time of degradable DOC in the photic zone, the importance of chemical and photochemical transformations modifying organic material to more (Keil and Kirchman 1994) or less (Lindell et al. 1995) refractive compounds would be expected to increase.

The high C : N ratios of accumulated DOM found by Williams (1995) can be explained within the framework of this model by assuming, for example, carbohydrate excretion by nutrient-limited phytoplankton as the main mechanism of release or by additional mechanisms such as a preferential degradation of dissolved organic forms containing N or P. It is actually more difficult to explain why dissolved organic forms of N (Duursma 1961; Williams 1995) and P (Duursma 1961; Thingstad and Rassoulzadegan 1995) apparently also accumulate during at least parts of the productive season. This phenomenon is not readily accounted for by the trophic mechanisms suggested here, and is probably an indication that a complete picture requires consideration also of interactions between these trophic mechanisms and mechanisms producing refractory DOM.

From the above analysis, the nature of what limits bacterial growth rates would seem to be a key aspect for understanding the regulation of the balance between DOC release and consumption. More experimental information on this under variable conditions such as how it correlates with areas where primary production is N, P, or Fe limited, and how it correlates with system oligotrophy and eutrophy, would therefore seem crucial for our understanding of the mechanisms mediating DOC accumulation and export.

Our use of the term "malfunctioning" microbial loop has been strictly in the sense of a DOC consumption unable to match DOC release. From other perspectives, such as a possible storage of energy in the ecosystem for consumption during dark and unproductive seasons, or for oceanic sequestration of carbon from the atmosphere, the proposed malfunctioning microbial loop may indeed function very well.

T. Frede Thingstad

Department of Microbiology
University of Bergen
Jahnebk. 5
N-5020 Bergen, Norway

Åke Hagström

Danish Environmental Research Institute
Fredriksborgv. 399, BP 358
DK-4000 Roskilde, Denmark

Fereidoun Rassoulzadegan

Station Zoologique
BP 28
F-06230 Villefranche-Sur-Mer, France

References

ARMSTRONG, R. A. 1994. Grazing limitation and nutrient limitation in marine ecosystems: Steady state solutions of an ecosystem model with multiple food chains. Limnol. Oceanogr. **39:** 597–608.

AZAM, F., T. FENCHEL, J. G. FIELD, J. S. GRAY, L. A. MEYER-REIL, AND F. THINGSTAD. 1983. The ecological role of water column microbes in the sea. Mar. Ecol. Prog. Ser. **10:** 257–263.

BILLEN, G. 1990. Delayed development of bacterioplankton with respect to phytoplankton: A clue to understanding their trophic relationships. Ergeb. Limnol. **34:** 191–201.

———, AND A. FONTIGNY. 1987. Dynamics of a *Phaeocystis*-dominated bloom in Belgian coastal waters. 2. Bacterioplankton dynamics. Mar. Ecol. Prog. Ser. **37:** 249–257.

———, P. SERVAIS, AND S. BECQUEVORT. 1990. Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: Bottom-up or top-down control? Hydrobiologia **207:** 37–42.

BJØRNSEN, P. K. 1988. Phytoplankton exudation of organic matter: Why do healthy cells do it? Limnol. Oceanogr. **33:** 151–154.

BRATBAK, G., M. HELDAL, T. F. THINGSTAD, B. RIEMANN, AND O. H. HASLUND. 1992. Incorporation of viruses into the budget

Acknowledgments

This work was supported by the commission of the European Communities, grants MAS2-CT93-0063 ("Medipelagos"), MAS2-CT92-0031 ("Meice"), and MAS3-CT95-0016 ("Medea").

of microbial C-transfer. A first approach. Mar. Ecol. Prog. Ser. **83:** 273–280.

———, AND T. F. THINGSTAD. 1985. Phytoplankton–bacteria interactions: An apparent paradox? Analysis of a model with both competition and commensalism. Mar. Ecol. Prog. Ser. **25:** 23–30.

BROPHY, J. E., AND D. J. CARLSON. 1989. Production of biologically refractory dissolved organic carbon by natural seawater microbial populations. Deep-Sea Res. **36:** 497–507.

CARLSON, C. A., H. W. DUCKLOW, AND A. F. MICHAELS. 1994. Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. Nature **371:** 405–408.

CHEN, R. F., B. FRY, C. S. HOPKINSON, D. J. REPETA, AND E. T. PELTZER. 1996. Dissolved organic carbon on Georges Bank. Cont. Shelf Res. **16:** 409–420.

CHO, B. C., AND F. AZAM. 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Mar. Ecol. Prog. Ser. **63:** 253–259.

COPIN-MONTÉGUT, G., AND B. AVRIL. 1993. Vertical distribution and temporal variation of dissolved organic carbon in the north-west Mediterranean Sea. Deep-Sea Res. I **40:** 1963–1972.

DRUFFEL, E. R. M., P. M. WILLIAMS, J. E. BAUER, AND R. ERTEL. 1992. Cycling of dissolved and particulate organic matter in the open ocean. J. Geophys. Res. **97:** 639–659.

DUNDAS, I. E. D. 1985. Fate and possible effects of excessive sperm released during spawning. Mar. Ecol. Prog. Ser. **30:** 287–290.

DUURSMA, E. K. 1961. Dissolved organic carbon, nitrogen, and phosphorus in the sea. Neth. J. Sea Res. **1:** 1–148.

EPPLEY, R. W., S. G. HORRIGAN, J. A. FUHRMAN, E. R. BROOKS, C. C. PRICE, AND K. SELLNER. 1981. Origins of dissolved organic matter in southern California coastal waters: Experiments on the role of zooplankton. Mar. Ecol. Prog. Ser. **6:** 149–159.

GOLDMAN, J. C., J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature **279:** 210–215.

HUTCHINSON, G. E. 1961. The paradox of the plankton. Am. Nat. **45:** 137–145.

ITTEKOT, V. 1982. Variations of dissolved organic matter during a plankton bloom: Qualitative aspects based on sugar and amino-acid analysis. Mar. Chem. **4:** 143–158.

JUMARS, P. A., D. L. PENRY, J. A. BAROSS, M. J. PERRY, AND B. W. FROST. 1989. Closing the microbial loop: Dissolved organic carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and adsorption in animals. Deep-Sea Res. **36:** 483–495.

KEIL, R. G., AND D. L. KIRCHMAN. 1994. Abiotic transformation of labile protein to refractory protein in sea water. Mar. Chem. **45:** 187–196.

KIRCHMAN, D. L., Y. SUZUKI, C. GARSIDE, AND H. W. DUCKLOW. 1991. High turnover rates of dissolved organic carbon during a spring phytoplankton bloom. Nature **352:** 612–614.

LEGENDRE, L., AND J. LE FÉVRE. 1995. Microbial food webs and the export of biogenic carbon in the oceans. Aquat. Microb. Ecol. **9:** 69–77.

LINDELL, M. J., W. GRANÉLI, AND L. J. TRANVIK. 1995. Enhanced bacterial growth in response to photochemical transformation of dissolved organic matter. Limnol. Oceanogr. **40:** 195–199.

NORLAND, S., K. M. FAGERBAKKE, AND M. HELDAL. 1995. Light element analysis of individual bacteria by X-ray microanalysis. Appl. Environ. Microbiol. **61:** 1357–1362.

OGURA, N. 1972. Rate and extent of decomposition of dissolved organic matter in surface seawater. Mar. Biol. **13:** 89–93.

PAKULSKI, J. D., AND R. BENNER. 1994. Abundance and distribution of carbohydrates in the ocean. Limnol. Oceanogr. **39:** 930–940.

PENGERUD, B., E. F. SKJOLDAL, AND T. F. THINGSTAD. 1987. The reciprocal interaction between degradation of glucose ecosystem structure. Studies in mixed chemostat cultures of marine bacteria, algae, and bacterivorous nanoflagellates. Mar. Ecol. Prog. Ser. **35:** 111–117.

POMEROY, L. R., J. E. SHELDON, W. M. SHELDON, JR., AND F. PETERS. 1995. Limits to growth and respiration of bacterioplankton in the Gulf of Mexico. Mar. Ecol. Prog. Ser. **117:** 259–268.

RASSOULZADEGAN, F., M. LAVAL-PEUTO, AND R. W. SHELDON. 1988. Partitioning of the food ration of marine ciliates between pico- and nanoplankton. Hydrobiologia **159:** 75–88.

SERVAIS, P., G. BILLEN, AND M.-C. HASCOET. 1987. Determination of the biodegradable fraction of dissolved organic matter in waters. Water Res. **21:** 445–450.

SØNDERGAARD, M., AND M. MIDDELBOE. 1995. A cross-system analysis of labile dissolved organic carbon. Mar. Ecol. Prog. Ser. **118:** 283–294.

TANOUE, E., S. NISHIYAMA, M. KAMO, AND A. TSUGITA. 1995. Bacterial-membranes—possible source of a major dissolved protein in seawater. Geochim. Cosmochim. Acta. **59:** 2643–2648.

THINGSTAD, T. F. 1995. Feedback mechanisms between degradation and primary production in the marine pelagic environment. *In* M. A. Beran [ed.], Carbon sequestration in the biosphere. NATO ASI Series Vol. 133. Springer-Verlag.

———, AND F. RASSOULZADEGAN. 1995. Nutrient limitations, microbial food webs, and "biological C-pumps": Suggested interactions in a P-limited Mediterranean. Mar. Ecol. Prog. Ser. **117:** 299–306.

———, AND E. SAKSHAUG. 1990. Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. Mar. Ecol. Prog. Ser. **21:** 47–62.

———, E. F. SKJOLDAL, AND R. A. BOHNE. 1993. Phosphorus cycling and algal-bacterial competition in Sandsfjord, western Norway. Mar. Ecol. Prog. Ser. **99:** 239–259.

WILLIAMS, P. J. LE B. 1990. The importance of losses during microbial growth: Commentary on the physiology, measurement and ecology of the release of dissolved organic material. Mar. Microb. Food Webs **4:** 175–206.

———. 1995. Evidence for seasonal accumulation of carbon-rich dissolved organic material, its scale in comparison with changes in particulate material and the consequential effect on net C/N assimilation ratios. Mar. Chem. **51:** 17–29.

WILLIAMS, P. M. 1986. Chemistry of the dissolved and particulate phases in the water column, p. 53–82. *In* R. W. Eppley [ed.], Plankton dynamics of the Southern California Bight. Springer.

ZWEIFEL, U. L., B. NORRMAN, AND Å. HAGSTRÖM. 1993. Consumption of dissolved organic carbon by bacteria and demand for inorganic nutrients Mar. Ecol. Prog. Ser. **101:** 23–32.

———, J. WIKNER, AND Å. HAGSTRÖM. 1995. Dynamics of dissolved organic carbon in a coastal ecosystem. Limnol. Oceanogr. **40:** 299–305.

Submitted: 15 November 1995
Accepted: 29 May 1996
Amended: 25 November 1996