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# Toward a Mechanistic Approach to Modeling Bacterial DOC Pathways: A Review

**Marie Eichinger[1, 2*], Jean-Christophe Poggiale[1, 2], and Richard Sempéré[1, 2]**

Dissolved organic carbon (DOC) can be mineralized into $CO_2$ through bacterial respiration, reenter the trophic chain if bacterial biomass is grazed, or be partly stored in a recalcitrant form for millennia in the deep ocean by bacterial production during DOC degradation. This review compares mathematical models used to represent these pathways in the context of the current knowledge of bacterial metabolism, and examines how they may be related to the biological carbon pump and the microbial carbon pump. In view of the ever-changing environments in which bacteria exist, the authors propose that models of DOC degradation should be based on data from experiments in which bacteria are subjected to external constraints, such as DOC availability, temperature, and ocean depth. Further, the need for combining experimental and mechanistic modeling approaches to advance our understanding of the factors that affect oceanic DOC cycling and organic carbon storage is discussed.

Modeling dissolved organic carbon (DOC) degradation remains challenging due to factors including the complex nature of DOC, the variety of microorganisms using different metabolic pathways necessary for DOC breakdown, and the various oceanic physicochemical conditions that regulate bacterial metabolism. In this review, we identify those variables (for example, DOC concentration and bacterial biomass) relevant to accurately model bacterial-driven DOC pathways and forcing factors (forces external to the system, acting upon it, for example, temperature and depth).

The Multi-G model represents DOC degradation using DOC concentration as a single variable. DOC concentration decay is assumed to be at a constant rate and is therefore represented by first order kinetics (Eq. 1, Table 1) (*1, 2*). Multi-G-based models do not include specific biological activity (Fig. 1A), even though bacteria are recognized as the main agents of DOC degradation (*3*). A more accurate representation of DOC dynamics requires the inclusion of more detailed information about bacterial metabolism (*4*). The Monod model is an example of the next generation of model, which includes bacterial biomass as a variable (Eq. 2, Table 1). This model is the most widely used in ecosystem studies, taking into account bacterial population growth as a result of DOC consumption (*5–7*). It assumes that assimilated DOC is instantaneously converted to bacterial biomass with constant bacterial growth efficiency (BGE), and that the complementary proportion (1-BGE) is used for bacterial respiration (Fig. 1B). Although the predicted results obtained when applying the Monod model agree well with experimental observations (*8*), certain parameters such as BGE vary widely as a function of DOC chemical characteristics (*9*) and environmental conditions [temperature (*10*), and depth (*8*)]. This model fails, however, when DOC availability changes suddenly, making it inappropriate for modeling natural ecosystems that are subject to frequent environmental variations (*11*).

Variability in DOC and nutrient quality and availability may have some effects on the physiological status of bacterial communities (*12*). These effects on bacterial stoichiometry have been modeled using the Droop equations, where, for example, carbon and phosphorus (*13*), or carbon, nitrogen, and phosphorus (*14*), are limiting. According to this model, population growth depends on a pool of internal nutrients inside the bacterial cells (Fig. 1C; Eq. 3, Table 1), such as an internal reserve of organic carbon that allows cells to survive periods of starvation. This can also be taken into account using the dynamic energy budget (DEB) model (*15*), where population growth resulting from DOC consumption is modeled using at least two bacterial variables, the reserve and the structure of the cell (Fig. 1D; Eq. 4, Table 1). The DEB model is also appropriate for handling variable resource environments and variable bacterial stoichiometry because it can be extended to deal with systems using several substrates (*15*) (Fig. 1E). Furthermore, DEB considers the concept of maintenance that reflects the fact that bacteria use intracellular DOC not only for growth but also for physiological activities that do not produce new biomass (osmotic regulation, maintenance of intracellular pH, macromolecule turnover) (*16, 17*). The importance of such considerations in changing environments has been demonstrated in experiments in which bacteria are exposed to episodic inputs of labile DOC (LDOC), where DOC utilization for maintenance is detectable during starvation (*11*). Maintenance cannot be neglected, since bacterial survival under starvation conditions is a fundamental aspect of bacterial existence and something bacteria experience often (*17*). In some studies of marine DOC cycling, maintenance modeling is restricted to the respiration process ($R_B$ in Eq. 3, Table 1) (*13, 16, 18*). These models may prove useful for estimating the contribution from bacteria to the biological carbon pump, but not to the microbial carbon pump (MCP), since the latter assesses the role of microbial processes in refractory DOC (RDOC) generation and in carbon storage in the ocean (*19*). By contrast, in the DEB model, maintenance activity incorporates not only respiration, but also a set of processes which can include RDOC production (Fig. 1D). This RDOC contributes to the total RDOC in the ocean. Since the DEB model accounts for this RDOC production explicitly, its use is relevant for connecting the biological carbon pump and the MCP.

Although RDOC production by marine bacteria has been studied both under controlled experimental conditions (*20–22*) and in situ (*23*), mechanisms of this production are still unresolved. Only a few models include bacterially derived DOC at either a microbial level (*11, 20, 24*) or at an ecosystem level (*25*). A study based on pure cultures indicated that bacterial RDOC production may occur as a stress response when LDOC availability is low; this can be represented using the DEB model where, in the case of starvation, maintenance costs are mainly paid not by bacterial reserve, but rather by bacterial structure, leading to the production of RDOC (*20*).

In order to extrapolate how long-term changes (e.g. warming) influence DOC dynamics and organic carbon storage in marine waters,

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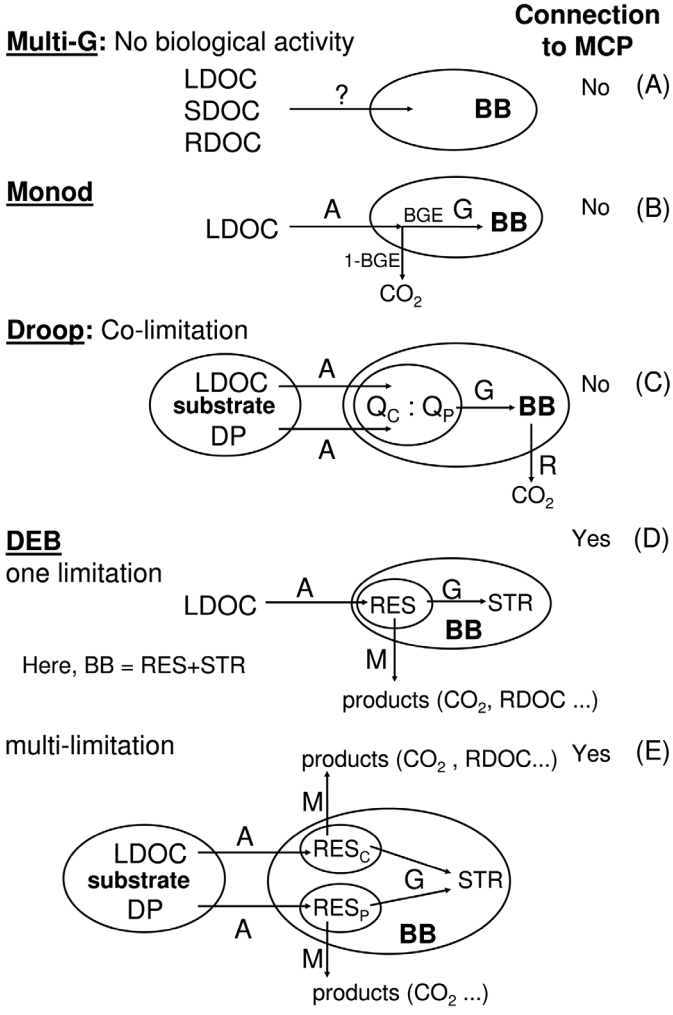
**Fig. 1**. Schematic representation of fluxes in Multi-G model (**A**), Monod model (**B**), Droop model with LDOC and dissolved phosphorus (DP) as limiting nutrients (**C**), DEB model with LDOC as the single limiting nutrient (**D**), and DEB model for two limiting nutrients, here LDOC and DP (**E**). Only the DEB model considers bacterial RDOC production, which can contribute to the total RDOC pool in the ocean. If these models are included in larger models accounting for primary production and export of organic carbon, then all models except the Multi-G can be indirectly linked to the biological carbon pump.

BB, bacterial biomass; BGE, bacterial growth efficiency; RES, reserve; STR, structure; LDOC, labile DOC; RDOC, refractory DOC; DP, dissolved phosphorus; $Q_C$, cellular carbon content; $Q_P$, cellular phosphorus content; $RES_C$, carbon reserve; $RES_P$, phosphorus reserve; A, assimilation; G, growth; R, respiration; M, maintenance.




mathematical models describing DOC concentration should account for the effects of these changes on the rates of DOC production and consumption. Few modeling studies consider the temperature effect on bacterial metabolic rates; some authors have used an exponential function to predict the effects of temperature changes on the rate of population growth (*7*), whereas others have applied the Q10 model to DOC assimilation and maintenance respiration (*24*) or to the population growth rate (*6*). The Q10 function represents one of the easiest ways to incorporate temperature dependence into a mathematical model. It estimates the change in a particular variable that would result from a temperature increase of 10°C. The Arrhenius function provides a more sophisticated way to consider temperature variations in a model, incorporating a high and low tolerance range (*15*). This representation might be useful in view of the wide range of temperatures in which bacteria can survive. However, to the best of our knowledge, it has never been used to model DOC generation and degradation by bacteria.

Although properties of bacterial metabolism like BGE (*8*) and bacterial production (*26*) are known to vary as a function of depth, the direct effects of continuously increasing pressure are poorly understood (*27*). Recent data suggest that bacterial production and extracellular hydrolytic enzyme activities are generally higher under in situ pressures than at atmospheric pressures, but the reasons for this remain unclear

**Table 1.** Equations of each model described in the review. t, time; LDOC, labile DOC; SDOC, semilabile DOC; RDOC, refractory DOC; BB, bacterial biomass, $B_c$, bacterial biomass in carbon, $V_{max}$ maximum LDOC uptake rate; K, half-saturation constant.

| Eq. No. | Model | Equations | State variables/parameter description |
|---|---|---|---|
| (1) | Multi-G | $[DOC] = [LDOC]e^{-k_1 t} + [SDOC]e^{-k_2 t} + [RDOC]$ | $k_1$ = LDOC degradation rate<br>$k_2$ = SDOC degradation rate |
| (2) | Monod | $\frac{dLDOC}{dt} = -V_{\max}\frac{LDOC}{K+LDOC}BB$<br>$\frac{dBB}{dt} = -BGE\ \frac{dLDOC}{dt}$ | BGE = bacterial growth efficiency (*8*) |
| (3) | Droop<br><br>Co-limitation between LDOC and dissolved P | $\frac{dLDOC}{dt} = -V_C\ B$<br>$\frac{dB_C}{dt} = V_C\ B - R_B\ B$<br>$\frac{dB}{dt} = \mu_B\ B$<br>$V_C = V_{\max}\frac{Q_C^{\max} - Q_C}{Q_C^{\max} - Q_C^{\min}}\frac{LDOC}{K+LDOC}$<br>$R_B = \rho_{gro}\ Q_C\ \mu_B + \rho_{\text{main}}\left(Q_C - Q_{\min}\right)$<br>$\mu_B = \mu_B^{\max}\left(1-\frac{Q_P^{\min}}{Q_P}\right)\left(1-\frac{Q_C^{\min}}{Q_C}\right)$ | B = bacterial number<br>$R_B$ = respiration rate<br>$\mu_B$ = specific growth rate<br>$\rho_{gro}$ and $\rho_{main}$ = portions of respiration allocated to growth and maintenance<br>$Q_C^{min}$, $Q_C^{max}$ and $Q_C$ = minimum, maximum and actual cellular carbon content, respectively<br>$Q_P^{min}$ and $Q_P$ = minimum and actual cellular phosphorus content, respectively (*13*) |
| (4) | DEB | $\frac{dLDOC}{dt} = -V_{\max}\frac{LDOC}{K+LDOC}LDOC\ .\ STR$<br>$\frac{dRES}{dt} = -eff_{RL}\frac{dLDOC}{dt} - maint_{RES}\ STR - eff_{RS}\frac{dSTR}{dt}$<br>$\frac{dSTR}{dt} = \frac{k_{RES}\ RES - maint_{RES}\ STR}{RES + eff_{RS}\ STR}STR$ | RES = energy reserve<br>STR = structural biomass<br>(with RES + STR = BB)<br>LDOC is assimilated into RES with efficiency $eff_{RL}$, maintenance ($maint_{RES}$) is supported by RES energy, $eff_{RS}$ is the efficiency of RES transfer to STR, and $k_{RES}$ is the reserve turnover rate (*20*) |

(*28*). In view of the number of bacteria present at depth, this issue needs to be more thoroughly investigated. Similarly, insufficient information on the effects of pH on bacteria-driven DOC degradation precludes its inclusion in current models. There is some evidence that lower pH increases bacterial production and degradation, but bacterial respiration and BGE have not yet been studied with respect to ocean acidification (*3*). Changes in seawater chemistry due to ocean warming and acidification are expected to enhance microbial activity and channel a greater fraction of the fixed carbon into DOC (*29, 30*), thus potentially increasing the importance of the MCP in the oceanic carbon flow. The relevance of the MCP in carbon cycling and storage, and how these changes might affect it should also be investigated using appropriate models.

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