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Modelling DOC assimilation and bacterial growth efficiency in biodegradation experiments: a case study in the Northeast Atlantic Ocean

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ABSTRACT: A Monod (1942) model was used to describe the interaction and dynamics between marine bacteria and labile-dissolved organic carbon (l-DOC) using data obtained from 36 biodegradation experiments. This model is governed by 2 state variables, DOC and bacterial biomass (BB), and 3 parameters, specific maximum assimilation rate (V_{max}), half-saturation constant (K_S) and bacterial growth efficiency (BGE). The calibrations were obtained from biodegradation experiments carried out in the Northeast Atlantic Ocean over different seasons and at different depths. We also conducted a sensitivity analysis to determine (1) which parameter had the greatest influence on the model, and (2) whether the model was robust with regard to experimental errors. Our results indicate that BGE is greater in surface layers than in deeper waters, with minimum values observed during winter. In contrast, the V_{max}/K_S ratio is inversely dependent on depth and does not show any seasonal trend. This reflects an increase in bacterial affinity for substrate with increasing depth (decrease of K_S) and/or better specific maximum assimilation rates (increase of V_{max}). The sensitivity and robustness analyses demonstrate that the model is more sensitive to the V_{max}/K_S ratio than to BGE, and that the parameters estimated are reliable. However, although the BGE values are close to those estimated experimentally, the use of a constant V_{max}/K_S ratio and BGE in a 1-dimensional model is not appropriate as these parameters should be described as variables that take depth and season into account.

KEY WORDS: Bacterial growth efficiency · Monod model · Bacterial biodegradation · Northeast Atlantic Ocean

INTRODUCTION

The global oceanic dissolved organic carbon (DOC) reservoir is about 685×10^{15} g C (Hansell & Carlson 1998), is recognised as one of the largest pools of reduced carbon on the planet (Carlson & Ducklow 1995) and is directly related to atmospheric CO_2 (Siegenthaler & Sarmiento 1993). Dissolved organic compounds are almost exclusively consumed by bacteria and are either incorporated into the microbial food web and/or respired as CO_2, in proportions that are difficult to determine. Depending on bacterial reactivity, DOC can be fractionated into several components. These include refractory material with turnover times of millennia, semi-labile material with turnover times of months to years and labile material with turnover times of hours to days (Williams & Drufell 1987, Bauer et al. 1992, Druffel et al. 1992, Carlson & Ducklow 1995, Hansell et al. 1995, Carlson 2002). The labile component of DOC (l-DOC) can be studied by measuring bacterial DOC consumption in biodegradation experiments (Amon & Benner 1996, Carlson & Ducklow 1996, Sempéré et al. 1998). Semi-labile and refractory-DOC are usually determined by examining DOC

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profiles throughout the water column (Wheeler et al. 1996, Hansell & Peltzer 1998, Wiebinga & de Baar 1998, Dafner et al. 2001, Sohrin & Sempéré 2005).

Bacterial respiration (BR) represents ~50 to 90% of total community respiration (Sherr & Sherr 1996, del Giorgio & Duarte 2002). Understanding heterotrophic bacterial metabolism (production of biomass plus respiration) is therefore paramount in determining the role of the biological pump in the carbon cycle. More recently, an effort has been made to provide a more accurate description of the relationship between DOC assimilation and bacterial production (BP) (Anderson & Williams 1999, Lancelot et al. 2002, Vichi et al. 2003). The bacterial carbon demand (BCD) can be calculated from BP by the use of bacterial growth efficiency (BGE = BP/BCD and BCD = BP + BR) (del Giorgio & Cole 1998, Rivkin & Legendre 2001). BGE ranges from <5 to 60%, median value being 24% (Jahnke & Craven 1995, del Giorgio & Cole 1998), and is usually determined by DOC biodegradation experiments or locally computed from *in situ* size-fractionated community respiration measurements and BP data (del Giorgio & Cole 1998).

Some biogeochemical models describe the interaction between DOC and bacteria but include other processes such as DOC production, the transfer of matter to higher trophic levels and different DOC pools (Baretta-Bekker et al. 1995, Blackburn et al. 1996, Anderson & Williams 1998, 1999, Anderson & Ducklow 2001, Spitz et al. 2001, Lancelot et al. 2002, Dearman et al. 2003). In these models, DOC uptake by bacteria are generally computed from Monod kinetics, which suggest a constant BGE (Taylor & Joint 1990, Baretta-Bekker et al. 1995, Blackburn et al. 1996, Anderson & Williams 1998, 1999, Lancelot et al. 2002). Biodegradation experiments produce a simple ecosystem (no autotrophs, no source of DOC and no grazers) which provides a reasonable data set that is easier to use for modelling bacterial utilisation of DOC. First-order kinetic models are often used in describing DOC and particulate organic carbon (POC) degradation (Harvey et al. 1995, Sempéré et al. 2000, Fujii et al. 2002, Panagiotopoulos et al. 2002), but these models only take into account the concentration of organic matter (OM) at any given time. Recent studies have indicated that a better understanding of the dynamics of OM in models requires an appropriate knowledge of the dynamics of the bacterial community (Talin et al. 2003 and references therein). Only a few aquatic biogeochemical studies describe model performance for bacteria, which is a poorly modelled state variable (Arhonditsis & Brett 2004). Some models have been developed to describe the interaction between bacteria and OM, but these include a mathematical formula for more than 1 potentially limiting factor, several bacterial communities and/or the respiration process (Thingstad & Pengrud 1985, Martinussen & Thingstad 1987, Thingstad 1987, Cajal-Medrano & Maske 1999, Touratier et al. 1999, Miki & Yamamura 2005).

Here, we report on the determination of BGE, estimated using 2 different methods: (1) experimental, by calculations obtained from BP and BR measured using biodegradation experiments, and (2) numerical, by estimating parameter values by finding the minimum distance between experimental kinetics and numerical simulations using the Monod (1942) model. The data used to determine both BGE come from the same experiments. However, in these experiments, only BP, bacterial abundance and oxygen consumption were measured. Thus, numerous hypotheses have to be made in order to estimate the necessary DOC data set and then estimate the parameters numerically. We are aware that these assumptions increase the errors in data, and thus in parameter estimations, but the current state of microbial knowledge and techniques precludes the achievement of better estimations with these data sets. Consequently, our approach is qualitative by suggesting a new method of BGE estimation and a new way of improving biogeochemical models. We show that BGE values obtained using both approaches are within the same range, varying with depth and season. We also demonstrate how robust the model is with regard to sensitivity to BGE and to parameter estimations using perturbed experimental data. Finally, we discuss the use of this model for describing bacterial and DOC dynamics in biodegradation experiments and thus in biogeochemical models.

MATERIALS AND METHODS

Experimental design. As part of the 'Programme Océan Multidisciplinaire Méso Echelle' (POMME), seawater samples were collected in the Northeast Atlantic Ocean (Fig. 1) over 3 seasons; winter (POMME 1; P1), spring (POMME 2; P2) and summer (POMME 3; P3) 2001 (for further details on POMME and on sampling techniques, see Mémery et al. 2005). It is beyond the scope of this study to present a detailed protocol and mesoscale variability aspects, and such data are available elsewhere (F. Van Wambeke et al. unpubl. data).

General design: Seawater was collected from 3 depths (5, 200 and 400 m) using Niskin bottles, then transferred immediately into large polycarbonate bottles without tubing. The protocol for seawater collection and for minimising organic carbon contamination is described in Sempéré et al. (2003). Following collection, seawater was filtered using a low vacuum (<50 mm Hg) through pre-combusted (450°C, 6 h)

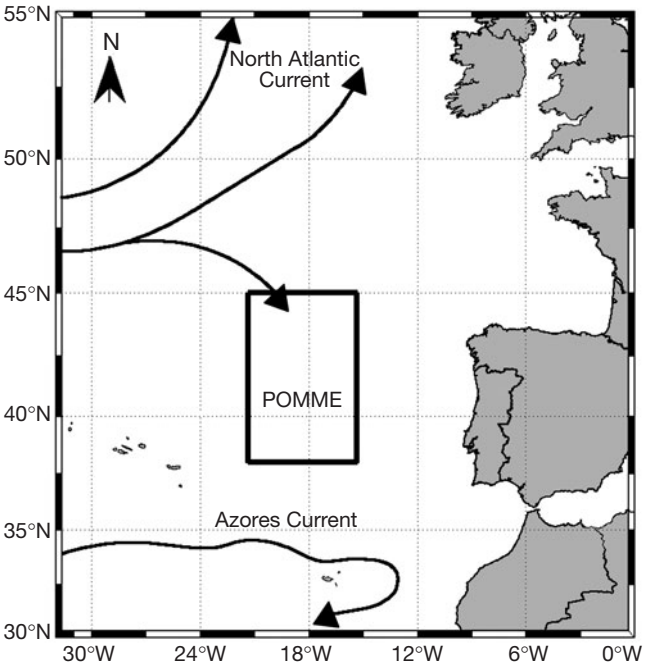

Fig. 1. POMME zone in the Northeast Atlantic Ocean studied during Leg 2 of POMME 1 (P1: 1–15 March 2001), POMME 2 (P2: 18 April–2 May 2001) and POMME 3 (P3: 19 September–3 October 2001) for BGE determination. Arrows represent principal currents: North Atlantic Current and Azores Current. See Mémery et al. (2005), Maixandeau et al. (2005) and Karayanni et al. (2005) for details on the hydrological situation at each site. Adapted from Guidi et al. (unpubl. data)

GF/F glass fibre filters in order to obtain bacterial seawater cultures. This experimental design removes all DOC sources and all predators, except for some viruses. A mean of 46% of the *in situ* bacterial cells was passed through the filters (F. Van Wambeke et al. unpubl. data). DOC was not measured. However, we could not exclude the possibility that the filtration process might induce some increase in DOC concentration and slightly modify the bacterial activity, particularly in the deep samples, because in some cases specific activity of bacteria after filtration increased compared to that *in situ* (F. Van Wambeke et al. unpubl. data). The bulk incubation culture was then sub-sampled by dispension into duplicate pre-combusted borosilicate bottles to determine BP and bacterial abundance, and also into quadruplicate 125 ml Winkler bottles for dissolved oxygen determination. The latter samples were fixed with Winkler reagents, and measurements were made using an automated Winkler titration system based on that described by Williams & Jenkinson (1982). Experimental bottles were incubated in the dark in a temperature controlled room (±1°C) over the course of the experiments. Samples were sacrificed and analysed for BP and dissolved oxygen using a time series of 0, 0.5, 1, 2, 5 and 10 d. Consequently, we must hypothesise that dynamics are identical in all bottles.

BP was calculated using the titrated leucine method (Kirchman 1993). The experimental estimation for BGE (BGE_E) was calculated by integrating data from time zero (t_0) to the BP peak, which refers to the maximum BP value in the time series, as follows:

$$BGE_E = \frac{IBP}{IBP + \frac{\Delta O_2}{\Delta t} t\, RQ} \quad (1)$$

where IBP (µM C) was time-integrated BP from t_0 to the BP peak with trapezoidal integration of discrete data. The conversion factor of leucine-carbon was 1.5 kg C mol^{-1} of leucine incorporated assuming an isotopic dilution of 1. The oxygen consumption rate $\Delta O_2/\Delta t$ (µM d^{-1}) was calculated assuming a linear regression model for the decrease in dissolved oxygen concentration with time (t). The respiratory quotient (RQ) was 0.8 (F. Van Wambeke et al. unpubl. data).

DOC and bacterial biomass estimations: Initial bacterial biomass (BB) was determined by epifluorescence microscopy after DAPI staining, assuming a carbon conversion factor (CCF) of 20 fg C $bacterium^{-1}$ (Lee & Fuhrman 1987). In order to estimate BB increase, the IBP (derived from the leucine method, see Eq. 1) was added to this initial value of BB for computing the BB for all other time points. Numerous hypotheses were made to assess DOC dynamics. Total organic carbon (TOC) was measured using high temperature catalytic oxidation (Sohrin & Sempéré 2005) on the *in situ* vertical profiles, but not for the biodegradation experiments. Initial values of DOC were thus estimated as the difference between *in situ* TOC and POC, which was deduced from total particulate carbon (TPC) measurements obtained using an optical particle counter (HIAC) (Merien 2003). As the proportion of DOC to TOC increases globally from 83% at 5 m to 92% at 200 m, we estimated that at 400 m DOC is close to TOC. We then assumed that initial DOC concentration in the batches was close to *in situ* DOC concentration. Finally, we estimated DOC concentrations over the course of the experiments on the assumption that the quantity of DOC consumed over a short period, which we assumed to be only l-DOC according to the duration of experiments, is equal to the sum of BB increase and CO_2 produced over the same period, estimated as:

$$\Delta CO_2/\Delta t = -RQ \times \Delta O_2/\Delta t \quad (2)$$

Monod (1942) model. The biodegradation model was set up on the basis of the following assumptions. (1) There is no source of DOC in the cultures. (2) Bacteria are the only organisms present (no flagellates and no viruses) (these first 2 assumptions are likely to be valid, since only the growth phase—and thus a short

period of time—is considered). (3) l-DOC was the limiting factor on bacterial growth, which is a reasonable assumption since nutrient concentrations measured in water column profiles during cruises were sufficient to sustain bacterial growth in the experiments considered (NO_3 concentrations ranged from 1.9 to 13.1 µM, except one value of 0.39 µM in spring, and PO_4 concentrations from 0.1 to 1.04 µM), except perhaps in surface water in late summer where values were lower (from undetectable to 0.04 µM for NO_3 and from 0.01 to 0.02 µM for PO_4) (F. Van Wambeke et al. unpubl. data). (4) We assumed that only the 1-DOC fraction is consumed by bacteria during the 10 d biodegradation experiments as well as in the model.

The Monod (1942) formula, which uses Michaelis-Menten kinetics, is one of the simplest and most widely used models for describing the interactions between 2 state variables, in this case bacterial C-biomass and DOC. Note that in this model the disappearing DOC is instantaneously taken up by bacteria and converted into C-biomass with a constant efficiency (numerical bacterial growth efficiency, BGE_N). Consequently, BGE_N is estimated using the model calibration and depends on the external limiting food concentration.

$$\frac{\mathrm{dDOC}}{\mathrm{d}t} = -\frac{V_{\max}\,\mathrm{DOC} \times \mathrm{BB}}{K_S + \mathrm{DOC}} \quad (3)$$

$$\frac{\mathrm{dBB}}{\mathrm{d}t} = \mathrm{BGE_N}\frac{V_{\max}\,\mathrm{DOC} \times \mathrm{BB}}{K_S + \mathrm{DOC}} \quad (4)$$

where BB is in µM C; DOC is concentration in µM C, with the assumption that l-DOC is the limiting food resource and the only fraction of DOC consumed; BGE_N is a fraction between 0 and 1; V_{max} is the specific maximum assimilation rate d^{-1}; and K_S is the half-saturation constant for DOC in µM C.

The parameters (BGE_N, V_{max} and K_S) were estimated, for each experiment, from all available DOC derived values and BB data. The parameter values were thus estimated using a non-linear regression that uses the least-squares method. The calibration is performed for each experiment in order to compare the parameters obtained from the model for different depths and seasons. Nevertheless, it should be pointed out that DOC estimations are representative of the total pool of DOC (l-DOC, semi-labile-DOC plus refractory-DOC), whereas the model only simulates the decrease of l-DOC, which constitutes the first and only fraction of DOC used by bacteria during the 10 d biodegradation experiments. This does not affect the parameter estimations, as semi-labile-DOC and refractory-DOC are supposed to be constant and unaffected during these biodegradation experiments. Thus, model parameters are representative of bacterial growth in batch cultures.

A sensitivity analysis was carried out to determine (1) which parameter has the most influence on the dynamics, and (2) the validity of parameter estimations according to experimental errors. First, the derivatives of the model were calculated with respect to the parameters, the highest derivative being the most influential parameter. This enables a quantitative comparison of parameter sensitivity. We then analysed the robustness of the parameter estimations with respect to the data. The measurement errors, the variability of environmental forcing parameters on the measurements and the assumptions made to assess DOC data may indeed indicate some variabilities in the observations used to calibrate the model. We have estimated that the sum of these variabilities was ≤30%. For 1 experiment, 500 extra sets of data were obtained by replacing each original data point in the course of the experiments by its value multiplied by $1 \pm p$, where $p \leq 0.3$ and is a random proportion that is uniformly distributed. Thus, 'perturbed' data represent the value that a data point could have if we consider the accuracy of the original data to be within the range of 70 to 100%. We then estimated parameters of the model for these 500 data sets using the same method as those for data sets without perturbation. This procedure provides information on parameter distribution and on the robustness of BGE_N estimations.

Comparison of methods for BGE estimation. The present study calculated BGE in 2 ways: as BGE_E and BGE_N. Both estimations implied assumptions about RQ and leucine-carbon conversion factors, which are supposed to be constant and equal in the 2 BGE estimations. The values of BGE_E may change with respect to BGE_N according to the method used to calculate the O_2 utilisation rate, the assumptions made to assess DOC data (as the CCF) and the integration time considered. BGE_E values are estimated using integrated data from t_0 to the BP peak and assuming a linear regression model for the decrease in dissolved oxygen concentration, whereas values for BGE_N are estimated using the least-squares method between the outputs of the 2 state variables of the model and the whole data set for each experiment. In order to compare the 2 methods, we calculated the relative quadratic distance (d) between BGE_E and BGE_N for each biodegradation experiment by taking BGE_E as reference:

$$d = \frac{|\mathrm{BGE_E} - \mathrm{BGE_N}|}{\mathrm{BGE_E}} \quad (5)$$

If d is low ($d \ll 1$), the 2 methods of BGE estimation are thus considered to be equivalent.

RESULTS

Model calibration and simulation

We performed a calibration of the model with the data for each experiment. The minimum distance between the model outputs and experimental data are obtained from high values of V_{max} and K_S in all experiments. Consequently, DOC can be neglected in comparison to K_S, that is K_S + DOC ≈ K_S. Then, Eqs. (3) & (4) can be approximated by the following system (Eqs. 6 & 7):

$$\frac{dDOC}{dt} = -\alpha\, DOC \times BB \quad (6)$$

$$\frac{dBB}{dt} = BGE_N\, \alpha\, DOC \times BB \quad (7)$$

where $\alpha = V_{max}/K_S$ in µM C^{-1} d^{-1} (8)

This simplified model can be solved analytically. Eqs. (A3) & (A4) in Appendix 1 allow the removal of the integration step for the calibration and simulation. The use of these equations enables analysis to be performed faster and provides a more precise calibration.

For most of the experiments (26 out of 36) the model (Eqs. 6 & 7) produces an accurate fit both qualitatively and quantitatively with parameters α and BGE_N (see Fig. 2). However, there is no agreement between the model outputs and data in the case of the other 10 experiments (see Fig. 3). Thus, these results have not been taken into account in the analysis of parameter variation according to depth and season. These inaccuracies are related to (1) missing BP or O_2 data due to problems with analysis precision (BP was at the detection limit, or quadruplicate Winkler bottles were highly variable), which made correct estimation of BB or DOC concentration difficult in Expts L, Q, O and FF ('nd' in Table 1); (2) the shape of the model, which is poorly suited to the shape of data in Expts C, J, II and U (e.g. in Expt C, BB data exhibit an exponential shape whereas the DOC data are linear); and (3) a stationary phase in bacterial data that was observed in Expts T and KK, whereas large amounts of DOC were still available (Fig. 3).

Sensitivity and robustness analyses

The derivatives of Eqs. (6) & (7) with respect to parameters were used in order to study the sensitivity of the model (Fig. 4, Appendix 2). Eqs. (A5) to (A8) represent the sensitivity of Eqs. (6) & (7) with respect to parameters α and BGE_N. In all cases, the sensitivity is equal to the product of $a \times DOC \times BB$, where a = BGE_N, 1, α and 0, respectively, for Eqs. (A5) to (A8). However, in all experiments, we observed that $0 < \alpha < BGE_N < 1$ (Tables 1 & 2). It follows that the model is more sensitive to $\alpha = V_{max}/K_S$ than to BGE_N (see Appendix 2 for more details). There is indeed a great difference in the order of magnitude of sensitivity to α as a function of DOC concentration and BB (Fig. 4b), which is between 20 and 100 times greater than the sensitivity to BGE_N (Fig. 4a). If we only consider sensitivity to α, since 1 > BGE_N, for the given values of DOC and BB, then Eq. (6) is more sensitive to a variation of α than Eq. (7) (Fig. 4b). Only Eq. (7) is sensitive to a variation in BGE_N (Fig. 4a).

We also analysed the robustness of the estimated parameters α and BGE_N with respect to the estimated

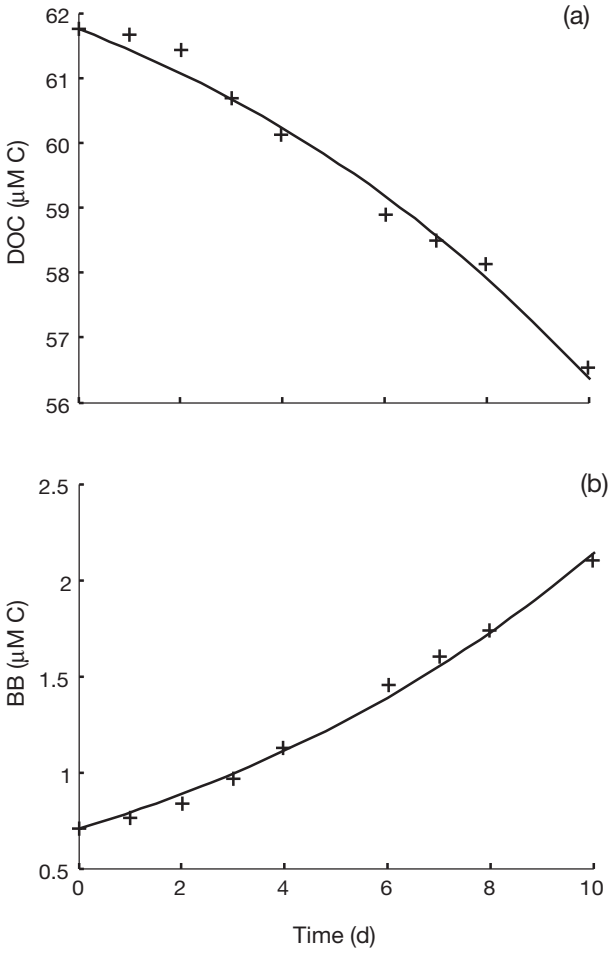

Fig. 2. Dynamics of (a) dissolved organic carbon (DOC) and (b) bacterial biomass (BB) for the biodegradation experiment carried out during spring at 5 m (Expt M, Table 1). +: data for BB and DOC recalculated from O_2 and bacterial production (BP) data during the biodegradation experiment. Lines: results of simulations of the Monod (1942) model with parameters estimated by non-linear regression, where α = 0.007 µM C^{-1} d^{-1} and BGE_N (numerical bacterial growth efficiency) = 0.27

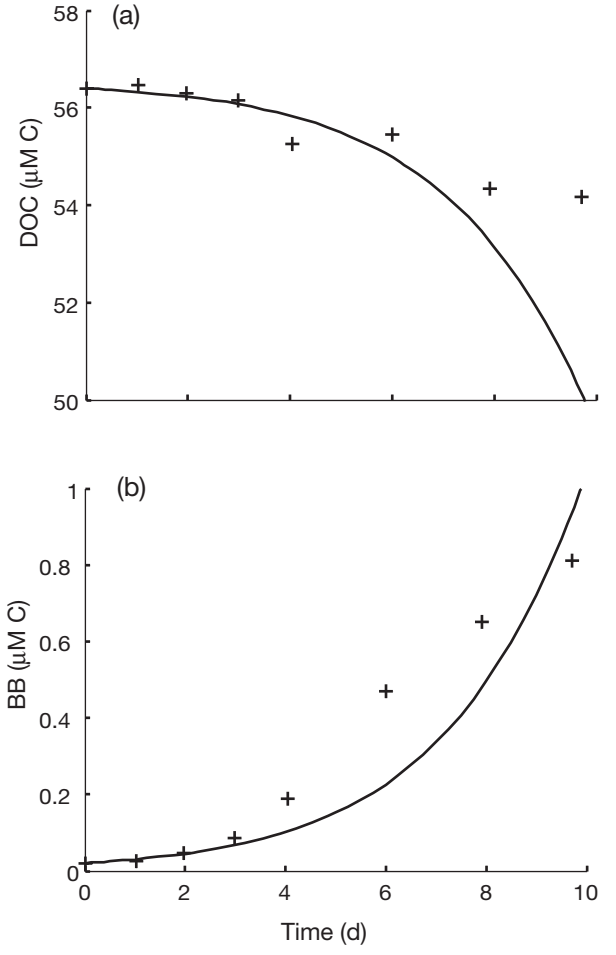

Fig. 3. Dynamics of (a) DOC and (b) BB for the biodegradation experiment carried out during spring at 200 m (Expt T, Table 1). **+**: data for BB and DOC recalculated from O_2 and BP data during biodegradation experiment. Lines: results of simulations of the Monod (1942) model with parameters estimated by non-linear regression, where $\alpha = 0.049$ µM C^{-1} d^{-1} and $BGE_N = 0.15$

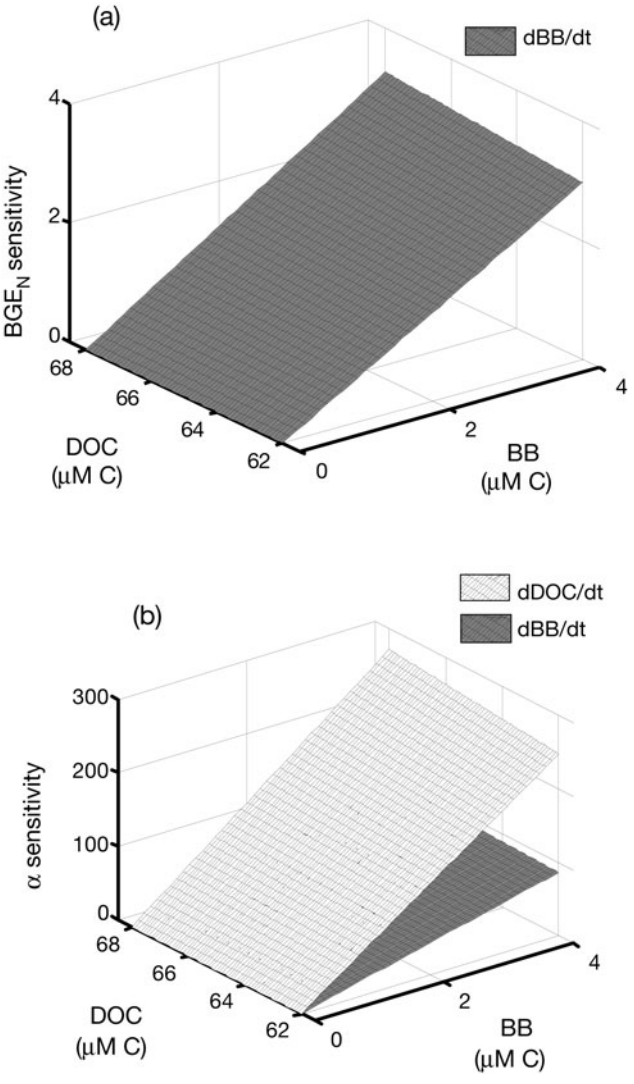

Fig. 4. Representation of sensitivity of parameters BGE_N and α as a function of variables BB and DOC in the biodegradation experiment carried out during summer at 5 m (Expt GG, Table 1). Sensitivity represented by a surface that corresponds to all possible combinations of the product $a \times DOC \times BB$, where $a = BGE_N$, 1, α or 0, according to corresponding sensitivity (Eqs. A5 to A8, respectively) (Appendix 2). DOC and BB can take all possible values in their own range of variation during the experiment ($\alpha = 0.012$ µM C^{-1} d^{-1} for Eq. A7 and $BGE_N = 0.35$ for Eq. A5). (a) sensitivity of $dBB \times dt^{-1}$ according to BGE_N, which corresponds to Eq. (A7) (sensitivity of $dDOC \times dt^{-1} = 0$). (b) sensitivity of both parts of model in relation to α (µM C^{-1} d^{-1}), which correspond to Eqs. (A5) & (A6)

data set. For each experimental data set, we simulated 500 extra sets of data with randomly pertubed data up to 30%, and we estimated model parameters for each of the extra sets. We termed the BGE_N and α estimated with the perturbed data 'BGE_P' and α_P, respectively. Then, for each experiment, we analysed the distribution of the 500 BGE_P estimated with their corresponding extra sets of data, with respect to the BGE_N estimated for the corresponding experiment without perturbation. The same analysis was performed for the parameter α. These simulations, which were performed for all experiments, provide a basis for studying how robust the model is according to the distribution of parameters (see Fig. 5).

In all experiments, the distribution of parameters following perturbation follows a unimodal low, and parameters estimated without perturbation are within or close to the modal class. In each experiment, 90 to 100% of the 500 perturbation simulations give rise to a $BGE_P < 0.4$, indicating a weak distribution of BGE_P. Moreover, >50% of the perturbation experiments give rise to $BGE_N - 0.1 < BGE_P < BGE_N + 0.1$. A small per-

Table 1. Comparison of experimental bacterial growth efficiency (BGE_E) and model parameters including numerical BGE (BGE_N) and α, estimated numerically with a non-linear regression, for the 3 depths and 3 seasons studied in the Northeast Atlantic Ocean during POMME (P1–3) cruises. Period of sampling for BGE determination: P1: 1–15 March 2001; P2: 18 April–2 May 2001; P3: 19 September–3 October 2001. Values in **bold** correspond to results that were not taken into account in further analyses because simulations did not match data (see 'Results; Model calibration and simulation'). nd: not determined

Expt	Winter (P1)			Expt	Spring (P2)			Expt	Summer (P3)		
	BGE_E	BGE_N	α		BGE_E	BGE_N	α		BGE_E	BGE_N	α
5 m											
A	0.04	0.07	0.013	M	0.21	0.27	0.007	AA	0.28	0.24	0.011
F	0.13	0.14	0.014	P	0.30	0.41	0.006	DD	0.30	0.28	0.013
I	0.18	0.17	0.016	S	0.36	0.40	0.006	GG	0.48	0.35	0.012
L	nd	nd	nd	V	0.26	0.19	0.011	JJ	0.35	0.29	0.016
200 m											
B	0.04	0.13	0.011	N	0.15	0.27	0.016	BB	0.09	0.11	0.043
D	0.15	0.25	0.007	T	0.16	**0.15**	**0.049**	EE	0.15	0.19	0.016
G	0.05	0.07	0.052	Q	0.20	nd	nd	HH	0.12	0.14	0.024
J	0.05	**0.10**	**0.016**	W	0.07	0.04	0.078	KK	0.18	**0.13**	**0.038**
400 m											
C	0.01	**0.05**	**0.024**	O	0.04	nd	nd	CC	0.08	0.09	0.045
E	0.06	0.09	0.040	R	0.02	0.26	0.017	FF	0.24	nd	nd
H	0.05	0.06	0.049	U	0.03	**0.10**	**0.119**	II	0.33	**0.21**	**0.027**
K	0.05	0.11	0.026	X	0.07	0.06	0.097	LL	0.13	0.14	0.035

centage of the results give a BGE_P close to 1 (not shown). This result could be related to the scattering of DOC data caused by the perturbation; indeed, this scattering does not give a satisfactory model fit and the calibration method produces a curve with a very small α_P. This indicates that the BB data, where the level of scattering is lower and thus well fitted, needs to be fitted using a very high value of BGE_P in order to balance the weak α_P. The values of α without perturbation are in the middle of the distribution and the highest α_P is double that of α without perturbation.

Parameters

For each experiment, values of α and BGE_N obtained by the parameterisation of the model are presented in relation to the BGE_E calculated experimentally from O_2 and BP data (Tables 1 & 2). For some experiments, there were no results because of experimental problems ('nd' in Table 1). BGE_E ranged from 0.01 to 0.48, whereas α and BGE_N ranged from 0.006 to 0.097 µM C^{-1} d^{-1} and 0.04 to 0.41, respectively. BGE values were also averaged at each depth for a given season, at each season for a given depth and at each depth for the whole year (Table 2). By calculating these means, the results where simulations were not possible or seemed inaccurate were excluded (see 'Results; Model calibration and simulation'). As the number of results for a given depth and season were small (n = 4 in general) and some were not taken into account in means, the standard deviations increase rapidly when we remove 1 or 2 results (n = 3 and 2, respectively, Table 2).

The relative quadratic distances d between BGE_E and BGE_N range from 0.07 to 12.00 (Fig. 6). All distances, except 6 out of 26, have $d < 0.5$ and all except 3 have $d < 1$, which suggests that the 2 methods of BGE estimation are quantitatively equivalent.

The results indicate that mean BGE_N decreases from the surface (5 m) to deeper waters (200 and 400 m) in spring and summer, whereas there is no significant relationship with depth in winter (Table 2). If we consider the annual means, we observe a decrease in BGE_N with depth. However, mean BGE_N varies according to season in the surface layer with a minimum mean in winter (P1). There were no significant differences in seasonal averages in spring and summer, owing to great variability within sites. In contrast, averaged α increased from the surface to deeper water whatever the season; however, there was no significant difference between 200 and 400 m as a result of high standard deviations of data among the stations studied. In contrast to BGE_N, α did not show any seasonal trend. Although BGE_E values are more abundant, the trends are the same as for BGE_N, i.e. minimum values observed in winter and at greater depths (Table 2). Finally, we have demonstrated that both BGE_E and BGE_N (experimental and numerical) presented the same variations according to depth, that they were minimum in winter and equivalent from a quantitative point of view.

Table 2. Model mean parameters α and BGE_N, and mean BGE_E estimated for different depths at different seasons and for the whole of 2001 (mean ± SD). See Table 1 for POMME (P1–3) cruise dates. n_N: number of values used to calculate means for numerical parameters α and BGE_N. n_E: number of values used to calculate mean BGE_E. For each individual cruise $n_E = 4$, except for mean calculated for P1 at 5 m, where $n_E = 3$

Depth (m)	Winter (P1)				Spring (P2)				Summer (P3)				Annual mean			
	α	BGE_N	n_N	BGE_E	α	BGE_N	n_N	BGE_E	α	BGE_N	n_N	BGE_E	α	BGE_N	n_N	BGE_E	n_E
5	0.014 ± 0.002	0.12 ± 0.05	3	0.12 ± 0.07	0.007 ± 0.002	0.32 ± 0.10	4	0.28 ± 0.06	0.013 ± 0.002	0.29 ± 0.05	4	0.35 ± 0.09	0.011 ± 0.004	0.25 ± 0.11	11	0.25 ± 0.12	11
200	0.024 ± 0.025	0.15 ± 0.09	3	0.07 ± 0.05	0.047 ± 0.044	0.15 ± 0.16	2	0.13 ± 0.04	0.028 ± 0.014	0.15 ± 0.04	3	0.13 ± 0.04	0.031 ± 0.025	0.15 ± 0.08	8	0.11 ± 0.05	12
400	0.038 ± 0.012	0.09 ± 0.03	3	0.04 ± 0.02	0.057 ± 0.056	0.16 ± 0.14	2	0.04 ± 0.02	0.040 ± 0.070	0.11 ± 0.04	2	0.18 ± 0.13	0.044 ± 0.026	0.11 ± 0.07	7	0.09 ± 0.10	12

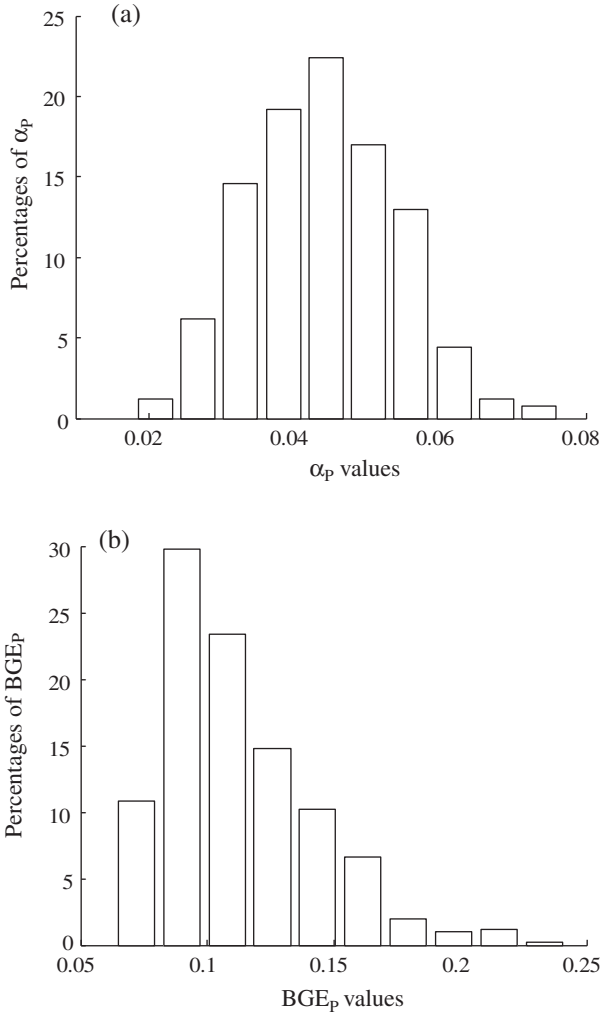

Fig. 5. Distribution of parameters (a) α_P (µM C^{-1} d^{-1}) and (b) BGE_P after 500 perturbations. Extra sets of data were obtained by replacing each initial data point by its value multiplied by $1 \pm p$, where $p \leq 0.3$ and is a random proportion uniformly distributed, for a biodegradation experiment carried out at 200 m during summer (Expt BB, Table 1). Results presented as the percentage of each value of (a) α_P and (b) BGE_P compared to all values obtained after perturbation. Values of α and BGE_N for data without perturbations are 0.043 µM C^{-1} d^{-1} and 0.11, respectively

DISCUSSION

Analysis of model results

The model fits the data in almost all simulations. However, in some cases, we observed that the model did not match the experimental data. For example, the experimental dynamics of BB seemed to reach a stationary phase even though there was still a significant concentration of DOC (47 and 54 µM C remaining for Expts KK and T, respectively) (Table 1, Fig. 3). The sta-

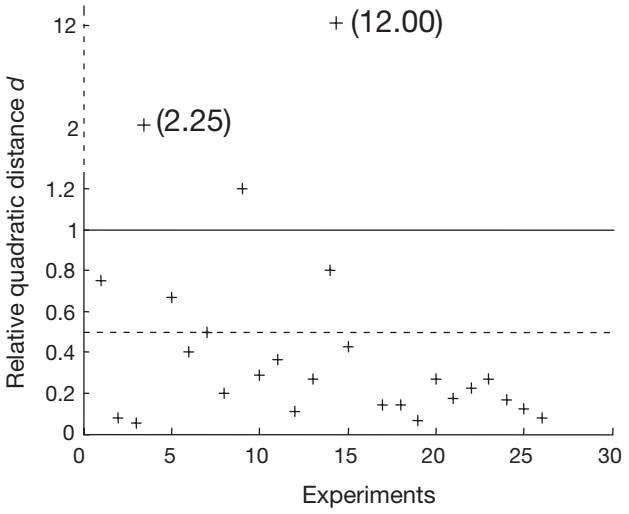

Fig. 6. Distribution of relative quadratic distance d (Eq. 5) between BGE_N and BGE_E. If $d > 1$ (solid line), the 2 methods of estimation give results that are distant; if $d < 0.5$ (dashed line), the 2 methods are considered equivalent; 2 distances are out of the scale and values are indicated in brackets (2.25 and 12.00)

tionary phases observed in these experiments are likely to be due to a complete exhaustion of l-DOC, because the remaining DOC in the batch is close to that found in deep waters (40 to 50 µM C) (Sohrin & Sempéré 2005) and *in situ* nutrient concentrations were sufficient to avoid limitation (see 'Materials and methods; Monod (1942) model'). This remaining DOC is represented by semi-labile and refractory-DOC poorly assimilated by bacteria and not represented in the model, and thus the bacterial stationary phase cannot be simulated.

Except for these biodegradation experiments, the sensitivity analysis has demonstrated that the Monod (1942) model is more sensitive to variation in V_{max}/K_S ratio than to BGE_N, indicating that the best estimations of both parameters require high precision in α values. Our results also demonstrate that a perturbation up to 30% of total variation in data affects parameter estimations within a reasonable range: parameters estimated without perturbation are always within or close to the modal class; the distributions of parameters with perturbed experimental data are not very large around the parameters estimated without perturbation; and >50% of the perturbation simulations give rise to $BGE_N - 0.1 < BGE_P < BGE_N + 0.1$. As such perturbations only influence the estimation of both parameters to a low order of magnitude, we can be sure that the parameters estimated without perturbation are reliable. However, for some of these perturbations we obtained BGE_P values close to 1. For these perturbations, the model does not match in the case of very small l-DOC variations (e.g. owing to a low signal-to-noise ratio of variations of O_2 data). As the relative quadratic distances d for most experiments are ≤0.5, our modelled estimations of BGE_N are close to the classical estimations of Eq. (1) (BGE_E). Moreover, we have demonstrated that the tendencies are the same when considering the 2 BGE (BGE_E and BGE_N). Consequently, the overall analysis of the model (qualitative and quantitative comparisons with experimental parameters, sensitivity and robustness analyses) shows that our numerical method of BGE estimation is well suited.

Biological analysis

The parameter values, revealed by calibration of the model, have shown a range of BGE_N values below 0.5 (0.04 to 0.41, Table 1), which is commonly observed in diverse aquatic habitats (del Giorgio & Cole 1998). The annual mean and standard deviations of BGE_N at 5 m (0.25 ± 0.11) are consistent with published data for the Gulf of Mexico (Pomeroy et al. 1995, Jørgensen et al. 1999), Sargasso Sea (Carlson & Ducklow 1996) and the Atlantic Jet in the Mediterranean Sea (Sempéré et al. 2003). BGE_N at 5 m was greater than at 200 and 400 m, and minimum values were observed in winter as was also the case in the surface layer of the North Sea (Reinthaler & Herndl 2005). In contrast, minimum values of α were reached at 5 m and no trend emerged with season. The fraction of refractory-DOC increases with depth (Carlson 2002). Bacteria probably consume, in addition to l-DOC, some semi-labile and refractory organic compounds. Therefore, the fraction of assimilated l-DOC probably decreases with depth, and it is conceivable that BGE decreases with depth. As α is the ratio between V_{max} and K_S, the increase in α reflects an increase in bacterial affinity for substrate with increasing depth (decrease of K_S) and/or better specific maximum assimilation rates (increase of V_{max}). These results suggest that the more refractory bulk DOC (representative of those observed below the productive layer, i.e. 200 m) (Sohrin & Sempéré 2005), as well as probable patchy distribution of l-DOC in deep waters, would explain lower BGE, higher affinity to the substrate and/or higher specific maximum assimilation rates.

Experimental problems

The data needed for the calibration were not directly measured. Patterns of change over time of DOC estimations are based on BP and BR, which were themselves estimated from indirect measurements (leucine incorporation and O_2 variations).

Hence, conversion factors (leucine to carbon, RQ) must be applied. The latter is not constant as bacteria can change their RQ (Kooijman 2000) according to changes in the quality and quantity of the substrate over the course of the experiments. However, the changes over time of these conversion factors has no influence on the comparison of BGE, as the same values were used in both cases (BGE_E and BGE_N) and the influence of these factors is discussed elsewhere (F. Van Wambeke et al. unpubl. data). Moreover, these changes of conversion factors over time have to be proven experimentally in order to be taken into account. It further results that the estimations of DOC concentrations may not be accurate and representative of the real variation in DOC in the experiments. Direct measurements of DOC would be more appropriate, but there is, for instance, no protocol which is sufficiently sensitive for oligotrophic waters. Nevertheless, even if data vary by up to 30% of the values without perturbation, the method of parameterisation is well suited. Consequently, estimated parameters are reliable. We have also assumed that the DOC concentration at a given time equals the initial DOC, minus the sum of CO_2 respired and BB produced. However, this hypothesis would be accurate only if the system behaves as a Monod (1942) model, i.e. if growth and respiration depend directly on the external concentration of the substrate. The presence of an internal carbon reservoir in bacteria (Ducklow & Carlson 1992, Cherrier et al. 1996) may indeed induce a time lag between assimilation and growth and/or respiration, which has not been taken into account in estimations of the data sets needed for calibration of the model.

Another bias is the difficulty in placing these results within a natural context. For example, the presence of viruses—which may induce a decrease in BGE and an increase in the growth rate of uninfected cells—cannot be ruled out (Middelboe et al. 1996). These are not represented in the model whereas they may in fact reduce bacterial abundance. Although great care was taken during filtration (Yoro et al. 1999), this process is likely to induce an increase in DOC due to particle breakdown (Carlson et al. 1999, Ducklow et al. 1999). However, increases in specific leucine incorporation rates at t_0 from biodegradation experiments compared to their respective *in situ* values occurred in less than half of the experiments (F. Van Wambeke et al. unpubl. data). The 10 d incubation experiments could also enable bacteria to use more refractory organic matter, thus lowering natural BGE (del Giorgio & Cole 1998, Carlson et al. 1999). Although these analytical biases are difficult to quantify, they should be kept in mind for comparisons and further interpretation.

Improvement of biogeochemical models

We have demonstrated using the Monod (1942) model that (1) parameters BGE_N and α are dependent on depth, and (2) BGE_N varies according to season, especially in the surface layer, in the Northeast Atlantic Ocean. Consequently, the use of a constant BGE_N and α in 1-dimensional biogeochemical models (Anderson & Williams 1999, Lancelot et al. 2002) may not be appropriate. It is necessary to find a better method to simulate the uptake of organic matter by bacteria, for example by expressing BGE_N and α as a function of depth, since the availability of l-DOC varies with depth. The seasonal changes in BGE_N should also be described, for example with temperature. Other environmental factors such as composition of organic nutrients, phages and physiological conditions may affect the BGE (Cajal-Medrano & Maske 2005). Moreover, BGE values could influence the existence and competition of bacterial communities living on distinct substrates (Miki & Yamamura 2005).

The time lag between assimilation of the substrate, respiration and growth may require mathematical descriptions for each of these kinetics. Some models that use variable BGE_N, such as the Droop (1968) model, take into account internal variable carbon storage (Grover 1991). In the case of DOC uptake by bacteria, this model allows bacteria to absorb the substrate in part of the cell, referred to here as the quota. Then, carbon stocked in the quota will be allocated for different bacterial processes including maintenance and growth. In contrast to the Monod (1942) model, the Droop (1968) model also allows bacteria to survive during a starvation period, and requires differentiation of assimilation and growth processes. These assumptions give a better understanding of the interaction between DOC and bacteria in biogeochemical models (Vichi et al. 2003) and allow a variable BGE to be considered as BGE = dBB/dDOC.

Previous studies indicate that bacteria supplied with phosphorus are able to store organic carbon, without dividing, thereby maintaining a higher BGE (Zweifel et al. 1993). The assumption of carbon storage has also been proposed with observation of a non-coupling between (1) the use of DOC and (2) BP and BR (Ducklow & Carlson 1992, Cherrier et al. 1996). It is also important to take into consideration the metabolic energy used for maintenance processes—i.e. processes that do not produce new biomass but maintain cell integrity—in bacterial modelling (Cajal-Medrano & Maske 1999, 2005). Some authors indicate that the addition of reserves and maintenance in a Monod (1942) model is necessary in order to obtain the bacterial dynamics in chemostats (Kooi & Kooijman 1994, Kooijman 2000). We have to test such mod-

els using data from biodegradation experiments and study the effects on biogeochemical models. In the first case, the substrate is constant in the cultures but there are changes in the populations, which proliferate or dominate in cultures; in contrast, in the second case, there are changes in the availability of the substrate over the course of the experiment. Consequently, the description of the interactions between bacteria and DOC in biogeochemical models should be reviewed in order to include some fundamental mechanisms such as the use of reserves and maintenance processes.

CONCLUSION

We have shown that Monod-type modelling constitutes a fast and cheap method to estimate BGE from bacterial biodegradation experiments (DOC and BB data). This model is not very sensitive to variation in parameters and is robust with regard to experimental errors. However, in order to obtain BGE estimations close to the natural BGE, accurate measured experimental data are required. Moreover, more experiments are needed to observe the decrease in BGE and increase in α with depth with the dynamics of both state variables recorded over different seasons: rigid sampling with regard to depth and time with replicates is essential. An experimental process using the most precise measurements available is crucial for the calibration and validation of any model. Moreover, DOC data is necessary to validate our approach and thus our results. The introduction of BGE as a function of depth and temperature in the model of Anderson & Williams (1999) could prove to be the way forward. Nevertheless, the Monod (1942) model was designed for a system in steady-state in the natural environment; however, there are always perturbations and the steady-state condition is rare. Consequently, models using time variable assimilation rate and BGE such as Droop (1968) and Dynamic Energy Budget models (Kooijman 2000) should be investigated more thoroughly in order to reproduce the observations more accurately.

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Appendix 1. Search for the analytical solutions of the model

The mass conservation law of the model (Eqs. 6 & 7) gives the following:

$$\mathrm{BGE_N}\frac{\mathrm{dDOC}}{\mathrm{d}t}+\frac{\mathrm{dBB}}{\mathrm{d}t}=0 \quad \text{(A1)}$$

Consequently, ($\mathrm{BGE_N}\times\mathrm{DOC}+\mathrm{BB}$) is a constant. If k_1 is this constant, then $\mathrm{DOC}=(k_1-\mathrm{BB})/\mathrm{BGE_N}$. The model and the conservation law produce the following for BB:

$$\frac{\mathrm{dBB}}{\mathrm{d}t}=\alpha\,(k_1-\mathrm{BB})\mathrm{BB}=\alpha\,k_1\,\mathrm{BB}\left(1-\frac{\mathrm{BB}}{k_1}\right) \quad \text{(A2)}$$

Eq. (A2) is a logistic equation with an analytic solution as follows:

$$\mathrm{BB}_t=\frac{\mathrm{BB}_0\,k_1}{\mathrm{BB}_0+[k_1-\mathrm{BB}_0]\mathrm{e}^{-\alpha\,k_1\,t}} \quad \text{(A3)}$$

where BB_0 is initial bacterial biomass (µM C), t is time (days), αk_1 is intrinsic growth rate (d^{-1}) and k_1 is carrying capacity (µM C).
The same reasoning can be applied to the second variable of the model:

$$\mathrm{DOC}_t=\frac{\mathrm{DOC}_0\,k_2}{\mathrm{DOC}_0+[k_2-\mathrm{DOC}_0]\mathrm{e}^{\alpha\,k_1\,t}} \quad \text{(A4)}$$

where DOC_0 is initial DOC concentration (µM C), and $k_2 = k_1/\mathrm{BGE_N}$ (µM C).

Appendix 2. Equations governing the sensitivity analysis

$$\left|\frac{\partial\left(\frac{\mathrm{dBB}}{\mathrm{d}t}\right)}{\partial\alpha}\right|=\mathrm{BGE_N}\times\mathrm{DOC}\times\mathrm{BB} \quad \text{(A5)}$$

$$\left|\frac{\partial\left(\frac{\mathrm{dDOC}}{\mathrm{d}t}\right)}{\partial\alpha}\right|=\mathrm{DOC}\times\mathrm{BB} \quad \text{(A6)}$$

$$\left|\frac{\partial\left(\frac{\mathrm{dBB}}{\mathrm{d}t}\right)}{\partial\mathrm{BGE_N}}\right|=\alpha\times\mathrm{DOC}\times\mathrm{BB} \quad \text{(A7)}$$

$$\left|\frac{\partial\left(\frac{\mathrm{dDOC}}{\mathrm{d}t}\right)}{\partial\mathrm{BGE_N}}\right|=0 \quad \text{(A8)}$$

In all experiments, $0<\alpha<\mathrm{BGE_N}<1$ (Tables 1 & 2). It follows that the values of Eqs. (A5) & (A6) are larger than those of Eqs. (A7) & (A8). We thus conclude that the model is more sensitive to $\alpha = V_{\max}/K_S$ than to $\mathrm{BGE_N}$.

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