

Analysis of Unstructured Kinetic Modeling for a Sulfate-Reducing Process Using *Desulfovibrio alaskensis* 6SR

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RESUMEN

En este artículo se presenta un análisis cinético de un proceso sulfato reductor tomando como caso de estudio a la cepa *Desulfovibrio alaskensis* 6SR. Este análisis consideró cinco modelos cinéticos no estructurados de tipo inhibición por producto, además se propone una expresión de ley de potencias para la producción del exopolisacárido (EPS) que se genera durante la fase de máxima producción de sulfuro de hidrógeno y conlleva a una condición de estrés. Cada modelo consideró las variables de estado de consumo de sulfato y lactato, producción de sulfuro de hidrógeno, acetato y biomasa. Los modelos considerados fueron validados por comparación con los datos experimentales generados obteniéndose coeficientes de correlación satisfactorios. El resultado de las simulaciones sugirió que el modelo de Levenspiel es la mejor representación matemática del crecimiento bacteriano y del proceso sulfato reductor al combinarse con el modelo de la ley de potencias para el EPS. Los parámetros cinéticos obtenidos fueron una $\mu_{\max} = 0.36$ 1/h, $K_s = 6559$ mg/l, $P^* = 610$ mg/l y $n = 0.89$, con un índice de correlación de $R^2 = 0.96$. El análisis cinético del proceso sulfato reductor permite dar una mayor aproximación de este tipo de crecimiento anaerobio para explorar su comportamiento bajo diferentes condiciones de operación según el interés biotecnológico deseado.

Palabras clave: *Sulfato reducción, modelos no estructurados, inhibición, cinética.*

ABSTRACT

This paper presents a kinetic analysis of sulfate reducing process considering as a case study *Desulfovibrio alaskensis* 6SR. Five unstructured kinetic models with product

inhibition were considered, and a power law kinetic expression to exo-polysaccharide (EPS) production was proposed. The EPS is generated when maximum production of sulfide takes place, which provokes a stress condition. All models presented satisfactory overall correlation coefficients and their performance is analyzed comparing the corresponding numerical simulations with the experimental data. The results of the simulations for each model suggest that Levenspiel's model is the best one to represent the bacterial growth, sulfate reducing process and the inhibition effect by sulfide, with the combination of the expression to EPS production. The kinetic parameters values obtained for this model are $\mu_{\max} = 0.36$ 1/h, $K_S = 6559$ mg/l, $P^* = 610$ mg/l and $n = 0.89$, and correlation coefficient of 0.96. The kinetic analysis of process sulfate reducing allows major approximation of anaerobic growth to explore the behavior in different operation conditions for biotechnology purposes.

Keywords: *Sulfate reducing, unstructured models, inhibition, kinetic.*

INTRODUCTION

Sulfate reducing bacteria (SRB) form a group of prokaryotes able to transform sulfate at sulfide and are widespread in anoxic habitats, they have an important role in both the sulfur and carbon cycles (Castro *et al.*, 2000; Wanger *et al.*, 1998). Approximately half of organic carbon is mineralized by SRB in anoxic ocean sediments (Jorgensen, 1982) or in wastewater treatment systems (Kühl, 1992). Some SRB can also decompose more persistent organic pollutants such as polycyclic aromatic hydrocarbons and polychlorinated biphenyls (Widdel & Rabus, 2001). Due to these characteristics, the SRB has been used to solve various environmental problems, e.g. in biological sulfate reduction, the produced sulfide can be used to precipitate metallic species

(Alvarez *et al.*, 2006; Katsoyiannis & Zouboulis, 2004; Muyzer & Stams, 2008). In contrast, the presence of SRB in the oil field contribute to the souring of water flooded oil reservoirs due to the production of sulfide, also the highly reactivity and toxicity of sulfide induces pitting metallic corrosion, causing great economic losses in pipeline systems of the petroleum industry and others (Videla & Herrera, 2005).

The SRB which thrive in environments under undesirable conditions, for example high levels of toxic elements such as sulfide and heavy metals, generally adopt special metabolic pathways and protective mechanisms to survive in these environments (Flemming & Wingender, 2001a, Flemming & Wingender, 2001b; Zhenming & Yan, 2005). Even if the SRB have the highest tolerance to

sulfide, their development is inhibited by the presence of high levels of sulfide (Caffrey & Voordouw, 2009), however they have the capability to produce special bioactive compounds such as extracellular polymeric substances (EPS) (Flemming & Wingender, 2001a). The EPS are produced during both suspended and biofilm growth to protecting microorganisms from predation, toxic agents, desiccation; also serving as surface adhesions, stabilizing enzymes, storing nutrient, etc. (Zhenming & Yan, 2005).

From the biotechnological point of view, the SRB are of great importance in environmental and industrial processes, for which demand a greater knowledge of the kinetic behavior of sulfate-reducing processes. However, the determination of kinetic parameters throughout *structured model* on basis of biomass components, such as: concentration of metabolites, enzymes, DNA, and/or RNA as a complex task (Arellano-Plaza *et al.*, 2007; Bailey & Ollis, 1986; Hyohak *et al.*, 2008). For this reason, the kinetic parameters more commonly used are estimated through *unstructured kinetic model* that use biomass, substrate, product measurements, as well as yield coefficients determined in the bulk of the reactor (Arellano-Plaza *et al.*, 2007; Hyohak *et al.*, 2008). Few kinetic models have obtained satisfactory

fitting of sulfate reducing kinetic (Neria-González *et al.*, 2009), in most cases Monod model is used, which does not takes into account the product inhibition phenomenon generated by sulfide accumulation inside bioreactor; much less the EPS production present at later stage of the reacting paths (Al-Zuhair *et al.*, 2008; Robinson & Tiedje; 1983). Beside, the well-know Monod expression is only applicable where the presence of toxic metabolic products is not important (Luong, 1985).

Nowadays, the sulfate reducing processes have more importance in the bioremediation field; therefore, a clear knowledge of the sulfate reducing kinetic and a mathematical model to describe satisfactorily the reacting behavior are needed. In this work the kinetic of sulfate reducing process, taken at *Desulfovibrio alaskensis* 6SR as strain model, was analyzed. The specific growth rate of 6SR strain is estimated through five unstructured kinetic models: (a) Haldane-Bulton, (b) Haldane-Levespiel, (c) Haldane-Luong, (d) Moser-Bulton, and (b) Levenspiel; all models includes a product inhibition (sulfide) term that take in consideration the inhibition effect by sulfur production: Mean while, the estimation of EPS production rate by means of power law model is carried-out. The goal is to find a kinetic model for specific growth rate and the mass balance expressions of

the different species (*X*, *S*, *P*, and EPS) to approximate satisfactorily the kinetic behavior in a batch bioreactor, in order to maximize or minimize the production of the desired metabolite (e.g. sulfide or EPS production).

MATERIALS AND METHODS

Organism, culture maintenance and purity test

Desulfovibrio alaskensis 6SR was maintained routinely in Hungate tubes with 5 mL of Postgate's B solid medium (Hungate; 1969; Postgate, 1981). The presence of black colonies indicated the growth of sulfate reducing bacteria. One black colony well defined and isolated was picked and quickly transferred at 45 mL sterile Postgate's C liquid medium in anaerobic conditions (Postgate, 1981), and subsequently a subcultures were made. The media were inoculated with 5 ml of culture and incubated at 37 °C. Each medium was prepared and dispensed in anaerobic conditions under a N₂ (99.998% purity) atmosphere, 120 and 160 ml serum bottles were filled with 45 and 95 mL of medium, respectively, and autoclaved at 121 °C.

Conditions of culture

The inoculum for kinetic study was cultured in 45 ml of Postgate's C medium at 37 °C for 30 h until culture

reached at the beginning of stationary phase. A 5 ml aliquot was taken from Postgate's C medium to inoculate 95 ml of fresh medium at 37 °C. The experiment was done using two series of triplicate independent cultures; each set of triplicate cultures were inoculated with 12 hours separated each other, the experimental run time was 72 hours. One set of independent cultures were used to measure EPS production. A culture was taken for day and the EPS was extracted.

Analytic Methods

The bacterial growing, consuming of sulfate, and sulfide production were monitored 3 or 4 hours each, the samples were taken carefully, avoiding contact with oxygen. The bacterial growing was followed through Optical Density (OD) methodology, the OD data were transformed into dry mass (mg/ml) through a dry mass *versus* OD standard curve. The consuming of sulfate in the medium was measured by the turbid metric method based on barium precipitation (Kolmert *et al.*, 2000). Also the production of sulfide was measured by a colorimetric method (Cord-Ruwisch, 1985). Each measuring was done using a Thermo SCIENTIFIC GENESYS 10uv Scanning Spectrophotometer.

The EPS was extracted by heat treatment and filtration. The bacterial

culture bottles were opened and placed in water bath at 50 °C for 15 minutes, each sample was vortexed once or twice, then the cellular suspension was passed through a nylon membrane 0.45µm, the filtrate was collected in 250 ml centrifuge bottle and EPS was then precipitated from it, adding an equal volume of cold ethanol overnight at -20 °C, followed by centrifugation at 2500 × g for 10 min at 4 °C (Hettich Zentrifugen UNIVERSAL 320R). The pelleted EPS was transferred at micro-centrifuge tube and washed in 70% (v/v) ice-cold ethanol. EPS was dried in oven (ECOSHEL DOV23A) at 70 °C for 24 h and before dry weight was recorded.

Data Analysis and mathematical model

The biomass, sulfate, sulfide, and EPS concentrations of each experimental data were averaged, in order to smooth the experimental behavior of each variable, see figure 1. The specific growth rate of *Desulfovibrio alaskensis* 6SR was evaluated with five different unstructured kinetic models (Haldane, 1930; Han & Levenspiel, 1988; Levenspiel, 1980; Luong, 1985; Moser 1958). In table 1 are shown the different product inhibition models (for high sulfide concentrations).

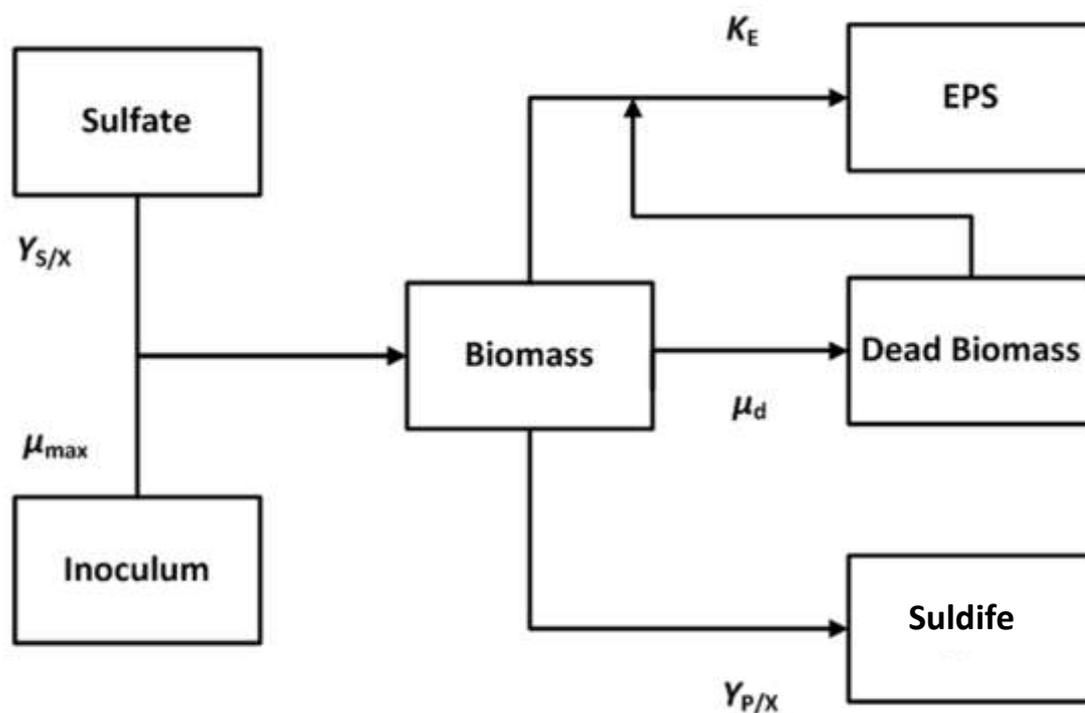


Fig. 1. Out line of sulfate reduction process for *Desulfovibrio alaskensis* 6SR.

Table 1. Unstructured kinetic models considered in this work.

Kinetic model		Equation	References
Haldane-Boulton	(1)	$\mu = \left[\frac{\mu_{\max} S}{K_S + S + (S^2/K_i)} \right] \left[\frac{K_P}{K_P + P} \right]$	Haldane, 1965; Boulton, 1980.
Haldane-Levenspiel	(2)	$\mu = \left[\frac{\mu_{\max} S}{K_S + S + (S^2/K_i)} \right] \left[1 - \frac{P}{K_P} \right]^m$	Haldane, 1965; Levenspiel, 1980
Haldane-Luong	(3)	$\mu = \left[\frac{\mu_{\max} S}{K_S + S + (S^2/K_i)} \right] \left[1 - \left(\frac{P}{K_P} \right)^m \right]$	Haldane, 1965; Luong, 1985.
Moser-Bulton	(4)	$\mu = \left[\frac{\mu_{\max} S^n}{K_S + S^n} \right] \left[\frac{K_P}{K_P + P} \right]$	Moser, 1958; Boulton, 1980.
Levenspiel	(5)	$\mu = \mu_{\max} \left[1 - \frac{P}{P^*} \right]^n \left[\frac{S}{K_S + S} \right]$	Levenspiel, 1980.

Estimations of kinetic parameters

The rate of change of experimental biomass production for the parametric

$$\left(\frac{dX}{dt} \right)_{ti} \cong \left(\frac{\Delta X}{\Delta t} \right) = \left(\frac{X_{i+1} - X_i}{t_{i+1} - t_i} \right) \quad (1)$$

The kinetic parameter estimations of the five unstructured kinetic models for specific growth rate were obtained by using nonlinear multivariable regressions through of Levenberg-Marquardt algorithm (POLYMATH 6.0 Professional software) employing experimental data of biomass, substrate, and product concentrations. The model predictions were comparing with experimental data through minimizing the error sum of least squares. The same methodology was

optimization was calculated using forward finite differences scheme according to the following equation:

used to estimate the production rate of EPS and the dead rate.

Model evaluation

According to the mass balances for biomass, substrate (sulfate) and product (sulfide), dead biomass and EPS concentrations, the following set or ordinary differential equations is proposed to modeling the sulfate-reducing process, in accordance with the reaction scheme showed in Figure 1.

Biomass (X):

$$\frac{dX}{dt} = r_X - \mu_d X \quad (2)$$

Substrate (S):

$$\frac{dS}{dt} = (-Y_{S/X})(r_X) \quad (3)$$

Product (P):

$$\frac{dP}{dt} = (Y_{P/X})(r_X) \quad (4)$$

$$\frac{dEPS}{dt} = K_E X^\varepsilon X_d \quad (5)$$

Dead rate (X_d):

$$\frac{dX_d}{dt} = \mu_d X \quad (6)$$

The specific growth rate models for r_x , considered in this work are Haldane-Bulton, Haldane-Levenspiel, Haldane-Luong, Moser-Bulton, and Levenspiel models. The yield coefficients by

substrate-biomass ($Y_{S/X}$) and product-biomass ($Y_{P/X}$) were calculated with the experimental data corresponding to exponential phase, using expressions (7) and (8).

$$Y_{S/X} = \frac{S_0 - S_1}{X_1 - X_0} \quad (7)$$

$$Y_{P/X} = \frac{P_1 - P_0}{X_1 - X_0} \quad (8)$$

To validate the mathematical models, experimental data were collected from two set batch cultures with the following initial concentrations: biomass ($X = 117$ mg/l), substrate ($SO_4^{2-} = 5000$ mg/l) and sulfide (34 mg/l). The values calculated of yields are $Y_{S/X} = 14.13$ and $Y_{P/X} = 2.14$. The simulation of the kinetic behavior was obtained integrating the set of differential equations (2-6) using the BioTecnología, Año 2013, Vol. 17 No. 2

specific growth parameter values (see Table 2) of the five unstructured kinetic models. The Runge-Kutta method (library ODE45 MATLAB™) was employed to solve the system given by equations (2-6). The performance of each model was evaluated by means of the corresponding correlation coefficient calculated by a linear regression between the experimental

and predicted data for the biomass,

substrate, and products concentrations.

Table 2. Kinetic parameters estimated for *Desulfovibrio alaskensis* 6SR and EPS.

Model	μ_{max}	k_s	k_i	k_p	P^*	n	m	K_E	ϵ
Haldane-Bulton	39.84	86070.00	9850.19	7.24	---	---	---	---	---
Haldane-Levenspiel	0.39	2227.03	2298.68	554.19	---	---	---	---	---
Haldane-Luong	7.00	2227.00	565.53	557.12	---	---	---	---	---
Moser-Bulton	10.55	1.26 E+9	---	2.70	---	2.53	2.53	---	---
Levenspiel	0.36	6550.00	---	---	610.00	0.89	0.89	---	---
EPS	---	---	---	---	---	--	---	9.78E-07	2

RESULTS AND DISCUSSION

Desulfovibrio alaskensis 6SR was taken as bacterium model for sulfate reducing process; this stain was isolated from a developed biofilm inside face of oil pipeline (Neria *et al.*, 2006). However, the strain 6SR have the ability of resistance high concentrations of heavy metals (Cd^{2+} , Pb^{2+} , Zn^{2+} and Cr^{6+}) in comparison with other species (López-Pérez *et al.*, 2013) is tolerant at oxygen, growths at pH 5.5–9.0 (7.0), 15–55 °C (4 °C) and in 30% (w/v) NaCl. These characteristics of growing are important in environmental processes and other as the biocorrosion (Videla & Herrera, 2005, Neria-González *et al.*, 2006; Padilla-Viveros *et al.*, 2006; Hernández-Gayosos *et al.*, 2004). For this reason, each day the sulfate-reducing bacteria are important in the biotechnological processes and for their anaerobic nature is difficult to study the

dynamic behavior in a laboratory. Then mathematical models, together with carefully designed experiments, make it possible to evaluate the behaviors of sulfate reducing process more rapidly than with laboratory experiments alone (Bellomo *et al.*, 2010; Bianca *et al.* 2009; Pérez-López *et al.*, 2012). Also, the number of state variables considered in the mathematic model can help to give a more real representation of biosystem (Bellouquid, 2010; Bellomo *et al.*, 2010). In this work the dynamic sulfate reducing process was analyzed considering four state variables using different mathematical models, see figure 1. The average of experimental date was graphed to analyze the evolution of growth of strain 6SR on base at consumption of sulfate, sulfide and production of biomass and EPS, figure 2. An induction phase of growth

of three hours and an exponential phase close to 40 hours were observed. Before 45 hours a maximum concentration of biomass and sulfide is over taken and a maximum consumption of sulfate is also reached; then the product formation kinetics is a simple stoichiometric connection between product formation and substrate utilization or cell growth. After of this time the sulfide is maintained constant and presented an inhibition by product affected the growth, and the consumption of sulfate decreases because the cell begin to die. In this phase, the EPS apparently not is related with the using substrate (sulfate), and such behavior can relate at a non-growth associated (Bailey & Ollis, 1986). In addition, the accumulation and toxicity of sulfide induces the producing of EPS as a cellular protective mechanism (Caffrey & Voordouw, 2009). Finely, at 170 hours, the four concentrations (biomass, sulfate, sulfide and EPS) enter in a steady state, the biomass stop to die, there is not consumption of sulfate and formation EPS is stopped. These results confirmed the use of the

no structure model with inhibition to analyze the dynamic for this process, Table 1. The predictions obtained for each mathematical model: Haldane-Bulton, Haldane-Levenspiel, Haldane-Luong, Moser-Bulton, and Levenspiel are represented in the figures 3-6, where can be observed that the mathematical models (Equations 2-6), which are based on mass balances principles; represent adequately the corresponding experimental data. Equation 2 considers the biomass concentration production as a function of sulfate and sulfide concentrations, as well as endogenous metabolism via first order biomass dead kinetic. Equations 3 and 4 represent the sulfate generation and the sulfide production, as a function of the specific microbial growth rate, considering the corresponding yield coefficients, which represents an assimilatory behavior. On other side, equation 5 is related with the EPS production, which is proposed as a function of life and dead biomass concentration, this last one variable, generated by the inhibitory effect of the sulfide concentration.

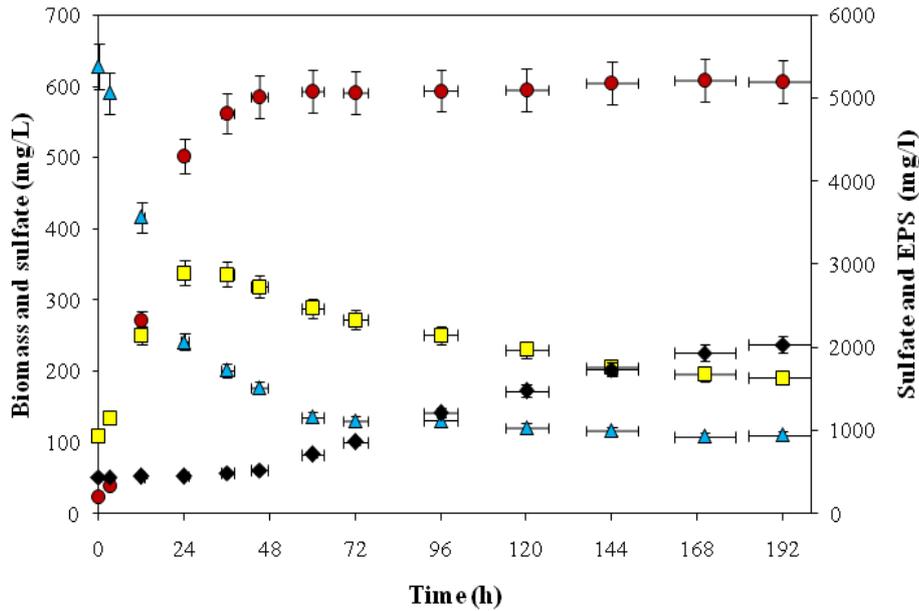


Fig. 2. Curve of growth for *Desulfovibrio alaskensis* 6SR, experimental date of in Postgate's C medium. The symbols indicate: (■) biomass, (▲) sulfate, (●) sulfide y (◆) EPS.

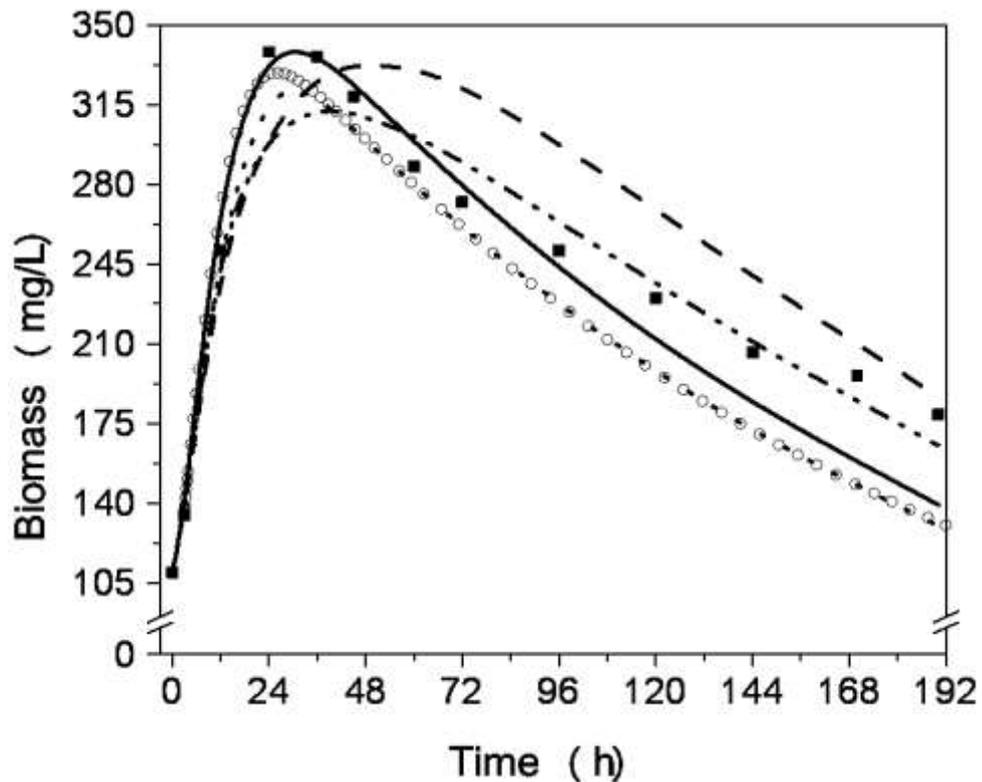


Fig. 3. Biomass prediction using kinetic models. The symbol (■) stands for experimental EPS data, Haldane and Bulton (---), Haldane and Levenspiel (···), Haldane and Luong (○○○), Moser and Bulton (-·-·-), and Levenspiel (—).

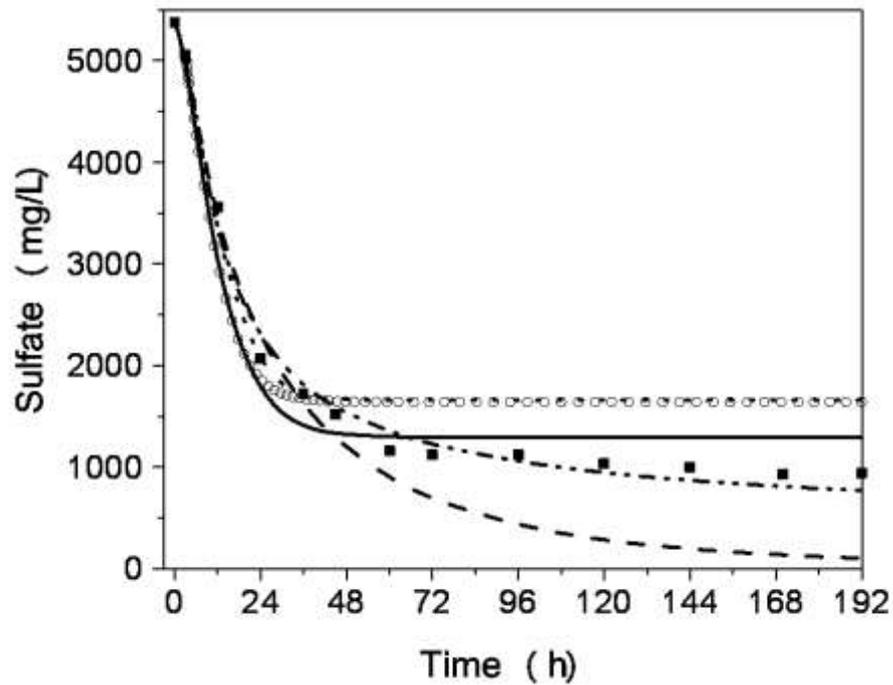


Fig. 4. Sulfate prediction under different kinetic models. The symbol (■) stands for experimental EPS data, Haldane and Bulton (---), Haldane and Levenspiel (-.-.-), Haldane and Luong (o o o), Moser and Bulton (- - - -), and Levenspiel (—).

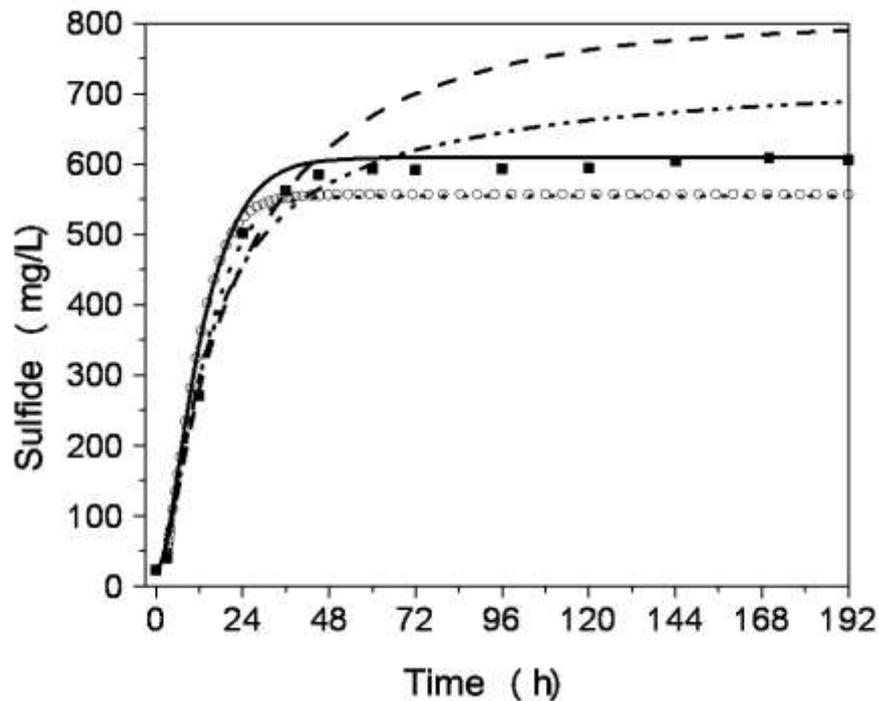


Fig. 5. Sulfide prediction under different kinetic models. The symbol (■) stands for experimental EPS data, Haldane and Bulton (---), Haldane and Levenspiel (-.-.-), Haldane and Luong (o o o), Moser and Bulton (- - - -), and Levenspiel (—).

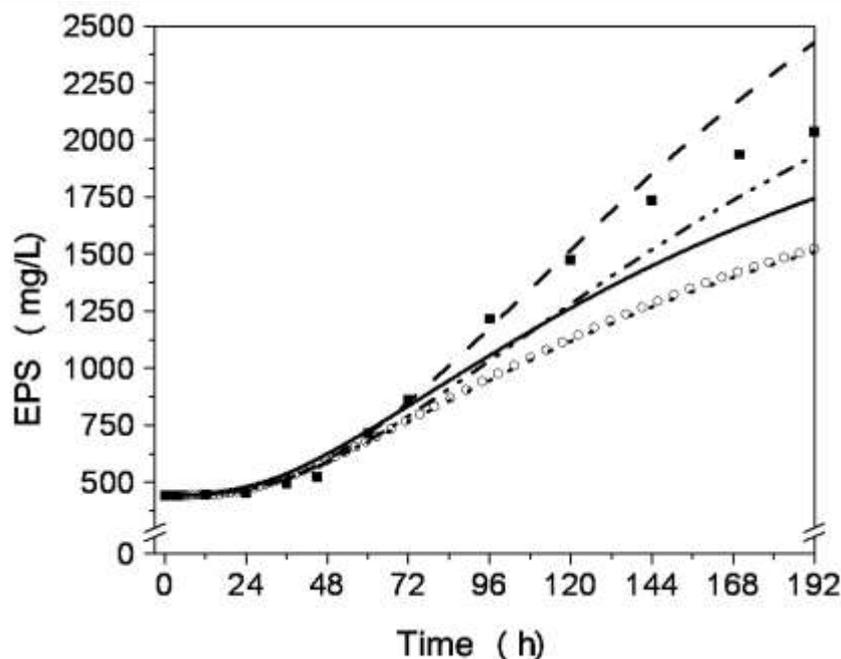


Fig. 6. EPS prediction under different kinetic models. The symbol (■) stands for experimental EPS data, Haldane and Bulton (---), Haldane and Levenspiel (•••), Haldane and Luong (◦◦◦), Moser and Bulton (-••-), and Levenspiel (—).

The kinetic parameters estimated on each model are displayed in Table 2, and overall correlation coefficients from each models were higher than 0.93 (Table 3). However the correlation coefficients for Levenspiel and Moser-Bulton models were the highest, 0.96 and 0.98, respectively. Strictly, the best kinetic model to be used to describe the bacterial growth should be the highest correlation coefficient (Arellano-Plaza *et al.*, 2007; Agarwal *et al.*, 2009), in this case Moser-Bulton (0.98), but the value of μ_{max} is higher than at maximum rate reported by Feio (0.13 1/h) (2004) and K_p does not represent the experimental inhibition concentration of sulfide (> 500 mg/l) and K_s exceed the experimental value, (Table 2). Haldane-

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Bulton model presents the same case and Haldane-Luong model only exceed the value of μ_{max} , so Haldane-Levenspiel and Levenspiel kinetic models would be employed, but Levenspiel model presented better overall correlation coefficients. Besides, all models represent the effect of substrate and product inhibition, except Levenspiel's model in which product inhibition is only considered. In previous publications has been mentioned that the Moser and Haldane models were designed to achieve better adjust to experimental data (Heijnen & Romein 1995; Trejos *et al.*, 2009), and in this case the corresponding models adjusts only in different parts of growth curve from all variables, but Levenspiel's

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model presented the best adjust along of the curve of growth see Fig. 7-10.

Table 3. Correlation coefficients calculated for each kinetic model.

Model	Correlation coefficient				Overall r^2
	Biomass	Sulfate	Sulfide	EPS	
Haldane-Bulton	0.88	0.92	0.94	0.98	0.94
Haldane-Levenspiel	0.92	0.87	0.98	0.93	0.94
Haldane-Luong	0.92	0.87	0.97	0.93	0.93
Moser-Bulton	0.95	0.99	0.97	0.99	0.98
Levenspiel	0.92	0.95	0.98	0.98	0.96

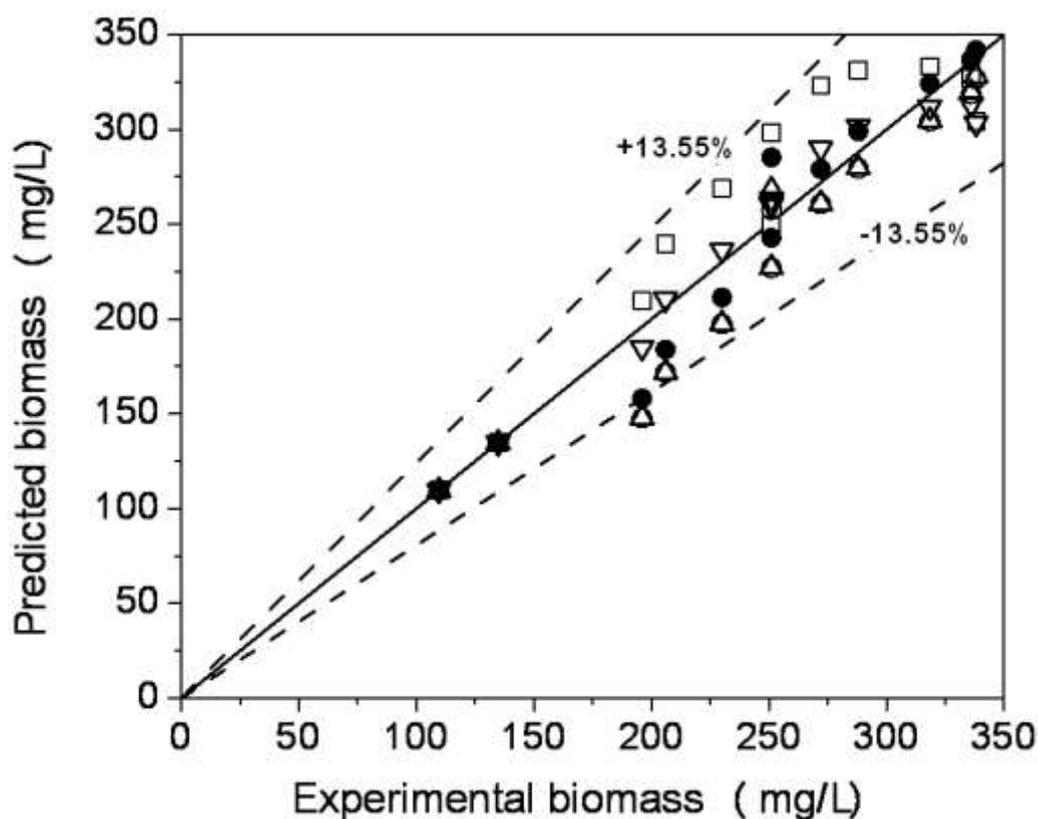


Fig.7. Error calculated from simulations of biomass for each model. The symbols represent models, Haldane and Bulton (\square), Haldane and Levenspiel (\circ), Haldane and Luong (\triangle), Moser and Bulton (∇), and Levenspiel (\bullet).

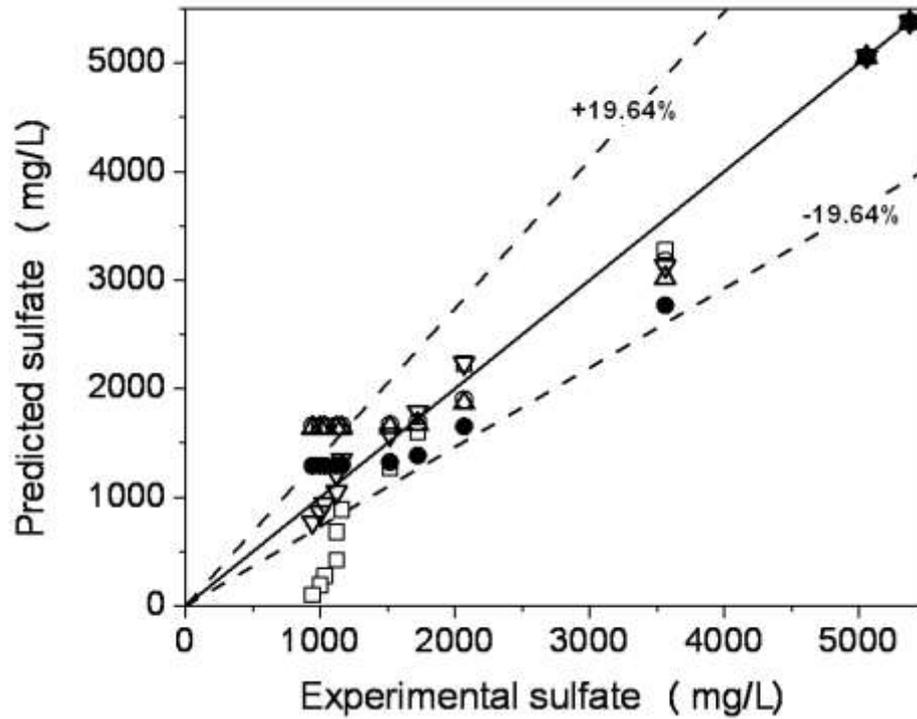


Fig.8. Error calculated from simulations of sulfate for each model. The symbols represent models, Haldane and Bulton (\square), Haldane and Levenspiel (\circ), Haldane and Luong (\triangle), Moser and Bulton (∇), and Levenspiel (\bullet).

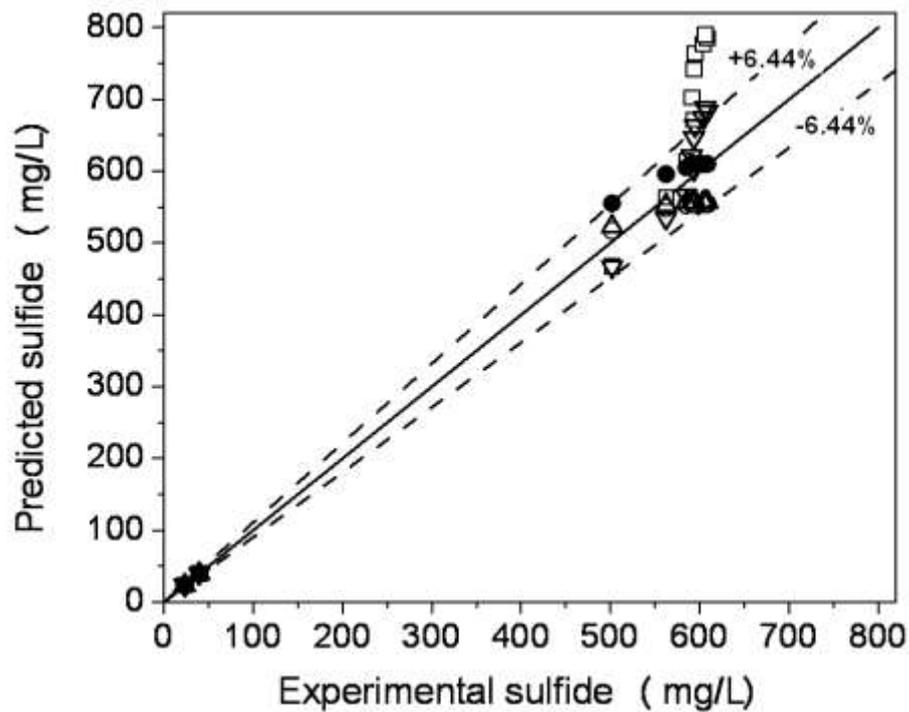


Fig.9. Error calculated from simulations of sulfide for each model. The symbols represent models, Haldane and Bulton (\square), Haldane and Levenspiel (\circ), Haldane and Luong (\triangle), Moser and Bulton (∇), and Levenspiel (\bullet).

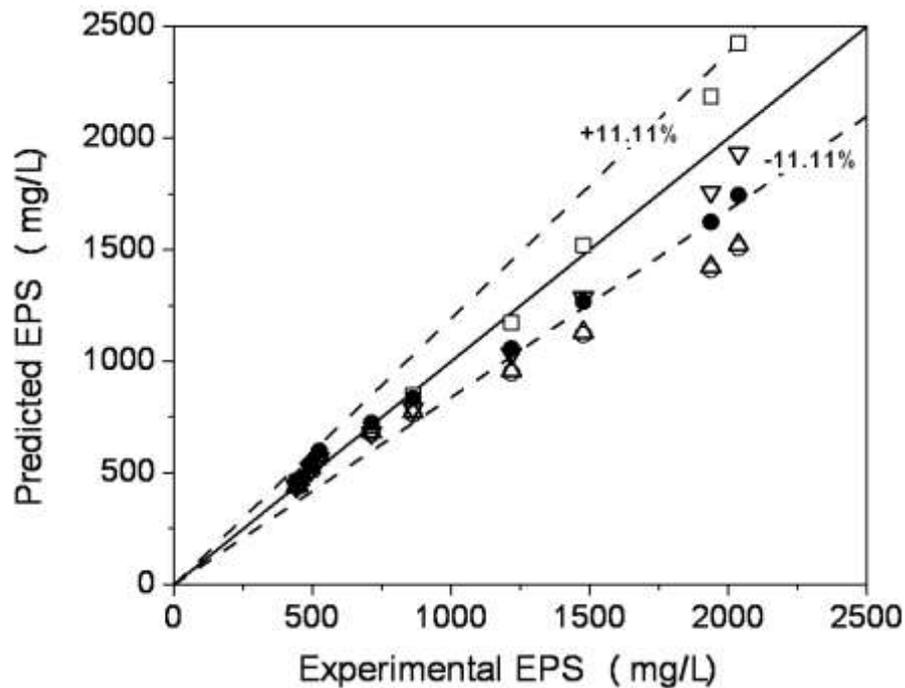


Fig.10. Error calculated from simulations of EPS for each model. The symbols represent models, Haldane and Bulton (□), Haldane and Levenspiel (○), Haldane and Luong (Δ), Moser and Bulton (▽), and Levenspiel (●).

In this kinetic analysis was observed that the effect of inhibition occurred approximately at 600 mg/l of sulfide. This effect is represented in all models, except on model Haldane-Bulton, see table 2, also correspond with previously date reported (Mossa & Harrison, 2006). The accumulation of sulfide in the environment affect the free multiplication cellular, then the kinetic behavior of sulfate-reducing process do not be represented by single Monod model and more when are considering more than two variables, due to poor fit (González-Silva *et al.*, 2009). In

consequence, the model of Levenspiel represented adequately the overall behavior of this process type, see Fig. 11. A mathematical model with more variables can describe better the real world, in the sense that their qualitative predictions are in accordance with the observed data. This is illustrated on some recently obtained results on cadmium removal using at *D. alaskensis* 6SR, where is remarked that the using mathematical model with more of one variable (López-Pérez *et al.* 2013) the cadmium removal can be estimated.

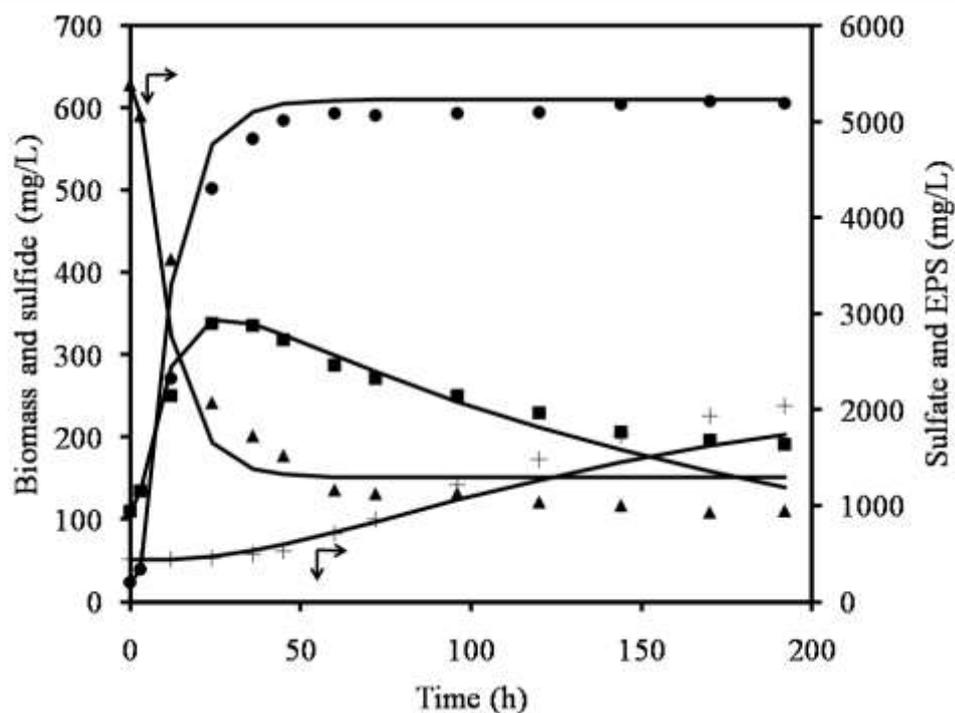


Fig.11. Comparison of the experimental and predicted data, employing model kinetics Levenspiel. Experimental biomass (■), experimental sulfate (▲), experimental sulfide (●), and experimental EPS (+). The continua line represents prediction data.

In conclusion, kinetic models are a grand tool in the bioprocesses allowing biochemical engineers to design, optimize, control microbial processes and, predicting the behavior of a bioprocess too (Bellouquid & Delitala, 2005). Then mathematical models, together with carefully designed experiments, make it possible to evaluate the behaviors of sulfate-reducing process more rapidly than with laboratory experiments alone, due at their anaerobic nature. So, the Levenspiel's model is the best model to represent the sulfate reducing process and the inhibition effect by sulfide, and with the combination of a mathematic BioTecnología, Año 2013, Vol. 17 No. 2

expression to EPS production kinetic, the overall behavior of system is satisfactory.

ACKNOWLEDGMENTS

J. C. Figueroa-Estrada would like to thank to Consejo Nacional de Ciencia y Tecnología (CONACyT) for the corresponding postgraduate scholarship.

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Nomenclature

X	: Biomass concentration (mg/l)
S	: Substrate concentration (mg /l)
P	: Product concentration (mg/l)
X_d	: Concentration of dead biomass (mg/l)
EPS	: Extracellular polymeric substances concentration (mg/l)
P^*	: Inhibitory product concentration (mg/l)
K_S, K_i, K_P	: Substrate affinity constant, inhibition constant, term inhibition (mg/l)
K_E	: Constant for EPS (1/h)
r_X	: Growth rate (mg-biomass/l per h)
r_d	: Death rate (mg-death biomass/l per h)
μ, μ_d, μ_{max}	: Specific growth rate, specific death rate, maximum rate growth (1/h)
$Y_{S/X}$: Substrate-biomass yield coefficient (mg-sulfate/mg-biomass)
$Y_{P/X}$: Product-biomass yield (mg-sulfide/mg-biomass)
m	: Exponential term for Luong model
n	: Exponential term for Moser model
ε	: Exponential term for EPS model