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Modelling the population dynamics and metabolic diversity of organisms relevant in anaerobic/anoxic/aerobic enhanced biological phosphorus removal processes

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ABSTRACT

In this study, enhanced biological phosphorus removal (EBPR) metabolic models are expanded in order to incorporate the competition between polyphosphate accumulating organisms (PAOs) and glycogen accumulating organisms (GAOs) under sequential anaerobic/anoxic/aerobic conditions, which are representative of most full-scale EBPR plants. Since PAOs and GAOs display different denitrification tendencies, which is dependent on the phylogenetic identity of the organism, the model was separated into six distinct biomass groups, constituting *Accumulibacter* Types I and II, as well as denitrifying and non-denitrifying *Competibacter* and *Defluviicoccus* GAOs. Denitrification was modelled as a multi-step process, with nitrate (NO_3), nitrite (NO_2), nitrous oxide (N_2O) and di-nitrogen gas (N_2) being the primary components. The model was calibrated and validated using literature data from enriched cultures of PAOs and GAOs, obtaining a good description of the observed biochemical transformations. A strong correlation was observed between *Accumulibacter* Types I and II, and nitrate-reducing and non-nitrate-reducing PAOs, respectively, where the abundance of each PAO subgroup was well predicted by the model during an acclimatisation period from anaerobic–aerobic to anaerobic–anoxic conditions. Interestingly, a strong interdependency was observed between the anaerobic, anoxic and aerobic kinetic parameters of PAOs and GAOs. This could be exploited when metabolic models are calibrated, since all of these parameters should be changed by an identical factor from their default value. Factors that influence these kinetic parameters include the fraction of active biomass, relative aerobic/anoxic fraction and the ratio of acetyl-CoA to propionyl-CoA. Employing a metabolic approach was found to be advantageous in describing the performance and population dynamics in such complex microbial ecosystems.
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1. Introduction

In the enhanced biological phosphorus removal (EBPR) process, the group of organisms primarily responsible for phosphorus (P) removal are known as the polyphosphate accumulating organisms (PAOs). In order to promote the development of PAO and, consequently, P removal, anaerobic followed by anoxic and/or aerobic conditions are generally

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employed. PAOs are able to take up carbon sources such as volatile fatty acids (VFAs) anaerobically and store them as polyhydroxyalkanoates (PHAs), providing them a selective advantage over most ordinary heterotrophs. However, glycogen accumulating organisms (GAOs) are also capable of anaerobic VFA uptake and therefore can also be enriched under similar conditions as PAOs, consuming the generally limited VFA supply, without contributing to P removal. In recent years, the competition between PAO and GAO has been studied intensively due to (a) its impact on phosphorus removal performance and efficiency, and (b) PAO-dominated systems have the potential to decrease operational costs through minimising the addition of supplemental additives (e.g. chemical precipitants, organic carbon sources) necessary to achieve sufficient P removal (Oehmen et al., 2007a). The addition of these chemicals is also undesirable since they result in higher sludge generation, increasing sludge disposal costs.

Among numerous operational and environmental factors, the carbon source (Pijuan et al., 2004; Oehmen et al., 2005b; Lu et al., 2006), pH (Filipe et al., 2001b; Schuler and Jenkins, 2002; Oehmen et al., 2005a) and temperature (Panswad et al., 2003; Lopez-Vazquez et al., 2007b, 2009a) have been observed to have a profound impact on the PAO–GAO competition. Recently, Lopez-Vazquez et al. (2009b) formulated a metabolic model that incorporates the combined effects of carbon source, pH and temperature on the metabolism of key EBPR microorganisms under anaerobic–aerobic conditions: specifically, *Accumulibacter* (PAO), *Competibacter* (GAO) and *Defluviicoccus* (GAO). In full-scale plants the EBPR process is invariably combined with nitrogen (N) removal. Different groups of PAOs and GAOs have shown varying denitrification capacities (Zeng et al., 2003c; Carvalho et al., 2007; Wang et al., 2008) that may have an important impact on their competition. This served as the motivation for the present study.

It has been postulated that denitrifying PAOs (or DPAOs) able to reduce nitrate correlate well with Type I *Accumulibacter*, while non-DPAOs (or simply, PAOs) that are unable to reduce nitrate but able to reduce nitrite have been correlated with Type II *Accumulibacter* (Carvalho et al., 2007; Flowers et al., 2009; Oehmen et al., 2010). Due to the fact that Type I and Type II *Accumulibacter* correlate strongly with the so-called DPAO and PAO, respectively, we have adopted the terms PAOI and PAOII to differentiate between their different denitrification tendencies in this manuscript. This was done to avoid confusion, since both organisms appear capable of nitrite reduction, while the only difference is that PAOI are capable of nitrate reduction as well. The term "PAO" seems better suited as a more general term to describe all organisms that contribute to enhanced biological phosphorus removal in activated sludge systems.

Kong et al. (2006) hypothesised that the different subgroups of *Competibacter* also display varying denitrifying capacities: (i) capable of nitrate and nitrite reduction (subgroup 6), (ii) able to reduce nitrate only (subgroups 1, 4 and 5) and (iii) unable to denitrify (subgroups 3 and 7). Wang et al. (2008) showed that an enrichment of *Defluviicoccus* Cluster I was able to reduce nitrate, but not nitrite, while Burow et al. (2007) suggested that *Defluviicoccus* Cluster II was unable to denitrify. It is clear from these studies that the denitrification activity of PAOs and GAOs depends on the abundance of the different subgroups enriched.

By expanding the metabolic model developed by Lopez-Vazquez et al. (2009b), the present study focuses on the calibration and validation of a metabolic model developed to describe the biochemical activity of 6 microbial groups of PAOs and GAOs, namely the nitrate-reducing and non-nitrate-reducing *Accumulibacter* (i.e. PAOI and PAOII, respectively), denitrifying and non-denitrifying *Competibacter* (DGB and GB, respectively) and denitrifying and non-denitrifying *Defluviicoccus* (DDEF and DEF, respectively). Strategies aimed at facilitating the calibration of metabolic models based on a small number of parameters are also addressed in this study. Since model calibration is a very important and challenging issue in activated sludge modelling, ensuring the ease of metabolic model calibration is crucial in order to increase its potential utility in practice. Further, the ability of this model to assess the population dynamics of DPAO and PAO in microbial enrichments will be illustrated.

2. Materials and methods

2.1. Model development

From a physiological perspective, the metabolic model developed in this study incorporates the different capabilities of PAOs and GAOs to denitrify by separating them into multiple distinct groups. For this purpose, denitrification by PAOs and GAOs was modelled as a multi-step process from nitrate to nitrite, followed by nitrite to N_2O, and finally N_2O to N_2. The stoichiometric matrix for PAOI and PAOII is shown in Appendix A, and that for GAOs and DGAOs (including GB, DGB, DEF and DDEF) is shown in Appendix B. In summary (see Fig. 1), PAOI are assumed to be capable of NO_3, NO_2 and N_2O reduction, while PAOII are capable of NO_2 and N_2O reduction only, as suggested from their metagenome (Garcia Martin et al., 2006). DGB is also considered to be capable of NO_3, NO_2 and N_2O reduction, while DDEF is capable of NO_3 reduction only and GB and DEF are not capable of denitrifying. These properties are consistent with the results obtained from the aforementioned literature studies.

It should be noted that PAOs and GAOs have been found to require a brief acclimation period (4–5 h) to induce denitrification enzymes after being exclusively exposed to anaerobic/aerobic conditions (Kuba et al., 1996b; Zeng et al., 2003a; Wang et al., 2008). In most systems, the organisms are exposed to anaerobic/anoxic/aerobic conditions, continuously exposing the bacteria to denitrifying conditions. Since the goal of this study was to model PAO and GAO steady-state metabolism, enzyme induction was not incorporated into the model. Nitrite accumulation (in the form of free nitrous acid: S_{HNO2}) is known to inhibit P uptake by PAOs (Saito et al., 2004; Zhou et al., 2007), and can lead to the undesirable production of N_2O (a powerful greenhouse gas) (Zhou et al., 2008). These aspects have been incorporated into the kinetic equations of the model.

2.2. Anaerobic stoichiometry

The anaerobic stoichiometry of PAOI and PAOII is modelled identically. The anaerobic processes consist of VFA uptake (as

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