Science of the Total Environment 775 (2021) 145760

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Generalized temperature dependence model for anammox process kinetics

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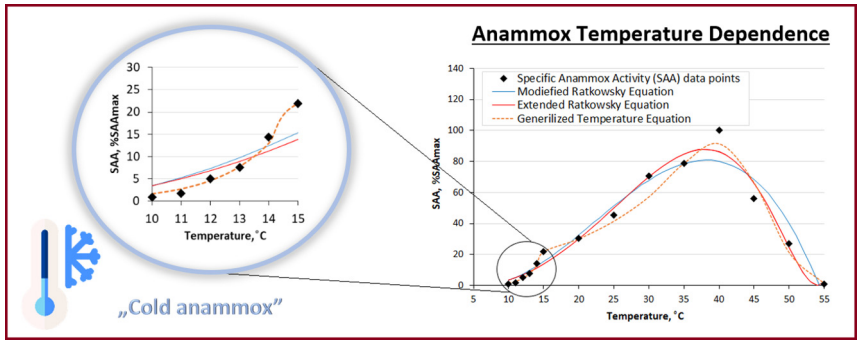
HIGHLIGHTS

- Anammox is strongly temperature dependent process.
- The temperature dependence of anammox cannot be described by a single equation.
- Ratkowsky equations describe the anammox activity in the entire temperature range.
- Ratkowsky equations cannot describe the temperature dependence at lower temperatures.
- The generalized temperature equation improves predictions at low temperatures (10–15 °C).

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 20 November 2020
Received in revised form 6 February 2021
Accepted 6 February 2021
Available online 11 February 2021

Editor: Yifeng Zhang

Keywords:
Activation energy
Anammox
Arrhenius equation
Ratkowsky equation
Temperature dependence

ABSTRACT

Temperature is a key operational factor influencing the anammox process kinetics. In particular, at temperatures below 15 °C, the specific anammox activity (SAA) considerably decreases. This study aimed to describe the temperature dependence of the anammox process kinetics in the temperature range from 10 to 55 °C, including the specific characteristics of "cold anammox". The commonly used Arrhenius and extended and modified Ratkowsky equations were examined. The Ratkowsky equations yielded a strong correlation (coefficient of determination, $R^2 = 0.93–0.96$) between the measured and predicted data over the analyzed temperature range (10–55 °C). However, these equations could not correctly reflect the anammox temperature dependence at temperatures below 15 °C ($R^2 = 0.36–0.48$). Therefore, a new generalized temperature model was proposed. The generalized temperature equation (GTE) considered the division of the analyzed temperature range into three temperature ranges: 10–15 °C, 15–35 °C and 35–55 °C. The ranges correspond to "cold anammox", "(low) mesophilic anammox" and "thermophilic anammox". The applied approach yielded a strong correlation between the measured and predicted SAA ($R^2 = 0.97$) over the temperature range from 10 to 55 °C and over the low-temperature range from 10 to 15 °C ($R^2 = 0.99$). Overall, the GTE could enhance the predictions of the temperature dependence of the anammox process kinetics. The GTE can help examine anammox-based bioaugmentation systems operating at both high temperatures (sidestream reactors) and low temperatures (mainstream reactors).

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https://doi.org/10.1016/j.scitotenv.2021.145760

Abbreviations

Anammox	anaerobic ammonium oxidation
AOB	ammonium oxidizing bacteria
NOB	nitrite oxidizing bacteria
OHO	ordinary heterotrophic organisms
SAA	specific anammox activity, g N $(g\ VSS \cdot d)^{-1}$
SAA_{ref}	reference specific anammox activity, %
MRE_i	modified Ratkowsky equation
ERE_i	extended Ratkowsky equation
GTE_i	generalized temperature equation
DO	dissolved oxygen concentration, mg O_2/L
HRT	hydraulic retention time, d
SRT	sludge retention time, d
NLR	nitrogen loading rate, kg N m^{-3} d^{-1}
NRE	nitrogen removal efficiency, %
SBR	sequencing batch reactor
UAB	upflow anaerobic biofilter/bioreactor
MBR	membrane bioreactor
ICR	internal circulation reactor

Symbols

T	temperature, K
μ	specific growth rate of anammox bacteria, d^{-1}
E_a	activation energy, kJ mol^{-1}
R	gas constant, J $(mol \cdot K)^{-1}$
A	pre-exponential factor in the Arrhenius equation, −
Θ	temperature coefficient, −
$b_{1,2}$	fitting parameter in the Ratkowsky equations, K^{-1} $d^{-0.5}$
$c_{1,2}$	fitting parameter in the Ratkowsky equations, K^{-1}

Subscripts

i	temperature range, °C
min	minimum value
max	maximum value
1	parameter in the ERE
2	parameter in the MRE

1. Introduction

Temperature is a key operational factor that considerably influences the rate of biochemical processes. However, maintaining the optimal temperature range may result in additional operational costs in wastewater treatment processes. To improve the energy efficiency of wastewater treatment plants (WWTPs), conventional nitrification-denitrification processes can be replaced by alternative technologies based on anaerobic ammonium oxidation (anammox). Anammox-based technologies are mainly used to realize nitrogen removal from wastewater with high concentrations of ammonium nitrogen and a deficit of organic carbon, such as effluents from anaerobic digesters and industrial wastewater streams. Despite numerous attempts, until now, this technology has not been applied in mainstream WWTPs. A notable challenge to the mainstream implementation of anammox-based technologies pertains to the low temperatures and seasonal temperature variations in municipal wastewater compared to the high and stable temperatures (~30 °C) involved in sidestream processes (Ali and Okabe, 2015; Cao et al., 2017; Hoekstra et al., 2019).

Although the optimum temperature for the growth and activity of anammox bacteria ranges from 35 to 40 °C (Strous et al., 1999; Isaka et al., 2008), these microorganisms can exist in natural ecosystems at both low (from −5 to 4 °C) and high (from 60 to 80 °C) temperatures (Cho et al., 2020). The occurrence of anammox bacteria over a wide temperature range indicates the potential of their use in various types of wastewater treatment systems. In recent years, numerous studies have reported on the anammox activity and possibility of operation of laboratory scale anammox reactors at extremely low temperatures (5–15 °C). Anammox performed at such temperatures is referred to as "cold anammox". These observations confirm that the process can not only be applied in sidestream but also in mainstream treatment systems. Therefore, certain recent studies focused on the intensification of the anammox activity at low temperatures (De Cocker et al., 2018; Straka et al., 2019; Kouba et al., 2019). The temperature dependence of the specific anammox activity (SAA) has been determined over a wide temperature range (10–55 °C) through both short- and long-term experiments (Dosta et al., 2008; Lotti et al., 2015; Sobotka et al., 2016; Park et al., 2017). According to the experiment results, the influence of the temperature on the SAA follows the trend described by the Arrhenius equation, albeit with a sharper decline at temperatures below 15 °C. Moreover, certain studies reported that at high temperatures (45–55 °C), the SAA was inhibited owing to the lysis of bacterial cells (Dosta et al., 2008; Isanta et al., 2015; Sobotka et al., 2016).

Mathematical models and simulations are being increasingly used to describe, predict and control anammox-based systems. In the literature, anammox-based systems have been modeled considering different factors, including temperature (Hao et al., 2002; Zhu et al., 2017), nitrogen content (De Pra et al., 2016), dissolved oxygen (DO) content (Seuntjens et al., 2018), chemical oxygen demand (Hao and van Loosdrecht, 2004) and granular flotation (Tan et al., 2020). The process temperature exerts a direct impact on the anammox process kinetics and an indirect impact on the properties of anammox granules, *e.g.* the granule settling velocity (Shi et al., 2017; Zhu et al., 2017).

The effect of temperature on the activity of microorganisms (*e.g.*, bacteria, archaea, fungi) is commonly described using two mathematical equations. The Arrhenius equation reflects the positive correlation between the SAA and temperature. Although this approach is simple, the general applicability is low. In contrast, the Ratkowsky equation is a basic approach that is used to describe the temperature dependence in situations in which the increasing temperature exerts a negative effect on the microbial activity. This equation can be expressed in two forms, namely, the extended Ratkowsky equation (ERE) and modified Ratkowsky equation (MRE). Both the ERE and MRE have been successfully used ($R^2 > 0.97$) to describe the effect of temperature on the growth rate and activity of various microorganisms in different temperature ranges, *e.g.*, soil bacteria (0–26 °C) (Nicola and Bååth, 2019; Nottingham et al., 2019), marine bacteria (5–35 °C) (Yi et al., 2005; van Gestel et al., 2020), and pathogenic bacteria (10–47 °C) (Juneja et al., 2009). The literature involves various studies on the anammox process kinetics, describing the influence of temperature on the SAA over wide temperature ranges. However, the current methods to describe this relationship cannot accurately reflect the differences in the temperature dependence of the anammox process at temperatures below 15 °C.

In this study, a novel approach was applied to describe the temperature dependence using a combination of the Arrhenius and Ratkowsky equations over three temperature ranges: 10–15 °C, 15–35 °C and 35–50 °C. The new generalized temperature dependence model is universal as it was developed based on extensive data from the literature, including results from different reactor types, operational conditions, and feed composition. The proposed approach could accurately describe the temperature dependence of the anammox process kinetics in a wide range of temperatures, corresponding to both sidestream and mainstream conditions. This knowledge can facilitate the successful operation of bioaugmentation systems implementing anammox at both high temperatures (sidestream reactors) and low temperatures (mainstream reactors).

2. Materials and methods

2.1. Experimental data

As mentioned previously, the effect of temperature on the SAA was investigated in short- and long-term experiments conducted by Sobotka

et al. (2016). The short-term experiments were conducted in two parallel 4 L batch reactors equipped with an automatic temperature control system and probes to realize the online monitoring of pH, DO and temperature. The anammox biomass originating from a laboratory scale anammox reactor operated at 30 °C was used. Ten different temperatures ranging from 10 to 55 °C (in intervals of 5 °C) were considered. The experiments were conducted under anoxic conditions in the presence of NH_4-N and NO_2-N. The initial NH_4-N and NO_2-N concentrations in the activity tests were approximately 30 mg NH_4-N L^{-1} and 40 mg NO_2-N L^{-1}, respectively. Samples to analyze the nitrogen forms (NH_4-N, NO_2-N, NO_3-N) were collected from the reactor at a frequency of 30 min. Based on the measured data, the SAA was determined for each examined temperature.

Due to the negative influence of low temperatures on the activity of anammox bacteria, as well as the natural ability of the bacteria to adapt to adverse environmental conditions, a comprehensive investigation on the influence of temperature on "cold anammox" was performed through a long-term experiment. The experiment was conducted in a 10 L sequencing batch reactor (SBR) and lasted 180 d. The SBR was fed with a synthetic autotrophic medium with a composition similar to sludge digester liquors (Dapena-Mora et al., 2004). The nitrite to ammonium molar ratio in the feeding media varied from 1.0 (at the lowest temperatures, 11 and 12 °C) to 1.3 (at temperatures ranging from 15 to 30 °C). The long-term experiment was divided into seven phases, in which the SBR operated at a temperature of 30, 20, 15, 14, 13, 12 and 11 °C. At each examined temperature, the SAA was determined three times per week. At temperatures below 15 °C, reducing the temperature by 1 °C resulted in unstable reactor operation. The effect of adaptation of anammox bacteria to lower temperatures was determined by averaging the measured SAA at a specific temperature over a period of several days of the stable operation at that temperature.

In addition, the literature data from 11 studies on the effect of temperature on the SAA were used to evaluate the temperature dependence model for anammox. The results clarified the corresponding temperature dependence in various reactors, *i.e.*, with suspended biomass, granular biomass and hybrid systems. These systems are briefly characterized in Table 1.

2.2. Equations describing the temperature dependence of anammox

The relationship between the chemical reaction rate and temperature is often described using the following form of the Arrhenius equation:

$$ln\,\mu = \frac{-E_a}{R \cdot T + \ln A} \quad (1)$$

where μ is the specific growth rate of anammox bacteria at temperature T (in K), E_a is the activation energy (kJ mol^{-1}), R is the gas constant (8.314 J K^{-1} mol^{-1}), and A is the "pre-exponential factor". The Arrhenius equation is commonly used to describe the relationship between biochemical process rates and temperature in situations in which an increase in the temperature does not inhibit the process. In the modeling of biochemical processes, the following simplified form of Eq. (1) is often used:

$$\mu_{T_1} = \mu_{T_{ref}} \cdot \theta^{(T_1 - T_{ref})} \quad (2)$$

where μ_{T1} and μ_{Tref} are the specific growth rates at the analyzed (T_1) and reference (T_{ref}) temperatures (°C), respectively, and θ is the dimensionless temperature dependence coefficient.

Furthermore, high temperatures lead to process inhibition, and the effect of temperature on the process rate can be modeled using the ERE (Ratkowsky et al., 1983):.

$$\mu = \left(b_1 \cdot (T - T_{min,1}) \cdot (1 - exp\,(c_1 (T - T_{max,1})))\right)^2 \quad (3)$$

where $T_{min,1}$ (K) and $T_{max,1}$ (K) are the minimum and maximum growth temperatures, respectively, b_1 is the regression coefficient of the square root of the growth rate constant *vs.* temperatures (K) below the maximum temperature, $T_{max,1}$ (K), and c_1 is an additional empirical parameter that allows the model to fit the data for temperatures above the optimal temperature (Ratkowsky et al., 1983).

Table 1
Summary of the reported studies on the temperature dependence of anammox in different nitrogen removal systems.

Reactor	Biomass/Dominant anammox genus	Operational conditions	Temperature, °C		Reference
			Enrichment	SAA_{max}	
SBR	Granular biomass, biofilm/ *Ca. K. stuttgartiensis*	pH: 7.0–8.0 HRT: 1 d	30	40	Dosta et al., 2008
UAB[a]	Immobilized biomass/ *Ca. B. sinica*	Operated in the dark	37	40	Oshiki et al., 2011
SBR	Granular biomass/—	pH: 7.5 pH: 7.8 ± 0.3	35	40	Zhu et al., 2017
SBR	Suspended biomass/ *Ca. Jettenia*	NLR: 0.408 ± 0.086 kg N m^{-3} d^{-1} pH: 6.9–7.5	31.6 ± 0.9	40	Tomaszewski et al., 2017
MBR	Immobilized biomass/ *Ca. B. sapporoensis*	HRT: 1 d SRT: 60 d	20–25	37	Narita et al., 2017
–	*Ca.B. anammoxidans, Ca. Scalindua species*	No data Operation time: 1000 d	32–35	35	Kocamemi et al., 2016
UAB[a]	Hybrid (suspended and immobilized biomass)/ *Ca. K. stuttgartiensis*	pH: 7.2 HRT: 9.6–4.0 h NLR: 1.2 kg N $m^{-3}d^{-1}$ Operation time: 262 d	35	35	Park et al., 2017
SBR	Granular biomass/—	pH: 7.5 HRT: 3 h Operation time: 345 d	35	35	Li et al., 2018
SBR	Suspended biomass/ *Ca. B. fulgida*	pH: 7.3 Stirrer: 200 rpm	30	35	Hu et al., 2013
ICR[b]	Granular biomass/ *Ca. B. fulgida*	No data Operation time: 1000 d	30–35	30	Lotti et al., 2015
UAB[a]	Granular biomass/—	pH: 7.2 HRT: 9.6–4.0 h	20	30	Park et al., 2017
MBR[c]	Immobilized biomass/ *Ca. Scalindua*	No data	28	30	Awata et al., 2013

[a] Upflow anaerobic biofilter/bioreactor.
[b] Internal circulation reactor.
[c] Membrane bioreactor.

The ERE describes the growth rates around the optimum temperature in the range constrained by $T_{min,1}$ and $T_{max,1}$. Usually, the estimated value of T_{min} is 2 to 3 °C lower than the actual minimum temperature at which growth is observed (McMeekin et al., 1993). However, at temperatures above $T_{max,1}$, Eq. (3) predicts positive growth rates, and thus, this equation cannot be applied for temperatures higher than $T_{max,1}$.

Modifications to the Ratkowsky equation were proposed by Zwietering et al. (1991) (Eq. (4)). In this case, the decreased microbial growth rates at temperatures higher than $T_{max,2}$ were expressed in terms of the exponential function, and thus, the extrapolation of $T_{max,2}$ did not lead to positive growth rate predictions.

$$\mu(T) = \left(b_2 \cdot (T - T_{min,2})\right)^2 \cdot (1 - \exp(c_2(T - T_{max,2}))) \quad (4)$$

Here, b_2 and c_2 are defined in a similar manner as b_1 and c_1, respectively, in Eq. (3).

2.3. Estimation of model parameters

In general, the Arrhenius and Ratkowsky equations contain unknown parameters (Table 2). To estimate these parameters, the generalized reduced gradient (GRG) nonlinear solving method (Frontline System, Inc., Incline Village, NV) was adopted. The GRG method, based on the generalized reduced gradient (GRG2) code, is often used for nonlinear optimization. The most accurate results are obtained for a smooth nonlinear function having a smooth (possibly curved) graph with no sharp 'breaks'. In the GRG solver methodology, the gradient or slope of the objective function is evaluated under variations in the decision variables (or input values) until the optimal solution is reached (the partial derivatives become zero). In the present study, the sum of the squares of the error (SSE) between the function and the fitted experimental data was minimized as follows:

$$\sum \left(Y_{T_n} - f(x)_{T_n}\right)^2 = SSE \quad (5)$$

where Y_{Tn} is the experimental observation (*i.e.*, SSA) at a given temperature, and $f(x)_{Tn}$ is the predicted value at that temperature.

The GRG nonlinear solving method enables optimization under constraints. In the present study, the examined temperature range (10–55 °C) was divided into three narrower intervals (10–15 °C, 15–35 °C and 35–55 °C). These intervals were chosen based on the specific temperature conditions reported in the literature (Zekker et al., 2015; Kouba et al., 2019; Vandekerckhove et al., 2020), pertaining to "cold anammox", "(low) mesophilic anammox" and "thermophilic anammox", respectively. In this manner, additional implicit constraints were established for solutions to the examined models (Table 2). The Arrhenius equation was used to describe the anammox temperature dependence in two ranges (10–15 and 15–35 °C). In each range, a different μ_{Tref} value was used. In general, the μ_{Tref} value can be considered to be linked to the highest SAA obtained in the analyzed temperature range. For the two Ratkowsky equations, the four parameters (b, c, T_{max} and T_{min}) were estimated separately.

Table 2
Examined temperature models, parameters and implicit constraints used in the present study.

Equation	Parameters	Constraints
Arrhenius	Θ, A, Ea	$\mu_{Tref\,(10-15)} = \mu_{15}$ $\mu_{Tref\,(15-35)} = \mu_{35}$
Extended Ratkowsky	b_1, c_1, $T_{min,1}$, $T_{max,1}$,	$T_{min} \leq T_{max}$
Modified Ratkowsky	b_2, c_2, $T_{min,2}$, $T_{max,2}$	$\mu_{15\,(10-15)} = \mu_{15\,(15-35)}$ $\mu_{35\,(15-35)} = \mu_{35\,(35-55)}$
Generalized model (this study)	Θ, A, Ea, b_1, b_2, c_1, c_2, $T_{min,1}$, $T_{min,2}$, $T_{max,1}$, $T_{max,2}$	$\mu_{Tref\,(10-15)} = \mu_{15}$ $\mu_{Tref\,(15-35)} = \mu_{35}$ $\mu_{15\,(10-15)} = \mu_{15\,(15-35)}$ $\mu_{35\,(15-35)} = \mu_{35\,(35-55)}$ $T_{min} \leq T_{max}$

3. Results and discussion

3.1. Effect of the temperature on the anammox process rate

The nitrogen removal efficiency (NRE) and SAA obtained in our experiments are summarized in Table Supplement 1. The highest SAA (1.19 g N (g VSS·d)$^{-1}$) was observed at a temperature of 40 °C, while the lowest SAA (0.01 g N (g VSS·d)$^{-1}$) occurred at both the extreme temperatures in the analyzed range (*i.e.*, 10 and 55 °C). At the lowest temperature (10 °C), the activity of anammox bacteria was considerably inhibited, although this inhibition was reversible. In contrast, during the test conducted at 55 °C, an irreversible loss in the activity of anammox bacteria was obtained, resulting from the lysis of the anammox bacteria cells. In the typical temperature range for the anammox process, *i.e.*, 30–40 °C, the SAA remained in the range of 0.87–1.19 g N (g VSS·d)$^{-1}$. An increase of 5 °C in the temperature above 40 °C led to a decrease of nearly 50% in the activity of anammox bacteria. Ultimately, the activity decreased to only 0.32 g N (g VSS·d)$^{-1}$ at 50 °C.

Numerous studies have confirmed that the optimum process temperature at which the maximum SAA (SAA_{max}) is attained is 40 °C (Dosta et al., 2008; Oshiki et al., 2011; Ali and Okabe, 2015; Zhu et al., 2017; Tomaszewski et al., 2017; Narita et al., 2017) (Table 3). However, in other studies, SAA_{max} occurred at 35 °C (Hu et al., 2013; Kocamemi et al., 2016; Park et al., 2017; Li et al., 2018) and even 30 °C (Lotti et al., 2015; Awata et al., 2015; Park et al., 2017). The lowest reference anammox activity (SAA_{ref} = 2.4–10% of SAA_{max}) was observed at a temperature of 5 °C (Oshiki et al., 2011; Ali and Okabe, 2015; Lotti et al., 2015; Narita et al., 2017; Li et al., 2018). At that temperature, the highest SAA value of 10% SAA_{max} in the MBR with *Ca. B. sapporoensis* as the dominant anammox genus was reported by Narita et al. (2017). The relatively high SAA value likely resulted from the high 16S rRNA gene similarity of *Ca. B. sapporoensis* to that of *Ca. Brocadia fulgida* (96%) and *Ca. Brocadia sinica* (93%), which often occurs at mainstream temperatures (Park et al., 2017; Nejidat et al., 2018).

Moreover, a negative but reversible effect of both low and high temperatures on the anammox activity was observed by Zhu et al. (2017) and Isaka et al. (2008), respectively. In the investigation of the short-term effect of temperature on the SAA, Zhu et al. (2017) observed inhibition of the anammox activity at a temperature of 10 °C and its subsequent recovery after raising the temperature from 10 to 35 °C. Isaka et al. (2008) recorded a reversible loss of anammox activity at 45 °C and almost complete recovery of the SAA after the cooling of the biomass. Furthermore, the complete and irreversible inhibition of the anammox activity by high temperatures was noted by Dalsgaard and Thamdrup (2002), Dosta et al. (2008) and Kocamemi et al. (2016). An irreversible loss of the anammox activity due to cell lysis was observed at temperatures of 55 °C (Sobotka et al., 2016) and 45 °C (Dosta et al., 2008). Furthermore, the complete inhibition of the anammox activity at 45 °C was reported by Kocamemi et al. (2016). A lower maximum temperature led to the total loss of the anammox activity at 37 °C, as indicated by Dalsgaard and Thamdrup (2002), who examined marine bottom sediments. This phenomenon occurred due to the considerably lower process temperature of marine anammox bacteria.

3.2. Description of the temperature dependence of the anammox process

The models describing the temperature dependence use specific ranges, and the prediction effectiveness (expressed in terms of R^2) is summarized in Table 4. Since the anammox process is commonly conducted at a temperature close to the optimal temperature, the temperature dependence is often described using the Arrhenius equation (Lotti et al., 2015; Xing et al., 2015; Park et al., 2017; Tomaszewski et al., 2017;

Table 3
Short-term effects of temperature on the relative SAA reported in the literature.

Enrichment temp. (°C)	SAAref (%) at a specific temperature											SAA (100%) (unit)	Dominant anammox genus	Reference
	5 °C	10 °C	15 °C	20 °C	25 °C	30 °C	35 °C	40 °C	45 °C	50 °C	55 °C			
30	–	5.0	12.0	17.0	21.0	33.0	48.0	100	62.0	–	–	0.42 gN (g VSS d)$^{-1}$	*Ca.K. stuttgartiensis*	Dosta et al., 2008
37	7.0	–	21.0	–	44.0	69.0	94.0	100	57.0	49.0	4.0	0.072 kgN m^{-3} d^{-1}	*Ca. B. sinica*	Oshiki et al., 2011
30	–	2.5	17.5	36.4	57.5	80.4	100	–	48.4	–	–	–	*Ca. B. fulgida*	Hu et al., 2013
30–35	2.4	20.2	44.6	72.3	–	100	–	–	–	–	–	0.559 g N (g VSS d)$^{-1}$	*Ca. B. fulgida*	Lotti et al., 2015
32–35	–	–	22.0	31.0	53.0	65.0	100	24[a]	–	–	–	0.049 g N_2-N (mg VSS·d)$^{-1}$	*Ca.B. anammoxidans* *Ca. Scalindua species*	Kocamemi et al., 2016
35	–	7.0	9.1	18.5	36.7	67.2	100	–	–	–	–	0.101 g N (g VSS d)$^{-1}$	*Ca. K. stuttgartiensis*	
20	–	16.2	27.5	43.5	74.6	100	65.6	–	–	–	–	–	–	Park et al., 2017
20	–	13.4	20.2	47.7	100	39.2	33.1	–	–	–	–	–	–	
35	–	0	6.0	32.0	56.0	80.0	100	100	60.0	2.0	–	0.5 g NH_4-N (g TSS d)$^{-1}$	–	Zhu et al., 2017
31.6 ± 0.9	–	4.0	20.0	26.0	46.0	58.0	71.0	100	–	–	–	–	*Ca. Jettenia*	Tomaszewski et al., 2017
37	10.0	5.0	–	–	44.0	–	–	100	84.0	–	–	–	*Ca. B. sapporoensis*	Narita et al., 2017
35	4.0	8.0	16.0	31.0	55.0	82.0	100	–	–	–	–	0.092 g (g d)$^{-1}$	–	Li et al., 2018
28	–	12.3	30.1	67.8	88.8	100[b] 70.3	5.8	1.8	–	–	–	3.5 μmol-$^{29}N_2$ (vial d)$^{-1}$	*Ca. Scalindua*	Awata et al., 2013
30	–	1.0	21.0	30.0	45.0	73.0	79.0	100	55.0	27.0	1.0	1.19 g N (gVSS d)$^{-1}$	*Ca. Brocadia*	Sobotka et al., 2016

[a] $T = 39$ °C.
[b] $T = 28$ °C.

Hoekstra et al., 2018; Kouba et al., 2019). A previous study (Sobotka et al., 2016) indicated that a single regression line could not accurately describe the effect of temperature on the anammox process. Similar observations were also reported by Lotti et al. (2015) and Tomaszewski et al. (2017). In both cases, the R^2 value obtained for the entire considered temperature range was below 0.9, suggesting an unsatisfactory description of the temperature dependence by a single regression line. Tomaszewski et al. (2017) obtained a higher R^2 for linear regression of the data set after dividing the entire analyzed temperature range (10–40 °C) into two subranges (10–20 and 20–40 °C). In many studies, the interval between the considered temperatures was set as 5 °C (Table 3), and thus, the change in the SAA trend could not be precisely observed. Consequently, the necessity to separately describe the temperature dependence of the anammox process at low temperatures has often been overlooked.

The effect of temperature on the anammox bacteria in a wide temperature range was investigated by Oshiki et al. (2011) (5–55 °C) and Zhu et al. (2017) (15–50 °C); however, only Zhu et al. (2017) examined all the equations, *i.e.*, the Arrhenius (10–35 °C), ERE and MRE (10–50 °C).

3.2.1. Complete temperature range (10–55 °C)

The temperature dependence of the anammox process in the temperature range from 10 to 55 °C was described using the ERE (3) and MRE (4) and is referred to as $ERE_{10–55}$ and $MRE_{10–55}$ henceforth, respectively. The results of parameter estimation are summarized in Table Supplement 2. The extreme temperatures (T_{min}, T_{max}) were similar, *i.e.*, (5.1 and 54.1 °C) *vs.* (6.0 and 54.3 °C), respectively, in $ERE_{10–55}$ and $MRE_{10–55}$.

The temperature dependence of anammox is illustrated in Fig. 1A. The equations can accurately describe the dependence (Fig. 1B), with a slightly higher coefficient of determination ($R^2 = 0.97$ *vs.* 0.93) for $ERE_{10–55}$. However, when only the low temperature range (10–15 °C) was considered, both the equations yielded an inaccurate description ($R^2 = 0.36–0.49$) of the temperature dependence (Fig. 1C). Therefore, a separate description of the temperature dependence for the low temperature range was proposed in the present study.

The temperature dependence of anammox in a wide temperature range (10–55 °C) was previously described by Zhu et al. (2017). The authors simulated the effect of temperature on the SAA in a wide temperature range by using three models: ERE, MRE, and cardinal temperature model with inflection (CITM). All the models were characterized by a high correlation ($R^2 > 0.988$), with the highest R^2 value (0.995) obtained using the ERE. However, due to the lack of SAA measurements at temperatures between 10 and 15 °C, Zhu et al. (2017) did not investigate the change in the SAA path at low temperatures.

Table 4
Overview of the literature data on the models describing the temperature dependence of the growth rate or activity of different bacterial species.

Model	Temperature range, °C	Measure of activity	R^2	Reference
Arrhenius equation	9–25	SAA	nd	Xing et al., 2015
Arrhenius equation	10–30	SAA	<0.9	Lotti et al., 2015
Arrhenius equation	10–35	SAA	nd	Park et al., 2017
Arrhenius equation	10–40	SAA	nd	Dosta et al., 2008
	10–20		0.94	
Arrhenius equation	20–40	SAA	0.99	Tomaszewski et al., 2017
	10–40		0.89	
Arrhenius equation	20–30	SAA	nd	Hoekstra et al., 2018
Arrhenius equation	10–30	SAA	0.9519	Kouba et al., 2019
Arrhenius equation	10–35		nd	
MRE	10–50	SAA	0.9886	Zhu et al., 2017
ERE			0.9949	
MRE	15–50	Growth of nitrifiers	nd	Van Hulle, 2007
ERE	−10 to 70	Bacterial growth	nd	Ratkowsky et al., 1983
MRE	10–47	Growth rate of *Salmonella*	0.986–0.990	Juneja et al., 2009
MRE	0–26	Bacterial growth in soil	0.978	Nicola and Bååth, 2019

nd – not determined.

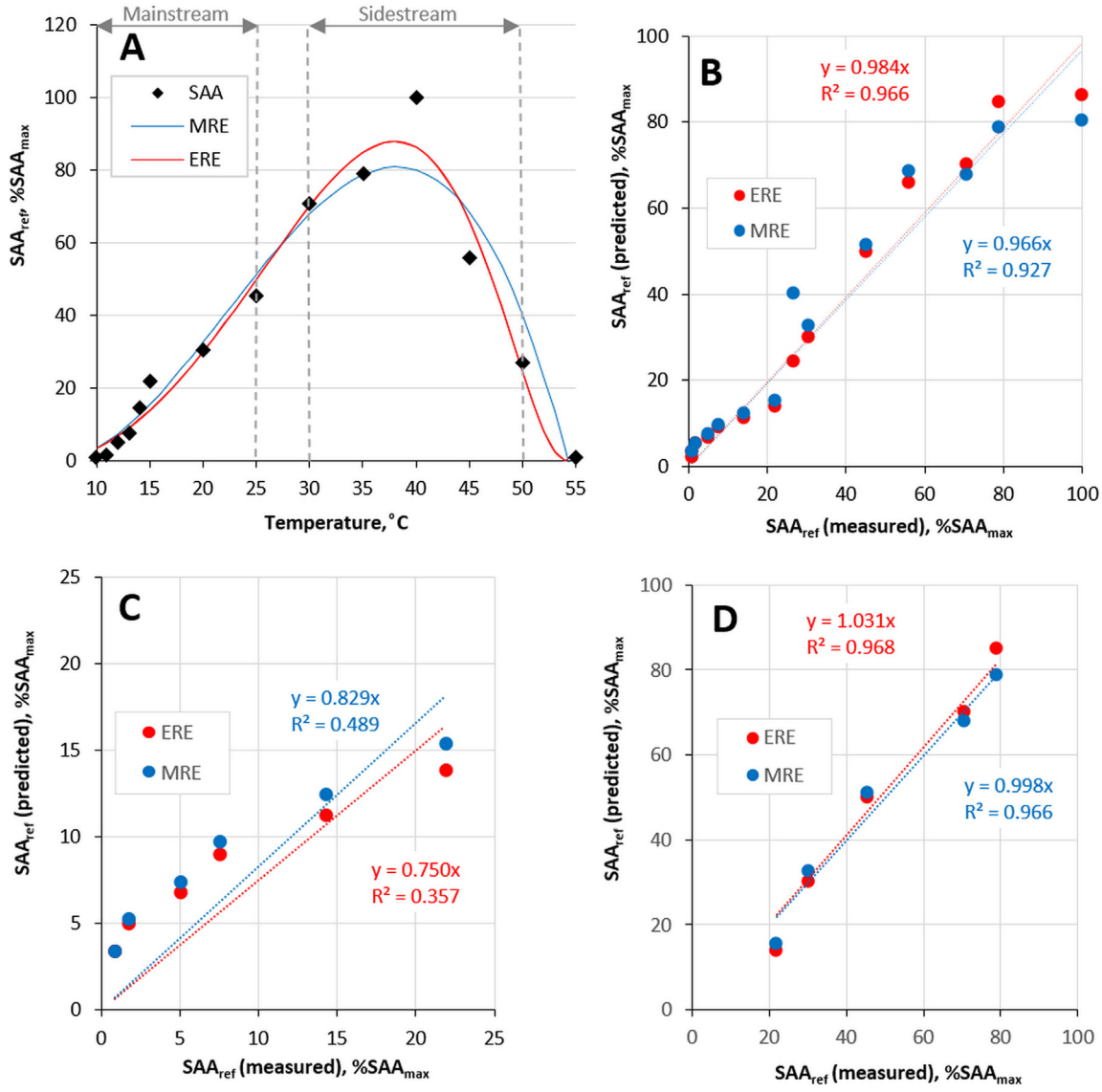

Fig. 1. Temperature dependence of the anammox process in the entire temperature range (10–55 °C): A) Description using the ERE and MRE; B) Comparison of the measured SAA_{ref} and predictions in the entire range; C) Comparison of the measured SAA_{ref} and predictions at low temperatures (10–15 °C); D) Comparison of the measured SAA_{ref} and predictions at moderate temperatures (15–35 °C) (Typical temperatures ranges for mainstream and sidestream systems are shown in Fig. 1A).

3.2.2. Low temperatures (10–15 °C)

In the new approach to describe the temperature dependence of anammox at low temperatures, the traditional Arrhenius equation was used with $T = 15$ °C as the reference temperature. The estimated temperature coefficient (θ) was 1.676.

This relationship is shown in Fig. 2A along with the experimental data. Predictions with a significantly higher accuracy were obtained ($R^2 = 0.989$) using this method than those obtained using both the Ratkowsky equations ($R^2 = 0.36$–0.49). These results suggest that the Arrhenius equation can serve as the base equation to describe the temperature dependence of anammox at low temperatures (<15 °C).

Most studies on the effects of low temperatures on the SAA considered only two temperatures, *i.e.*, 10 and 15 °C (Table 3). Therefore, except for those reported by Sobotka et al. (2016), no data are available regarding the temperature dependence of anammox at temperatures between 10 and 15 °C. Thus, the results of Sobotka et al. (2016) were compared with similar data from Lotti et al. (2015), who investigated the anammox activity in three different wastewater treatment systems (internal circulation reactor in Dokhaven, airlift reactor in Olburgen, MBR), after normalization at $T = 30$ °C (Fig. 3). The line (solid and dashed for the temperature range 15–30 °C and 10–15 °C) represents the Arrhenius equation using T = 30 °C as the reference temperature and an activation energy (Ea) equal to 65.7 kJ mol^{-1}. The obtained SAA trend was similar in both studies, including that for the range 10–15 °C. Lotti et al. (2015) noted that the Arrhenius model predictions were correct only in the temperature range of 15–35 °C. Moreover, the authors emphasized that the Arrhenius model could not be reliably used at temperatures lower than 15 °C. The detailed data from Sobotka et al. (2016) indicated deviations from a general Arrhenius equation for the temperature range of 10–15 °C. Therefore, the temperature dependence of "cold anammox" must be described separately.

3.2.3. Adaptation of the anammox biomass to low temperatures and resulting temperature dependence relationship

Adaptation is a natural phenomenon among bacteria, and the adaptation of anammox bacteria to mainstream temperatures has been studied, *e.g.*, at 15 °C (Dosta et al., 2008), 12 °C (Hu et al., 2013; Sobotka et al., 2016), 10 °C (Lotti et al., 2015; Li et al., 2018; De Cocker et al., 2018) and 9 °C (Jin et al., 2013). Based on the literature data, it can be inferred that the adaptation of the anammox biomass to a temperature lower than the process temperature can enhance the N removal efficiency in the system. Dosta et al. (2008) first demonstrated the positive effect of

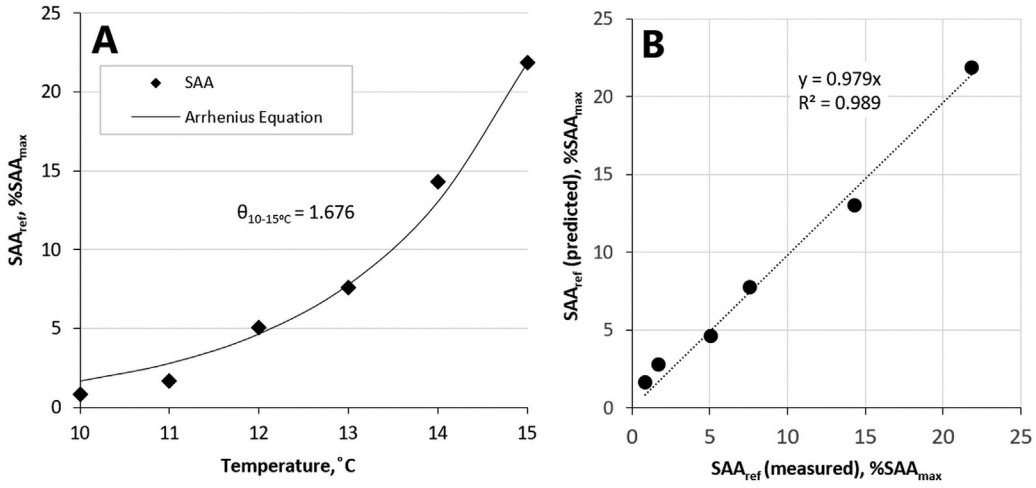

Fig. 2. Temperature dependence of the anammox process at temperatures ranging from 10 to 15 °C: A) Description using the Arrhenius equation; B) Comparison of measured SAA_{ref} and predictions by the Arrhenius model.

gradual adaptation. The observed SAA at T = 15 °C was more than three times higher for the adapted biomass than that of the nonadapted biomass.

Another method is to adapt the biomass directly to the target temperature. Lotti et al. (2015) realized the adaptation of biomass originating from a one stage deammonification reactor operating at 30–35 °C to temperatures of 20 and 10 °C. The results confirmed that the biomass adapted to the lower temperature exhibited a lower sensitivity to the temperature changes and higher SAA at low temperatures than those for nonadapted sludge. In this case, the authors implemented a long-term (8 and 6 months at 20 °C and 10 °C, respectively) adaptation of the sludge to the target temperature.

While changing the operational temperatures in the anammox systems, the quantitative and qualitative compositions of the microbial community may change. To date, seventeen species of anammox bacteria have been discovered and described, which belong to five genera: "*Candidatus Kuenenia*", "*Candidatus Brocadia*", "*Candidatus Scalindua*", "*Candidatus Jettenia*" and "*Candidatus Anammoxoglobus*" (Schmid et al., 2005; Kartal et al., 2007, 2008). The literature data suggest that the most common genera in anammox-based wastewater treatment systems are *Ca. Kuenenia* and *Ca. Brocadia*. He et al. (2018) analyzed the effects of temperature on anammox performance and community structure. In the course of reducing the temperature in the lab scale anammox upflow anaerobic sludge blanket (UASB) reactor from 33 to 13 °C, the authors observed an increase in *Ca. Kuenenia* abundance, ranging from approximately 2 to 55% of the total microbial community. Moreover, domination of *Ca. Kuenenia* at lower temperatures (20 °C and below) was observed by Taotao et al. (2015). De Cocker et al. (2018) compared two long-term-operated anammox SBRs. In the first reactor, the temperature was constant (30 °C), while in the second reactor, the temperature was gradually decreased from 30 to 10 °C. The authors observed a switch from *Ca. Brocadia* to *Ca. Kuenenia* at low temperatures. Moreover, Li et al. (2019) noted that seasonal temperature variations (29–11 °C) in a UASB reactor caused a decrease in the *Ca. Brocadia* abundance and a gradual increase in *Ca. Kuenenia*. The domination of *Ca. Brocadia* in systems operating at higher temperatures has been widely observed (Puyol et al., 2013; Laureni et al., 2015; Wang et al., 2017; Pradhan et al., 2020). Nevertheless, *Ca. Brocadia* (especially *Ca. Brocadia flugida*) appeared as the dominant anammox bacteria at ambient temperatures, as reported by Hendrickx et al. (2014), Persson et al. (2014), Lotti et al. (2014), Rodriguez-Sanchez et al. (2016), Sobotka et al. (2016) and Zhang et al. (2020). The results obtained in these studies indicated that the representatives of *Ca. Brocadia* can grow at temperatures lower than originally assumed. Nevertheless, it should be emphasized that the differentiation of *Ca. Brocadia* and *Ca. Kuenenia* pertains to not only the temperature but also the different affinities of the bacteria for substrates (ammonium and nitrite) and the absence of oxygen inhibition and competition/partnerships with other bacteria (AOB, NOB and OHO) (De Cocker et al., 2018).

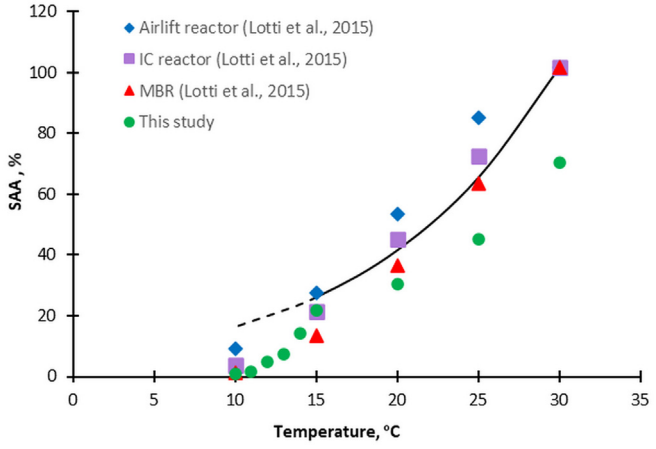

Fig. 3. Comparison of the results of temperature influence on SAA obtained by Sobotka et al. (2016) and Lotti et al. (2015).

3.2.4. Medium temperatures (15–35 °C)

At ambient temperatures, the temperature dependence can be described using all the considered equations (Arrhenius, ERE and MRE). In this study, the same ERE and MRE as those adopted in the analysis of the complete temperature range were used. As shown in Fig. 1D, both ERE_{10-55} and MRE_{10-55} yielded a strong correlation between the measured data and model predictions (R^2 = 0.966–0.968). When using the Arrhenius equation in the temperature range 15–35 °C, T = 35 °C was used as a reference temperature for the anammox process, and the temperature coefficient was 1.066.

Fig. 4A shows the temperature dependence of the anammox process in the medium temperature range, as obtained using the Arrhenius equation. As shown in Fig. 4B, this equation could accurately describe (R^2 = 0.948) the temperature dependence of anammox at temperatures between 15 and 35 °C.

For the anammox process in the temperature range 15–35 °C, the calculated θ ranged from 1.066 (Sobotka et al., 2016) to 1.37 (Straka et al., 2019). Gilbert et al. (2015) calculated θ for suspended, granular and attached anammox biomasses after 10 weeks of adaptation to a

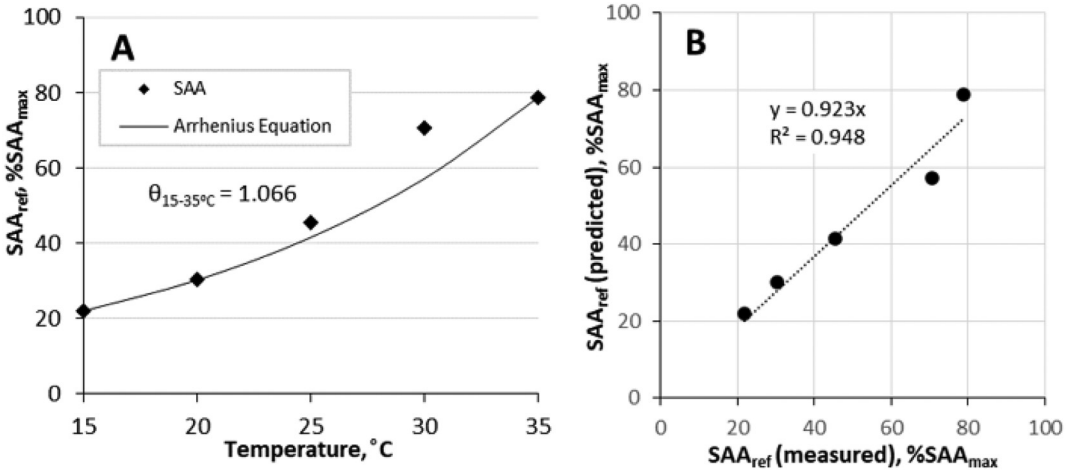

Fig. 4. Temperature dependence of the anammox process in the temperature range from 15 to 35 °C: A) Description using the Arrhenius equation; B) Comparison of the measured SAA_{ref} and the value predicted by the Arrhenius model.

temperature of 20 °C, and obtained values of 1.20 ± 0.09, 1.17 ± 0.07 and 1.14 ± 0.03, respectively.

3.2.5. Activation energy (E_a)

For the low and medium temperatures, at which the temperature dependence was described using the Arrhenius equation, the Ea of the anammox reaction was determined from the Arrhenius plot (Fig. 5). The low value of the coefficient of determination ($R^2 = 0.751$) of the linear regression indicated that a single Ea could not be used. Therefore, two Arrhenius regression lines were plotted from the data. The high determination coefficient ($R^2 \approx 0.98$) of each regression line confirmed the appropriateness of that approach. The Ea values in the two analyzed temperature ranges were 448.4 kJ mol^{-1} (10–15 °C) and 50.5 kJ mol^{-1} (15–35 °C). These results showed that the Ea was almost 10 times higher at low temperatures (10–15 °C) than that at medium temperatures (15–35 °C), which indicated the higher sensitivity of the anammox bacteria to the temperature in the analyzed temperature range. A similar relationship, *i.e.*, an increase in Ea with decreasing temperature was observed in other studies (Isaka et al., 2008; Lotti et al., 2015; Tomaszewski et al., 2017; Zhu et al., 2017; Li et al., 2018). A comparison of the Ea values for the anammox reaction reported in the literature is presented in Table 5. At low temperatures (10–15 °C), Ea remained in the range of 109 to 360 ± 140 kJ mol^{-1} (Lotti et al., 2015; Li et al., 2018; Kouba et al., 2019). The Ea obtained by Sobotka et al. (2016) at temperatures below 15 °C ($Ea_{10-15°C}$ = 448.4 kJ mol^{-1}) was at least two times as high as that noted by Lotti et al. (2015) ($Ea_{0-15°C}$ = 230.0 ± 8.3 kJ mol^{-1}) and Li et al. (2018) ($Ea_{10-18°C}$ = 109 kJ mol^{-1}). This discrepancy was likely a result of the differences in the inoculum biomass used in the individual studies and the rather narrow temperature range for which this value was determined (entirely within the "discomfort zone" of anammox bacteria). The Ea obtained at low temperatures was approximately 360 ± 140 kJ mol^{-1}, as presented by Kouba et al. (2019). In both the studies, the anammox genus was *Ca. Brocadia*. The Ea obtained in the temperature range 15–35 °C (50.5 kJ mol^{-1}) was lower than the corresponding literature data for granular anammox sludge. Dosta et al. (2008) reported an Ea value of 63 kJ mol^{-1} in the temperature range of 10–40 °C. At medium temperatures (15–30/35 °C), the Ea of the anammox reaction in the systems with granular biomass was reported to range from 42 (Jin et al., 2013) to 83.1 kJ mol^{-1} (Lotti et al., 2015). The relatively low value of Ea (50.5 kJ mol^{-1}) obtained by Sobotka et al. (2016) indicates a low sensitivity of the biomass to high temperatures, which was observed during batch tests, in which a high activity of anammox bacteria was observed in the temperature range of 35–50 °C (SAA_{max} of 40 °C). The different literature data on Ea suggest that anammox is not an elementary reaction but consists of different partial reactions affecting the process rate, including the production of hydrazine from ammonia and hydroxylamine, oxidation of hydrazine to N_2 and production of hydroxylamine by reducing NO_2^-. Moreover, the

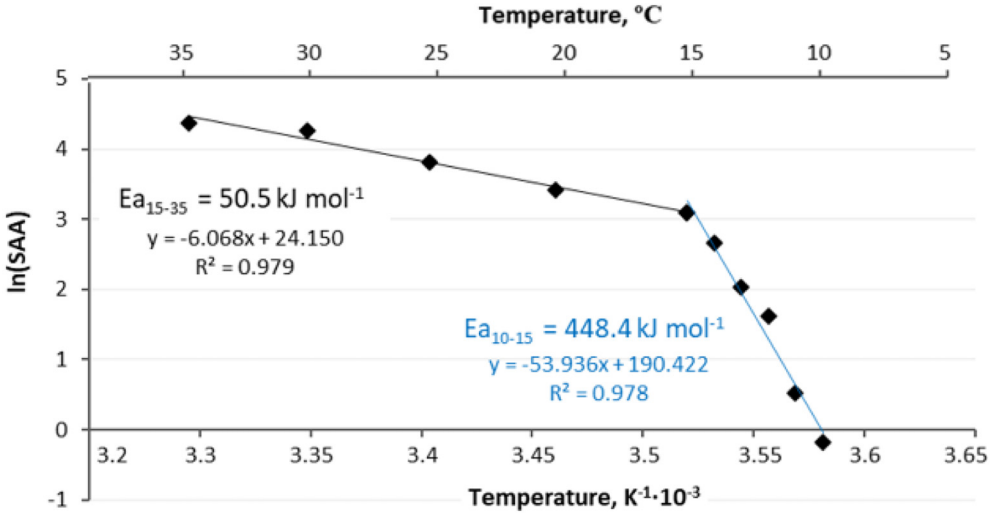

Fig. 5. Arrhenius plot for the anammox reaction at temperatures between 10 and 35 °C.

Table 5
Comparison of Ea values for the anammox reaction, as reported in the literature.

Temperature range, °C	T_{opt}, °C	Type of biomass/Species	E_a, kJ mol^{-1}	References
10–15	*nd*	Suspended	230.5 ± 8.3	Lotti et al., 2015
10–15	32	Suspended/Flocks/*Ca. Brocadia*	360 ± 140	
10–15	37	Granules/*Ca. Brocadia*	248	Kouba et al., 2019
10–15	14	Immobilized/Biofilm/*Ca. Brocadia*	193	
11–15	30	Granular/*Ca. Brocadia*	448.4	This study
10–18	*nd*	Granular/*nd*	109	Li et al., 2018
10–20	*nd*	Suspended	72	Hendrickx et al., 2012
10–25	25	Granular	107	
10–30	30	Granular	73	Park et al., 2017
10–35	35	Granular	89	
10–40	35–40	Immobilized	63	Dosta et al., 2008
10–40	35–40	Granular	63	
15–20	*Nd*	Suspended	104.9 ± 13.3	Lotti et al., 2015
15–25	35–40	Granular	95.9	Zhu et al., 2017
15–25	*nd*	Suspended/*Ca. Brocadia fulgida, Anammoxoglobus propionicus*	72.4	Kwak et al., 2020
15–30	*nd*	Suspended	83.1	Lotti et al., 2015
15–30	*nd*	Granular	83.1	
15–30	32	Suspended/Flocks/*Ca. Brocadia*	89 ± 20	
15–30	37	Granules/*Ca. Brocadia*	76 ± 26	Kouba et al., 2019
15–30	14	Immobilized/Biofilm/*Ca. Brocadia*	78 ± 7	
15–35	>35	Granular	43	Jin et al., 2013
15–35	35–40	Granular	69.5	Zhu et al., 2017
15–35	30	Granular/*Ca. Brocadia*	50.5	This study
18–35	*nd*	Granular/*nd*	42	Li et al., 2018
20–25	*nd*	Suspended	67.6 ± 7.1	Lotti et al., 2015
25–30	*nd*	Suspended	46.6 ± 2.7	
25–35	35–40	Granular	43.2	Zhu et al., 2017
25–35	*nd*	Granular/*nd*	46	Li et al., 2018
20–35	*nd*	Suspended/*Ca. Kuenenia stuttgartiensis, Anammoxoglobus propionicus.*	5.8	Kwak et al., 2020
20–43	*nd*	*nd*	70	Strous et al., 1999
28–37	37	Immobilized/*Ca. Kuenenia stuttgartiensis, Ca. Brocadia anammoxidans*	93	Isaka et al., 2008

nd – no data

dominant anammox bacteria may vary depending on the temperature, especially in the lower ranges (Park et al., 2017). In addition to temperature, Ea can be affected by several other factors, such as types of seed culture, reactor types, variable levels of anammox enrichment and reactor operating conditions (Kwak et al., 2020).

3.2.6. High temperatures (35–55 °C)

Under thermophilic conditions the temperature dependence can only be described using both the Ratkowsky equations. To verify the results obtained using $ERE_{10–55}$ and $MRE_{10–55}$, an additional set of Ratkowsky equations for temperatures in the range of 35–55 °C was determined using Eq. (6). These equations, named $ERE_{35–55}$ and $MRE_{35–55}$, were developed based on the SAA results (Sobotka et al., 2016) for thermophilic conditions and optimized to obtain the highest possible correlation between the measured data and model predictions.

$$\mu_{35-55} = \begin{cases} \left[533.5(T-297)\left(1-e^{(7.9\cdot10^{-5}(T-327))}\right)\right]^2 \\ [4.1(T-273)]^2\cdot\left(1-e^{(2\cdot10^{-4}(T-328))}\right) \end{cases} \quad (6)$$

The results of the ERE and MRE parameter estimation in the temperature range from 35 to 55 °C are summarized in Table Supplement 2.

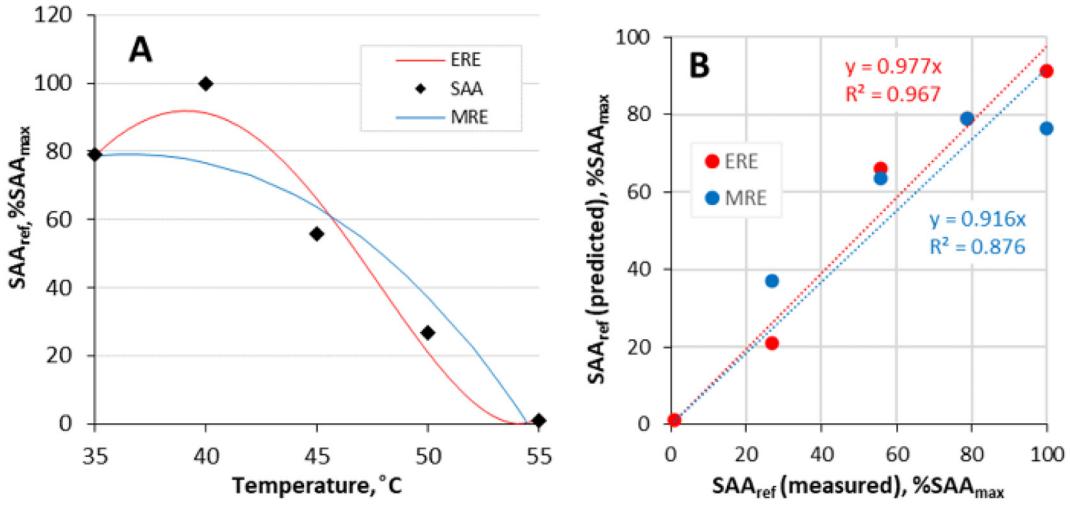

Fig. 6. Temperature dependence of the anammox process in the temperature range 35–55 °C: A) Description using the ERE and MRE; B) Comparison of the measured SAA_{ref} and values predicted by the ERE and MRE.

The optimization of the Ratkowsky equations for only high temperatures resulted in both cases exhibiting a slightly higher R^2. The extrapolated T_{min} in ERE_{35-55} and MRE_{35-55} was 0.85 °C (273.00 K) and 24.9 °C (297.03 K), respectively. The estimated T_{max} was comparable in both equations, *i.e.*, 55.3 °C (327.47 K, ERE_{35-55}) and 55.4 °C (327.50 K, MRE_{35-55}). The temperature dependence of the anammox process in the temperature range from 35 to 55 °C is graphically presented in Fig. 6.

Despite the growing interest in anammox conducted at thermophilic conditions, the feasibility of this process remains unclear. Recently, thermophilic anammox was investigated by Vandekerckhove et al.

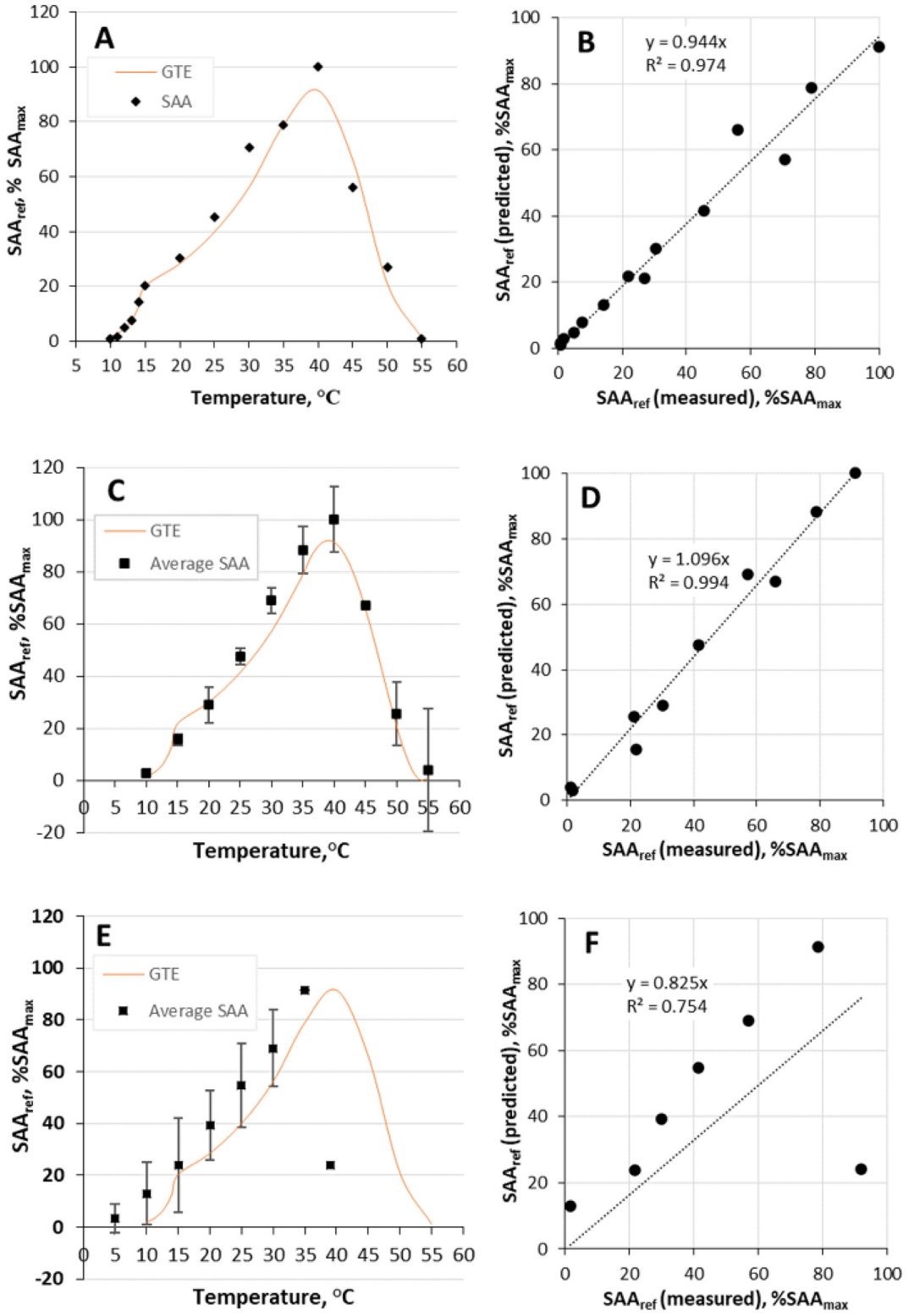

Fig. 7. Description of the anammox temperature dependence using the GTE (A) and comparison of measured SAA_{ref} values and model predictions by the GTE (B). Description of the literature data with T_{opt} = 40 °C (C) and T_{opt} = 30–35 °C (E) using the GTE. Comparison of measured literature values of SAA_{ref} with T_{opt} = 40 °C (D) and T_{opt} = 30–35 °C (F) and the model predictions obtained using the GTE.

(2020) by gradually increasing (0.05–0.07 °C d^{-1}) the process temperature from 38 to 48 °C. During this long-term adaptation, the temperature dependence of the process rate was described by a linear equation using the least squares method, and it yielded an R^2 value of 0.92.

3.2.7. Generalized temperature dependence model

Based on the results obtained for the entire temperature range, a generalized temperature equation (GTE) is proposed:

$$\mu_{GTE} = \begin{cases} \mu_{15} \cdot 1.676^{(T-15)} \; for \; T(10-15^{\circ}C) \\ \mu_{35} \cdot 1.066^{(T-35)} \; for \; T(15-35^{\circ}C) \\ \left[77.9(T-297)\left(1-e^{(5.8 \cdot 10^{-5}(T-327))}\right)\right]^2 \; for \; T(35-55^{\circ}C) \end{cases} \quad (7)$$

The R^2 values obtained for the entire range (10–55 °C) and specific temperature ranges (10–15, 15–35 and 35–55 °C) are summarized in Table Supplement 3. Although both ERE_{10-55} and MRE_{10-55} could effectively describe the anammox temperature dependence in the entire range ($R^2 = 0.93–0.97$), the description of the temperature dependence of "cold anammox" at temperatures below 15 °C ($R^2 = 0.36–0.48$) was inadequate.

A comparison of the GTE predictions *vs.* observed SAA is presented in Fig. 7A. A strong correlation ($R^2 > 0.95$) was observed not only in the entire range (10–55 °C) but also in all the specific ranges (10–15, 15–35 and 35–55 °C). In the range 10–55 °C, the highest correlation ($R^2 = 0.97$) was obtained using the ERE_{10-55} and GTE. However, only the GTE could accurately describe the temperature dependence of "cold and classic anammox" simultaneously. At temperatures below 15 °C, the GTE used $AR_{10-15,}$ which provided the most accurate description of the temperature dependence of "cold anammox" ($R^2 \approx 0.99$).

To describe the influence of temperature on the SAA with the Arrhenius equation, two separate ranges were considered with different θ values. Due to the strong inhibitory effect of low temperatures on the anammox activity, the SAA trend was not stable. The application of a single temperature coefficient over a wide range, *e.g.*, 10–40 °C, adversely influenced the correlation between the measured and predicted SAA, especially at temperatures below 15 °C.

The GTE was validated using the available literature data (Table 3) for the temperature range from 10 to 55 °C. In terms of the optimum temperature (40 *vs.* 30–35 °C), the data were grouped into two sets. This approach allowed the assessment of the applicability of the GTE in systems with different characteristics, *e.g.*, optimum temperature. The average SAA values for the literature data with the corresponding standard deviations and GTE predictions are presented in Fig. 7C (40 °C) and 7E (30–35 °C). The GTE provided a strong correlation ($R^2 \approx 0.99$, Fig. 7D) against the literature data with the maximum SAA observed at 40 °C. When the GTE was examined against the literature data pertaining to systems with a different optimal temperature, the correlation decreased ($R^2 \approx 0.76$, Fig. 7F) and the predicted SAAs were underestimated (except for the highest temperature, $T = 40$ °C). These results confirmed the applicability of the proposed equation to systems with similar characteristics, including a similar optimum temperature.

4. Conclusions

The anammox process kinetics over the entire activity range (10–55 °C) cannot be described by one equation. Notably, the measured data and predictions obtained with both the Ratkowsky equations are highly inconsistent in the temperature range of 10–15 °C.

The Arrhenius equation, applicable in the range of 10–35 °C, should be divided into two subregions (10–15 °C and 15–35 °C) to separately characterize "cold anammox" and "(low) mesophilic anammox", respectively.

The proposed GTE is the most universal temperature developed so far. It can enhance the description of the anammox temperature dependence ($R^2 > 0.95$) over the entire activity range, including the range in which "cold anammox" occurs (<15 °C). In practical applications, the GTE can help examine anammox-based bioaugmentation systems operated at both high temperatures (sidestream reactors) and low temperatures (mainstream reactors).

CRediT authorship contribution statement

D. Sobotka: Methodology, Data curation, Investigation, Writing – original draft, Visualization. **J. Zhai:** Writing – review & editing. **J. Makinia:** Conceptualization, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.145760.

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