

## Model development for the growth of microalgae: A review

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### ABSTRACT

Despite attracting many attentions in the past decades, microalgal cultivation still faces many challenges for industrialisation. Growth, as one of the most crucial characteristics of a microalgal cultivation system, has been a significant subject for modelling. This paper presents a review of available models in the literature regarding the effect of process parameters such as light, temperature, nutrients, oxygen accumulation, salinity, and pH and carbon, on the growth rate of microalgal cells to understand their application in large-scale microalgal production. The existing models are classified based on the process conditions or parameters they considered in the formulation, and where multiple parameters were included the model was broken into separate functions, and each function was presented in the associated section. The most prominent result of this review is the huge gap between models and their validity for outdoor systems. It seems that to find suitable models for a real condition application, a new pathway is needed where models are developed based on the behaviour of the outdoor cultures in long-term. There are some effects such as adaptation which are difficult to model in short-term modelling while if the long-term approach is used these effects can be considered negligible. These characteristics of outdoor cultivation help in simplification of the models and less struggle in their validation. Moreover, using saline water is an effective way to improve the viability of algal production which requires understanding the relationship between growth and salinity of the medium. Such models are missing in the literature.

### 1. Introduction

Microalgae are unicellular photosynthetic organisms with multiple beneficial characteristics that can potentially be used to overcome some of today's issues. They have high carbon dioxide fixation rate which can be used in flue gas treatment and the emission rate of this gas [1–3]. They use nutrients such as phosphorus and nitrogen which can be provided from industrial or municipal wastewater, making them a suitable option for waste water treatment [4–6]. Moreover, in case of marine microalgae there is no need for potable water since they can grow in saline water which facilitates the provision of water for large scale cultivation [7]. Another key attribute of microalgae is their low land requirement. They use significantly less area to grow compared to other crops due to their high photosynthetic efficiency per area [8–10]. Microalgae can be cultivated even in non-arable lands; thus, they do not impact agricultural land availability [2,8,11]. In addition to these traits, microalgae are capable of producing multiple valuable products which can be used in various industries such as food, cosmetics, pharmaceutical, etc [3,12–14]. One of the products that have attracted many attentions is biofuel. Algal biofuel is produced from the lipid stored in algal cells [15] which is extracted and converted to biodiesel. High

productivity, being renewable, carbon emission mitigation, compatibility of algal biofuel with current diesel engines, and its low pollution are just a few of many advantages of using microalgae as a source of biofuel [3,16–18]. However, production of algal biofuel is still in the research stage and has not been fully commercialised yet [19].

Various systems are common for the algal cultivation of which closed photobioreactors (PBR), and open ponds are used more frequently. While construction and operation of open ponds are easy and relatively inexpensive, they have some disadvantages such as poor illumination and loss of water due to evaporation [20]. Also compared to closed PBRs, open ponds have the high risk of contamination which can directly affect production costs and annual productivity [21].

On the pathway to mass production, many process issues need to be resolved, and the growth and biomass production of algae should be well understood and optimised to make efficient operation and process control viable [22]. An important step for this purpose is mathematical modelling in which the effect of each process condition (temperature, light, etc.) is mathematically related to the key production parameters (growth rate, productivity, etc.) so that the effect of every change in the process conditions can be observed without the necessity to experimentally test the effects separately. Modelling kinetic of algal growth is

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vital for both estimation and optimisation of production parameters and control of process conditions which is of great importance in the industrialisation of algal biofuel production. For a model to be reliable, all the influential process conditions should be included in it which is difficult but crucial to do. Many process conditions influence the growth of microalgae and to control and optimise the industrial production of algal biofuel, an accurate mathematical model is vital. A successful model should include the effects of all parameters and their contribution, and when it is joint with reactor model should be able to predict the performance and productivity of a cultivation system for different operating conditions.

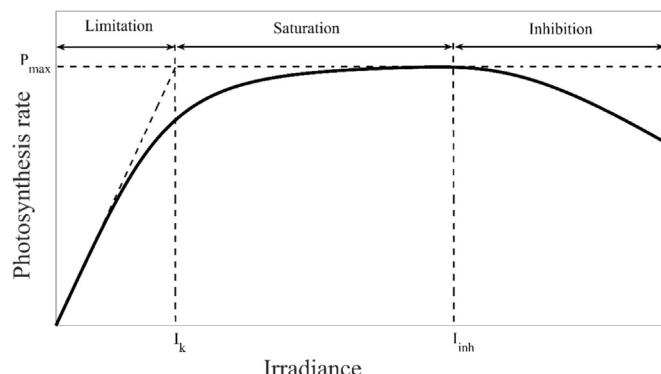
This paper presents a review of the existing models and how their formulations evolved over time to become more accurate. Although all the current models are listed in the tables to show this evolution; only the most prominent models have been discussed and compared. Finally, the effectiveness of current models for large-scale production is discussed to elaborate a pathway to improve modelling approaches and make the models more applicable in real conditions. While many of these models have been reviewed to see their performance in laboratory scale, the novelty of this study is in two folds: (1) understanding how the current models can be adapted for use in large-scale production of microalgae, and (2) realising the gap in research regarding modelling the simultaneous impact of various factors such as salinity, light, and temperature.

## 2. Effective process conditions

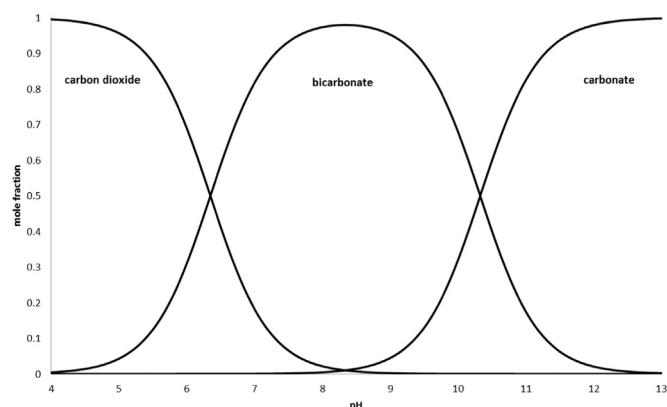
In the past century, many studies were conducted to understand the impact of each process parameter on the growth and productivity of algal cultures. The parameters that are discussed in this review are light, temperature, nutrients, pH, salinity, and dissolved oxygen. The effects of these parameters have been studied through many experiments and many models have been suggested, of which a summary of prominent ones can be found here.

### 2.1. Light

Algae use light as a source of energy for photosynthesis, and therefore it is the most important parameter in the modelling of microalgal growth. Microalgal cells experience three light zones based on the intensity of the light (See Fig. 2): (1) photolimited, (2) photo-saturated, and (3) photoinhibited zone. A common phenomenon inside a turbid media like algae culture is light attenuation, where light intensity decreases as it goes deeper into the media [23] due to absorption of light by cells, and as the photons penetrate into the culture, more of them are absorbed [24]. To show this effect, usually Beer-Lambert Law is used which suggests that light intensity exponentially decreases with depth [25–27].



**Fig. 1.** A schematic of PI curve showing three light regions: (1) light limited, (2) light saturated, and (3) light inhibited.



**Fig. 2.** Distribution of inorganic carbon forms with pH.

$$I = I_0 e^{-kz} \quad (1)$$

Where  $I$  is light intensity,  $I_0$  is light intensity entering the media perpendicular to surface,  $z$  is depth, and  $k$  is attenuation rate. Although this relation is used widely, researchers have used different definitions for  $k$  and how it is calculated. Some researchers described it as a linear function of biomass concentration [28] or chlorophyll concentration [29], while others related  $k$  to both chlorophyll as well as biomass concentration in the media and even took into account a constant which describes the behaviour of the culture without any cells [25]. Sukenik et al. [30] assumed light attenuation rate to be a linear function of just chlorophyll amount while this dependency varies for different wavelengths. Despite its popularity, Beer-Lambert Law is based on the assumption that light is not scattered in the media which is not correct when it comes to microalgal cultures. Therefore, some researchers proposed models taking into account light scattering in order to overcome this issue [31,32].

Another factor that plays a vital role in the light exposure of algae is hydrodynamics of the culture, and how cells move within the media as when they are closer to the light source, they will be subject to more light and vice versa. This effect is critically important to determine how much light a cell may absorb and from which photosynthesis and growth rate can be calculated. Most attempts in modelling the effect of light focused on equations to describe photosynthesis and light relationship (commonly presented in form of PI curve) [33]. Photosynthesis in this relationship is expressed in various forms such as electron transfer rate (ETR), oxygen evolution, and carbon dioxide consumption, and sometimes is replaced by specific growth rate. Despite the differences between these forms, all result in the same shape of PI curve [22,34,35].

Many models have been suggested in the last few decades, a summary of which can be seen in Table 1, but here we are reviewing the details of the most prominent models. One of the earliest models that can be found in the literature was suggested by Baly [36] and later used by Tamiya [37], reporting that based on their experiments this function had approximately the same shape as their results. This equation is similar to the renowned equation proposed by Monod [38] for effect of substrates on growth of bacteria which is widely used for microalgal growth as well. In this equation, if substrate concentration is replaced by irradiance, it results in Baly and Tamiya's equation. This equation contains two key elements: 1) the maximum specific growth rate ( $\mu_{max}$ ) which indicates the maximum achievable specific growth rate when culture is in light saturated condition, 2) light half-saturation constant ( $K_I$ ) at which the specific growth rate is half its maximum value. Parameter  $K_I$  is often compared to light saturation irradiance ( $I_k$ ), which is the irradiance that defines light saturated region (Fig. 1). In this model the difference between two parameters are significant as  $K_I$  is associated with half the amount of maximum specific growth rate while at  $I_k$  the  $\mu$  almost reaches its maximum value. This difference is

**Table 1**  
Models describing the effect of light.

Source	Formula	System	Alga	Parameters
Tamiya et al. [37] a.k.a. Monod model	$\mu = \mu_{max} \frac{I}{I + K_I}$	(1)	Indoor	<i>Chlorella ellipsoidea</i>
Lee et al. [33]			Indoor	<i>Spirulina platensis</i>
Molina Grima et al. [59]			Indoor	<i>Isochrysis galbana</i>
Jeon et al. [69]		Indoor	<i>Haematococcus pluvialis</i>	$\mu_{max} = 0.1351(h^{-1})$ $K_I = 13.9136(W/m^2)$ at 820 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.109 h^{-1}$ $K_I = 763.7 \mu E m^{-2}s^{-1}$ at 1630 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.0514 h^{-1}$ $K_I = 177.2 \mu E m^{-2}s^{-1}$ at 3270 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.0448 h^{-1}$ $K_I = 769.2 \mu E m^{-2}s^{-1}$ cell concentration 0.215 g L <sup>-1</sup> $P_{max} = 43.5 mg g^{-1} h^{-1}$ $K_I = 177.2 \mu E m^{-2}s^{-1}$ cell concentration 0.123 g L <sup>-1</sup> $P_{max} = 51.7 mg g^{-1} h^{-1}$ $K_I = 254.4 \mu E m^{-2}s^{-1}$
Haario et al. [70]		Outdoor	Diatom	$\mu_{max} = 0.0886 day^{-1}$ $K_I = 61.9(W/m^2)$ <i>Chrysophycea</i> $\mu_{max} = 0.0465 day^{-1}$ $K_I = 115(W/m^2)$ <i>Cyanobacteria</i> $\mu_{max} = 0.329 day^{-1}$ $K_I = 16.4(W/m^2)$ <i>Minor species</i> $\mu_{max} = 0.212 day^{-1}$ $K_I = 134(W/m^2)$
Filali et al. [71]		Indoor	<i>Chlorella vulgaris</i>	$\mu_{max} = 0.08 h^{-1}$ $K_I = 0.14 \mu E s^{-1} 10^9 cell^{-1}$
Franz et al. [72]		Indoor	<i>Chlamydomonas reinhardtii</i>	$\mu_{max} = 1.4 day^{-1}$ $K_I = 215 \mu mol.m^{-2}.s^{-1}$
Ifrim et al. [73]		Indoor	<i>Chlamydomonas reinhardtii</i>	$K_I = 120 \mu mol.m^{-2}s^{-1}$ $\mu_{max} = 0.16 h^{-1}$
Bechet et al. [74] Kasiri et al. [75]		Indoor	<i>Chlorella vulgaris</i>	values are reported at six different temperatures in [74]
Chalup and Laws [76] and, Laws and Chalup [77]	$\mu = \mu_{max} \frac{I}{I + K_I} - \mu_r$	(2)	Indoor	<i>Pavlova lutheri</i> $\mu_{max} = 1.95 day^{-1}$ $K_I = 10.8 mol quantum^{-2} day^{-1}$
Smith [39]	$P = P_{max} \left( \frac{I^2}{I^2 + K_I^2} \right)^{1/2}$	(3)	indoor	Gigartina harveyana $\mu_r = 0.03 day^{-1}$
Bannister [40]	$\mu = \mu_{max} \frac{I}{(I^m + K_I^m)^{1/m}}$	(4)	Indoor	<i>Chlorella pyrenoidosa</i> $\mu_{max} = 2.48 day^{-1}$ $m = 1.8$ $K_I = 5.7 \mu E m^{-2}s^{-1}$
Lee et al. [33]	$\mu_{ave} = \mu_{max} \frac{I_{ave}}{(I_{ave}^m + K_I^m)^{1/m}}$	(5)	Indoor	<i>Spirulina platensis</i> $\mu_{max} = 0.2976(h^{-1})$ $K_I = 15.01(W/m^2)$ $m = 0.4970$
Molina Grima et al. [78]	$\mu = \mu_{max} \frac{I^m}{I^m + K_I^m}$	(6)	Indoor	<i>Isochrysis galbana</i> $\mu_{max} = 0.0426(h^{-1})$ $K_I = 10.92(W.m^{-2})$ $m = 5.13$
Molina Grima et al. [28]		Indoor	<i>Isochrysis galbana</i>	$\mu_{max} = 0.046(h^{-1})$ $K_I = 9.67 \times 10^{15} (quanta cm^{-2}) m = 1.7$
Molina Grima et al. [59]		Indoor	<i>Isochrysis galbana</i>	at 820 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.0465 h^{-1}$ $K_I = 195.6 \mu E m^{-2}s^{-1}$ $m = 2.11$ at 1630 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.0448 h^{-1}$ $K_I = 140.6 \mu E m^{-2}s^{-1}$ $m = 1.58$ at 3270 $\mu E m^{-2}s^{-1}$ $\mu_{max} = 0.0459 h^{-1}$ $K_I = 808.2 \mu E m^{-2}s^{-1}$ $m = 0.98$

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**Table 1** (continued)

Source	Formula	System	Alga	Parameters
Concas et al. [79]		Indoor	<i>Spirulina platensis</i>	$\mu_{max} = 2.06 \times 10^{-5} (s^{-1})$ $K_I = 160 \mu Em^{-2}s^{-1}$ $m = 1.49$
Pegallapati and Nirmalakhandan [80]		Indoor	<i>Nannochloropsis salina</i>	$\mu_{max} = 1.2 (day^{-1})$ $K_I = 181 \mu Em^{-2}s^{-1}$ $m = 1.75$
			<i>Scenedesmus sp.</i>	$\mu_{max} = 1.4 (day^{-1})$ $K_I = 131 \mu Em^{-2}s^{-1}$ $m = 2.7$
Fernandez et al. [81]		Outdoor light	<i>Scenedesmus almeriensis</i>	$K_I = 69 \mu Em^{-2}s^{-1}$ $m = 0.87$
Costache et al. [82]	$P = P_{max} \frac{I^m}{I^m + (K_I \exp(k_e I))^m}$	(7)	Indoor	$Scenedesmus almeriensis$ $P_{max} = 4.6 \times 10^{-5}$ (mol O <sub>2</sub> g biomass <sup>-1</sup> min <sup>-1</sup> ) $k_e = 1.85 \times 10^{-3} m^2 s \mu E^{-1}$ $K_I = 76.35 \mu Em^{-2}s^{-1}$
Fernandez et al. [83]		Outdoor	<i>Scenedesmus almeriensis</i>	$K_I = 139.3 \mu Em^{-2}s^{-1}$ $k_e = 0.002 m^2 s \mu E^{-1}$ $m = 1.045$
Molina Grima [59]	$\mu = \mu_{max} \frac{I^{m_{app}}}{I^{m_{app}} + K_{app}^{m_{app}}}$ $m_{app} = \frac{n_2}{l_0}$ $K_{app} = I_K + \left( \frac{l_0}{K_I} \right)^{n_1}$	(8)	Indoor	<i>Isochrysis galbana</i> $\mu_{max} = 0.0444 (h^{-1})$ $I_K = 170.68 (\mu Em^{-2}s^{-1})$ $K_I = 2217.2 (\mu Em^{-2}s^{-1})$ $n_1 = 12.8$ $n_2 = 2728.8 (\mu Em^{-2}s^{-1})$
Garcia-Malea et al. [60]	$\mu = \mu_{max} \frac{I^{m_{app}}}{I^{m_{app}} + K_{app}^{m_{app}}}$ $m_{app} = a + b I_0$ $K_{app} = c + d I_0$	(9)	indoor	<i>Haematococcus pluvialis</i> $\mu_{max} = 0.11 h^{-1}$ $a = 2.32$ $b = -0.00008 (\mu Em^{-2}s^{-1})^{-1}$ $c = 98.7 \mu Em^{-2}s^{-1}$ $d = 0.034$
Aiba [34]	$P = P_{max} \frac{I}{I + K_I + \frac{I^2}{K_I}}$	(10)	–	–
Megard et al. [55] Lee et al. [33]		Indoor Indoor vessel	Various species <i>Spirulina platensis</i>	$\mu_{max} = 5.4849 (h^{-1})$ $K_I = 959.2 (W/m2)$ $K_i = 0.5817 (m2/W)$
Molina Grima et al. [59]		Indoor	<i>Isochrysis galbana</i>	at 820 $\mu Em^{-2}s^{-1}$ $\mu_{max} = 0.1088 h^{-1}$ $K_I = 195.1 \mu Em^{-2}s^{-1}$ $K_i = \infty$ at 1630 $\mu Em^{-2}s^{-1}$ $\mu_{max} = 0.0513 h^{-1}$ $K_I = 145.2 \mu Em^{-2}s^{-1}$ $K_i = \infty$ at 3270 $\mu Em^{-2}s^{-1}$ $\mu_{max} = 0.0449 h^{-1}$ $K_I = 697.2 \mu Em^{-2}s^{-1}$ $K_i = \infty$
Fouchardet al. [84]		indoor	<i>Chlamydomonas reinhardtii</i>	$\mu_{max} = 0.2274 h^{-1}$ $K_I = 81.38 \mu mol photon m^{-2}s^{-1}$ $K_i = 2500 \mu mol photon m^{-2}s^{-1}$
Ippoliti et al. [12]		Indoor and outdoor	<i>Isochrysis galbana</i>	$P_{max} = 1075 mg O_2 (g biomass. h)^{-1}$ $K_I = 311.8 \mu Em^{-2}s^{-1}$ $K_i = 1253 \mu Em^{-2}s^{-1}$
Concas et al. [3]	$\mu = \mu_{max} \frac{I}{I + K_I + \frac{I^2}{K_I}}$	(11)	Indoor	<i>Nannochloris eucaryotum</i> $K_I = 60 \mu Em^{-2}s^{-1}$ $K_i = 130 \mu Em^{-2}s^{-1}$
Mirzaie et al. [85]		Indoor	<i>Chlorella vulgaris</i>	$K_I = 1.56 \mu mol photons m^{-2}s^{-1}$ $K_i = 15.42 \mu mol photons m^{-2}s^{-1}$
Peeters [54]	$\mu = \mu_{max} (1 + \beta_I) \cdot \frac{2x_I}{x_I^2 + 2\beta_I x_I + 1}$ $x_I = \frac{I}{I_{opt}}$	(12)		
Dauta et al. [58]		indoor	<i>Chlorella Vulgaris</i>	$\mu_{max} = 1.3 day^{-1}$ $I_{opt} = 140 \mu Em^{-2}s^{-1}$

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**Table 1** (continued)

Source	Formula	System	Alga	Parameters
Talbot et al. [86]	$\mu = \mu_{max}(1+\beta_I) \cdot \frac{2x_I}{x_I^2 + 2\beta_I x_I + 1}$ $x_I = \frac{I}{I_{opt}}$ $y = \mu_{max}, I_{opt}, \text{or } \beta$ $y = y_{max} \left( \frac{T}{\theta_{opt}} w^u \right)^\alpha$ $w = \frac{\theta_0 - T}{\theta_0 - \theta_{opt}}$ $u = \frac{\theta_0 - \theta_{opt}}{\theta_{opt}}$	(13) indoor	<i>Oscillatoria agardhii</i>	$\mu_{max} = 0.58 \text{ day}^{-1}$ $I_{opt} = 150 \mu E m^{-2} s^{-1}$ $\mu_{max} = 0.77 \text{ day}^{-1}$ $I_{opt} = 270 \mu E m^{-2} s^{-1}$ $\mu_{max} = 1.32 \text{ day}^{-1}$ $I_{opt} = 125 \mu E m^{-2} s^{-1}$ $I_{opt}:$ $y_{max} = 101 \mu E m^{-2} s^{-1}$ $\theta_{opt} = 24^\circ C, \theta_0 = 43^\circ C,$ $\alpha = 1.6$ $\mu_{max}:$ $y_{max} = 0.5 \text{ day}^{-1}, \theta_{opt} = 37^\circ C$ $\theta_0 = 43^\circ C, \alpha = 0.3$ $\beta:$ $y_{max} = 2.3, \theta_{opt} = 18^\circ C$ $\theta_0 = 43^\circ C, \alpha = 1.9$ $I_{opt}:$ $y_{max} = 174 \mu E m^{-2} s^{-1}$ $\theta_{opt} = 29^\circ C, \theta_0 = 43^\circ C, \alpha = 1.2$ $\mu_{max}:$ $y_{max} = 1.1 \text{ day}^{-1}, \theta_{opt} = 37^\circ C$ $\theta_0 = 43^\circ C, \alpha = 0.2$ $\beta:$ $y_{max} = 2.2, \theta_{opt} = 22^\circ C$ $\theta_0 = 43^\circ C, \alpha = 1.5$ $I_{opt}:$ $y_{max} = 541 \mu E m^{-2} s^{-1}$ $\theta_{opt} = 30^\circ C, \theta_0 = 43^\circ C, \alpha = 4.8$ $\mu_{max}:$ $y_{max} = 1.7 \text{ day}^{-1}, \theta_{opt} = 37^\circ C$ $\theta_0 = 43^\circ C, \alpha = 2.7$ $\beta:$ $y_{max} = 5.4, \theta_{opt} = 23^\circ C$ $\theta_0 = 43^\circ C, \alpha = 5$ $\beta_I = 538 (\mu \text{mol photon} m^{-2} s^{-1})$ $\beta_{T,I} = 0.56$
Dermoun et al. [87]	$\mu = \mu_{max}(1+\beta_I) \cdot \frac{2x_I}{x_I^2 + 2\beta_I x_I + 1}$ $x_I = \frac{I}{I_{opt}}$ $\mu_{max}(T) = \gamma(1+\beta_I^g) \cdot \frac{2x_g}{x_g^2 + 2\beta_{T,g} x_g + 1}$ $x_g = \frac{T - \theta_{g,0}}{\theta_{g,opt} - \theta_{g,0}}$ $I_{opt}(T) = \rho_I(1+\beta_{T,I}) \cdot \frac{2x_{T,I}}{x_{T,I}^2 + 2\beta_{T,I} x_{T,I} + 1}$ $x_{T,I} = \frac{T - \theta_{I,0}}{\theta_{T,opt} - \theta_{I,0}}$	(14) Indoor	<i>Pophyridium cruentum</i>	$\theta_{I,0} = 4.7^\circ C$ $\theta_{I,opt} = 12.3^\circ C$ $\gamma = 1.4 (\text{day}^{-1})$ $\beta_{T,g} = 0.02$ $\theta_{g,0} = 4.7^\circ C$ $\theta_{g,opt} = 20.5^\circ C$
Grobbelaar [88]	$\mu_m = \mu_m(T) \cdot \frac{I}{I + K_I(T)} (1 - \alpha(T) \cdot I) - r(T)$ $\mu_m = \mu_0 \theta_\mu^{\frac{T-10}{10}}$ $K_I = K_{I0} \theta_K^{\frac{T-10}{10}}$ $\alpha = \alpha_0 \theta_\alpha^{\frac{T-10}{10}}$ $r(T) = r_0 \theta_r^{\frac{T-10}{10}} - r_1$ $\mu_{ave} = \frac{I_{ave}}{K_1 + K_2 J_{ave}}$	(15) Outdoor	<i>Scenedesmus obliquus</i> , <i>Coelastrum sphaericum</i>	$K_1 = 177.9 (W/m^2/h)$ $K_2 = 0.1083 (m^2/h/W)$ $\mu_{max} = 2 \text{ day}^{-1}$ $\alpha = 0.05 \mu E^{-1} m^2 s \text{ day}^{-1}$ $I_{opt} = 275 \mu E m^{-2} s^{-1}$
Lee et al. [33]	$\mu = \mu_{max} \frac{I}{I + \frac{\mu_{max}}{\alpha} \left( \frac{I}{I_{opt}} - 1 \right)^2}$	(16) Indoor vessel	<i>Spirulina platensis</i>	$\mu_{max} = 1.85 \text{ day}^{-1}$ $\alpha = 0.12 \text{ day}^{-1}$ $I_{opt} = 2.03 \times 10^8 \mu E m^{-2} s^{-1}$
Bernard and Remond [15]	$\mu = \mu_{max} \frac{I}{I + \frac{\mu_{max}}{\alpha} \left( \frac{I}{I_{opt}} - 1 \right)^2}$	(17)	<i>Nannochloropsis oceanica</i> <i>Chlorella pyrenoidosa</i>	$\mu_{max} = 2 \text{ day}^{-1}$ $\alpha = 0.05 \mu E^{-1} m^2 s \text{ day}^{-1}$ $I_{opt} = 275 \mu E m^{-2} s^{-1}$

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**Table 1** (continued)

Source	Formula	System	Alga	Parameters
Munoz-Tamayo et al. [89]			<i>Tisochrysis lutea</i>	$\mu_{max} = 0.76\text{day}^{-1}$ $\alpha = 0.008\mu E^{-1}\text{m}^2\text{s day}^{-1}$ $I_{opt} = 548\mu Em^{-2}\text{s}^{-1}$ $V = 0.75L$ $X_0 = 0.01905\text{kg.m}^{-3}$ $K = 0.8\text{kg.mol}^{-1}$ $r_m = 0.13\text{mol.kg}^{-1}$ $a = 0.0023(\text{m}^2/\text{W/h})$ $b = 0.0254(\text{h}^{-1})$
Ogbonna et al. [90]	$\mu = K \left( \frac{I_a}{X \cdot V} - r_m (1 - V_F) \right)$	(18)	Indoor	<i>Chlorella pyrenoidosa</i>
Lee et al. [33]	$\mu_{ave} = aI_{ave} + b$	(19)	Indoor vessel	<i>Spirulina platensis</i>
Van Oorschot [49] a.k.a. Poisson model	$P = P_{max} \left( 1 - \exp \left( - \frac{\alpha I}{P_{max}} \right) \right)$ or $P = P_{max} \left( 1 - \exp \left( - \frac{I}{K_I} \right) \right)$	(20)		
Molina Grima et al. [59]		Indoor	<i>Isochrysis galbana</i>	at $820\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.064\text{h}^{-1}$ $K_I = 456.8\mu Em^{-2}\text{s}^{-1}$ at $1630\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.043\text{h}^{-1}$ $K_I = 195.2\mu Em^{-2}\text{s}^{-1}$ at $3270\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.034\text{h}^{-1}$ $K_I = 724.7\mu Em^{-2}\text{s}^{-1}$
Geider et al. [91] Geider et al. [92]		Indoor Indoor	Various species <i>Thalassiosira pzedonana</i> <i>Pavlova lutheri</i> <i>Skeletonema costatum</i> <i>Isochrysis galbana</i>	Parameters can be found in [91] $\alpha = 1 \times 10^{-5} \text{g Cm}^{-2} (\text{g Chl a}) \mu \text{mol photons}^{-1} \mu_{max} = 5.1 \text{day}^{-1}$ $\alpha = 0.46 \times 10^{-5} \text{g Cm}^{-2} (\text{g Chl a}) \mu \text{mol photons}^{-1} \mu_{max} = 3 \text{day}^{-1}$ $\alpha = 1.38 \text{g Cm}^{-2} (\text{g Chl a}) \mu \text{mol photons}^{-1} \mu_{max} = 3 \text{day}^{-1}$ $\alpha = 0.46 \text{g Cm}^{-2} (\text{g Chl a}) \mu \text{mol photons}^{-1} \mu_{max} = 3 \text{day}^{-1}$
Meseck et al. [93]		Indoor	<i>Tetraselmis chui</i>	$\mu_{max} = 0.77\text{day}^{-1}$ $K_I = 7.14\mu Em^{-2}\text{day}^{-1}$
Bechet et al. [74] Steele [52]	$P = P_{max} \cdot \frac{I}{I_{opt}} e^{1-I/I_{opt}}$	(21) Indoor Outdoor	<i>Chlorella vulgaris</i> Sea phytoplanktons	
Molina Grima et al. [59]		Indoor	<i>Isochrysis galbana</i>	at $820\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.0521\text{h}^{-1}$ $I_{opt} = 1020.3\mu Em^{-2}\text{s}^{-1}$ at $1630\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.0484\text{h}^{-1}$ $I_{opt} = 741.9\mu Em^{-2}\text{s}^{-1}$ at $3270\mu Em^{-2}\text{s}^{-1}$ $\mu_{max} = 0.32\text{h}^{-1}$ $I_{opt} = 2217.9\mu Em^{-2}\text{s}^{-1}$
Baquerisse et al. [94]		Indoor	<i>Porphyridium purpureum</i>	
James and Boriah [95]		Indoor	<i>Phaeodactylum tricornutum</i>	
Marsullo et al. [96]		Indoor	<i>Phaeodactylum tricornutum</i> <i>Thalassiosira pseuinana</i>	$\mu_{max} = 1.392\text{day}^{-1}$ $I_{opt} = 37.118\text{Wm}^{-2}$ $\mu_{max} = 3.288\text{day}^{-1}$ $I_{opt} = 21.834\text{Wm}^{-2}$
Chalker [48]	$P = P_{max} \tanh(\alpha I)$	(22)	Indoor	<i>Gymnodinium microadriaticum</i> $P_{max} = 36\text{mol O}_2\text{h}^{-1} (\text{mol Chl a})^{-1}$ $\alpha = 4.6E^{-1}\text{m}^2\text{h}$
Bechet et al. [74] Lee and Zhang [76]		Indoor Indoor	<i>Chlorella vulgaris</i> <i>Chlorella sp.</i>	$\alpha = 0.0590\mu \text{mol photon}^{-1}\text{m}^2\text{s}$
Collins and Boylen [97]	$\mu = \mu_{max}(T) \frac{I}{I + K_I(T)} - r(T)$ $\mu_{max} = \mu_0 e^{k_\mu T}$ $K_I(T) = K_{I0} e^{k_K T}$ $r = r_0 e^{k_r T}$	(23)	Indoor	$\mu_0 = 0.098 \left( \frac{gC}{gDW} \text{day}^{-1} \right)$ $k_\mu = 0.0854(\text{°C}^{-1})$ $K_{I0} = 32.05 \left( \frac{\mu E}{m^2 s} \right)$ $k_K = 0.078(\text{°C}^{-1})$ $r_0 = 0.072 \left( \frac{gC}{gDW} \text{day}^{-1} \right)$ $k_r = 0.067(\text{°C}^{-1})$

(continued on next page)

**Table 1** (continued)

Source	Formula	System	Alga	Parameters
Guterman [98]	$\mu = \mu_p - r$ $\mu_p = qI \left( \frac{1 - (T - T_{opt})^2}{\Delta T^2} \right)$ $r = (aT + b) \cdot \frac{\Delta T}{H}$	(24) Outdoor	<i>Spirulina platensis</i>	$q = 5.679 \text{ min}^{-1} \text{ klux}^{-1}$ $T_{opt} = 33^\circ \text{C}$ $\Delta T = 25^\circ \text{C}$ $a = -0.231 \text{ min}^{-1} \text{ C}^{-1}$ $b = 0.343 \text{ min}^{-1}$
Carvalho and Malcata [99]	$\mu = \mu_{max} \left( 1 - \frac{X}{X_{max}} \right)$ $\mu_{max} = \frac{K_1 I}{K_2 T + I} e^{-\frac{K_3 I}{RT}}$	(25) indoor	<i>Pavlova lutheri</i>	$K_1 = -2.72 \text{ day}^{-1}$ $K_2 = -2.86 \text{ }^\circ \text{C}^{-1}$ $K_3 = 129 \times 10^2 J \cdot mol^{-1}$
Muller-Feuga [100]	$\mu = \mu_{max} \frac{2(1 - \rho_e)(\varphi - \rho_e)}{(1 - \rho_e)^2 + (\varphi - \rho_e)^2}$ $\varphi = \frac{I}{I_{opt}}, \rho_e = \frac{I_e}{I_{opt}}$	(26) Indoor	<i>Pophyridium cruentum</i>	$\mu_{max} = 1.06 \text{ day}^{-1}$ $I_{opt} = 485 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ $I_e = 42 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$
Lee and Zhang [76]		Indoor	<i>Chlorella</i> sp.	$I_{opt} = 54 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ $I_e = 1 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ $\mu_{max} = 0.7 \text{ day}^{-1}$
Rubio Camacho et al. [63]	$x_e^* = \frac{1}{2} \left( \left( 1 - \kappa - \frac{\alpha_I}{I} \right) + \sqrt{\left( 1 - \kappa - \frac{\alpha_I}{I} \right)^2 + 4\kappa} \right)$ Light limited: $\frac{\mu}{\mu_{max}} = \frac{I}{\alpha_I} (1 - x_e^*)$ Photoinhibited: $\kappa = \kappa_t (1 + \delta \sqrt{I})$ $\alpha_I = \alpha_{t,t} (1 + \delta \sqrt{I})$ $\frac{\mu}{\mu_{max}} = \frac{I}{\alpha_I} \frac{(1 - x_e^*)}{1 + \delta \sqrt{I}}$	(27) Indoor	<i>Chlorella pyrenoidosa</i>	

due to the nature of the equation as it has low curvature and reaches the maximum value at a low pace.

Later, Smith [39] used a new model similar to Baly's model with some modifications. By substituting irradiance and saturation constant with the square of their value, the model reached a larger curvature and therefore made model closer in shape to a typical PI curve. Bannister et al. [40] employed the same idea but instead of using square values, they used power  $m$  of them (also referred to as shape factor) which enabled the model to adjust its curvature based on the experimental data. Using values 1 and 2 for  $m$  transforms the equation into Baly and Smith's models respectively; however, after testing the model on the data from various experiments [41–45] Bannister proposed that the value of  $m$  must be between 2 and 3.

Jassby and Platt [46,47] used data from 188 experiments on light saturation curve at Nova Scotia coastal waters and compared eight different models including the ones that were developed by Baly and Smith. After an extensive comparison, they concluded that a hyperbolic tangent function was the best fit to the experimental data. Chalker [48] performed a similar study and compared four different types of equations and confirmed that as Jassby and Platt [46] concluded the hyperbolic tangent function gives the best results. Bannister stated that hyperbolic tangent function closely matches his model when  $m$  is 2.5, which is consistent with the proposed limits for  $m$  [40].

Van Oorschot [49] used an exponential equation known as Poisson function to describe the effect of light. Although this model showed to be a better fit to experimental data than Baly's model, in the analysis by Jassby and Platt [46] it did not perform as good as hyperbolic tangent function.

So far all the equations suggest that as light intensity tends to infinity, the growth rate approaches its maximum value while this contradicts the experiment where after a certain intensity, the growth rate will drop again [50,51]. This effect known as photoinhibition needs to be reflected in the model as well. Therefore, Steel [52] proposed a model to describe this effect:

$$\mu = \mu_{max} \cdot \frac{I}{I_{opt}} e^{1 - \frac{I}{I_{opt}}} \quad (2)$$

In this model when the intensity reaches  $I_{opt}$ , the growth rate will be at its maximum value, and any increase in light intensity results in lower growth rate. However, Steele [52] reported that in the shallow cultures the amount of discrepancy was relatively high. Later, Crill [53] defined photosynthetic factories where light is trapped and initiates the photosynthetic reactions and by incorporating probability functions, the same formula as Steele's was derived.

Another equation later proposed by Aiba [34], Peeters and Eilers [54] and Megard et al. [55] added an inhibition term to Tamiya's equation:

$$\mu = \mu_{max} \cdot \frac{I}{K_I + I + I^2/K_I} \quad (3)$$

Eilers and Peeters [56,57] improved Crill's model [53] and proposed a new model based on the dynamic study of photosynthesis. They assumed photosynthetic units (PSU) can experience three states: (1) resting state, (2) activated state, and (3) deactivated or damaged state. Then by defining the rate of state changes they managed to formulate the effect of light on photosynthesis at steady state conditions. Peeters and Eilers [54] also rearranged the model to show the effect of irradiance on photosynthesis based on optimum irradiance.

$$\mu = \mu_{max} (1 + \beta_I) \cdot \frac{2x_I}{x_I^2 + 2\beta_I x_I + 1} x_I = I/I_{opt} \quad (4)$$

Dauta et al. [58] compared Peeters and Eilers equation with Steels equation for four different microalgae species and found former to be more accurate. In a study Lee et al. [33] modified Aiba's equation to reduce the number of constants and facilitate parameter estimation.

$$\mu = \mu_{max} \cdot \frac{I}{K_I + K_i \cdot I^2} \quad (5)$$

Even though the above equation still seems to have three parameters, by introducing  $K_I = K_I/\mu_{max}$  and  $K_i = K_i/\mu_{max}$ , the number of parameters will be reduced to two. They used experimental data for growth of *Spirulina platensis* and compared the new equation with the models by Baly [36], Bannister [40], and Aiba [34] and concluded that their model besides Aiba's are the only ones able to perform well at high

irradiance while their model had a smaller mean square deviation in general.

Molina Grima et al. [28] developed a model based on Bannister's model using average intensity which later was enhanced by replacing the shape factor,  $m$ , and the photo-saturation constant,  $K_I$ , by apparent values which could be calculated using specific relations [59]:

$$\mu = \mu_{max} \cdot \frac{I_{ave}^{n_{app}}}{I_{app}^{n_{app}} + I_{ave}^{n_{app}}} \quad (6)$$

$$n_{app} = n_2/I \quad (7)$$

$$I_{app} = I_k + \left( \frac{I}{K_I} \right)^{n_1} \quad (8)$$

where  $n_1$ ,  $n_2$  are model constants.

They assumed that photo-inhibition is caused by the damaged photosystem at a high light intensity which is the case only where the light enters the culture. Thus, due to light attenuation, photo-inhibition does not happen in the depth of the culture as the light intensity drops significantly. On the other hand, regeneration of photosystem is not bounded by the cell location and can happen anywhere in the culture. Therefore, the growth rate should be related to both incident and average light intensity.

Another modification of Bannister's model was done by Garcia-Malea et al. [60] where the shape factor and the saturation constant were related linearly to irradiance at the surface:

$$\mu = \mu_{max} \cdot \frac{I_{av}^{a+bI_0}}{(c + dI_0)^{a+bI_0} + I_{av}^{a+bI_0}} \quad (9)$$

In 2000, Han et al. [35] argued that since microalgae experience variable irradiance, using static modelling is not the best approach. Therefore, they involved the dynamic aspect of light in the model to reach more accuracy. They used the same idea as Peeters and Eilers [54,56,57] but instead of simplifying the model for steady state condition, they kept the dynamic characteristics of the model. Due to consideration of light history of cells this model could potentially be valuable for hydrodynamic study of microalgal culture, where cells experience various light conditions [61,62]. It also enables the model to account for unique phenomenon in microalgae cultures known as flash light effect [63]. However, in this paper we have not reviewed dynamic models, as a summary of them can be found in Bechet et al. [51].

### 2.1.1. Light spectrum

Although light is one of the most important factors in the growth of microalgae, it is not only the intensity of light that is important but also its spectrum as well. Microalgae have been shown to grow in certain wavelengths of light better than the others, and thus some researchers studied this effect as well [30]. This light range, which is also known as photosynthetically active radiation (PAR), is responsible for providing energy for the reactions and its wavelength ranges from 400 nm to 700 nm [30]. Blanken et al. [27] took this effect into account and assumed the effective light intensity is caused by these wavelengths and considering light attenuation, he proposed a formula for light intensity inside the culture:

$$I(z) = \sum_{\lambda=400}^{700} I_\lambda(0) e^{a_x C_x z} \Delta \lambda \quad (10)$$

where  $I_\lambda(0)$  is light intensity at surface for wavelength  $\lambda$ ,  $a_x$  is light absorption rate,  $C_x$  is biomass concentration, and  $z$  is depth of the point at which light intensity is calculated.

Ritchie [64] made the range of effective wavelengths even narrower by considering only blue (425–500 nm) and red (640–700 nm) light. Using the results of McCree [65] he added average quantum efficiency and calculated photosynthetically useable radiation (PUR).

$$I_{PUR} \approx 0.668 \times \int_{425}^{500} I_\lambda d\lambda + 0.819 \times \int_{640}^{700} I_\lambda d\lambda \quad (11)$$

The highest solar irradiance on the surface of the earth can reach about  $2220 \mu\text{mol m}^{-2} \text{s}^{-1}$ , of which, according to Eq. (11), only about  $767 \mu\text{mol m}^{-2} \text{s}^{-1}$  can be used for photosynthesis [65]. The usable light intensity calculated in Eq. (11) may replace irradiance in most of the presented growth models.

Moreover, wavelengths out of PAR range do not stimulate growth but may have inhibitory effects. Studies show that UV irradiation can cause inhibition of photosynthesis and even death of algal cells and consequently limit growth rate [66–68].

## 2.2. Nutrients

Microalgae require various nutrients for growth and when they undergo nutrient limitation the growth can be affected significantly. Nitrogen and phosphorus compounds play an important role on the growth and the organic composition of algal cells [101,102]. There are also many micronutrients such as cobalt, iron, molybdenum, and manganese, which are necessary for optimum growth of microalgae [103]. Many models have been used to explain the effect of nutrients on the growth of microalgae, a summary of which can be found in Table 2. Monod [38] introduced one of the first growth models which was initially intended for bacterial cultures but later was used by many researchers for algal cultures as well. He tried to study the biochemistry of bacteria using bacterial growth where he just limited the study to positive growth and neglected the death rate. He used a Michaelis-Menten equation to describe the growth rate as a function of the concentration of nutrient.

$$\mu = \mu_{max} \frac{S}{K_s + S} \quad (12)$$

Where  $\mu$  is specific growth rate,  $\mu_{max}$  is maximum specific growth rate,  $S$  is concentration of the limiting nutrient, and  $K_s$  is concentration of limiting nutrient at which the specific growth rate is half of its maximum value.

Many studies used this model as a basis and found the parameters of this model for their specific alga type [104–107]. Goldman et al. [104] divided the growth based on the concentration of limiting nutrient into three areas. The first area is the low concentration of nutrient which is defined as a concentration in which specific growth rate is less than half of its maximum value. In this area, the specific growth rate is in a linear relationship with limiting nutrient concentration.

$$\mu = \mu_{max} \cdot \frac{S}{K_s} \quad (13)$$

The second area is where Monod equation applies till when the specific growth rate is almost reached the maximum value. The third area is the constant growth rate area where based on Monod equation given  $K_s \ll S$  then  $\mu = \mu_{max}$  and further increase in concentration will not result in any change in the specific growth rate.

Despite its popularity among researchers, Monod equation failed when high concentration of nutrients had negative effect on growth. Andrews [108] used Monod equation and performed some modifications to add the inhibitory effect of high concentrations which may be significant during transient conditions like system start-up. For this purpose he added an inhibitory term to the equation:

$$\mu = \mu_{max} \cdot \frac{S}{S + K_s + \frac{S^2}{K_i}} \quad (14)$$

where  $K_i$  is inhibition constant and  $\mu_{max}$  is a theoretical value representing maximum specific growth rate if there was no inhibition. Andrews pointed out that this equation does not follow a theoretical basis and is empirically derived and lacks the effects of organism death, inhibitory effect of products, and delayed response of microalgae to

**Table 2**  
Models considering effect of nutrients.

Source	Model	System	Alga type	Estimation
Monod [38]	$\mu = \mu_{max} \frac{S}{K_S + S}$	(1)		
Haario et al. [70]		Outdoor	Diatom	$\mu_{max} = 0.0886 \text{ day}^{-1}$ $N: K_S = 14.5 (\mu\text{g/L})$ $P: K_S = 10.4 (\mu\text{g/L})$
			<i>Chrysophycea</i>	$\mu_{max} = 0.0465 \text{ day}^{-1}$ $N: K_S = 32.9 (\mu\text{g/L})$ $P: K_S = 8.27 (\mu\text{g/L})$
			<i>Cyanobacteria</i>	$\mu_{max} = 0.329 \text{ day}^{-1}$ $N: K_S = 21 (\mu\text{g/L})$ $P: K_S = 5.5 (\mu\text{g/L})$
			<i>Minor species</i>	$\mu_{max} = 0.212 \text{ day}^{-1}$ $N: K_S = 45.7 (\mu\text{g/L})$ $P: K_S = 77.3 (\mu\text{g/L})$
Xin et al. [107]			<i>Scenedesmus</i> sp.	$N: K_S = 12.1 \text{ mg L}^{-1}$ $P: K_S = 0.27 \text{ mg L}^{-1}$
Concas et al. [79]		Indoor	<i>Spirulina platensis</i>	$N: K_S = 5.314 \text{ g m}^{-3}$ $P: K_S = 0.028 \text{ gm}^{-3}$
Spijkerman et al. [129]		Indoor	<i>Chlamydomonas acidiphila</i>	Multiplicative model: $\mu_{max} = 0.073 h^{-1}$ $C: K_S = 0.38 \mu M$ $P: K_S = 1.09 nM$ Threshold model: $\mu_{max} = 0.076 h^{-1}$ $C: K_S = 1.43 \mu M$ $P: K_S = 1.46 nM$
Jayaraman and Rhinehart [18]			<i>Gladieria sulphuraria</i>	
Chen et al. [130]			<i>Microcystis aeruginosa</i>	$P: K_S = 0.025 (\text{mg L}^{-1})$
Marsullo et al. [96]		Indoor	<i>Phaeodactylum tricornutum</i>	$N:$ $K_S = 0.001 \text{ mol.m}^{-3}$
			<i>Thalassiosira pseuinana</i>	$N:$ $K_S = 0.001 \text{ mol.m}^{-3}$
Lee and Zhang [76]			<i>Chlorella</i> sp.	$N: K_S = 0.1 \text{ mg L}^{-1}$
Concas et al. [3]		Indoor	<i>Nannochloris eucaryotum</i>	$N: K_S = 5.4 \times 10^{-4} \text{ g L}^{-1}$ $P: K_S = 2.5 \times 10^{-5} \text{ g L}^{-1}$
Fre et al. [131]		Indoor	<i>Dunaliella tertiolecta</i>	$75 \text{ mg L}^{-1}$ of sodium nitrate $\mu_{max} = 0.02790 h^{-1}$ $K_S = 0.9 \times 10^{-4} \text{ g L}^{-1}$ $300 \text{ mg L}^{-1}$ of sodium nitrate $\mu_{max} = 0.02804 h^{-1}$ $K_S = 8.52 \times 10^{-4} \text{ g L}^{-1}$ $600 \text{ mg L}^{-1}$ of sodium nitrate $\mu_{max} = 0.02567 h^{-1}$ $K_S = 2.374 \times 10^{-3} \text{ g L}^{-1}$ $900 \text{ mg L}^{-1}$ of sodium nitrate $\mu_{max} = 0.02617 h^{-1}$ $K_S = 3.944 \times 10^{-3} \text{ g L}^{-1}$
Martinez Sancho et al. [112] and Martinez et al. [113]	$\mu = \frac{\mu_{m1}S + \mu_{m2}K_S}{K_S + S}$	(2)	<i>Scenedesmus obliquus</i>	$\mu_{m1} = 0.0466 h^{-1}$ $\mu_{m2} = 0.0256 h^{-1}$ $K_S = 0.2 \mu M$
Martinez et al. [113]	$\mu = \frac{\mu_{m1}K_IS + \mu_{m2}S^2 + \mu_{m3}K_SK_I}{K_SK_I + K_IS + S^2}$	(3)	<i>Scenedesmus obliquus</i>	Values at different temperatures are reported in [113]
Andrews [108]	$\mu = \mu_{max} \frac{S}{K_S + S^2 / K_IS}$	(4)		
Zhang et al. [132]		Indoor	<i>Chlamydomonas reinhardtii</i>	For nitrate: $K_S = 2.6085 \text{ g L}^{-1}$ $K_IS = 0.1065 \text{ g L}^{-1}$ For ammonium chloride: $K_S = 2.2956 \text{ g L}^{-1}$ $K_IS = 0.1557 \text{ g L}^{-1}$ For urea: $K_S = 2.3978 \text{ g L}^{-1}$ $K_IS = 0.0708 \text{ g L}^{-1}$
Kasiri et al. [75]		Indoor	<i>Chlorella kessleri</i>	$\mu_{max} = 0.73 \text{ day}^{-1}$ $K_S = 722 \text{ mg L}^{-1}$ $K_I = 1.28 \times 10^4 \text{ mg L}^{-1}$

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**Table 2** (continued)

Source	Model	System	Alga type	Estimation
Mirzaie et al. [85]		Indoor	<i>Chlorella vulgaris</i>	$\mu_{max} = 0.13 day^{-1}$ $K_S = 0.117 g L^{-1}$ $K_{IS} = 0.073 g L^{-1}$
Lee and Zhang [76]		Indoor	<i>Chlorella</i> sp.	$N:K_S = 1.78 mg L^{-1}$ $K_{IS} = 364 mg L^{-1}$
Spijkerman et al. [129] <sup>a</sup>	$\mu = \mu_{max} \frac{C}{K_C + C}$ $K_C = \frac{\mu_{max}}{\alpha C_{max}} \times \frac{K_P + P}{P}$	(5)	Indoor Chlamydomonas acidophila	$\mu_{max} = 0.059 h^{-1}$ $K_P = 0.7 nM$ $\alpha C_{max} = 0.039$
Spijkerman et al. [129] <sup>a</sup>	$\mu = \mu_{max} \frac{P}{K_P + P}$ $K_P = \frac{\mu_{max}}{\alpha P_{max}} \times \frac{K_C + C}{C}$	(6)	Indoor Chlamydomonas acidophila	$\mu_{max} = 0.066 h^{-1}$ $K_C = 0.77 \mu M$ $\alpha P_{max} = 0.075$
Droop [110]	$\mu = \mu'_{max} \left(1 - \frac{Q_{min}}{Q}\right)$	(7)	<i>Monochrysis lutheri</i>	
Burmester [133]			<i>Monochrysis lutheri</i>	$\mu_{max} = 1.03 (day^{-1})$ $Q_{min} = 7.02 \times 10^{-16} mol. cell^{-1}$
Packer et al. [29]		Indoor	<i>Pseudochlorococcum</i> sp.	$\mu_{max} = 3.26 day^{-1}$ $Q_{min} = 0.0278 g N.(g dw)^{-1}$
Wu et al. [134]		Indoor	<i>Scenedesmus</i> sp.	$\mu_{max} = 0.34 day^{-1}$ $Q_{min} = 0.019%$
Fre et al. [131]		Indoor	<i>Dunaliella tertiolecta</i>	75 mg L <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.04669 h^{-1}$ $Q_{min} = 0.02634 mg.g^{-1}$ 300 mg L <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.04319 h^{-1}$ $Q_{min} = 0.03505 mg.g^{-1}$ 600 mg L <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.05289 h^{-1}$ $Q_{min} = 0.08543 mg.g^{-1}$ 900 mg L <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.04628 h^{-1}$ $Q_{min} = 0.1179 mg.g^{-1}$
Guest et al. [126]	$\mu = \mu'_{max} \left(1 - \left(\frac{Q_{min}}{Q}\right)^4\right)$	(8)	Indoor <i>Chlamydomonas reinhardtii</i>	
Geider [92]	$\mu = \mu'_{max} \left(\frac{Q - Q_{min}}{Q_{max} - Q_{min}}\right)$	(9)	Indoor <i>Thalassiosira pseodonana</i> <i>Pavlova lutheri</i> <i>Skeletonema costatum</i> <i>Isochrysis galbana</i>	$Q_{min} = 0.04 \left(\frac{g N}{g C}\right)$ $Q_{max} = 0.2 \left(\frac{g N}{g C}\right)$ $Q_{min} = 0.04 \left(\frac{g N}{g C}\right)$ $Q_{max} = 0.2 \left(\frac{g N}{g C}\right)$ $Q_{min} = 0.04 \left(\frac{g N}{g C}\right)$ $Q_{max} = 0.2 \left(\frac{g N}{g C}\right)$ $Q_{min} = 0.04 \left(\frac{g N}{g C}\right)$ $Q_{max} = 0.167 \left(\frac{g N}{g C}\right)$
Caperon and Meyer [122,123]	$\mu = \mu'_{max} \frac{Q - Q_{min}}{K_C + Q - Q_{min}}$	(10)	Indoor <i>Coccochloris</i> <i>Cyclotella</i> <i>Dunaliella</i>	$\mu_{max} = 0.090 (h^{-1})$ $Q_{min} = 0.075 \left(\frac{mol N}{mol C}\right)$ $K = 0.057 \left(\frac{mol N}{mol C}\right)$ $\mu_{max} = 0.087 (h^{-1})$ $Q_{min} = 0.043 \left(\frac{mol N}{mol C}\right)$ $K = 0.053 \left(\frac{mol N}{mol C}\right)$ $\mu_{max} = 0.076 (h^{-1})$ $Q_{min} = 0.044 \left(\frac{mol N}{mol C}\right)$ $K = 0.034 \left(\frac{mol N}{mol C}\right)$
Flynn [111]	$\mu = \mu'_{max} \frac{\hat{Q}(1 + k_Q)}{\hat{Q} + k_Q}$ $\hat{Q} = \frac{Q - Q_{min}}{Q_{max} - Q_{min}}$	(11)		

(continued on next page)

**Table 2** (continued)

Source	Model	System	Alga type	Estimation
Chapelle et al. [135]			<i>Alexandrium minutum</i>	$\mu_{max} = 0.55 day^{-1}$ $Q_{min} = 3.7 pg. cell^{-1}$ $Q_{max} = 32.6 pg. cell^{-1}$ $K_Q = 4.24$
Bougaran et al. [120]	$\mu = \mu'_{max} \frac{\left(1 - \frac{Q_{min}}{Q}\right)}{\left(1 - \frac{Q_{min}}{Q_{max}}\right)}$	(12) Indoor	<i>Selenastrum minutum</i>	$\mu_{max} = 0.67 day^{-1}$ $Q_{min} = 5.5 pg. cell^{-1}$ $Q_{max} = 15.6 pg. cell^{-1}$ $K_Q = 1.34$
Fouchardet al. [84]	$\frac{\mu}{\mu'_{max}} = f(Q)$ $\frac{f(Q) - f_{min}}{1 - f_{min}} = \frac{\exp(k \cdot \frac{Q}{Q_m}) - 1}{\exp(k) - 1}$	(13) indoor	<i>Chlamydomonas reinhardtii</i>	$\mu_{max} = 1.58 (day^{-1})$ N: $Q_{min} = 0.06 \left(\frac{mol N}{mol C}\right)$ $Q_{max} = 0.21 \left(\frac{mol N}{mol C}\right)$ P: $Q_{min} = 0.0018 \left(\frac{mol N}{mol C}\right)$ $Q_{max} = 0.015 \left(\frac{mol N}{mol C}\right)$ $\mu_{max} = 1.5 (day^{-1})$ N: $Q_{min} = 0.065 \left(\frac{mol N}{mol C}\right)$ $Q_{max} = 0.14 \left(\frac{mol N}{mol C}\right)$ P: $Q_{min} = 0.0009 \left(\frac{mol N}{mol C}\right)$ $Q_{max} = 0.006 \left(\frac{mol N}{mol C}\right)$ $Q_m = 7 mg Sulfur (mg biomass)^{-1} k = 0.3389$ $f_{min} = 0.0674$
De La Hoz Siegler et al. [136,137] <sup>b,c</sup>	$\mu = \mu'_{max} \frac{\tilde{q}}{K_q + \tilde{q}} \exp\left(-\frac{\tilde{q}}{K_l}\right)$ $\bar{q} = \frac{1}{t} \int_0^t \tilde{q} dt$ $\tilde{q} = \frac{Q}{X + L + Q}$	(14) Indoor	<i>Auxenochlorella protothecoides</i>	$\mu_{max} = 11.12 day^{-1}$ $K_q = 0.0022$ $K_l = 0.016$
Abdollahi and Dubljevic [138]		Indoor	<i>Auxenochlorella protothecoides</i>	$\mu_m = 14.18 day^{-1}$ $K_q = 0.0041$ $K_l = 0.016$
He et al. [139] <sup>c</sup>	$\mu = \mu_{max} \left(1 - \frac{X}{X_{max}}\right)$	(15) Indoor	<i>Isochrysis galbana</i>	N: 25 mg of sodium nitrate $\mu_{max} = 0.721 day^{-1}$ $X_{max} = 387.9 mg L^{-1}$ 50 mg of sodium nitrate $\mu_{max} = 0.568 day^{-1}$ $X_{max} = 538.28 mg L^{-1}$ 75 mg of sodium nitrate $\mu_{max} = 0.448 day^{-1}$ $X_{max} = 670.58 mg L^{-1}$ 100 mg of sodium nitrate $\mu_{max} = 0.416 day^{-1}$ $X_{max} = 835.41 mg L^{-1}$ Reported in [140] for various ammonium concentrations
Tavatia et al. [140] <sup>c</sup>	$\mu = \mu_{max} \alpha(t) \left(1 - \frac{X}{X_{max}}\right)$ $\alpha(t) = \frac{e^{-h_0}}{e^{-\mu_{max} t} + e^{-h_0} - e^{-\mu_{max} t - h_0}}$	(16)		(continued on next page)

**Table 2** (continued)

Source	Model	System	Alga type	Estimation
Fre et al. [131] <sup>c</sup>	$\mu = \mu_{max} \left( \frac{S}{K_S + S} \right) \left( \frac{X}{X + K_X} \right)$	(17)	Indoor	<i>Dunaliella tertiolecta</i> 300mgL <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.02858h^{-1}$ $K_S = 5.05 \times 10^{-4} g.L^{-1}$ $K_X = 5.474 g.L^{-1}$ 600mgL <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.02889h^{-1}$ $K_S = 5.232 \times 10^{-3} g.L^{-1}$ $K_X = 3.958 g.L^{-1}$ 900mgL <sup>-1</sup> of sodium nitrate $\mu_{max} = 0.02870h^{-1}$ $K_S = 5.851 \times 10^{-3} g.L^{-1}$ $K_X = 3.932 g.L^{-1}$

<sup>a</sup> C and P are concentration of carbon and phosphorus in the media respectively, and  $\alpha_{Cmax}$  and  $\alpha_{Pmax}$  are model constant regarding these values.

<sup>b</sup> X is the concentration of biomass, L is the concentration of lipid and Q is nitrogen concentration within the cell.

<sup>c</sup>  $X_{max}$  is the maximum sustainable concentration of biomass.

variations of nutrients concentration; however, this model has proven to be more successful in explaining microalgae growth compared to Monod equation.

Applying the above models many studies used concentration of nutrients in the culture and related it to the growth rate [36,39,106,107]; However, some believed that the concentration in the media does not have an immediate effect on the specific growth rate unless a long-term rate is studied [109,110]. Also, it has been reported that even when the concentration of nutrients in the culture dropped to zero, microalgal growth was not immediately ceased [109–111]. Martinez Sancho et al. [112] tried to resolve this issue with classical Monod model by introducing an extra parameter in the model. They examined different models for phosphorus-limited cultures, including a modified form of Monod equation which showed a better fit to the experimental results:

$$\mu = \frac{\mu_{m1}S + \mu_{m2}K_S}{K_S + S} \quad (15)$$

In this model  $\mu_{m1}$  is maximum specific growth rate, and  $\mu_{m2}$  is specific growth rate when there is no phosphorus. By adding the specific growth rate at zero phosphorus concentration they tried to explain the ongoing growth after consumption of all nutrients. Later, they examined other models for inhibitory effect of substrate where they modified Andrew's equation and formed a new model [113].

$$\mu = \frac{\mu_{m1}K_iS + \mu_{m2}S^2 + \mu_{m3}K_SK_i}{K_SK_i + K_iS + S^2} \quad (16)$$

Where  $\mu_{m1}$  is maximum specific growth rate,  $\mu_{m2}$  is inhibited growth rate, and  $\mu_{m3}$  is the specific growth rate when there is no phosphorus. Also  $K_S$  and  $K_i$  are model constants to account for saturation and inhibition by substrate, respectively.

Another approach was presented by introducing the concept of intercellular concentration or cell quota where it is assumed that nutrients are stored within the cell before it is used. Droop [110,114,115] suggested that cell quota, which is customarily represented by Q and is defined as the concentration of nutrient within the cell divided by cell mass, could be used as an effective parameter to calculate the specific growth rate:

$$\mu = \mu'_{max} \left( 1 - \frac{k_Q}{Q} \right) \quad (17)$$

$k_Q$  is the saturation constant which later was referred to by some researchers [2,116] as  $Q_{min}$  implying that if the cell quota of a specific nutrient is less than  $Q_{min}$ , the growth rate will be zero. Therefore, when the substrate concentration reaches zero in the culture, there is still nutrients stored in the cell to support cell growth. This model proved to

be successful in describing the behaviour of microalgae in natural systems when nitrogen and phosphorus are both limited [2,117,118]. Droop's equation has become a well-known model and has been frequently used by many researchers [25,29,101,119] because it is able to uncouple the growth rate and the absorption of the nutrients [120]. Sommer [121] compared Monod and Droop models using data from a eutrophic lake in Germany and found Monod model to be significantly less accurate than Droop. He also explained while Monod model has limitation in its application due to luxury uptake of nutrients, Droop model is difficult to apply as cell quota is difficult to measure.

Caperon and Meyer [122,123] used the same concept as Droop and proposed another model using Michaelis-Menten form of equation:

$$\mu = \mu'_{max} \frac{Q - Q_{min}}{Q - Q_{min} + K_C} \quad (18)$$

Where  $K_C$  is the model constant.

This model was developed to explain steady state growth rate under nutrient-limited condition. Later, Flynn [111] used the same model as a basis to explain co-limitation of nitrogen and phosphorus. He assumed that at  $Q_{max}$  the specific growth rate is maximised which led to the following equation:

$$\mu = \mu'_{max} \frac{\frac{Q - Q_{min}}{Q - Q_{min} + K_C}}{\frac{Q_{max} - Q_{min}}{Q_{max} - Q_{min} + K_C}} \quad (19)$$

Another assumption was that  $K_C$  is a linear function of  $Q_{max} - Q_{min}$  which ultimately resulted in Eq. (19):

$$\mu = \mu'_{max} \frac{(1+K_Q)(Q - Q_{min})}{(Q - Q_{min}) + K_Q(Q_{max} - Q_{min})} \quad (20)$$

where  $K_Q$  is the model constant.

Eq. (20) can be simplified to:

$$\mu = \mu'_{max} \frac{\hat{Q}(1+K_Q)}{\hat{Q} + K_Q} \quad (21)$$

$$\hat{Q} = \frac{Q - Q_{min}}{Q_{max} - Q_{min}} \quad (22)$$

In this model, if the quota reaches its maximum value, which is finite, the growth rate will be at its maximum as well, but this statement does not apply to Droop's model. In Droop's model in order to reach the maximum growth rate, the cell quota needs to approach infinity which is not a realistic assumption. However, Droop [124] explained that  $\mu'_{max}$  is merely a mathematical concept which can only be achieved when  $\hat{Q}$  approaches infinity and it is different from maximum specific growth rate in Monod equation ( $\mu_{max}$ ) and its value is larger than  $\mu_{max}$  [125].

**Table 3**

Models considering the effect of temperature.

Source	Model	System	Alga type	Estimation
Ratkowsky et al. [142]	$\sqrt{\mu} = b(T - T_0)$	(1)	For Bacteria	
Ratkowsky et al. [143]	$\sqrt{\mu} = b(T - T_{min})(1 - e^{c(T - T_{max})})$	(2)	For Bacteria	
Zwieterin et al. [147]	$\mu = b(T - T_{min})^2(1 - e^{c(T - T_{max})})$	(3)	For bacteria	
James and Boriah [95]	$\mu = \mu_{max} \exp(-k_t(T - T_{opt})^2)$	(4)	Indoor <i>Phaeodactylum tricornutum</i>	$T_{opt} = 20^\circ C$ $k_t = 0.007^\circ C^{-2}$ $T_{opt} = 25^\circ C$ $s = \frac{1}{\sqrt{k_t}} = 13^\circ C$
Franz et al. [72]	-	-	-	
Jayaraman and Rhinehart [18]	-	-	<i>Gladieria sulphuraria</i>	$T_{opt} = 323K$ $k_t = 0.0001K^{-2}$
Dauta et al. [58]	$\mu = \begin{cases} \mu_{max} \exp\left(-2.3\left(\frac{T - T_{opt}}{T_L - T_{opt}}\right)^2\right), & T < T_{opt} \\ \mu_{max} \exp\left(-2.3\left(\frac{T - T_{opt}}{T_U - T_{opt}}\right)^2\right), & T \geq T_{opt} \end{cases}$	(5)	Indoor <i>Chlorella Vulgaris</i>	$T_{opt} = 30^\circ C$
Franz et al. [72]	$\frac{\mu}{\mu_{max}} = \begin{cases} \exp\left(-\left(\frac{T - T_{opt}}{s}\right)^2\right), & T \leq T_{av,day} \\ 1, & T_{av,day} < T \leq T_{av,day} + 8 \\ \exp\left(-\left(\frac{T - T_{opt} + 8}{s}\right)^2\right), & T > T_{av,day} + 8 \end{cases}$	(6)	Outdoor <i>Fragilaria crotonensis</i> <i>Straurostrum pingue</i> <i>Synechocystis minimata</i> <i>Chlamydomonas reinhardtii</i>	$T_{opt} = 25^\circ C$ $T_{opt} = 27^\circ C$ $T_{opt} = 32^\circ C$ • Tromsø: $T_{opt} = 7^\circ C$ $s = 5^\circ C$ • Fehmarn: $T_{opt} = 11^\circ C$ $s = 5^\circ C$ • Karlsruhe: $T_{opt} = 13^\circ C$ $s = 6^\circ C$ • Madrid: $T_{opt} = 17$ • Tamanrasset: $T_{opt} = 25^\circ C$ • Manaus: $T_{opt} = 28^\circ C$ $s = 10^\circ C$
James et al. [157]	$\frac{\mu}{\mu_{max}} = \begin{cases} \exp(-K_1(T - T_1)^2), & T \leq T_1 \\ 1, & T_1 < T \leq T_2 \\ \exp(-K_2(T - T_2)^2), & T > T_2 \end{cases}$	(7)		
Costache [82]	$P = P_{max}(k_1 e^{E_1/RT} - k_2 e^{E_2/RT})$	(8)	Indoor <i>Scenedesmus almeriensis</i>	$k_1 = 4.99 \times 10^7$ $k_2 = 1.66 \times 10^{13}$ $E_1 = 4.27 \times 10^4 mol.J^{-1}$ $E_2 = 7.71 \times 10^4 mol.J^{-1}$
Bitaube Perez et al. [158]	$\mu = \mu_{max} \left( k_1 \exp\left(\frac{E_1(T - T_0)}{RT}\right) - k_2 \exp\left(\frac{E_2(T - T_0)}{RT}\right) \right)$	(9)	Indoor <i>Phaeodactylum tricornutum</i>	$k_1 = 0.26 h^{-1}$ $k_2 = 0.18 h^{-1}$ $E_1 = 28 kcal. mol^{-1}$ $E_2 = 39 kcal. mol^{-1}$ $T_0 = 293K$
Tevatia et al. [159]	$\mu = \mu_{max} \left( \frac{e^{E_1/RT}}{1 + K_T e^{E_2/RT}} \right)$	(10)		
Sharpe and DeMichele [145]	$\mu = \frac{\frac{\phi}{RT} \Delta H_A}{1 + e^{\frac{\Delta S_L}{R}} - \frac{\Delta H_L}{RT} + e^{\frac{\Delta S_H}{R}} - \frac{\Delta H_H}{RT}}$	(11)		$\phi = 32.69(K^{-1}s^{-1})$ $\Delta H_A = 12939 \left( \frac{cal}{mol} \right)$ $\Delta S_H = 180.2 \left( \frac{cal}{mol.K} \right)$ $\Delta H_H = 56977 \left( \frac{cal}{mol} \right)$ $\Delta S_L = -184.4 \left( \frac{cal}{mol.K} \right)$ $\Delta H_L = -54632 \left( \frac{cal}{mol} \right)$
Eppley [153]	$\mu = \mu_0 1.066^T$	(12)	indoor Approximately 130 species	$\mu_0 = 0.851 \text{ doublings per day}$
Moisan [160]	$\mu = \begin{cases} \log(2)*0.851*1.066^T \frac{ T - T_{opt} ^3}{T_{low}}, & T \leq T_{opt} \\ \log(2)*0.851*1.066^T \frac{ T - T_{opt} ^3}{T_{high}}, & T > T_{opt} \end{cases}$	(13)		
Norberg [161]	$\mu = 0.59 \left( 1 - \left( \frac{T - Z}{w} \right)^2 \right) e^{0.0633T}$	(14)		
Haario et al. [70]	$\mu = \mu_{ref} \theta^{T-20}$	(15)	outdoor Diatom	$\mu_{ref} = 0.0886 day^{-1}$ $\theta = 1.14$

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**Table 3** (continued)

Source	Model	System	Alga type	Estimation
Lee and Zhang [76]			<i>Chrysophycea</i> <i>Cyanobacteria</i> <i>Minor species</i>	$\mu_{ref} = 0.0465\text{day}^{-1}$ $\theta = 1.07$ $\mu_{ref} = 0.329\text{day}^{-1}$ $\theta = 1.16$ $\mu_{ref} = 0.212\text{day}^{-1}$ $\theta = 1.13$
Pegallapati and Nirmalakhandan [80]	$\mu = \mu_{ref} 1.066^{T-20}$	(16) Indoor	<i>Chlorella</i> sp.	When coupled with Chalker [48] model of light: $\theta = 1.35$ When coupled with Muller-Feuga [100] model of light: $\theta = 1.16$ $\mu_{ref} = 1.2\text{day}^{-1}$
Ketheesan and Nirmalakhandan [154]		Indoor and outdoor	<i>Nannochloropsis salina</i> <i>Scenedesmus</i> sp.	Indoor: $\mu_{ref} = 1.4\text{day}^{-1}$ Outdoor: $\mu_{ref} = 2.0\text{day}^{-1}$ $\mu_{ref} = 1.15\text{day}^{-1}$
Sukenik et al. [30,156]	$P = P_{ref} \exp\left(-E_0\left(\frac{1}{T} - \frac{1}{T_{ref}}\right)\right)$	(17) Indoor	<i>Dunaliella tertiolecta</i>	$E_0 = 3500\text{ K}$
Geider et al. [92]			<i>Pavlova lutheri</i> <i>Skeletonema costatum</i> <i>Thalassiosira pseudonana</i> <i>Isocrysis galbana</i>	
Chen et al. [130]	$\mu = \mu_{max} c_1 e^{c_2  T - T_{opt} }$	(18)	<i>Micrcystis aeruginosa</i>	$c_1 = 1.57$ $c_2 = 0.24$
Carvalho and Malcata [99]	$\mu = \mu_{max} \left(1 - \frac{X}{X_{max}}\right)$ $\mu_{max} = \frac{K_1 I}{K_2 T + I} e^{-\frac{K_2 I}{RT}}$ $X_{max} = (K_4 + K_5 T) e^{-\frac{K_6 L}{RT}}$	(19) indoor	<i>Pavlova lutheri</i>	$K_1 = -2.72\text{day}^{-1}$ $K_2 = -2.86^\circ\text{C}^{-1}$ $K_3 = 129 \times 10^3 J.\text{mol}^{-1}$ $K_4 = 1.19 \times 10^8 \text{cell. mL}^{-1}$ $K_5 = -3.69 \times 10^5 \text{cell.(mL. }^\circ\text{C)}^{-1}$ $K_6 = -12.4 J.\text{mol}^{-1}$
Bernard and Remond [15]	$\mu = \mu_{max} \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})(a(T) - b(T))}$ $a(T) = (T_{opt} - T_{min})(T - T_{opt})$ $b(T) = (T - T_{opt})(T_{opt} + T_{min} - 2T)$ $T_{min} < T < T_{max}$	(20) Indoor	Various species	Parameters are available in [15]
Munoz-Tamayo [89]		Indoor		$\mu_{max} = 0.76\text{day}^{-1}$ $T_{min} = -0.2^\circ\text{C}$ $T_{opt} = 26.7^\circ\text{C}$ $T_{max} = 33.3^\circ\text{C}$
Ippoliti et al. [12]	$P = P_{max} \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})(a(T) - b(T))}$ $a(T) = (T_{opt} - T_{min})(T - T_{opt})$ $b(T) = (T - T_{opt})(T_{opt} + T_{min} - 2T)$ $T_{min} < T < T_{max}$	(21) Indoor and outdoor	<i>Isochrysis galbana</i>	$T_{min} = 11.88^\circ\text{C}$ $T_{opt} = 35.73^\circ\text{C}$ $T_{max} = 46.15^\circ\text{C}$
Rarrek et al. [162]	$f(T) = 1 -  T - T_{opt}  / T_{dep}$	(22)		$T_{opt} = 25^\circ\text{C}$ $T_{dep} = 0.05\text{K}^{-1}$
Blanchard et al. [152]	$P = P_{max} \phi_T^\beta e^{\beta(1 - \phi_T)}$ $\phi_T = \frac{T_{max} - T}{T_{max} - T_{opt}}$	(23) Indoor	<i>Benthic diatom</i>	Isolated in September 1995 $P_{max} = 5.81 \mu\text{g C} (\mu\text{g Chl a})^{-1} h^{-1} T_{opt} = 25.3^\circ\text{C}$ $T_{max} = 38.2^\circ\text{C}$ $\beta = 1.76$ Isolated in December 1995 $P_{max} = 3.04 \mu\text{g C} (\mu\text{g Chl a})^{-1} h^{-1} T_{opt} = 25.4^\circ\text{C}$ $T_{max} = 34.9^\circ\text{C}$ $\beta = 1.03$
Slegers et al. [163]		Indoor	<i>Phaeodactylum tricornutum</i> <i>Thalassiosira pseuinana</i>	$T_{opt} = 21.64^\circ\text{C}$ $T_{max} = 30.31^\circ\text{C}$ $\beta = 1.57$ $T_{opt} = 24.73^\circ\text{C}$ $T_{max} = 31.4^\circ\text{C}$ $\beta = 1.83$
Quinn et al. [116]	$\mu = \mu_{max} \frac{2k_T}{1 + k_T^2}$ $k_T = \exp\left(\frac{E_a}{RT_{opt}} - \frac{E_a}{RT}\right)$	(24) Outdoor	<i>Nannochloropsis</i> <i>occulta</i>	$E_a = 63 \text{kJ mol}^{-1}$ $T_{opt} = 23^\circ\text{C}$

Bougaran et al. [120] proposed a threshold coupling model that considered both phosphorus and nitrogen limitation where the minimum quota function is related to the specific growth rate. They proposed the same form of function for both N and P:

$$\mu = \mu'_{\max} \frac{1 - \frac{Q_{min}}{Q}}{1 - \frac{Q_{min}}{Q_{max}}} \quad (23)$$

This equation resolves the infinite quota problem with Droop's model by adding a maximum quota as well as maintaining the simplicity of the equation.

Another model was proposed by Guest et al. [126] which used the same condition as Bougaran (threshold model for N and P) and Droop's model as a basis.

$$\mu = \mu'_{\max} \left( 1 - \left( \frac{Q_{min}}{Q} \right)^4 \right) \quad (24)$$

Even though this equation still has the same issue with infinite quota as Droop's model, due to the fourth power, the function rapidly reaches the vicinity of its maximum value where its difference from maximum is negligible for common values of Q. This makes the model appropriate when compared to the experimental data.

Another aspect of modelling the effect of nutrient, is understanding the relationship when there is more than one nutrient involved. Haefner [127] presented five methods for combining multiple parameters: (1) Liebig's law of minimum, (2) multiplication, (3) arithmetic average, (4) mean resistance, and (5) additive rates.

Liebig's law of minimum, which is also known as threshold model, assumes that the most limited nutrient determines the rate of growth. Therefore, it describes the growth to be related to minimum value of nutrients functions:

$$\mu = \mu_{\max} \min(f(S_1), f(S_2), f(S_3)) \quad (25)$$

The function of each nutrient can be any of the discussed models such as Monod or Droop models.

Multiplication method assumes that all the nutrients affect the growth at the same time and not only limitation in one nutrient lowers the growth rate, but multiple limitations deteriorate the situation. It relates the final value to be relative to multiplication of all functions:

$$\mu = \mu_{\max} \cdot f(S_1) \cdot f(S_2) \cdot f(S_3) \quad (26)$$

The third method is using the arithmetic average of the functions:

$$\mu = \mu_{\max} \frac{f(S_1) + f(S_2) + f(S_3)}{3} \quad (27)$$

Mean resistance method is inspired by the effect of a resistance in an electrical circuit and uses the reverse of each function:

$$\mu = \mu_{\max} \frac{1}{\frac{1}{f(S_1)} + \frac{1}{f(S_2)} + \frac{1}{f(S_3)}} \quad (28)$$

Haefner [127] added the fifth method (additive rates) based on a study by O'Neill et al. [128] where they compared eight different methods of simultaneous limitation by applying them to data from terrestrial and aquatic experiments, and found additive model to be the most accurate.

$$\mu = \mu_{\max} \frac{S_1 S_2}{K_1 S_2 + S_1 S_2 + K_2 S_1} \quad (29)$$

As can be seen, this equation is based on the Monod model.

Among all the mentioned methods, two approaches are the most common among the researchers when modelling co-limitation of nutrients: threshold model and multiplicative model [2]. Multiplicative model, unlike threshold model, has been used widely and not only for co-limitation, but also for connecting the effects of other parameters such as light and temperature; however, Haefner [127] stated that in

practice using multiplication appears to underestimate growth when the number of limiting nutrients increase.

Law of the minimum was employed in the model proposed by Bougaran et al. [120] and Guest et al. [126]. As in the latter study, the co-limited relationship was expressed with the following equation:

$$\mu = \mu_{\max} \min \left( \left( 1 - \left( \frac{Q_{P,min}}{Q_P} \right)^4 \right), \left( 1 - \left( \frac{Q_{N,min}}{Q_N} \right)^4 \right) \right) \quad (30)$$

### 2.3. Temperature

After nutrient and light, temperature plays the most crucial role in the growth of microalgae [15]. Many studies have been undertaken to understand the effect of temperature on the growth rate and many models have been proposed in a variety of forms (Table 3). This diversity in the form of models suggests the complicated nature of the relationship between growth and temperature.

Many of the models for effect of temperature on the growth of microalgae are inspired from bacterial or other microbial growth models. Hence, all seem to follow similar trends.

One of the first models is known as Hinshelwood model [141] which was derived using Arrhenius law for growth of bacteria and later was used for microalgae growth:

$$\mu = k_1 e^{-\frac{E_1}{T}} - k_2 e^{-\frac{E_2}{T}} \quad (31)$$

where T is absolute temperature and  $k_1$ ,  $k_2$ ,  $E_1$ , and  $E_2$  are model parameters.  $E_1$  and  $E_2$  replaced the activation energy over gas constant ( $\frac{E_a}{R}$ ) in the original form of Arrhenius law and  $k_1$  and  $k_2$  are pre-exponential factors. Thermodynamically, in this equation, the first term can be interpreted as the production (growth) rate and the second term as the consumption (death) rate of the bacteria due to high temperature. However, as the temperature is decreased in this model, specific growth rate declines but never reaches zero except at temperature of absolute zero. This makes the model unrealistic at low temperatures.

Ratkowsky et al. [142] explain that Van't Hoff and Arrhenius relations cannot provide a good approximation of the temperature dependency of the growth rate. They plotted the logarithm of the growth rate against the reciprocal of absolute temperature and suggested the following model which uses the square root of growth rate:

$$\sqrt{\mu} = b(T - T_{min}) \quad (32)$$

where  $T_{min}$  is the temperature below which no growth takes place and  $b$  is the model constant.

However, this equation worked well from the minimum temperature to the optimum temperature, where the growth rate is at its maximum value, but for higher temperatures this equation is not valid. When the temperature is increased beyond the optimum value, the growth rate starts to decrease while this equation does not predict this effect. To cover this flaw, an extension of this model was proposed [143]. In the new model an exponential term was added to correct the previous equation for higher temperatures:

$$\sqrt{\mu} = b(T - T_{min})(1 - e^{c(T - T_{max})}) \quad (33)$$

where  $T_{max}$  is the maximum temperature limit for growth and  $c$  is a model constant. They applied this model to 30 sets of data for various bacteria and found this model to be fairly accurate.

Sharpe et al. [144,145] proposed a model considering three energy states: (1) inactivation due to low temperature, (2) inactivation due to high temperature, and (3) active (developing) state. They modelled the transition between the states and used a different equation for the kinetic rates to describe the growth rate changes with temperature:

$$\mu = \frac{T \exp\left(\frac{(\phi - \frac{\Delta H_A}{T})}{R}\right)}{1 + \exp\left(\frac{(\Delta S_L - \frac{\Delta H_L}{T})}{R}\right) + \exp\left(\frac{(\Delta S_H - \frac{\Delta H_H}{T})}{R}\right)} \quad (34)$$

In this equation  $R$  is the universal gas constant, and the rest of the parameters are defined as follows:

- $\Delta H_A$ : enthalpy of activation of growth
- $\Delta S_L$ : entropy change of low temperature inactivation
- $\Delta H_L$ : enthalpy change of low temperature inactivation
- $\Delta S_H$ : entropy change of high temperature inactivation
- $\Delta H_H$ : enthalpy change of high temperature inactivation
- $\phi$ : is the model constant

Schoolfield et al. [146] described this formulation to be unsuitable for regression due to high correlation of parameters. They explained that the complexity of the model makes parameter estimation sometimes impossible. Therefore, they reformulated the function to facilitate the regression process.

$$\mu = \frac{\mu_{25} \frac{T}{298} \exp\left(\frac{\Delta H_A}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right)}{1 + \exp\left(\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right) + \exp\left(\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right)} \quad (35)$$

Schoolfield et al. [146] used 25 °C (298 K) as the reference temperature and included specific growth rate at this temperature ( $\mu_{25}$ ) as one of the parameters in the model. The reason for selection of 25 °C as the reference temperature was mainly due to observed high activity for most microalgae around this temperature. In Eq. (34)  $T_L$  and  $T_H$  are temperatures of half-inactivation at low and high temperature, respectively.

Zwietering et al. [147] modified the extended Ratkowsky model, so that the growth rate is related to the square of the first term but not the exponential term.

$$\mu = (b(T - T_{min}))^2(1 - e^{c(T - T_{max})}) \quad (36)$$

Then, they compared the modified model with several other models including Schoolfield [146] and Ratkowsky [142,143] models for growth of enzymes and reported that despite having only four parameters, their model had less deviation from experimental data than more complicated models like Schoolfield's. Lobry et al [148] suggested a new empirical model using three cardinal temperatures ( $T_{min}$ ,  $T_{opt}$  and  $T_{max}$ ). The growth takes place when the temperature is between  $T_{min}$  and  $T_{max}$ , therefore, out of this range there is no positive growth and at  $T_{opt}$  the specific growth rate reaches its maximum value. These three temperatures are part of the characteristics of each species and having a model based on these values facilitates the application of the model.

$$\mu = \mu_{max} \frac{(T_{max} - T)(T - T_{min})}{(T - T_{opt})^2 + (T_{max} - T)(T - T_{min})} \quad (37)$$

This model was unable to predict the suboptimal curve of growth with temperature, thus it was modified and cardinal temperature model with inflection (CTMI) was introduced [141]:

$$\mu = \mu_{max} \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})[(T_{opt} - T_{min})(T - T_{opt}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T)]} \quad (38)$$

Rosso et al. [141] compared the new model with Ratkowsky [143] and Zwietering [147] model for 47 sets of data of various bacterial species. The comparison showed that CTMI was able to show a better fit for 21 of the 47 sets while Ratkowsky model performed better for 20 of

the 47 sets and in the remaining six sets Zwietering model had the lowest deviation. The performance of this model was very close to that of Ratkowsky model, but its ease of use and meaningful parameters made CTMI a powerful tool which later was used by Bernard et al. for microalgal cultures [15]. They used CTMI for various algal species and showed its good fit with experimental data. However, it must be mentioned that CTMI has certain limitations in terms of its applicability. To have positive values for  $\mu$  all across the valid range, the average of  $T_{min}$  and  $T_{max}$  should be less than  $T_{opt}$  or in other words  $T_{opt}$  needs to be closer to  $T_{max}$  than  $T_{min}$ , otherwise the model will produce negative numbers for growth [15].

In 1999 Yan and Hunt [149] used cardinal temperatures to predict the change in photosynthetic rate of plants by temperature, modifying previous models by Yin et al. [150] and Gao et al. [151] for growth in crops.

$$\mu = \mu_{max} \frac{T_{max} - T}{T_{max} - T_{opt}} \left( \frac{T - T_{min}}{T_{opt} - T_{min}} \right)^{\frac{T_{opt} - T_{min}}{T_{max} - T_{opt}}} \quad (39)$$

The model, then was further simplified by assuming  $T_{min}$  to be zero which led to the following equation:

$$\mu = \mu_{max} \frac{T_{max} - T}{T_{max} - T_{opt}} \left( \frac{T}{T_{opt}} \right)^{\frac{T_{opt}}{T_{max} - T_{opt}}} \quad (40)$$

Another model was proposed by Blanchard et al. [152] for the change in growth of motile benthic diatoms with temperature. Although, the model seems to fit the experimental data acceptably, it is observed that in suboptimal temperatures the model predicted a smaller degree of curvature compared to that of experiments.

Some studies used a normal distribution model (Gaussian curve) to predict the effect of temperature [18,95]. In this model, growth is maximum around  $T_{opt}$  and as the temperature decreases or increases the growth will change in a Gaussian bell-shape. In a study, Franz et al. [72] used Gaussian curve to explain the effect of temperature and assumed that microalgal strains had adapted to local climate, and therefore, had the best performance at average temperature of their specific geographical location. They suggested two equations: the first one assumes  $T_{opt}$  to be average temperature for all the studied locations:

$$\mu = \mu_{max} \exp\left(-\left(\frac{T - T_{opt}}{s}\right)^2\right) \quad (41)$$

and the second equation takes  $T_{ave,day}$  equal to the average temperature of each location:

$$\begin{cases} \mu = \mu_{max} \exp\left(-\left(\frac{T - T_{ave,day}}{s}\right)^2\right); T \leq T_{ave,day} \\ \mu = \mu_{max} \exp\left(-\left(\frac{T - T_{ave,day} + 8}{s}\right)^2\right); T > T_{ave,day} \end{cases} \quad (42)$$

$$\mu = \mu_{max}; T_{ave,day} < T \leq T_{ave,day} + 8 \quad (43)$$

$$\begin{cases} \mu = \mu_{max} \exp\left(-\left(\frac{T - T_{ave,day} + 8}{s}\right)^2\right); T_{ave,day} + 8 < T \\ \mu = \mu_{max} \exp\left(-\left(\frac{T - T_{ave,day}}{s}\right)^2\right); T \geq T_{ave,day} \end{cases} \quad (44)$$

where  $s$  is a model constant.

As it can be seen, in the second model the growth rate stays at the maximum value for a temperature range of 8 °C which is due to the hypothesis that temperature has less effect on the growth rate when the light intensity is low [72] and ultimately makes the model application very limited. Moreover, the change in growth with temperature does not fully fit a Gaussian distribution as based on experimental data the change is not symmetrical. Dauta et al. [58] have also used the same basis for their model but added skewness to the functions to get the asymmetry in the shape of the model.

Eppley [153] proposed a very simple model for growth of various species of phytoplankton in the sea using about 200 data points.

$$\mu = 0.851 \times 1.066^T \quad (45)$$

Here  $T$  is temperature in degrees Celcius. This model is surprisingly simple and easy to use and many other researchers utilised it as a basis for their models [70,76,80,154]. However, this model only performs as an envelope for various species or in other words as the author stated the equation is “useful as a generalisation of the maximum  $\mu$  to be expected for a photosynthetic unicellular algae.” [153]

So far in all the discussed models the effect of temperature was as an independent and separate function which could be coupled with that of other limiting factors. But there are studies that included the effect of temperature in other functions such as light [155]. For instance, Dermoun et al. [87] (Eq. (14) in Table 1) and Talbot et al. [86] (Eq. (13) in Table 1) used the Peeters and Eilers model [54,56] for light but considered the constants to be temperature dependant. Grobbelaar [88] used the same principle but applied it to Baly’s model [36].

$$\mu = a_1 a_2 \frac{K_S a_3^\theta I}{I + K_S a_3^\theta} \quad (46)$$

In this equation  $a_1$ ,  $a_2$ , and  $a_3$  are model constants,  $K_S$  is light saturation constant, and  $\theta$  is temperature factor calculated via following equation:

$$\theta = \frac{T-10}{10} \quad (47)$$

where  $T$  is temperature in °C.

As it can be seen, the effect of temperature on the growth of microalgae can be difficult to model and having numerous equations in variety of forms is a proof for it. Most of the studies reviewed here used a standalone function to describe this effect with a few cases where it was combined with light function. There are also studies where photosynthesis was described as a function of temperature and was later used to calculate specific growth rate or productivity assuming they have a linear relationships [30,91,92,156]:

$$P = P_{ref} \exp \left( -E_0 \left( \frac{1}{T} - \frac{1}{T_{ref}} \right) \right) \quad (48)$$

where  $P_{ref}$  is photosynthesis rate at  $T_{ref}$ . Eq. (48) was inspired by Van ‘t Hoff equation which was originally derived to describe variation of equilibrium constant with temperature in a chemical reaction.

#### 2.4. pH and carbon

For each strain of microalgae, there is an optimum pH where the growth rate is maximised [164]. But pH is a parameter which is closely affected by the amount of carbon in the media, as carbon dioxide injection is a common way to lower pH level [165]. In modelling approaches, their effects are considered together, thus only one of them is included in the models. Moreover, carbon is one of the main nutrients for algal growth and in many studies the same models used for nutrients, was applied to carbon as well [80,104,129]. However in the studies considering the effect of pH, the models were diverse. Also, in some studies pH was maintained constant using other means while carbon dioxide concentration was varied [17]. Table 4 summarises the models considering the effect of pH or carbon on the growth of microalgae.

Dissolved inorganic carbon in a culture can be in different forms such as carbon dioxide, carbonate, and bicarbonate [166] and they do not contribute equally to the growth. Algal cells use carbon dioxide to a larger extent compared to bicarbonate and barely use carbonate [167]. For pH levels between 6.5 and 10, where most of algal cells grow, bicarbonates are the dominant form of carbon (Fig. 2).

As mentioned before models that include the effect of carbon concentration treat carbon as a nutrient. Goldman et al. [104] used Monod model (Eq. (8) in Table 4) to relate specific growth rate to total inorganic carbon for *Scenedesmus quadricauda* and *Selenastrum*

*capricornutum*. To calculate total inorganic carbon they added the amount of carbonic acid, bicarbonate and carbonate, as well as aqueous carbon dioxide. They stated that algal growth should be related to total inorganic carbon not one specific form of it. However, King and Novak [168] used the data from Goldman et al. [104] and argued that specific growth rate is a function of free carbon dioxide and not total inorganic carbon. Lee and Zhang [76] also used aqueous carbon dioxide in Monod model (Eq. (8) in Table 4) for growth of *Chlorella* sp. when concentration of carbon dioxide is below 50 mg L<sup>-1</sup>. For higher concentrations Andrews model was utilised to include the inhibitory effect of carbon caused by low pH as a result of high carbon concentration. Baquerisse et al. [94] selected Steele model [52], which was originally used for irradiance, and replaced light parameters with carbon dioxide parameters to explain the growth kinetic of *Porphyridium purpureum*.

The second type of models are those where pH level is incorporated directly into the model. Bailey and Ollis [169] derived a model for the effect of pH on the reaction rate of enzymes:

$$\mu = \mu_{max} \frac{1}{1 + \frac{[H^+]}{K_H} + \frac{K_{OH}}{[H^+]}} \quad (49)$$

In this equation  $K_H$  and  $K_{OH}$  are model parameters and  $[H^+]$  is hydrogen ion concentration which can be calculated from  $pH$  ( $[H^+] = 10^{-pH}$ ). They classified enzymes into three groups: (1) catalytically active, (2) acid inactive, and (3) basic inactive. The same formulation was used by Tang et al. [170] for bacterium *Clostridium formicoaceticum* and later by Bitaube Perez et al. [158] for *Phaeodactylum tricornutum*. Zhang et al. [132] modified this model by adding a third constant to denominator and resulting in Eq. (50):

$$\mu = \mu_{max} \frac{1}{K_1 + \frac{[H^+]}{K_H} + \frac{K_{OH}}{[H^+]}} \quad (50)$$

where  $K_H$ ,  $K_{OH}$  and  $K_1$  are model parameters Jayaraman and Rhinehart [18] included pH as a parameter in their model assuming only carbon dioxide concentration is responsible for pH changes. Therefore, instead of using carbon dioxide concentration as an input, they used a function of pH to describe the effect of carbon.

$$\mu = \mu_{max} \cdot \frac{1}{1 + e^{\lambda(pH - pH_{opt})}} \quad (51)$$

Where  $pH_{opt}$  is the pH at which growth is maximised and  $\lambda$  is the model constant.

Costache et al. [82] used a model based on Arrhenius equation to describe the effect of pH on Photosynthesis rate which showed a close fit to experimental data for *Scenedesmus almeriensis*:

$$P = P_{max} (B_1 e^{-C_1/pH} - B_2 e^{C_2/pH}) \quad (52)$$

In this equation  $B_1$ ,  $B_2$ ,  $C_1$ , and  $C_2$  are model constants and  $P$  and  $P_{max}$  are photosynthesis rate and its maximum value respectively. Filali et al. [71], however, considered all three types of inorganic carbon ( $CO_2$ ,  $HCO_3^-$ , and  $CO_3^{2-}$ ) and by using equilibrium constants and pH, calculated the total amount of inorganic carbon.

$$\mu = \mu_{max} \cdot \frac{[TIC]}{X \cdot K_{CL} + [TIC]} \quad (53)$$

$$[CO_2] = \frac{[TIC]}{1 + \frac{K_1}{[H^+]} + \frac{K_2 K_3}{[H^+]^2}} \quad (54)$$

$$[H^+] = 10^{-pH} \quad (55)$$



Where  $[TIC]$  is the molar concentration of total inorganic carbon,  $K_1$  and  $K_2$  are equilibrium constants of  $HCO_3^-$  and  $CO_3^{2-}$  formation (Eqs. (55) and (56)),  $X$  is biomass concentration, and  $K_{CL}$  is carbon saturation

**Table 4**

Models considering the effect of pH or carbon concentration.

Source	Formula	System	Alga type	Estimation
Jayaraman and Rhinehart [18]	$\mu = \mu_{max} \frac{1}{1 + \exp(\lambda(pH - pH_{opt}))}$	(1)	<i>Gladieria sulphuraria</i>	$pH_{opt} = 2.5$
Costache [82]	$P = P_{max}(B_1 e^{-C_1/pH} - B_2 e^{C_2/pH})$	(2)	Indoor <i>Scenedesmus almeriensis</i>	$B_1 = 2.5$ $B_2 = 533$ $C_1 = 6.45$ $C_2 = 69.2$
Fernandez et al. [83]			Outdoor <i>Scenedesmus almeriensis</i>	$B_1 = 2.4098$ $B_2 = 533.01$ $C_1 = 6.2684$ $C_2 = 68.8062$
Bailey and Ollis [169]	$\mu = \mu_{max} \frac{1}{1 + \frac{[H^+]}{K_H} + \frac{K_{OH}}{[H^+]}}$	(3)		
Tang et al. [170] Bitaube Perez et al. [158]		Indoor	<i>Phaeodactylum tricornutum</i>	$\mu_{max} = 0.064 h^{-1}$ $K_H = 2.3 \times 10^{-6} mol.L^{-1}$ $K_{OH} = 1.2 \times 10^{-10} mol.L^{-1}$
Zhang et al. [132]	$\mu = \mu_{max} \frac{1}{K_1 + \frac{[H^+]}{K_H} + \frac{K_{OH}}{[H^+]}}$	(4)	Indoor <i>Chlamydomonas reinhardtii</i>	For nitrate: $\mu_{max} = 1.4528 h^{-1}$ $K_1 = 0.7602$ $K_H = 0.401 \times 10^7 mol.L^{-1}$ $K_{OH} = 0.865 \times 10^7 mol.L^{-1}$ For ammonium nitrate: $\mu_{max} = 1.2942 h^{-1}$ $K_1 = 1.1835$ $K_H = 0.2826 \times 10^7 mol.L^{-1}$ $K_{OH} = 0.666 \times 10^7 mol.L^{-1}$ For urea: $\mu_{max} = 1.4198 h^{-1}$ $K_1 = 0.3499$ $K_H = 0.2609 \times 10^7 mol.L^{-1}$ $K_{OH} = 0.8042 \times 10^7 mol.L^{-1}$
Rarrek et al. [162]	$\mu = \mu_{max} (1 -  pH - pH_{opt}  p H_{dep})$ $pH_{dep}$ : model parameter $pH_{opt}$ : pH associated with maximum growth	(5)		$pH_{opt} = 8.5$ $pH_{dep} = 0.3$
Ifrim et al. [171]	$\mu = \mu_{max} x_{pH} e^{1-x_{pH}}$ $x_{pH} = \frac{pH - pH_{min}}{pH_{max} - pH}$ $pH_{min}$ : minimum pH for growth $pH_{max}$ : maximum pH for growth	(6)		
Ippoliti et al. [12]	$P = P_{max} \frac{(pH - pH_{max})(pH - pH_{min})^2}{(pH_{opt} - pH_{min})(a(pH) - b(pH))}$ $a(pH) = (pH_{opt} - pH_{min})(pH - pH_{opt})$ $b(pH) = (pH_{opt} - pH_{max})(pH_{opt} + pH_{min} - 2pH)$ $pH_{min}$ : minimum pH for growth $pH_{max}$ : maximum pH for growth $pH_{opt}$ : pH associated with maximum growth	(7)	Indoor and outdoor <i>Isochrysis galbana</i>	$pH_{opt} = 7.34$ $pH_{min} = 2.24$ $pH_{max} = 10$
Monod model [38]	$\mu = \mu_{max} \frac{C}{K_S + C}$	(8)	Indoor <i>Scenedesmus quadricauda</i>	$\mu = 2.29 day^{-1}$ $pH 7.1–7.21$ $K_S = 0.3 mg.L^{-1}$ $pH 7.25–7.39$ $K_S = 0.36 mg.L^{-1}$ $pH 7.44–7.61$ $K_S = 0.71 mg.L^{-1}$
Goldman et al. [104]			Indoor <i>Selenastrum capricornutum</i>	$\mu = 2.45 day^{-1}$ $pH 7.05–7.23$ $K_S = 0.4 mg.L^{-1}$ $pH 7.25–7.39$ $K_S = 1.0 mg.L^{-1}$ $pH 7.43–7.59$ $K_S = 1.2 mg.L^{-1}$
Hsueh et al. [105]		Indoor <i>Nannochloropsis sp.</i>		$K_S = 1.9 mM$ $\mu_{max} = 3.5 day^{-1}$
Marsullo et al. [96]		Indoor <i>Phaeodactylum tricornutum</i> <i>Thalassiosira pseuinana</i>		$C:$ $K_S = 0.001 mol.m^{-3}$ $C:$ $K_S = 0.001 mol.m^{-3}$ $N:K_S = 3.6 mgL^{-1}$
Lee and Zhang [76]			<i>Chlorella sp.</i>	

(continued on next page)

**Table 4** (continued)

Source	Formula		System	Alga type	Estimation
Filali et al. [71]	$\mu = \mu_{max} \frac{[TIC]}{X \cdot K_{CL} + [TIC]}$ X: biomass concentration $K_{CL}$ : model parameter	(9)	Indoor	<i>Chlorella vulgaris</i>	$\mu_{max} = 0.08h^{-1}$ $K_S = 1.28 \times 10^{-5} mol \cdot 10^9 cell^{-1}$
De La Hoz Siegler et al. [136,137]	$\mu = \mu_{max} \frac{C}{K_S + C + \frac{C^2}{K_i}}$	(10)	Indoor	<i>Auxenochlorella protothecoides</i> (Heterotroph)	$\mu_{max} = 11.12 day^{-1}$ $K_S = 15.03 gL^{-1}$ $K_i = 47.4 gL^{-1}$
Pegallapati and Nirmalakhandan [80]			Indoor	<i>Nannochloropsis salina</i>	$\mu_{max} = 1.2 (day^{-1})$ $K_S = 2.316 \times 10^{-6} M$ $K_i = 0.0046 M$
Abdollahi et al. [138]			Indoor	<i>Scenedesmus</i> sp.	$\mu_{max} = 1.4 (day^{-1})$ $K_S = 9.818 \times 10^{-4} M$ $K_i = 1 M$
Lee and Zhang [76]				<i>Chlorella</i> sp.	$\mu_{max} = 14.18 day^{-1}$ $K_S = 8.45 gL^{-1}$ $K_i = 49.5 gL^{-1}$
Kasiri et al. [75]	$\mu = \mu_{max} \frac{C - C_0}{K_S + (C - C_0) + \frac{C^2}{K_i}}$ $C_0$ : minimum concentration of carbon for growth	(11)	Indoor	<i>Chlorella kessleri</i>	$\mu_{max} = 0.73 day^{-1}$ $K_S = 3.75 mgL^{-1}$ $K_i = 1.79 \times 10^3 mgL^{-1}$
Baquerisse et al. [94]	$\mu = \mu_{max} \cdot \frac{C}{C_{opt}} e^{1 - \frac{C}{C_{opt}}}$ $C_{opt}$ : carbon concentration associated with maximum growth	(12)	Indoor	<i>Porphyridium purpureum</i>	

constant. They used mass transfer equations to calculate the amount of carbon dioxide in the culture and using the above equations determined total inorganic carbon concentration and specific growth rate.

$$[CO_2^*] = \frac{p_{CO_2}}{H_{CO_2}} \quad (58)$$

$$\frac{dTIC}{dt} = k_L a ([CO_2^*] - [CO_2]) \quad (59)$$

$p_{CO_2}$  is partial pressure of carbon dioxide in the air,  $H_{CO_2}$  is Henry's constant for solubility of carbon dioxide in the medium,  $[CO_2^*]$  is the maximum obtainable concentration of carbon dioxide in the medium, and  $k_L a$  is the mass transfer coefficient.

Ifrim et al. [171] presented an equation in which they used minimum and maximum pH thresholds for growth:

$$\mu = \mu_{max} \frac{pH - pH_{max}}{pH_{min} - pH} e^{1 - \frac{pH - pH_{max}}{pH_{min} - pH}} \quad (60)$$

Ippoliti et al. [12] proposed an equation (Eq. (7) in Table 4) based on CTMI (originally developed to describe the effect of temperature on growth). They used pH thresholds as well as optimum pH for growth, which showed to be a good fit to the experimental data.

In most studies carbon dioxide is assumed to be in excess, and therefore its effect is neglected while in large-scale cultivation, the limitation of carbon is a common issue in microalgal cultures [166] particularly at high culture densities or when there is no carbon dioxide injection into the system and increasing the amount of carbon dioxide significantly improves the productivity [164]. Despite this, there are very few researchers who included  $CO_2$  in their model as a limiting factor and mostly the same approach as other nutrients has been employed.

## 2.5. Salinity

microalgae production is a process that requires massive amount of water, and procuring it is a major challenge. Yang et al. [172] reported that to produce one kilogram of biodiesel, 3726 kg of water is needed.

The cost of using fresh water significantly affects the viability of microalgae production. Considering the majority of areas where microalgae can have highest productivity have limited or no access to freshwater [7], use of saline water, in the form of seawater or underground saline water, is an inevitable option to grow microalgae in large scale [7]. However, there is another challenge when any type of saline water is used. Areas with high intensity of sunlight are the best locations for cultivating microalgae as a higher level of irradiance accelerates the growth rate. On the other hand, higher light intensity means more evaporation, especially for open ponds, which causes an increase in salinity level [173]. Some types of microalgae are compatible with high-salinity water: (1) marine, (2) halotolerant, and (3) halophilic microalgae [174]. Salinity is an important parameter for the growth of these microalgae [175], and different types of microalgae have different reactions to high salinity [175,176]. Some strains of marine microalgae such as *Tetraselmis* sp. show higher productivities compared to freshwater microalgae [177,178]. Fábregas et al. [179] observed the maximum cell density for *Tetraselmis suecica* in the range of 2.5–3.5% salinity, and below this range, the density dropped in proportion to salinity. Laing and Utting [180] found this range to be 2.5–3% for *Tetraselmis suecica* and 1.5–2.5% for *Isochrysis galbana*. Controlling the salinity of the culture is a difficult task, especially when one of the goals is to minimise the consumption of freshwater and also maximise nutrients utilisation. Fon Sing [181] discussed the importance of recycling the media to use the unconsumed nutrients which will eventually reduce the cost of production. However, using this strategy means a constant increase in the salinity of the media which can significantly affect photosynthesis and consequently growth rate [182]. But despite incredible advancements in understanding the physiology of salinity effects [183], its relationship with growth is still not clear [182]. Salinity can affect microalgae in three ways: (a) causing osmotic stress, (b) uptake or loss of ions which results in ion stress, and (c) causing changes in cellular ionic ratios [183]. None of those has been a subject of mathematical modelling. Any change in osmotic pressure leads to inhibition of photosynthesis or can cause swelling which may result in the cells being burst [184]. The effect of salinity becomes more critical considering that elevated salinity level in the culture puts the cells

under stress [185]. The stressed cells grow slower and start accumulating lipids [186,187] which is not a desirable behaviour in growth phase when cell number growth is the goal. If saline water is to be used for microalgae cultivation, it is vital to understand the effect of salinity on growth and how changes in salinity, whether it is gradual (due to evaporation) or sudden (due to the addition of recycled medium), affects the growth. But despite the importance of this process parameter, to the extent of authors' knowledge, no effort has been made to include this effect in mathematical models.

## 2.6. Oxygen

Oxygen build-up in the culture is a major issue in microalgal growth [188–190] as oxygen is a by-product of photosynthesis [191] and its concentration can reach over four times of air saturation in the culture [192] which constrains photosynthesis rate. This can happen in both closed photo bioreactors and open ponds; however, due to diffusion to atmosphere and use of paddle wheels, high concentration of dissolved oxygen is less prominent in open ponds [188]. This effect was first discovered by Warburg in 1920, who observed that photosynthesis of *Chlorella* was dropped significantly when culture was exposed to pure oxygen [193]. Inhibition of growth by elevated oxygen, mostly referred to as Warburg effect, has been observed in many plants as well [194]. Many researchers have reported a decrease in productivity when a high concentration of oxygen was present in algal cultures [188,192,195]. Ugwu et al. [191] demonstrated a decrease in the productivity when dissolved oxygen was increased from 120% of air saturation to 300%. When the culture was stripped of oxygen, photosynthesis rate of *C. vulgaris* was increased and when the medium was exposed to pure oxygen, the photosynthesis rate dropped by 35% [189]. Turner et al. [193] showed that when *Chlorella pyrenoidosa* was exposed to less than 20% oxygen concentration in gas phase, no significant increase in the photosynthesis was observed but when oxygen level exceeded 20%, inhibition up to 42% was recorded. Also in a test for *Chlorella vulgaris*, they observed that when the culture was exposed to air again, the level of inhibition decreased; however, they could not conclude if this is always reversible. Merrett and Armitage [196] found that decreasing oxygen level in air from 21% to 2% result in an increase in cell number for *Euglena gracilis* but when the same experiment was done for *Chlamydomonas reinhardtii* no such effect was observed. Torzillo et al. [197] believe that high oxygen concentration causes sensitivity to photo-inhibition and therefore lowers productivity while lowering the temperature can deteriorate the situation and increase the sensitivity. Richmond [188] reported that in extremely high concentration of oxygen photooxidative death can happen. Although the limiting effect of accumulated oxygen on the photosynthesis and growth is well

accepted and attempts have been made to predict the concentration of oxygen in the microalgal culture [189], very few models can be found to describe this effect [82,198] (Table 5). Miyachi et al. [199] proposed a second order equation for degree of inhibition:

$$H = 1 - \frac{P}{P_{max}} = \frac{[O_2]^2}{K_O + [O_2]^2} \quad (61)$$

where  $H$  is degree of inhibition,  $K_O$  is model constant,  $P$  is photosynthesis rate at the absence of oxygen (replaced by nitrogen) and  $[O_2]$  is oxygen partial pressure in gas phase. Fernandez et al. [81], however, used a first order Eq. (61) which resulted in Eq. (62).

$$P = P_{max} \frac{K_O}{K_O + [O_2]} \quad (62)$$

In a study to simulate a biocoil Photobioreactor, Concas et al. [3] used a linear function to describe the inhibitory effect of oxygen:

$$\mu = \mu_{max} \left( 1 - \frac{[O_2]}{[O_2]_{max}} \right) \quad (63)$$

In this equation  $[O_2]_{max}$  is oxygen concentration at which growth becomes zero. Costache et al. [82] related photosynthesis rate to the rate of oxygen generation and developed the following equation:

$$P = P_{max} \left( 1 - \left( \frac{[O_2]}{K_{O_2}} \right)^z \right) \quad (64)$$

where  $K_{O_2}$  and  $z$  are the model constants.

## 3. Gaps and pathways for future researches

Despite the extensive and detailed studies in the modelling of the growth rate of microalgae, there is still room for improvement. Some of the gaps have been reported in previous reviews [2,51]; however there are still a number of areas which have not been addressed. The following areas are the most important areas of research to achieve better models for application in industrial systems:

### 3.1. Light

Light is one of the most important parameters in modelling the microalgae growth, and almost all suggested models have included the effect of this parameter and are thoroughly reviewed by Bechet et al. [51] and Lee et al. [2]. This does not mean that no more study can be done in this area. Contrarily, there are still a few ambiguities when it comes to irradiance. Firstly, how the light intensity should be utilised is

**Table 5**  
Models considering the effect of dissolved oxygen.

Source	Formula	System	Alga	Estimation
Miyachi et al. [199]	$P = P_{max} \frac{K_O^2}{K_O + [O_2]^2}$ (1)			
Turner and Brittain [200]		Indoor	<i>Chlorella</i>	$at CO_2 = 1 \times 10^{-6} mol L^{-1}$ $K_O = 0.42 atm$ $at CO_2 = 91 \times 10^{-6} mol L^{-1}$ $K_O = 1.71 atm$
Costache et al. [82]	$P = P_{max} \left( 1 - \left( \frac{[O_2]}{K_O} \right)^z \right)$ (2)	Indoor	<i>Scenedesmus almeriensis</i>	$K_O = 32.08 mg L^{-1}$ $z = 5.49$
Fernandez et al. [83]		Outdoor	<i>Scenedesmus almeriensis</i>	$K_O = 0.8373 mol m^{-3}$ $z = 5.4333$
Ippoliti et al. [12]		Indoor and outdoor	<i>Isochrysis galbana</i>	$K_O = 19.99 mg L^{-1}$ $z = 2.9$
Concas et al. [79]	$\mu = \mu_{max} \left( 1 - \frac{[O_2]}{[O_2]_{max}} \right)$ (3)	Indoor	<i>Spirulina platensis</i>	$\mu_{max} = 2.06 \times 10^{-5} s^{-1}$ $[O_2]_{max} = 47.9 g m^{-3}$
Fernandez et al. [81]	$P = P_{max} \frac{K_O}{K_O + [O_2]}$ (4)	Outdoor light	<i>Scenedesmus almeriensis</i>	$K_O = 1.13 mol O_2 m^{-3}$

still a subject of debate, whether incident irradiance is more proper or average irradiance [2]. Some studies use incident [29,34,72] while some use average light intensity [71,154] and a few cases use both at the same time [59]. It must be well understood that which irradiance needs to be used and where it should be used to have the best outcome.

Additionally, it is widely known that just a particular spectrum of light (PAR) is influential on photosynthesis, and some wavelengths are absorbed better than the others. Considering that wavelengths have different penetration depth and therefore different distribution throughout the culture, it is clear that light spectrum and wavelength has a role to play in the growth models which is neglected in all the models. The only models where wavelengths played a role in light distribution in the culture was by Blanken et al. [27]. Therefore, more studies need to be done to formulate the effect of wavelength, as in the existing models, it is assumed that all wavelengths have the same effect on the growth rate.

The light application form is another debatable subject. As discussed by Bechet et al. [51], it is usually used in form of photon flux density (PFD), conventionally reported in  $\mu\text{E m}^{-2} \text{s}^{-1}$  or  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ , or energy flux ( $\text{W m}^{-2}$ ). Despite the popularity of the former, the latter is more convenient in energy studies. Using PFD is more justifiable considering the efficiency of photons with different wavelengths (as mentioned before), and energy flux is more applicable when looking at the amount of energy that is required for reactions within a cell. This issue has also been discussed previously in a review by Lee et al. [2]. The summary of their review shows the diversity of the manner in which effect of light was interpreted. However, to this day, no clear solution has been suggested.

Another issue which has been mentioned in previous studies [51], is the difference between indoor and outdoor data. Majority of the models have been derived and tested using indoor data, while outdoor cultures experience entirely different growth conditions. In case of light exposure, while indoor data are collected using artificial lights and under constant irradiance, in an outdoor environment sun is the only source of light and the intensity of this light is constantly changing throughout the day. All these make the results of parameter estimation from an indoor data rather useless for outdoor modelling.

It has been realised through this research that the most critical gap in the majority of the studies is lack of focus on the ultimate application of microalgae. Whether the goal is biofuel or any other product, the production is done outdoor and in large scale and if the model is trying to predict the productivity over a long period of time, a new approach to modelling is needed as some of the effects discussed in the models lose their significance. For instance, as illustrated by Tredici [201] due to light attenuation only a few centimetres of the culture is in the light-saturated zone, while the majority of the culture is photolimited and maybe only a few millimetres in the photoinhibited zone. This implies that the culture as a whole is severely light-limited. In other words, if long-term production data is used, as found by authors in a yet unpublished work, the culture does not experience photosaturation or photoinhibition at a significant level. However, the issue with this approach is the need for a large amount of outdoor data which is an extremely time-consuming task.

### 3.2. Temperature

The effect of temperature has been studied widely for microalgae and also for other photosynthetic organisms. In most cases its function has been included in the model in the form of multiplication; however, there are some cases where effects of light and temperature were coupled together using more complex functions. When the temperature is solely studied, the growth seems to increase exponentially at first but then it slows down and abruptly declines to zero in a narrow temperature range. This sharp drop is often associated with the death of algal cells due to disruption in the metabolism [202] as a result of deactivation of enzymes or modification of proteins [203]. The short

span of declining growth phase imposes limitations in measuring growth between optimum and maximum temperature, as the growth is sensitive to slight temperature variations in this range. Thus, it is more difficult to obtain suitable data points in this range, which result in high uncertainty in parameter estimation [203]. Bernard and Remond [15] found rather large confidence intervals for the cardinal temperatures especially when there was only one data point for growth above optimum temperature. Since the result of parameter estimation and its stability highly depends on the number of data points, the challenge here is to acquire more growth rates at various temperatures specifically at levels higher than optimum temperature.

Temperature also has impacts on chemical reactions and enzymatic activities, which suggest that all other reactions around an algal cell, such as nutrient uptake, will be affected by temperature variations. Moreover, temperature affects pH and also gas absorption in the media which have an influence on growth directly or indirectly. All these suggest that there is still much more to temperature than just its direct effect on growth which needs to be investigated further.

Furthermore, all the reviewed models in this paper describe the growth under constant temperature, but when it comes to variating temperatures, which is the case in outdoor cultures, none of the models is able to explain how algal growth rate reacts to these changes and how fast they adapt to the new temperature. As we know temperature is changing during the day and despite the fact that temperature variation in the culture is smaller than the air, the temperature fluctuation is significant enough to influence cells activity.

### 3.3. Temperature and relationship with light

There is no doubt that temperature affects the growth rate, and there is a minimum and a maximum temperature between which growth can take place. Some of the suggested models are accurate but in a narrow range, and some are solely empirical correlations with no theory behind them. There are also many cases where the relationship between temperature and light has been simplified to a multiplication of light and temperature functions [15,72,96,204], while just a few studies coupled the effect of light and temperature in one equation [86,87,97,99]. Furthermore, the effect of temperature on photoinhibition is another issue that has not been widely modelled and in many cases, the photoinhibition effect is overestimated especially when the light intensity at different depths is used to calculate photoinhibition.

As mentioned before lack of validation based on outdoor data is a serious problem in microalgal growth modelling, but what makes the situation more complicated is the fact that in most cases high daily irradiance is associated with higher temperatures. Therefore, when outdoor data is being used it is rather difficult to observe to what extent the change in growth is due to change in irradiance and to what extent due to temperature variation.

In their study, Bechet et al. [51] reviewed various light and temperature models to find the most suitable approach for modelling the outdoor systems. They suggested the use of uncoupled models where the interdependency between light and temperature is neglected. The reason for this suggestion is the complexity of the models for this relationship which may lead to overfitting. However, this approach may cause an error in the prediction if this interdependency is significant.

### 3.4. Carbon-pH relationship and its effect

Carbon is the primary nutrient for the growth of algal cells, and in dense cultures, it is a limiting factor. It also directly affects pH of the culture which is another important parameter for the growth of the microalgae. Therefore, a good understanding of the relationship between pH and carbon concentration in the medium and also between growth rate and these two parameters is required. The existing models lack a justified relation between these two as all of them used one of these two parameters to determine growth rate. But while carbon

dioxide concentration has a substantial effect on pH of the media it is not the only parameter that manipulates it. The model proposed by Jayaraman and Rhinehart [18] suggests that lower pH results in a higher growth rate which is acceptable to a certain value but further decreasing pH value beyond that point will cause a drop in the growth rate [205]. The approach used by Filali et al. [71] showed better results; however, it used pH solely to calculate the amount of inorganic carbon which was used in a Monod-type model. Hence, high amount of carbon will increase the growth rate in this model and makes it unable to determine an optimum pH for growing microalgae. This suggests that this model may only be applicable in a narrow range of pH. The problem with mentioned models is that even though they show the positive effect of elevated carbon concentration on microalgae growth, they fail to show its adverse effect at very low pH values. Therefore, when only carbon concentration is used, models considering an inhibitory effect for carbon [80,94] are more appropriate. On the other hand, since determining the amount of carbon in a culture can be more difficult than pH, the models using pH are easier to implement. Moreover, the majority of these models are able to predict an optimum pH for growth which means they are considering the limiting effect of high and low pH.

The main issue with the existing models is considering the effect of pH and carbon content as a whole, which is not exactly correct. The reason for this consideration is the use of carbon dioxide injection as a mean for pH control, which ties these parameters together and makes observing the effect of each of them independently impossible. In an attempt to uncouple the pH and carbon content, where the buffer was used to control pH instead of carbon dioxide injection, Bartley et al. [165], observed optimum pH for *Nannochloropsis salina* to be higher than previous studies [206–208]. This may suggest that the reason many researchers find better growth at lower pH levels could be because of the presence of more carbon dioxide. However, more studies seem necessary in this area to approve it, and also to see the effect of pH and carbon content on the growth of microalgae separately.

### 3.5. Salinity

Salinity is an influential parameter if saline water is to be used for microalgal cultivation. As discussed before, using saline water has multiple advantages when it comes to economy of microalgal systems. The effect of salinity is widely accepted, and some explanations have been provided to clarify the mechanism of this effect [183]. However, no model is proposed including salinity as a parameter and describing the impact of changes in salinity on the growth rate, which leaves this area wide open for investigation and model development. Understanding the effect of salinity on growth not only helps in predicting growth rate but also in designing suitable strategies to maximise productivity while minimising the costs. For instance, implementation of medium recycling causes a constant increase in salinity level of the medium which may make maintaining an optimal level of production difficult. Two strategies are commonly known to overcome this issue. First, starting from microalgae with lower salinity tolerance and as the salinity level rises using the medium for the strains with higher tolerance [174]. The second approach is to use strains of microalgae which have high productivity over a wide range of salinity [209]. Either of these approaches requires a good understanding of the effect of salinity on key production measurements such as growth.

### 3.6. Indoor vs outdoor

As mentioned before, despite the large number of models that were developed to describe the growth of microalgae, there is no clear evidence suggesting that any of the models are reliable to be used for outdoor cultures. The gap between controlled-condition modelling and real-situation modelling is still significant. This gap can be observed from different aspects. First of all, in a controlled condition usually only

one or two process parameters are changing and the rest are kept constant so that observation of the effects of those parameters are more clear and more reliable. Despite being beneficial to see the effect of one process parameter decoupled from other parameters, this approach overlooks how multiple process parameters interact. In a real outdoor condition all the parameters are in constant variation, hence if there is an overlooked interaction between two parameters, the model will not be able to predict reliable values. Moreover, the continuous variation of process parameters is another aspect that has not been included in the models. All the models that are reviewed in this paper found the growth rate based on a constant value of the process parameters which means the model determines a steady-state value for the growth rate. But since in an outdoor condition all the parameters are changing, these models are unable to predict how cells respond to these fluctuations dynamically and how fast do they adapt to a new condition. This issue is valid for all the process parameters and hence makes modelling more challenging. Acclimation is a major phenomenon in microalgae. As the process conditions change, the cells try to adapt to the new condition. In a more complicated situation, a major factor such as light varies at different locations in a culture. As discussed before, at each time the majority of the culture is light-limited which causes cells to adapt to low light intensity. Therefore, when they are exposed to regions with high irradiance, they do not use the light efficiently [201]. If the modelling is based on long-term outdoor data, acclimation will become less of an issue, as for some outdoor conditions, such as irradiance and temperature, the average over an extended period hardly changes radically but often in a gradual manner by changes in the seasons. So the cells have already been provided sufficient time to adapt to the new condition which facilitates the modelling process. Finally, to make it more complicated, we need to realise that hydrodynamics in a culture also play a major role in the conditions each cell experiences which has a significant effect on the light history of cells, absorption of carbon dioxide from atmosphere and release of produced oxygen.

### 3.7. Comprehensive growth models

A comprehensive growth model is a model that takes into account the effect of multiple process parameters to predict growth rate under outdoor conditions and lack of such a model is noticeable. There are major challenges in the path to a successful comprehensive model. These models tie various process parameters together and as the number of the process parameters increase the model becomes more difficult to validate. Having more process parameters is associated with having more model constants which implies that massive amount of data is required for parameter estimation and model validation. Obtaining datasets large enough to properly serve such a model may require extensive time and resources.

Having a large number of constants in a model also causes another issue with the model called overfitting. Overfitting happens due to high degree of freedom in a model as a result of numerous model constants and makes the result of parameter estimation unreliable even if the model produces a low error in its predictions. Commonly, as a result of overfitting, the model may converge to unrealistic values for its constants and when tested against a second set of data for validation, it may result in significantly larger error values.

## 4. Practical implications of this study

Modelling a biological system is a challenging task since there are thousands of reactions involved within each cell to be included. The typical mindset towards modelling such systems is to model general characteristics of the system without getting involved in too much detail of cell metabolism. There are numerous metabolic reactions involved, and the data needed to model them are often difficult to obtain which makes such modelling practically impossible. The majority of the models discussed in this paper tried to model a microalgal system based

on indoor laboratory data. However, since one of the goals of using microalgae is for commercial production, focusing on indoor data seems impractical. There are numerous effects to be included in the modelling which is another main challenge. However, by changing the focus from short-term indoor data to long-term outdoor, some of the issues could be resolved or ameliorated. An excellent example of this difference is the importance of acclimation which is crucial in short-term but insignificant in long-term studies.

Moreover, outdoor data comes with its specific pattern that could potentially facilitate modelling. For instance, light and temperature variation throughout a day follows a particular pattern with minor changes due to weather conditions. An ideal short-term model would be able to predict the influence of these changes on the growth, but as discussed before, developing such a model is a difficult task. On the other hand, long-term modelling can resolve the issue since the average over an extended period changes gradually and commonly does not have drastic fluctuations. Although, the short term modelling has the potential to provide more accurate results, in reality, long-term modelling can provide solutions that are easier to develop and to apply. A demonstration of this approach can be seen in the authors' previous works [210,211].

Salinity is another factor that has a significant role in practice. As discussed earlier, using saline water in the form of seawater or saline underground water facilitates the provision of water where there is little access to freshwater. More importantly, it considerably reduces the total cost of production. The cost of maintaining a microalgae culture is rather high, and any step in lowering the cost is an advancement towards a viable production. Using saline water, however, requires a good understanding of the relationship between salinity of the medium and production indicators such as growth. A model to describe this relationship is still missing from the literature, having which could improve the predictions for productivity and profitability of an algal system.

## 5. Conclusion

A review of available models considering the effects of light, temperature, nutrients, pH, carbon concentration, and oxygen on the growth of microalgae is presented. Salinity is one of the key parameters in the growth of marine algae which has not been considered in the modelling so far. There is clear evidence to show the benefits of using saline water for growing microalgae, but due to evaporation and recycling, the salinity of the media will increase continuously if such type of water is used. Therefore, it is vital to model the effect of salinity on growth in order to achieve a practical model for microalgal production. Also, as discussed before in a review by Bechet et al. [51], when it comes to outdoor cultivation, not many models have been validated for this condition. Even if a model has performed well on laboratory data, given that outdoor cultivation is associated with a different source of light and many uncontrollable conditions, its reliability is still questionable. This issue is more significant when it comes to the effect of light as by nature the artificial light sources that are used in the labs have different spectra and intensity compared to sunlight. Thus, a validation using outdoor data is necessary for the models to certify their usability in a real condition. Additionally, these conditions fluctuate regularly and this behaviour is not included in most of the models. If a model is going to be used for outdoor data, especially when the model is used for process control, predicting its response to the variations in process conditions is critical. Modelling the effects of these variations on growth is an extremely difficult task. However, if modelling is done for a longer period, instead of the instantaneous response to changes, some of the issues may not be valid as they affect short-term growth and not long-term. For instance, the specific growth rate of a culture within a week or a fortnight can sum up the effects of process conditions and neglect the small variations which are insignificant in large scales.

Furthermore, the majority of the discussed models were designed to

consider the effect of only one or two parameters while in reality, all the mentioned parameters will be playing a notable role in the growth. Therefore, a combination of various models is needed to form a comprehensive model which can predict growth under various changes in the process conditions. However, developing a comprehensive model itself will bring up new issues as these models have a large number of constants and require extensive experimental data for parameter estimation and validation. Overfitting is another common issue when the number of model constants grows. However, one way to avoid these issues to some extent, is by studying a culture as bulk and in wider timeframes. This means instead of studying the effect of the parameters at different depths, and within small time intervals, the overall performance of a model can be studied for a culture in longer periods. Moreover, outdoor cultures usually experience a more or less same pattern of conditions. For instance, the changes in light and temperature within a day is generally similar in most days with only slight changes due to the day of the year and weather conditions. Furthermore, in long-term, the range in which a certain process parameter varies is not wide. Daily solar irradiance for a particular location is within a relatively narrow range, and therefore it is unnecessary to model the effect of irradiance for a broad range. These patterns and correlations between process parameters can be helpful in simplification of the models and construction of a model with a lower number of constants which would be easier to apply and verify. Such a model may not have the meaningfulness of the detailed mechanistic models in terms of formulating what happens inside a cell, but it may be more applicable in large scale cultures and for long-term cultivation of microalgae.

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