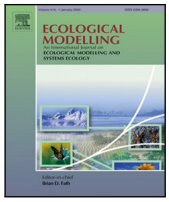
Ecological Modelling 466 (2022) 109887

Contents lists available at ScienceDirect

Ecological Modelling

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



Mathematical comparison and empirical review of the Monod and Droop forms for resource-based population dynamics☆

Hao Wang, Pablo Venegas Garcia, Shohel Ahmed, Christopher M. Heggerud *

Department of Mathematical and Statistical Sciences, University of Alberta, Canada

ARTICLE INFO

Keywords:
Droop form
Monod form
Transient dynamics
Asymptotic dynamics

ABSTRACT

Almost all biological models use either the Droop or Monod form to describe the resource-based growth of a living organism. Empirical evidence overwhelmingly suggests the Droop form describes data more accurately than the Monod form, however, the Monod form is more popular due to its simplicity. Focusing on phytoplankton, we illustrate the underlying logics behind these two forms via conceptual comparison, experimental data validation, transient, and asymptotic dynamics. The conceptual illustration provides the primary difference in their mechanisms via a paradox. Data validation is tested via field and laboratory experiments. The Droop and Monod forms have consistent asymptotic dynamics in the closed nutrient case, whereas the transient dynamics are significantly different when the nutrient uptake rate is small. In addition, we decipher Michael Droop's private last statements on unifying the Droop and Monod forms as well as simplifying the Droop form. This article aims to guide future model development with any resource-based growth.

1. Introduction

The Monod and Droop forms are ubiquitous in modelling the resource-based growth. However, a systematic comparison between the two forms has seemingly eluded the literature. We start with some of Michael Droop's last statements on these two popular forms and their possible future development. We then present a paradox and resolve it with a conceptual graph of the cell life cycle. We conclude this section by reviewing the history of population growth and introducing the background of Monod and Droop and their modified forms.

For better readability, we introduce the notations in the quotes of Michael Droop as follows: S is the substrate (or nutrient or resource) concentration, u is the cell (or population) concentration, Q is the nutrient content per cell, and t is time.

1.1. Michael Droop's last statements

"For the present, I would have thought that the rate function relating consumption and biomass is (in the steady state)

$$-dS/dt = Qdu/dt,$$

which neither the Monod nor the Droop model can avoid. Monod, of course, assumes constant Q for all growth rates (OK for carbon for an obvious reason) and applies only to steady states, while in the Droop model the per capita growth rate and Q have a functional relationship (which cannot apply to carbon for the same obvious reason)." - Michael Droop (in a personal email correspondence with the first author on November 12, 2006).

We have shown this logic in Section 2.1.

"There is one thing that was always in the back of my mind. That is that knowing the growth parameters of a single organism concerning one or two nutrients does not get the poor ecologist very far (he needs four parameters per nutrient per a plethora of species). His life would be much simpler if it were possible for the sum of a many-species population of a coherent body of water could be specified by a mere four parameters per nutrient. I am impressed by the fact that some functions (e.g. the Langmuir isotherm) have a fractal quality, in that they tend to turn up on successively higher levels of organization. This suggests that some such simplification may be possible. Against this is the fact that every increase in organizational level is likely to introduce properties that are not predictable from those observed in the immediately lower level. I think a mathematical approach would be interesting and possibly useful. For instance, the mention of fractals suggests that something akin to affine transforms worked with functions might create

☆ This work was partially supported by an NSERC Individual Discovery Grant, Canada (RGPIN-2020-03911) and an NSERC Discovery Accelerator Supplement Award, Canada (RGPAS-2020-00090).

* Corresponding author.
E-mail address: cheggeru@ualberta.ca (C.M. Heggerud).

https://doi.org/10.1016/j.ecolmodel.2022.109887
Received 21 May 2021; Received in revised form 3 December 2021; Accepted 23 January 2022
Available online 9 February 2022

a whole from a lot of similar parts." - Michael Droop (in a personal email correspondence with the first author on November 12, 2006).

Droop was concerned that an ecologist cannot get the whole picture with only knowing the growth parameters of an organism. Rather, if an ecologist wants to make solid modelling efforts, they would need more parameters, such as the uptake rates, half saturation constant (uptake efficiency), minimum cell quota, and the intrinsic growth rate. Each of these parameters, except perhaps the intrinsic growth, would be required for each nutrient element involved. For example, if we consider harmful algal blooms instead of a single species dynamic, we could potentially simplify the entire lake dynamics by considering four parameters for a single resource. This may give a good indication to overall algal abundance, but says very little about the species composition. As a possible extension, Droop compared the Langmuir isotherm to a phytoplankton population. The Langmuir isotherm is a model of the Monod form that describes the adsorption of a gas to a surface based on the pressure. This model is the gold standard for adsorption. In essence, a process that is incredibly complex like adsorption can be described well by a simple mathematical model that is comparable to the Monod model in simplicity and form. Droop believed there should be something similar to phytoplankton dynamics. However, he mentioned that ecology may not be as simple as physics due to the increase of organizational levels. For instance, the ecological process is stochastic, or that there are not enough 'particles' for the law of large numbers to apply. The mention of fractals seems a mere example of one angle to take. The idea of fractals may be analogous to a lattice or connected network, where each node behaves independently but with similar dynamics (e.g., the Langmuir equation, where a surface is made up of many adsorption 'sites' but the overall volume of adsorbed gas is simplified to a single equation). On the community level of phytoplankton, is there something similar? The Droop model partly answers this question. Every cell is assumed to possess the same cell quota and size, but this is far from the reality.

Lastly, how affine transforms would relate to phytoplankton is still puzzling us. Most likely, Droop claims that phytoplankton dynamics and the model parameters for each nutrient element or species are related to one another by some transformation. Although the discovery of such a transform would indeed simplify the theoretical framework and have substantial impacts in phytoplankton modelling, there seems to be thus far no progress made on such an achievement.

1.2. Availability ≠ growth.

Paradox

Ideal assumptions:

- An immediate recycling of nutrient from algal death and exudation.
- The total nutrient is conserved.
- Nutrient is either in algae or in media.

Question: Is more nutrient available in media good or bad for algae?
Answer 1: More nutrient in media gives more available nutrient for algal growth, then it is good for algae.
Answer 2: Due to the conservation law of matter, more nutrient in media means less nutrient for algal growth, then it is bad for algae.

Interestingly there is a paradox that occurs when considering nutrient availability and algal dynamics. If we consider a system in which matter is closed and conserved, then more nutrient in the media would imply that there is less nutrient in the phytoplankton population, which is unfavourable to the phytoplankton. However, more nutrient in the media also implies that there is more nutrient available for phytoplankton to uptake and grow, which of course is favourable to the phytoplankton. This paradox can be partly explained by considering timescales. In the case that phytoplankton can uptake nutrient quickly, then extra nutrient in the media will quickly be relocated to the phytoplankton, benefiting the phytoplankton. On the other hand, if nutrient uptake is slow then the nutrient content of the phytoplankton will remain low for a much longer period of time. We can only answer this paradox by considering nutrient uptake rates, however the Monod approach fails to do so.

When taking a process based approach to model algal dynamics, there are three main processes to consider. The first process is the uptake of available essential nutrients. The second process is the cell growth and division. The third process is the mortality and resultant nutrient recycling. In the Droop formulation all of these processes are modelled separately. That is, Droop considered nutrient uptake and growth to be distinct processes by tracking internal nutrient storage. In contrast, Monod considered nutrient uptake and growth to be a simultaneous process neglecting internal storage by assuming homeostasis, or the regulation of a species internal elemental composition (Persson et al., 2010). The life cycle of algal cells is shown in Fig. 1 to highlight the difference between the Monod and Droop formulations.

1.3. History of Droop and Monod forms

To begin the history of mathematical formulations for population growth, we summarize Droop's personal view (Droop, 1983) and start with the idea of exponential population growth popularized by Malthus (Bacaër, 2011). Under circumstances where resources and space are unlimited, the rate of change of a population is proportional to its own size:

$$\frac{dx}{dt} = \mu x, \tag{1}$$

where μ is often recognized as the specific growth rate and x represents the population density. The population (or biomass) for this model can only be limited when the growth rate tends to zero. Considering the size of a population should be limited by physical conditions, in 1845 Verhulst proposed that the growth rate should be a of the biomass:

$$\mu = \mu_M \left(1 - \frac{x}{K_s}\right), \tag{2}$$

which is widely recognized as the logistic law (Bacaër, 2011; Verhulst, 1845). Here, μ_M is the maximum specific growth rate and K_s is the carrying capacity. A breakthrough after many unsuccessful attempts to derive a law of growth from chemical or physical principles was made in 1932 by Teissier (Droop, 1983; Tiesser, 1942) who related the asymptotic dependence of growth to the concentration of resource:

$$\frac{d\mu}{ds} = \frac{\mu_M - \mu}{K_s}, \tag{3}$$

where s is the resource concentration and K_s is a constant with the same dimension. Ten years later Monod introduced a simpler, and now widely used, model known as the Monod function (Monod, 1942):

$$\mu = \mu_M \frac{s}{K_s + s}. \tag{4}$$

In Teissier's and Monod's works, they postulated that the instantaneous change of biomass with respect to the substrate should be in constant proportion (Droop, 1968):

$$\frac{dx}{ds} = -Y, \tag{5}$$

where Y denotes the yield coefficient. This assumes a constant chemical cell composition, although this assumption may not always be true. However, this assumption can be justified when the chemical is carbon since it contributes vastly as energy-carrying molecules on the cell composition (Herbert, 1961). In 1939, Ketchum observed a phenomenon called luxury uptake by studying the uptake of phosphorus in algae (Ketchum, 1939). In 1962, this phenomenon was studied in

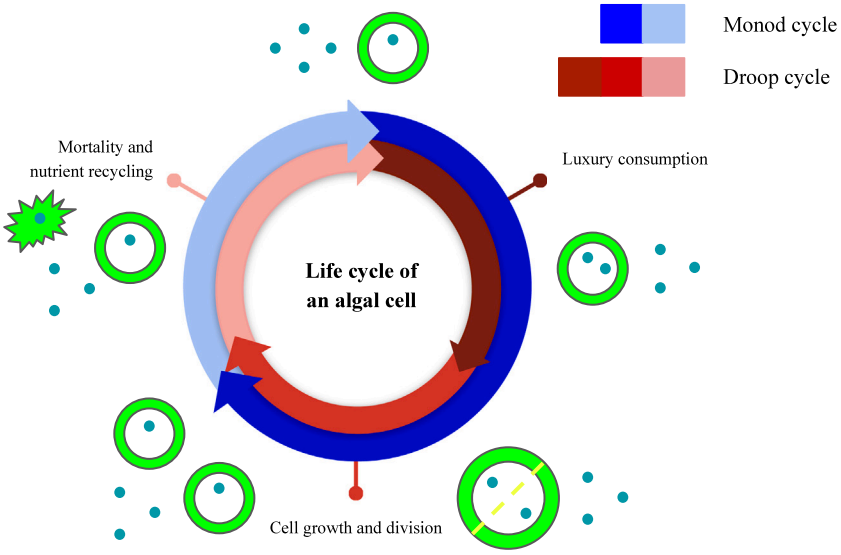


Fig. 1. Life cycle of an algal cell under the Monod and Droop formulations. In the Monod formulation it is assumed that nutrient consumption and growth/cell division are simultaneous processes, whereas in the Droop formulation they are considered separately.

detail by Kuenzler and Ketchum, and they found that an algal species, *Phaeodactylum tricornutum*, can uptake and deplete phosphorus in a controlled environment before its cells start to divide (Kuenzler and Ketchum, 1962). This observation gives a clear insight that the algal growth is not always directly related to the external concentration of the substrate. Obviously the Monod Eq. (4) is incapable of describing this particular situation. In the presence of luxury consumption, a general relation between the algal growth and the external substrate concentration would be impossible to find unless we consider the steady-state case (Droop, 1983).

The concept of internal nutrient pool in cells was introduced by Droop during his work on exploring mechanisms of nutrient-limitation in chemostat experiments. In 1968, Droop introduced a mathematical model with nutrient limitation developed for *Monochrysis lutheri* after he pointed out that “the amount of vitamin in the cells controls the rate of growth" (Droop, 1968). In fact, Droop proposed the following model, referred to as the Droop model, to describe the relation between growth rate and cell quota (Q):

$$\mu = \mu_M \left(1 - \frac{q_m}{Q}\right), \tag{6}$$

where the cell quota (Q) is defined as the weight of nutrient per cell and the subsistence quota q_m is the minimum cell quota required for the basic cell structure. This model has been successfully used to describe the relationship between different organisms and nutrients, and a list of reports showing this relation can be found in Droop (1983).

A numerical comparison is made between the growth rates of the Monod model (4) and the Droop model (6) in Fig. 2. Note that the growth rates are significantly different when the nutrient required for growth is scarce, that is, the cell quota Q in the Droop form is low, or the available resource S in the Monod form is low. However, as these values increase the two models show similar dynamics. This indicates that in the case of plentiful nutrient and uptake, the two models will give similar growth rates.

Under steady-state conditions and taking the Michaelis–Menten uptake into account, the Monod and Droop forms are equivalent by simple algebraic manipulations (Burmaster, 1979). Different approaches beyond these two typical forms have been proposed in the literature, specifically Sunda et al. (2009) suggested a modified version for the Monod form or the Michaelis–Menten uptake (Sunda et al., 2009):

$$\mu = \begin{cases} \mu_M (s - s_0)/(K_s + s - s_0), & \text{if } s > s_0, \\ 0, & \text{otherwise,} \end{cases} \tag{7}$$

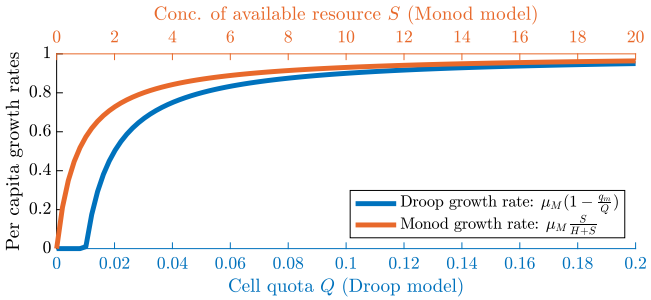


Fig. 2. The growth rate of the Monod model, Eq. (4), as a function of S in orange (on the top x-axis), and the growth rate of the Droop model, Eq. (6), as a function of Q in blue (on the bottom x-axis). In both models, $\mu_M = 1$ with $H = 0.75$ and $q_m = 0.01$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where s_0 is a threshold parameter at which the growth rate or substrate update rate is zero. The modified Monod form fits data more accurately than the standard Monod form. However, this approach predicts a higher maximum growth rate than the experimental one, which could be undesirable in many circumstances. The modified Michaelis–Menten uptake rate given by (7), together with the Droop growth, provides a better data fit. For convenience, we call the Droop growth with the modified Michaelis–Menten uptake as the modified Droop form in this article.

2. Monod vs. Droop in the ODE setting

It has been well agreed upon that the steady state dynamics of the Droop and Monod forms are equivalent when appropriately parameterized from both the mathematical and ecological perspectives. However, even though most papers agree that the Droop model is superior in the context of capturing transient dynamics, there is no true consensus as many complex nonlinear interactions occur in nature. Here we discuss the Monod and Droop formulations of a chemostat model under a well-mixed assumption. The features of each model are highlighted and their dynamics are compared numerically and mathematically in several biological situations. Furthermore, we address the paradox discussed in Section 1.2 by exploring limiting cases of the models.

Table 1
Summary of parameters and variables used in the Monod and Droop models (9) and (8), respectively.

Parameters		Used in:	
Symbol	Description	Monod	Droop
μ_M	Maximum specific growth rate	✓	✓
a	Input nutrient concentration	✓	✓
D	Dilution rate	✓	✓
q_M	Minimum cell quota	✗	✓
θ	Yield constant (Homeostatic cell quota)	✓	✗
H	Half sat. conts. for uptake and growth	✓	✗
K	Half sat. conts. for uptake	✗	✓
ρ_M	Maximum nutrient uptake rate	✗	✓
Variables			
S	Substrate/nutrient/resource concentration	✓	✓
u	Cell/population concentration	✓	✓
Q	Cell quota	✗	✓

2.1. Monod and Droop formulated chemostat models

We propose the following simple chemostat model for an arbitrary organism where the growth function follows the Droop formulation:

$$\frac{dS}{dt} = (a - S)D - f(S,Q)u, \tag{8a}$$
$$\frac{du}{dt} = \mu_M\left(1 - \frac{q_m}{Q}\right)u - Du, \tag{8b}$$
$$\frac{dQ}{dt} = f(S,Q) - \mu_M\left(1 - \frac{q_m}{Q}\right)Q, \tag{8c}$$

where S, u, and Q represent the substrate/nutrient/resource concentration, the cell/population concentration, and the cell quota (or per capita nutrient content), respectively. Parameter descriptions are given in Table 1. The uptake function $f(S,Q)$ can take different forms. For example, $f(S,Q)$ may be a saturating function in both S and Q if there is a biological maximum cell quota (Heggerud et al., 2020; Wang et al., 2007), or it may be a function of only S if luxury consumption is unbounded (no maximum cell quota) (Haefner, 2005). The parameters a and D are the input nutrient concentration and the dilution rate, respectively. The term $\mu_M(1 - \frac{q_m}{Q})$ is the Droop growth term described in Eq. (6).

Monod proposed a simpler model that does not consider uptake and growth as separate processes as described in Fig. 1:

$$\frac{dS}{dt} = (a - S)D - \theta\frac{\mu_M S}{H + S}u, \tag{9a}$$
$$\frac{du}{dt} = \frac{\mu_M S}{H + S}u - Du, \tag{9b}$$

where θ is the homeostatic nutrient ratio of the organism. That is, θ is the amount of nutrient consumed for each new cell formed. Again, the parameters and variables are summarized in Table 1. In our proceedings, we consider carbon to be plentiful and S to be the concentration of some other limiting nutrient (P, N, Fe, Si, etc.). In this sense we assume that when a cell uptakes the limiting nutrient they also consume enough carbon to maintain their cell quota (Q in Droop form, and θ in Monod form). However, in the original formulation of the Monod model, carbon limitation was studied (Monod, 1942). When the element is carbon, the parameter θ in model (9) would be replaced with $1/\gamma$ where $\gamma \in (0,1)$ is a yield constant that accounts for carbon energy loss as governed by the second law of thermodynamics. H is the half saturation constant for uptake and growth. The other parameters are defined similarly to that of the Droop formulation.

The units of the state variables in studying organismal growth can vary. Typically, S will be measured in the concentration of nutrient, u is measured in the concentration of either cells, biomass, or mass of carbon, and Q is measured in the mass of nutrient per cell, or the mass ratio of nutrient to carbon.

2.1.1. Closed element case

For simplicity we discuss the ODE models described above but for a closed nutrient case. That is, there should be no dilution or addition of nutrient to the system. The Droop model (8) is simplified as follows:

$$\frac{dS}{dt} = -f(S,Q)u, \tag{10a}$$
$$\frac{du}{dt} = \mu_M\left(1 - \frac{q_m}{Q}\right)u, \tag{10b}$$
$$\frac{dQ}{dt} = f(S,Q) - \mu_M\left(1 - \frac{q_m}{Q}\right)Q. \tag{10c}$$

The closed nutrient condition implies

$$\frac{d}{dt}(S + uQ) = 0 \Rightarrow S + uQ = R_D = S(0) + Q(0)u(0) \tag{11}$$

and

$$-\frac{dS}{dt} = f(S,Q)u = \left[\frac{dQ}{dt} + \mu_M\left(1 - \frac{q_m}{Q}\right)Q\right]\frac{du}{\mu_M(1 - \frac{q_m}{Q})dt}. \tag{12}$$

In the steady state case for Q, the right hand side of Eq. (12) reduces to

$$-\frac{dS}{dt} = Q\frac{du}{dt}. \tag{13}$$

The cell quota is for the conversion between carbon (for u) and nutrient (for S). There is no nutrient loss unlike energy.

Now, in the closed nutrient case the Monod model (9) is simplified as follows:

$$\frac{dS}{dt} = -\theta\frac{\mu_M S}{H + S}u, \tag{14a}$$
$$\frac{du}{dt} = \frac{\mu_M S}{H + S}u, \tag{14b}$$

for which

$$\frac{d}{dt}(S + \theta u) = 0 \Rightarrow S + \theta u = R_M = S(0) + \theta u(0) = constant \tag{15}$$

and

$$-\frac{dS}{dt} = \theta\frac{du}{dt}. \tag{16}$$

Here θ is the fixed cell quota. In the steady state case, this is consistent to the Droop form if the fixed cell quota θ (strict homeostasis, see (Wang et al., 2012, 2018)) of the Monod model is consistent to the asymptotic value of the varying cell quota Q in the Droop model.

Additionally, the quantities R_D and R_M represent the total nutrients of the whole system in the Droop and Monod models, respectively. In the closed nutrient case, these values are constant.

2.1.2. Connecting Droop to Monod via multi-scale analysis

To begin we consider the Droop closed nutrient system (10) with the uptake function

$$f(S,Q) = f(S) = \rho_m\frac{S}{K + S}, \tag{17}$$

where ρ_m is the maximum uptake rate and K is the half saturation constant for uptake. In the following, we show that when $f(S)$ is large the Droop formulation will give qualitatively similar dynamics to the Monod formulation in (14).

By assuming that ρ_m is a large parameter we can rewrite system (10) as a system perturbed by the parameter $\epsilon = 1/\rho_m$:

$$\epsilon\frac{dS}{dt} = -\frac{S}{K + S}u, \tag{18a}$$
$$\frac{du}{dt} = \mu_M\left(1 - \frac{q_m}{Q}\right)u, \tag{18b}$$
$$\epsilon\frac{dQ}{dt} = \frac{S}{K + S} - \epsilon\mu_M\left(1 - \frac{q_m}{Q}\right)Q. \tag{18c}$$

By applying an asymptotic expansion in ϵ to the state variables (for example, $S(t) = S^0(t) + \epsilon S^1(t) + \mathcal{O}(\epsilon^2)$) we are able to create fast and slow subsystems that operate on separate timescales.

First, to arrive at the fast subsystem and obtain the $\mathcal{O}(1)$ approximation of the fast system we substitute the time variable with $\tau = t/\epsilon$ and let $\epsilon \to 0$. We denote the first order solutions to the fast subsystem with a tilde ($S^0(t) \to \tilde{S}(\tau)$) and the reduced system is as follows:

$$\frac{d\tilde{S}}{d\tau} = -\frac{\tilde{S}}{K+\tilde{S}}\tilde{u}, \tag{19a}$$

$$\frac{d\tilde{u}}{d\tau} = 0, \tag{19b}$$

$$\frac{d\tilde{Q}}{d\tau} = \frac{\tilde{S}}{K+\tilde{S}}. \tag{19c}$$

The dynamics of (19) are obvious, as $\tau \to \infty$, $\tilde{S}$ goes to zero, $\tilde{Q}$ goes to $S(0)/u(0)+Q(0)$ and $\tilde{u}$ remains constant. Additionally, recall the condition that in a closed nutrient system, $S+uQ = S_0+u_0Q_0 = constant$. This condition is to be held in both the fast and slow systems. It is clearly held in the fast system. In summary, with large uptake, the fast dynamics show all of the substrate being uptook by the species by an increase in the cell quota, but the species abundance remains constant.

To obtain the first order approximation of the slow system, we denote the first order solutions to the slow subsystem with a hat ($S^0(t) \to \hat{S}(\tau)$) and let $\epsilon \to 0$ in system (18). We arrive at

$$0 = -\frac{\hat{S}}{K+\hat{S}}\hat{u}, \tag{20a}$$

$$\frac{d\hat{u}}{dt} = \mu_M\left(1-\frac{q_m}{\hat{Q}}\right)\hat{u}, \tag{20b}$$

$$0 = \frac{\hat{S}}{K+\hat{S}}, \tag{20c}$$

$$\hat{Q} = \frac{S_0+u_0Q_0-\hat{S}}{\hat{u}}. \tag{20d}$$

The slow system dynamics have $\hat{u}$ growing to a positive equilibrium while the cell quota ($\hat{Q}$) tends to its biological minimum value (q_m) with no substrate in the media. As in previous studies (Heggerud et al., 2020; Hek, 2010) the first order approximation is a fairly good approximation of the full system dynamics. Furthermore, we emphasize that the fast dynamics of the population ($\tilde{u}$) is constant. This implies that the entirety of the species abundance dynamics happens on the slow time scale.

Now, we wish to compare these dynamics to that of the Monod formulation given by Eq. (14). To correctly compare we must consider the similarities in parameter values. Mainly, the maximum growth rate should be consistent for both models. Additionally, the fixed cell quota θ and the minimum cell quota q_m should also be the same. Note that the fixed cell quota θ would actually be more reasonable to match the equilibrium value of the varying cell quota Q in the Droop model in the case of closed nutrient, and in this example those values are identical. However, as we see in Section 2.1.3 with an open system, this is not the case. Lastly, we must compare the half saturation constant for Monod growth/uptake (H) to the half saturation constant for Droop uptake (K). In the Monod model, the half saturation constant can be interpreted similarly to the half saturation that arises from the law of mass action. In other words, the half saturation constant here is a constant describing how efficient a cell is at finding nutrient and immediately growing, that is a small value of H means that cells are still able to grow well when the substrate concentration is low, whereas a high value of H means that cells require a high substrate concentration to grow. The interpretation for K in the Droop model is similar, but only regarding uptake and does not consider growth. Now, as mentioned in Sections 1.2 and 2.1, the Monod form assumes uptake and growth are simultaneous processes, thus H and K cannot differ drastically for the same system but they are certainly not equivalent. However, if they did differ significantly, we note that the model with the higher respective half saturation constant will have a longer transient. In Fig. 3 we take the Monod half saturation constant to be 0.5 and the Droop half saturation constant to be one.

In comparing the dynamics of the two models, we also see that the Monod dynamics solely occur on the faster timescale. This comparison is visualized in Fig. 3. Hence, in the situation where the uptake function is large and the system is closed to nutrients we can argue that there is no qualitative difference between the Droop and Monod models in either transient, nor asymptotic dynamics of the organism.

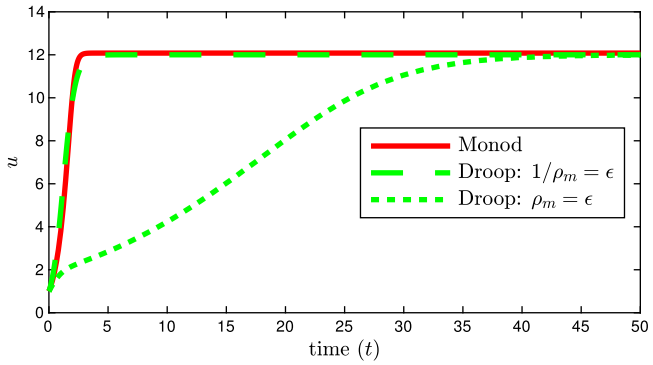


Fig. 3. Comparison of Monod dynamics with Droop dynamics for small uptake rate $\epsilon = \rho_m \ll 1$ and for large uptake rates $\epsilon = 1/\rho_m \ll 1$. The parameters used in this model comparison are similar to the parameters fit to data in Sunda et al. (2009).

2.1.3. Comparison of steady states

We attempt to find conditions that result in similar steady states between the two models. We begin by considering a system with closed nutrient, i.e. $D = 0$ in (8) and (9), with $f(S,Q)$ as in (17). The total nutrient for the Droop system (10) for all time is given by $R_D = S_0 + Q_0u_0$, whereas the total nutrient for the Monod system (14) for all time is $R_M = S_0 + \theta u_0$. If $\theta \neq Q_0$ then the total nutrient in the systems will be different, and naturally this results in different equilibrium values. Now, if we assume that the initial conditions between the two systems vary such that $R_D = R_M$, then by choosing $\theta = Q^*$ (the equilibrium value for the Droop quota) then it is easy to see that the asymptotic dynamics are identical, as $S \to 0$ in both systems.

In the case of closed nutrient, the positive steady states for both the Droop and Monod formulations are globally stable. The proof is trivial with the argument of constant nutrient and a strictly decreasing S and increasing u.

In the case of the open nutrient systems (i.e., $D > 0$), the asymptotic dynamics change. Note that the transient dynamics are nonequivalent, but in certain parameter regions are qualitatively similar. When it exists, the positive equilibrium for the Monod case is

$$S^* = \frac{DH}{\mu_M - D}, \tag{21}$$

$$u^* = \frac{a}{\theta} - \frac{DH}{\theta(\mu - D)}, \tag{22}$$

whereas the positive equilibrium in the Droop case is

$$S^* = \frac{K\mu_M(Q^*-q)}{\rho_M - \mu_M(Q^*-q)}, \tag{23}$$

$$u^* = D\left[\frac{a\rho-(a+K)\mu(Q^*-q)}{(\rho-\mu(Q^*-q))\mu(Q^*-q)}\right], \tag{24}$$

$$Q^* = \frac{-\mu_M q_m}{D-\mu_m}. \tag{25}$$

Both systems exhibit the extinction equilibrium for all values of D, the dilution rate. The positive equilibria in the Monod and Droop models are nonequivalent, and any direct comparison is difficult to interpret. We obtain some numerical observations shown in Fig. 4. We note that the equilibria are the same for $D = 0$, when the initial conditions are such that the total nutrient is the same in both systems. Furthermore, we fix θ for all simulations to be equal to Q^* when $D = 0$ (i.e. $Q^* = q_m = \theta$). Note that in the case of $D = 0$ the steady state values for u^* in both systems are satisfied by all values of u, thus the actual steady state value is determined by the initial conditions. Furthermore

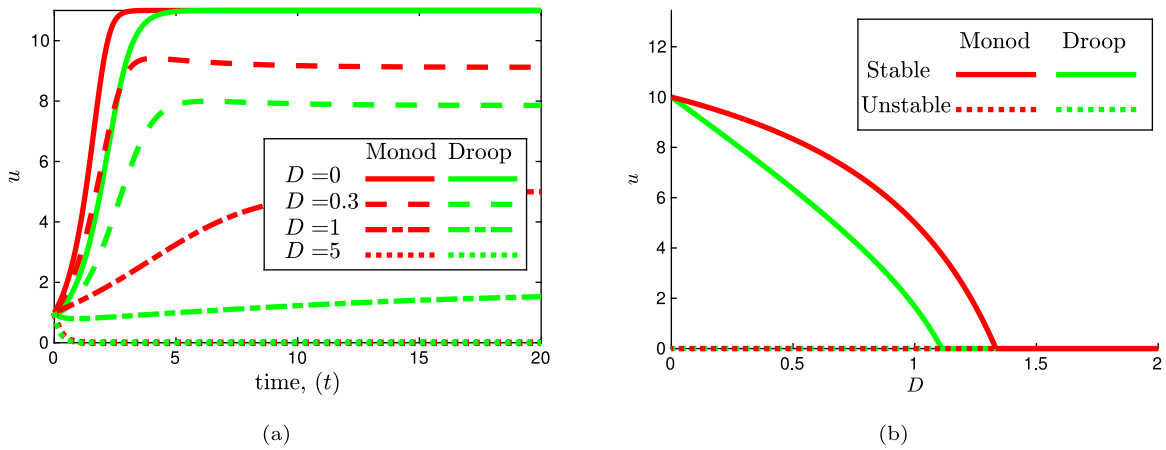


Fig. 4. (a): A direct comparison of long term dynamics of the Monod and Droop models for several values of D. The curves for $D = 0$, and $D = 5$ overlap significantly for both models. (b): Bifurcation plots of both models. The trivial equilibria exist and are structurally similar for both models.

it is important to note that if we manipulate θ such that $\theta = Q^*$ for the open systems, then the asymptotic dynamics may become closer in value, but may still differ, depending on the remaining parameters. We further notice that both systems are topologically equivalent (see bifurcation structure in Fig. 4), but that the transcritical bifurcations occur at slightly different values for D. For intermediate values of D, the asymptotic dynamics are not equivalent if we do not allow other parameters to change.

2.1.4. Comparison of transients

We explore the case if the uptake rate is small. That is, $\epsilon = \rho_m$ is treated as a small perturbation parameter. In this situation the system is written as

$$\frac{dS}{dt} = -\epsilon \frac{S}{K+S} u, \tag{26a}$$

$$\frac{du}{dt} = \mu_M \left(1 - \frac{q_m}{Q}\right) u, \tag{26b}$$

$$\frac{dQ}{dt} = \epsilon \frac{S}{K+S} - \mu_M \left(1 - \frac{q_m}{Q}\right) Q. \tag{26c}$$

Here the slower timescale is $\tau = \epsilon t$ and the intermediate timescale is t. Note that we denote this timescale as the intermediate timescale as it is consistent with the slow timescale in the discussion of large ρ_m.

As before we apply the asymptotic expansion and let $\epsilon \to 0$. Then on the intermediate timescale the dynamics are

$$\frac{d\hat{S}}{dt} = 0, \tag{27a}$$

$$\frac{d\hat{u}}{dt} = \mu_M \left(1 - \frac{q_m}{\hat{Q}}\right) \hat{u}, \tag{27b}$$

$$\frac{d\hat{Q}}{dt} = -\mu_M \left(1 - \frac{q_m}{\hat{Q}}\right) \hat{Q}. \tag{27c}$$

And the slowest timescale (denote the first order solution with a bar $(S(t) \to \bar{S}(\tau))$):

$$\frac{d\bar{S}}{d\tau} = -\frac{\bar{S}}{K+\bar{S}} \bar{u}, \tag{28a}$$

$$0 = \mu_M \left(1 - \frac{q_m}{\bar{Q}}\right) \bar{u}, \tag{28b}$$

$$0 = -\mu_M \left(1 - \frac{q_m}{\bar{Q}}\right) \bar{Q}. \tag{28c}$$

We can see mathematically that the nutrient in the medium are held constant on the intermediate scale, while the species dynamics are not. On the other hand, the species dynamics are restricted to a slow manifold while the nutrient changes slowly (restricted algebraically). This in essence means that under the assumption of slow uptake rates the species dynamics and nutrient dynamics occur on different timescales. The fast–slow analysis here is again a good approximation of the full dynamics, which ensures we can draw the above conclusion of separation of timescales. However, in the case of the Monod dynamics as discussed in 2.1.2, the dynamics of the nutrient and organism occur on the same timescale. This discrepancy explains why transient dynamics are not consistent between the Droop and Monod models. Fig. 3 shows that the Monod and Droop dynamics do not give similar transient dynamics in the case of smaller uptake rates. These limiting cases offer insight towards the paradox discussed in Section 1.2 in that the paradox does not consider any transient dynamics or allows for the explicit reliance on nutrient uptake mechanisms.

3. Monod vs. Droop in the PDE setting

To further the comparison of the Droop and Monod models, we consider a spatially explicit scenario in which we assume the chemostat is not well–mixed. This assumption leads directly to the use of partial differential equations (PDE) to model such systems. As such, we consider reaction–diffusion models for the Droop and Monod forms under the assumption that the molecular movement of nutrient and microorganism follows Fick's law of diffusion (Hsu et al., 2014; Chang et al., 2021; Zhang et al., 2021). The features of each model are highlighted and a comparison of the dynamics is given numerically.

3.1. Spatially explicit Monod and Droop formulated chemostat models

We now introduce the chemostat models using both the Monod and Droop frameworks under explicit spatial consideration. The chemostat is assumed to have spatial domain $\Omega = [0, 1]$. Under the Droop formulation, we consider the following system of reaction–diffusion equations with the internal storage of nutrient:

$$\frac{\partial S}{\partial t} = d \frac{\partial^2 S}{\partial x^2} - f(S, \frac{U}{u}) u, \tag{29a}$$

$$\frac{\partial u}{\partial t} = d \frac{\partial^2 u}{\partial x^2} + \mu(\frac{U}{u}) u, \tag{29b}$$

$$\frac{\partial U}{\partial t} = d \frac{\partial^2 U}{\partial x^2} + f(S, \frac{U}{u}) u, \tag{29c}$$

with boundary conditions

$$\frac{\partial S}{\partial x}(0,t) = -a, \quad \frac{\partial S}{\partial x}(1,t) + \alpha S(1,t) = 0, \tag{29d}$$

$$\frac{\partial u}{\partial x}(0,t) = 0, \quad \frac{\partial u}{\partial x}(1,t) + \alpha u(1,t) = 0, \tag{29e}$$

$$\frac{\partial U}{\partial x}(0,t) = 0, \quad \frac{\partial U}{\partial x}(1,t) + \alpha U(1,t) = 0, \tag{29f}$$

Table 2
Summary of parameters and variables used in the Monod and Droop models (31) and (29), respectively.

Parameters		Used in:	
Symbol	Description	Monod	Droop
μ_M	Maximum specific growth rate	✓	✓
a	Input nutrient concentration	✓	✓
d	Diffusion coefficient	✓	✓
α	Advection rate across the boundary (sinking)	✓	✓
q_M	Minimum cell quota	✗	✓
θ	Yield constant (Homeostatic cell quota)	✓	✗
H	Half sat. conts. for uptake and growth	✓	✗
K	Half sat. conts. for uptake	✗	✓
ρ_M	Maximum nutrient uptake rate	✗	✓
Variables			
S	Substrate/nutrient/resource concentration	✓	✓
u	Cell/population concentration	✓	✓
U	Total nutrient in the population	✗	✓
Q	Cell quota	✗	✓

and initial conditions

$$S(x,0) = S_0(x) \geq 0, \tag{30a}$$

$$u(x,0) = u_0(x) \geq 0, u_0(x) \not\equiv 0, \tag{30b}$$

$$U(x,0) = U_0(x) \geq 0, U_0(x) \not\equiv 0, \tag{30c}$$

where $S(x,t)$, $u(x,t)$ and $Q(x,t)$ are the nutrient concentration, the species density, and the cell quota $Q(x,t)$ of the species at position x and time t, respectively. The variable $U(x,t) = u(x,t)Q(x,t)$ is the total amount of stored (internal) nutrient of the species. The parameter d is the diffusion coefficient, a is the nutrient influx rate, and α is the advection rate across one boundary. Here, $f(S,Q)$ is defined as the uptake function and $\mu(Q)$ is the Droop growth function. Likewise, the Monod model has the following form without internal storage:

$$\frac{\partial S}{\partial t} = d\frac{\partial^2 S}{\partial x^2} - \theta\beta(S)u, \tag{31a}$$

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + \beta(S)u, \tag{31b}$$

with boundary conditions

$$\frac{\partial S}{\partial x}(0,t) = -a, \quad \frac{\partial S}{\partial x}(1,t) + \alpha S(1,t) = 0, \tag{31c}$$

$$\frac{\partial u}{\partial x}(0,t) = 0, \quad \frac{\partial u}{\partial x}(1,t) + \alpha u(1,t) = 0, \tag{31d}$$

and initial conditions

$$S(x,0) = S_0(x) \geq 0, \tag{32a}$$

$$u(x,0) = u_0(x) \geq 0, \ u_0(x) \not\equiv 0, \tag{32b}$$

where the function $\beta(S)$ describes the nutrient uptake and growth rate of the species at the concentration of nutrient S, and θ is the fixed cell quota. As with the ODE models we take

$$\mu(Q) = \mu_M\left(1 - \frac{q_m}{Q}\right), \ f(S,Q) = \rho_m\frac{S}{K+S}, \ U = uQ, \ \beta(S) = \frac{\mu_M S}{H+S}, \tag{33}$$

where all parameters are summarized in Table 2.

3.1.1. Numerical comparison

In this section we numerically compare the Droop (29) and Monod (31) formulations for a spatially explicit model. Note that a rigorous comparison of transient and steady state dynamics is possible with the models (29) and (31), however it is beyond the scope of this paper. Instead we provide a numerical comparison of the transient and long term dynamics of both models. For different uptake rates, both models show similar asymptotic but the transient dynamics differ significantly (see Fig. 5).

The cell/population concentration approaches the unique positive steady state (see Fig. 5(b)) in the presence of nutrient input ($a = 1$) or becomes extinct (see Fig. 5(c)) in the absence of nutrient input ($a = 0$). This observation agrees with an analytic study on the Droop model in the PDE setting in an unstirred chemostat Hsu et al. (2010). Furthermore, we simulated the case for closed nutrient (no input $a = 0$ and no output $\alpha = 0$) under different maximum uptake rates ρ_m. The results are similar to that of ODE case where the asymptotic dynamics are comparable but the transient dynamics can differ significantly for various maximum uptake rates.

Now we discuss both models under different spatial intervals, the results are shown in Fig. 6. For a small spatial domain size ($x \in [0, 0.1]$), both models result in extinction. This happens due to the narrow size of the domain and proximity of every point in the domain to the boundary. That is, the species and substrate near the boundary are lost from the system due to a relatively high sinking rate ($\alpha = 10$). However, with the same input and output rates, in the intermediate domain ($x \in [0, 0.3]$) (see Fig. 6(b)), the Monod model still results in an extinction whereas the Droop model is able to yield species persistence. This happens due to the difference between the half saturation constant for Monod growth/uptake ($H = 1$) and the half saturation constant for Droop uptake ($K = .5$). A small value of H in the Monod model means that the cells are efficient at finding nutrient and growing immediately, whereas a high value of H means the cell requires a high concentration to grow. The interpretation for K in the Droop model is similar but only considers uptake. With the high uptake rate and low half saturation constant, the Droop formulation benefits in this domain. Lastly, in the case of large spatial domain ($x \in [0, 1]$), both substrate and species stay far enough away from the loss due to sinking–boundary so that the species is able to persist in both models.

We note that the domain size can act as a bifurcation parameter for both models. Furthermore, the bifurcation point (with respect to domain size) that corresponds to the transition from extinction to persistence also depends on other model parameters. To this end, there is certainly a parameter region such that the Monod and Droop models would both show similar dynamics, or that the Monod model shows extinction and the Droop model shows persistence in the intermediate domain size. In our simulations we consider just one set of parameters values and show the transition from extinction to persistence for each model as we increase the domain size. Furthermore, this dependence on the spatial domain is implicitly related to the available nutrient via the effects of the boundary conditions. This shows some insight towards the paradox discussed in Section 1.2, as a smaller domain may be less favourable to the Monod model under the assumption that a larger proportion of nutrients are lost at the boundary leading to a decreased growth rate, whereas in the Droop form, under large uptake rate nutrient is quickly uptook and placed into the population allowing for a delayed growth.

4. Empirical evidence

Both Monod and Droop approaches have been tested and compared in many empirical experiments. The nature of the experiments can differ and thus we separate them into three categories: field experiments, uncontrolled laboratory experiments, and controlled laboratory experiments. Field experiments refer to those experiments where the study takes place in nature rather than in a laboratory. For uncontrolled laboratory experiments, important parameters will remain uncontrolled, and for controlled laboratory experiments those critical parameters are under control. In this section, we discuss some representative experiments in the literature.

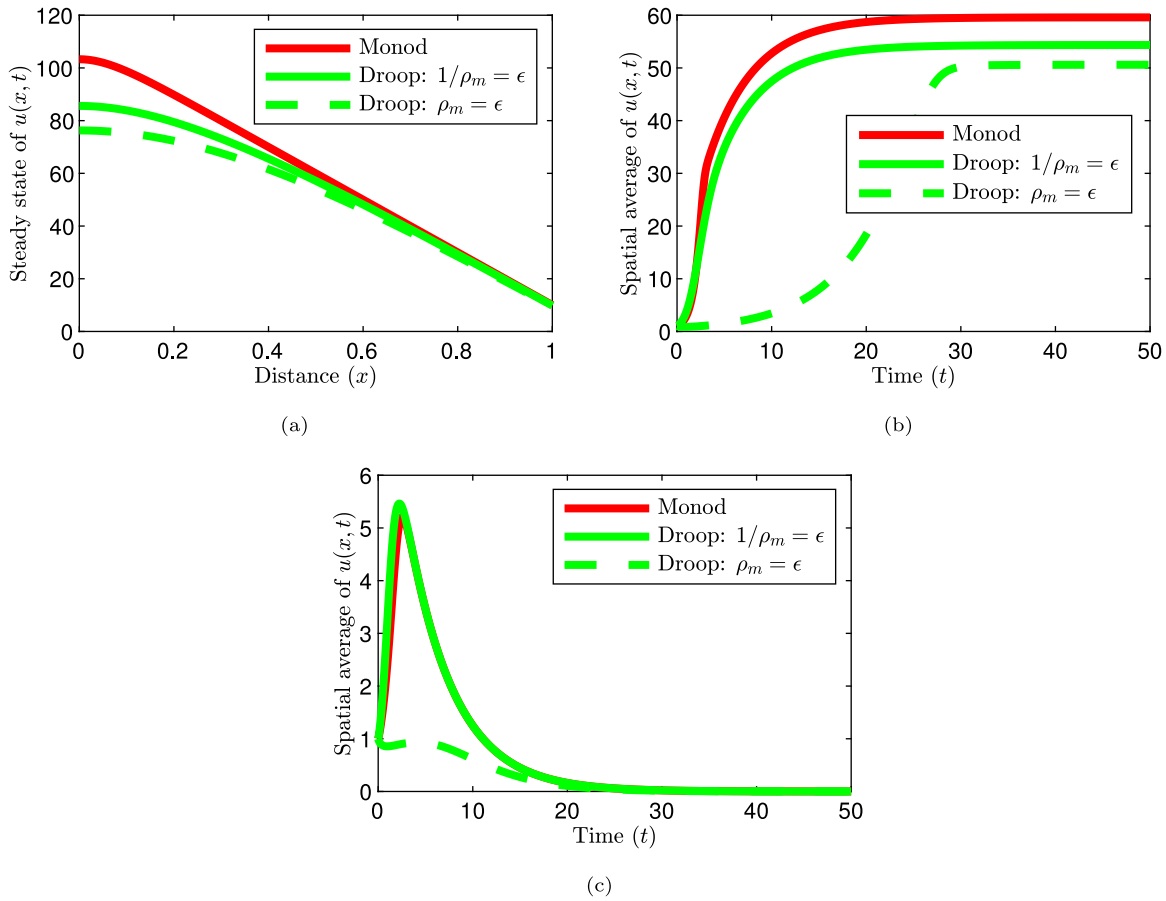


Fig. 5. Spatial and temporal dynamics of the Droop and Monod models under different maximum uptake rates ρ_m and different nutrient input rates a. Panel (a) plots the spatial distributions at equilibria, and panels (b)(c) plot the spatially average concentration over time. We choose $a = 1$ in panels (a)(b), $a = 0$ in (c), and other parameters are $K = 0.5$, $\mu_M = 2$, $q_m = 0.1$, $d = 0.1$, $\theta = 0.1$, $H = 0.5$, $u_0 = 1$, $U_0 = 0.1$, $\alpha = 10$.

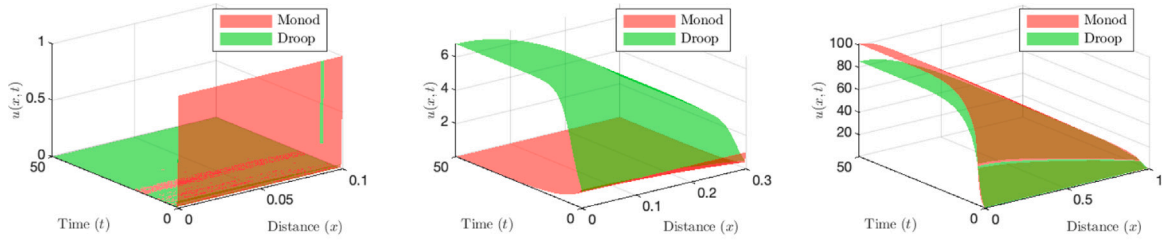


Fig. 6. Droop vs Monod model under different spatial domain when (a): $x \in [0, 0.1]$, (b): $x \in [0, 0.3]$, and (c): $x \in [0, 1]$. Other parameters are $\rho_m = 20$, $K = 0.5$, $\mu_M = 2$, $q_m = 0.1$, $d = 0.1$, $\theta = 0.1$, $H = 1$, $\alpha = 10$, $S_0 = a = 1$, $u_0 = 1$, $U_0 = 0.1$.

4.1. Field experiment

The nutrient uptake kinetics given by Monod and Droop forms have been studied and compared to understand under which circumstances a model would produce a better data fit in large experiments. For example, in Akoglu (2020) field data was collected and used from the Cilician Basin to compare the seasonal phytoplankton biomass and nutrient dynamics to the predictions produced by a simple model. The model had two variations that allowed the data to be compared to both the Monod or Droop uptake kinetics. The biomass from data was compared to the biomass predicted by the model by using the root mean square distance (RMSD). Furthermore, simulated nutrients such as nitrogen and phosphorus were also compared with the data samples. The simulated biomass and nutrient dynamics were in general more realistic when Droop uptake kinetics were considered compared to the Monod form. A reasonable explanation is because, given an oligotrophic environment such as the Celician Basin, Droop kinetics are suitable for describing the phenomena of nutrient luxury consumption. In Fig. 7 we show the plot adapted from Akoglu (2020) used as an empirical comparison between Monod and Droop predictions in a basic model. By a simple RMSD data comparison, the simulated biomass data using Droop uptake kinetics was more realistic than the biomass simulated when Monod form was considered. However, if the general trend of the seasonal bloom dynamics is preferred, the Monod form could be more appropriate due to its simplicity.

4.2. Uncontrolled laboratory experiments

The Monod form predicts the growth rate in terms of the substrate availability. In contrast, the Droop form predicts the growth rate based

on the cell quota. In Sommer (1991), a large scale experiment was designed to better understand the impact of nutrient limitations on the growth rate of phytoplankton. Samples for this experiment were taken weekly from a lake in Germany for almost one year. The experiment allowed the indirect cell quota calculations of different phytoplankton species under different limiting–nutrient environments. A comparison between the Monod and Droop forms as growth rate predictors was made, and the results showed the Droop form did better at predicting growth rates than the Monod form. In Fig. 8(a) we plot the empirical comparison between Monod and Droop growth rate predictions in terms of external substrate (Ammonium) for *Ceratium hirundinella*. Data used was taken from Sommer (1991), and nonlinear regression (MATLAB) was used to estimate parameters. In Fig. 8 the standard and modified Monod's curves (see Eqs. (4) and (7)) are shown in red, whereas green curves corresponds to Droop's forms with standard and modified Michaelis–Menten uptake rate as suggested in Sunda et al. (2009). The maximum uptake rate, the half-saturation constants for the uptake rate, and the hypothetical maximum growth rates were fitted to the data from Sommer (1991) using Eqs. (A.3) and (A.6). The subsistence quota was fixed and taken from the same data set. The minimum amount of ammonium at which the uptake rate is zero was fixed as the first ammonium sample from the data (see Table A.4).

4.3. Controlled laboratory experiments

The competitiveness of two cyanobacterial species where limited amounts of phosphorus was injected continuously, or by pulses, in the media was studied in Ducobu et al. (1998). A mathematical model was proposed considering the dynamics given by the Droop form. The Droop model predicted the data better than the Monod form. It was empirically shown how transients using the Monod form were entirely dependent on the amount of phosphorus in the media. Therefore, predictions may lead to unsatisfying results.

Basic mathematical models have been used to compare predictions of algal biomass considering Monod and Droop dynamics. In Sunda et al. (2009), it has been stated and shown empirically that these models are equivalent in steady-state conditions. Data was produced by growing algae in a cyclostat under ammonia-limiting circumstances. Both mathematical models were able to successfully fit the data considering both Monod and Droop forms. However, the Monod form needs to be slightly modified and the maximum growth rate was larger than expected. Also, both models were tested by a simulated single pulse of nutrient into the system to show the differences between transients (Sunda et al., 2009). In Fig. 8(b) we plot the empirical comparison between Monod and Droop growth rate predictions in terms of external substrate (Ammonium) for *T. pseudonana*. Data used was taken from Sunda et al. (2009). To estimate parameters we used the nonlinear regression function in MATLAB. To fit the Monod curve (see Eq. (4)) we fixed the maximum growth rate experimentally estimated as $\mu_M = 1.45\ \text{day}^{-1}$. Sunda suggested a modified version for the Monod form and Michaelis-Menten equation for the Droop form for a better fit (see Eqs. (7) and (A.4)). We only plotted the Droop curve with the usual Michaelis–Menten uptake rate (see Eq. (A.3)) since these three curves were practically the same. However, the maximum growth rate corresponding to the Monod modified form was numerically estimated as $\mu_M = 2.904\ \text{day}^{-1}$ which is significantly higher. It is possible to fit the data better by modifying the Monod form, or Michaelis–Menten uptake rate. However, these modifications could lead to inaccurate numerical estimations of parameters from those observed in laboratory (see Table A.5).

Droop and Monod forms were developed under steady–state conditions, but they are often used to describe transients of a system. In Ghaffar et al. (2017) these forms were tested for short periods of time when the equilibrium of the system has not been reached yet. This experiment consisted on batch culture methods which means that the culture was not maintained with constant inflow and outflow of culture medium and cells. Phosphorus was considered as the limiting nutrient and it was added in different bottles at different concentrations to measure the uptake kinetics. The main goal of this experiment was to compare transient dynamics observed in laboratory against Droop and Monod based growth rate predictions. The duration of the experiments lasted six days with samples drawn on the third and sixth day to estimate *Microcystis* biomass density, dissolved phosphorus in the media, and intracellular phosphorus (cell phosphorus media) under a controlled environment. The data showed a poor prediction for the Droop form using estimates of cell quota, and a limited prediction for the Monod form. The experiment was divided temporally in two sets of data. One set corresponded to the relationship between growth rate and phosphorus concentrations, or growth rate against the measured cell quota, from the zeroth day to the third day, and the other set corresponded from the third day to the sixth day. The Monod form presented the best fit but only for the first set using the relationship between the growth rate and phosphorus concentration in the media. For the second set, and for the other two sets which corresponded to the growth rate against the cell quota, both forms failed to fit the data. It was concluded a poor description of transient dynamics by these models for short periods of time and a completeness for these forms was suggested for more accurate predictions. The experiment showed highly complex relationships between the external and internal phosphorus concentrations, and cell growth that changed over time. It was suggested to consider intracellular and external nutrients when modelling algal growth, and that changes in intracellular phosphorus were best related to growth rather than absolute concentrations in transient conditions.

5. Discussion

In this paper we have attempted to shed light on the similarities and differences between the Monod and Droop forms for resource explicit population modelling. Biologically speaking, the assumption that growth and uptake are distinct processes is more reasonable and applies to a broader range of problems. This assumption creates a key difference between the two models. The Droop form considers uptake and growth as two separate processes, whereas the Monod form considers them as a single process (see Fig. 1). Under various mathematical and biological assumptions the applicability of each model varies, and neither model should be treated as a universally suitable model. However, we have provided some insights as to under what scenarios each model may be suitable or unsuitable.

5.1. Summary

In the ODE setting, we showed that when the Droop uptake is large the two models are qualitatively similar in both transient and asymptotic dynamics. That is, when the Droop uptake parameter (ρ_m) is large, the uptake of nutrient occurs on a faster timescale and thus the growth dynamics of both the Droop and Monod models occur on the same timescale. However, when the uptake is small, there is a significant difference between the two transient dynamics due to the uptake dynamics occurring on the same, or slower timescale of the population dynamics. In certain biological situations, such a cold temperatures and various stresses (Sterner and Grover, 1998), slow uptake may be reasonable but the Monod model does not allow this separation.

We also showed that under certain conditions the asymptotic dynamics can differ significantly. The difference arises from the homeostatic assumption in the Monod model and allocation of nutrient. For example, with a change in washout or nutrient supply, the Droop cell quota is able to increase or decrease accordingly. If the Droop cell quota equilibrium is above the fixed Monod cell quota (θ), then for similar nutrient dynamics we can expect the Droop model to show a lower population density. This can be seen more clearly by comparing the

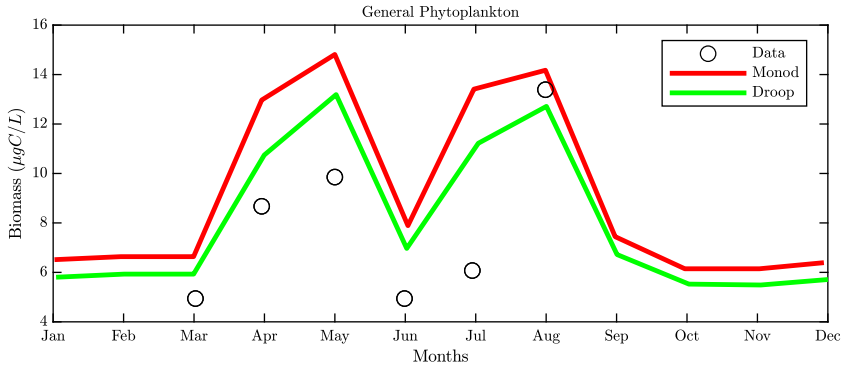


Fig. 7. Empirical comparisons between Monod and Droop forms..
Source: Plot was adapted from Akoglu (2020).

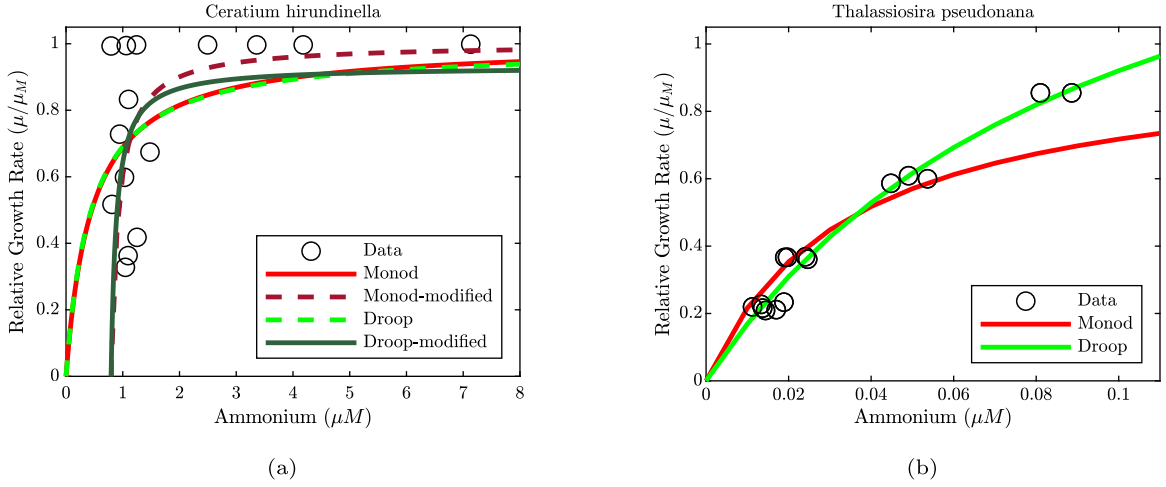


Fig. 8. Empirical comparison between Monod and Droop forms. Data points on panel (a) were taken from Sommer (1991) and data points on panel (b) were taken from Sunda et al. (2009). The legend Droop-modified refers to Droop form predictions but using the modified Michaelis–Menten equation as suggested in Sunda et al. (2009) (see Eqs. (A.3) and (A.6)). The x-axis in both panels represent the substrate S in micromole units.

total nutrient equations, $R_D(t) = S(t)+Q(t)u(t)$ and $R_M(t) = S(t)+\theta u(t)$, for both models. However, in Fig. 4 we considered a fixed value of $\theta = q_m$ for all simulations. It is reasonable to assume that with an increase in nutrient supply the value of θ would exceed the minimum cell quota. Hence, it is likely the case that if θ was similar to the value of the cell quota equilibrium, the asymptotic dynamics of the two models could be much closer. Furthermore, we have shown a bifurcation diagram of the two models in Fig. 4(b) with bifurcation parameter D (exchange rate). The bifurcation plot shows that the equilibrium values are not consistent for a given value of D. This result is clear by highlighting the differences between Eqs. (22) and (24). It should be noted that one could choose parameter values such that the difference between the equilibrium equations, or bifurcation curves is minimized. However, this minimization comes with little biological intuition as is seemingly purely mathematical. Furthermore, the convergence of the asymptotic dynamics is ambiguously dependent on the parameters of the ecological system at hand, and not the applicability of the models.

In the PDE setting we have shown in Fig. 5 that two models have similar asymptotic dynamics, but that under varying uptake rates the transient dynamics may differ. This result and its biological interpretation is similar to that of the ODE case. However, when the spatial domain is varied we can see a departure in the dynamics. That is, due to conservation laws the Monod model is more sensitive to available nutrient as described in Section 1.2. In turn the Monod model will be more likely to show extinction than the Droop model when the space size is decreased for the same nutrient inputs. Furthermore, the half saturation constants can act as bifurcation parameters separating species persistence from the extinction equilibrium. This is explainable by interpreting the half saturation constant as the amount of nutrient required for a cell to find nutrient and grow at half its maximum rate. Hence, there is a critical threshold for the half saturation constant required for persistence in a spatially explicit setting for both models. Moreover, there likely exists a parameter region such that the Droop model shows persistence for a smaller domain than the Droop model.

Another main difference between the two forms is mathematical simplicity. It is clear that the Monod form is much more mathematically tractable than the Droop form. For example, in the ODE case to model a single species using the simplest models, it is required to use a minimum of three parameters with two variables in the Monod formulation, but four parameters with three variables in the Droop formulation. For every additional species we add to the system, we are required to add additional three parameters and one variable in the Monod case, but four parameters and two variables in the Droop case. Although it is difficult to extend both models to consider many species, it is much more difficult in the Droop case.

5.2. Conclusion

For accurate predictions in algal growth population models, it would be ideal to have access to all kinds of parameters needed for each species and each nutrient. However, estimating these parameters could be a very difficult task due to experiment complexity and economical reasons. Mathematical models are of great advantage to describe such predictions at low costs, but the dynamics that arise will depend on the

model in use. In algal growth prediction models, the Monod form has been preferred over the Droop form due its simplicity. The Monod form does not only represent a great advantage for a modeller, but also for an ecologist since the growth rate of an algae species could be described by only an external substrate pool. In other words, to use the Monod form it would require a few and simpler measurements of parameters compared to a more complex and larger number of parameters needed if the Droop form is considered.

It has been shown empirically and mathematically that under steady–state conditions the prediction of algal growth rate using the Monod or Droop form can be equivalent. However, limitations arise using the Monod form if luxury consumption or transient dynamics are critical. On the contrary, the Droop form was designed to capture the luxury consumption phenomenon, and transient dynamics are generally better approached. Our paradox in Section 1.2 is partially resolved here.

We have highlighted several differences and similarities between the Monod and Droop models. Michael Droop's statements (see Section 1.1) alluded to the steady state similarities between the two models, and we showed an in-depth study of this in Section 2. Although we have shown additional nuances to the steady state comparison that Droop did not discuss in his correspondence. However, our study has shown the relative cumbersomeness of the Droop model compared to the Monod model only highlighting the importance of Droop's second statement. That is, in extending the models to a system with many species the Droop formulation would soon be too complex for any reasonable analysis while the Monod model may be too biologically simple in its assumptions. This indeed begs of another method or model to consider multiple interacting species in this framework.

In this paper we highlighted several similarities and differences between the two well established resource explicit population models of Monod and Droop. We provided an in-depth mathematical exploration of the models assumptions and derivations, as well as provided numerical simulations and some mathematical analysis to highlight relevant aspects of their dynamics. The areas in which these models can be applied have significant overlap, however the results may depend heavily on which model is chosen. Depending on the research question or assumptions being made, one model may be favourable or inapplicable. In the following section we provide a Table 3 to summarize under which scenarios we recommend the models to be used. In conclusion the Droop model is more mechanistically and ecologically driven, and thus should generally be favoured over the Monod model. However, while the Droop model shows more prowess in resource explicit modelling, it comes with the caveat of additional mathematical complexity.

5.3. Guidelines

In this section we provide guidelines, shown in Table 3, on the applicability of either the Droop or Monod models. First we consider various mathematical situations in which the models do or do not apply. Although the Droop formulation is more ecologically considerate, it comes at the cost of mathematical complexity and this complexity would resonate through in any mathematical analysis. Thus the Monod model is preferred for studies that involve rigorous mathematics. It has also been shown in Figs. 3 and 5 that the transient dynamics of both models are consistent when the Droop uptake rate (ρ_m) is large. However, these figures also show significant differences in the transient dynamics for small Droop uptake rates. These differences are explained by the separation of timescales between uptake and growth that only the Droop formulation permits, as discussed in Section 2.1.4. Furthermore, in a closed nutrient system eventually all the nutrient will be found in the population, if the Droop cell quota (Q) and homeostatic nutrient ratio (θ) are similar then the population abundance will also be similar. This result applies to both the PDE and ODE setting. On the other hand, when the system is open the asymptotic dynamics depart as shown graphically in Figs. 6 and 4(a), and mathematically in Eqs. (22) and (24). However, by adjusting parameter values one could achieve equality of the steady values, which is evident in steady state parameter fitting (Burmaster, 1979). When considering spatially explicit models, one should be careful about choosing the model parameters as domain size can act as a bifurcation parameter for both models. There is certainly a parameter region where the Monod and Droop models show similar dynamics, as in a smaller and large spatial domain both models behave similarly as seen in Figs. 6(a) and 6(c) respectively. However, the Monod model shows extinction and the Droop shows persistence in the intermediate domain size (see Fig. 6(b)).

Next we discuss the applicability of the models under various ecological considerations. If the population being considered exhibits luxury consumption or internal storage of the resource then the Droop model must be used. The Monod model assumes the species is homeostatic with respect to the resource while the Droop form allows for variable internal content. Moreover, the biological research question at hand can dictate which model is the preferred choice. If addressing questions pertaining to complex population dynamics, such as seasonal dynamics, nutrient allocation, or population health then the Droop model is preferred as the Droop model considers more biological mechanisms. However, if the questions being asked relate to simple population trends like persistence or extinction conditions, then the Monod model can do a sufficient job at matching this type of data with the reduced model complexity (Akoglu, 2020). Lastly, in considering a closed eutrophic system we refer to the paradox proposed in Section 1.2. That is, in an eutrophic setting the uptake rates of the population must be taken into account to fully understand the dynamics. By construction the Monod model does not allow for the explicit consideration of nutrient uptake and therefore may fall short in accurately modelling this dynamic.

In order to represent the seasonal biomass and nutrient dynamics, both the models can be considered (see Section 4.1). However, the Droop model could be useful for accurate predictions, whereas the Monod model is sufficient for the general prediction of seasonal blooms. Since the Monod model is more sensitive to the available nutrient as described in Section 1.2, the Droop model can be appropriate to discuss the most nutrient capacity in an organism.

5.4. Future work

There are several pathways that one can follow in advancing the knowledge of resource explicit population modelling. The Droop model is a true process based model, but comes at the cost of additional mathematical complexity. In some instances, this mathematical complexity is too much to make deep dynamical conclusions. On the other hand the Monod model is much more mathematically palatable but also makes certain biological assumptions that could be deemed unreasonable in many circumstances. To our best knowledge, there has been no successful attempt at formulating a mechanistic model, while maintaining a relatively simple mathematical model although variations of the Droop and Monod models have been proposed (Darvehei et al., 2018; Lee et al., 2015). Droop's statement refers to this aspect on a larger community level scale as discussed in Section 1.1. Droop proposed that all the additional parameters needed to model multiple species can be simplified by the use of an affine transformation. In other words, using existing data and tools we may be able to greatly simplify the addition of species by using a single parameter for each additional species, but not lose the benefit of using the Droop form.

We also highlight another possible direction for future work that involves a deeper study of transient dynamics. The study of transient dynamics in ecological systems has shown to become increasingly important. Most ecological concerns and questions occur on a short, or relatively short timescale especially those that exhibit stochastic perturbations (Hastings et al., 2018). In this sense, the study of asymptotic dynamics is less crucial. Unfortunately, the popularity of the Monod

Table 3
The applicability of the Monod or Droop form in different scenarios.

Situation	Monod	Droop	Reason
Mathematical simplicity required	Yes	No	Droop requires more parameters and a cell quota equation
Transients with large uptake rate	Yes	Yes	See Figs. 3 and 5
Transients with small uptake rate	No	Yes	See Figs. 3 and 5
Asymptotic dynamics in closed nutrient	Yes	Yes	Steady states are equivalent (see Section 2.1.3)
Asymptotic dynamics in open nutrient	No*	Yes	Steady states are (*in general) not equivalent. (see Eqs. (22) and (24))
Variable space scale	Yes	Yes	See Section 3.1.1 and Fig. 6
Luxury consumption is possible	No	Yes	Monod form assumes homeostasis
Complex population trends	No	Yes	See Section 4.1
Simple population trends	Yes	No	See Section 4.1
Closed eutrophic system	No	Yes	See Section 1.2

model implies that either transient dynamics have historically been neglected, or that they may be misinformative. Moreover, more realistic modelling approaches such as multi–stage nutrient uptake kinetics can be crucial for understanding transients and the underlying mechanisms that drive certain systems (Jiang et al., 2019). A more rigorous study of transient dynamics would greatly benefit the fields relating to resource based population models and their usefulness in application to management and policy making (Hastings et al., 2018).

Finally, the theory of resource explicit models in the PDE setting begs for more rigour. The models presented in this paper are what we consider to be toy models, and are merely some first attempts at considering ecological stoichiometry in a spatially explicit resource based population model (Hsu et al., 2014). As such, to be certain these models are reasonable (as with any PDE model) a true process based derivation should be proposed. This derivation could be akin to the use of master equation for describing a physical Markov systems (Székely and Burrage, 2014), the application of Fick's law in deriving the diffusion equation (Mazumdar, 1999; Othmer et al., 1988), or the rigorous mathematical and physical derivation of the telegraphers equation (Othmer et al., 1988). In any sense the consideration of variable internal stoichiometry in a spatially explicit setting is far from trivial, but a meticulous derivation of the internal nutrient dynamics must be considered to properly advance this important area of research.

CRediT authorship contribution statement

Hao Wang: Conceptualization, Methodology, Validation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Pablo Venegas Garcia:** Software, Formal analysis, Writing – original draft, Writing – Review & Editing, Visualization. **Shohel Ahmed:** Software, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Christopher M. Heggerud:** Conceptualization, Software, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision.

Declaration of competing interest

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

Appendix. Data fitting

To data fit the relative growth rate in terms of a substrate we used Eq. (4) or Eq. (7) for Monod and Monod-modified relative growth rate predictions. However, to fit the data using the Droop form we did the following. From Eq. (6),

$$Q = \frac{q_m}{1 - \frac{\mu}{\mu_M}}. \tag{A.1}$$

Considering Eqs. (8) and (17) for $dQ/dt = 0$, we obtain

$$\frac{\rho_m S}{K + S} = \mu \frac{q_m}{1 - \frac{\mu}{\mu_M}}, \tag{A.2}$$

Table A.4
Parameters fitted to data points taken from Sommer (1991) for different relative growth rate forms. Bold numbers are fixed parameters observed in the experiment.

Fig. 8(a)	Monod	Monod-modified	Droop	Droop-modified
μ_M	**0.26**	2.62	2.4285	3.93
K_s	0.45	0.133	–	–
s_0	–	**0.794**	–	**0.794**
ρ_m	–	–	38.64	2.9818
K	–	–	217.64	2.638
q_m	–	–	**0.033**	**0.033**

Table A.5
Parameters fitted to data points taken from Sunda et al. (2009) for different relative growth rate forms. Bold numbers are fixed parameters observed in the experiment.

Fig. 8(b)	Monod	Monod-modified	Droop	Droop-modified
μ_M	**1.45**	2.904	3.63	4.25
K_s	0.034	0.109	–	–
s_0	–	−0.0009	–	−0.0009
ρ_m	–	–	1.158	6.35
K	–	–	0.393	0.346
q_m	–	–	0.1054	0.694

thus Droop's relative growth rate in terms of a substrate at the steady state is given by

$$\frac{\mu}{\mu_M} = \frac{\rho_m S}{\mu_M q_m (K + S) + \rho_m S}. \tag{A.3}$$

We take the modified uptake function $f(S)$ as suggested in Sunda et al. (2009)

$$f(S) = \begin{cases} \rho_m (S - s_0)/(K + S - s_0), & \text{if } S > s_0, \\ 0, & \text{otherwise.} \end{cases} \tag{A.4}$$

Then by using the same procedure as before, when $dQ/dt = 0$,

$$\frac{\rho_m (S - s_0)}{K + S - s_0} = \mu \frac{q_m}{1 - \frac{\mu}{\mu_M}}. \tag{A.5}$$

In this way, the relative growth rate given by the Droop-modified form is given by

$$\frac{\mu}{\mu_M} = \frac{\rho_m (S - s_0)}{\mu_M q_m (K + S - s_0) + \rho_m (S - s_0)}. \tag{A.6}$$

In Fig. 8 we have used Eqs. (4), (7), (A.3) and (A.6). The parameters estimated for each experiment are given in Tables A.4 and A.5.

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