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# Models of Phytoplankton Nutrient Uptake and Coupling with Plankton Dynamics

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## ABSTRACT

Phytoplankton are the autotrophic components of the plankton community and a key factor of oceans, seas and freshwater basins ecosystems. Over much of the ocean, their growth is limited by their uptake of nitrogen (as nitrate), which has most commonly been described by the hyperbolic Michaelis-Menten (MM) equation. Here, we review some developments in nutrient uptake and growth modeling of phytoplankton in order to show the important progress on the knowledge of its kinetics that has been made up to now. On the other hand, plankton plays an important role in the ecology of the ocean and climate because of their participation in the global carbon cycle at the base of the food chain. In the past years, a larger number of researchers have attempted to model the relationship between nutrient, phytoplankton and zooplankton, to investigate the dynamics in plankton model. In this chapter is described a simple nutrient-phytoplankton-zooplankton (NPZ) model, indicating the most important simplifications considered by expert researchers in this field.

**Keywords:** Phytoplankton; Nutrient uptake; Growth; Half-saturation constant; Plankton dynamics; NPZ models

# THE PLANKTON COMMUNITY

"Plankton" is from a Greek word for "wanderer." It is a term that groups the various organisms that float freely in the seas, oceans, rivers, lakes, reservoirs, etc. They range in size from the tiniest microscopic organisms to much larger animals such as jellyfish.

Plankton can be divided into two large groups: planktonic plants and planktonic animals. The first, also called phytoplankton, are the primary producers of the food chain in the sea and in freshwater. They are autotrophs, making their own food, using the process of photosynthesis. The animal plankton, also called zooplankton, eat food for energy. These heterotrophs feed on the microscopic world of the sea and transfer energy up the food pyramid to fishes, marine mammals, and humans. For many years, scientists have been interested in studying plankton, because they are the base of the food chain in marine and freshwater ecosystems.

## One-Celled Organisms

The plankton organisms can be classified according to size. The smallest are commonly referred as microbes, e.g. bacteria, protists (algae and protozoans), and fungi. Although they are microscopic organisms (in the micrometer size range), their abundance makes them of great importance in the aquatic life.

Bacteria are prokaryotic cells and are distinguished from the eukaryotes by their lack of intracellular organelles. Moreover, prokaryotic genetic material is not enclosed in a nuclear membrane. There are over 10000 species of bacteria.

Protists are one-called organisms and belong to the group eukaryotes. These cells contain organelles such as nucleus and mitochondria and/or chloroplasts. Protozoa are animal-like protists and algae are photosynthetic protists. These are over 60000 species of protists. The major groups are: ciliophora (e.g. Paramecium, Vorticella); rhizopoda (e.g. Amoeba); actinopoda (e.g. Heliozoan); zoomastigophora (e.g. Giardia); euglenophyta (e.g. Euglena); chlorophyta (e.g. Chlorella); cryptophyta (e.g. Cryptomona); dinoflagellata (e.g. Ceratium); chrysophyta (e.g. diatoms), etc.

Aquatic fungi include several groups of true fungi as well as morphologically similar buy distantly related, protists-like water molds and slime molds. There are over 50000 species of true fungi, 700 species of water-molds, and 800 species of slime molds. Fungi occur wherever there is sufficient organic material for growth. They compete with bacteria and tend to be most successful when the food supply is difficult to decompose plant or animal polymers.

## Macroinvertebrates

Other plankton organisms that are easily overlooked in the aquatic medium are the macroinvertebrates (also called small invertebrates). Because of their numbers, they are of major importance to aquatic ecology. These organisms are the primary consumers of the microbes, previously described, and they are the favorite food of larger organisms, such as fish.

Macroinvertebrates can be classified in rotifers (e.g. Ascomorpha, Brachionus, Keratella, Floscularia); annelida (e.g. Tibifex, Aelosoma); branchiopoda (e.g. Daphnia, Bosmina); copepod (e.g. Calanoida, Cyclopoida); malacostracans (e.g. Amphipoda, Mysidacea, Decapoda); insects (e.g. Coleoptera, Hemiptera).

## MODELS OF NUTRIENT UPTAKE AND GROWTH IN PHYTOPLANKTON

Monod in 1949 [1] extended the MM enzyme kinetics to growth of whole organism such as bacteria. Later, Dugdale [2] introduced MM to represent the effect of nutrient concentration on phytoplankton nutrient uptake rate:

$$V = \frac{V_{\max}[S_\infty]}{K_\infty + [S_\infty]} \qquad (1)$$

Where $[S_\infty]$ is the ambient nutrient concentration, $V_{max}$ is the maximal uptake rate, and $K_\infty$ is the MM bulk half-saturation coefficient, which is the nutrient concentration when the uptake rate is half that $V_{max}$. This equation has become the standard representation of nutrient-limited uptake and growth in classical competition theory as well as for modern ocean ecosystem models.

In this section we review some development in nutrient uptake and growth modeling of phytoplankton beyond the MM framework.

## PHYTOPLANKTON NUTRIENT UPTAKE

Nutrient uptake refers to processes necessary for moving a nutrient ion from the outside to the inside of a cell [3]. These processes are carried out by uptake sites, proteins on the cell membrane where nutrient ions are captured from the surrounding medium and transported into the cytoplasm [4]. The formalism of phytoplankton nutrient uptake was commonly represented as an analogy of enzymatic kinetics where the role of the enzymes is played by uptake sites. The uptake process can then be described by the reaction [4,8]:

$$S_0 + E_f \underset{\kappa_{-1}}{\overset{\kappa_1}{\leftrightarrow}} ES_0 \xrightarrow{\kappa_2} S_i + E_f \qquad (2)$$

Where $S_0$ represents the nutrient ion concentration in the vicinity of the cell (local concentration), $E_f$ is the unoccupied uptake site, $ES_0$ is the uptake site-nutrient ion compound, $S_i$ represents the nutrient ion concentration incorporated by uptake sites into the cell and $K_1$, $K_{-1}$ and $K_2$ are the rate constants. The reaction scheme 2, as indicated in [4], describes a process in which nutrient ions hit an uptake site at a constant encounter rate $K_1$ and the site remains occupied until the enzyme–ion pair is completely dissociated inside the cytoplasm, which occurs at a constant rate $K_2$. An ion–transporter complex can be dissociated outside the cell at a rate $K_{-1}$ (rebound process), although it is considered that this process occurs at a frequency too small to be taken into account.

The analogy assumes that the uptake sites are not consumed during the uptake process, and their concentrations are much less than the nutrient ion concentration presented in the medium [4].

By applying the law of mass action, which states that the rate of a reaction is proportional to the product of the concentrations of the reactants, it is possible to deduce an equation for the nutrient uptake [4]:

$$V = \frac{\kappa_2 [E][S_0]}{\kappa_2 / \kappa_1 + [S_0]} = \frac{V_{max}[S_0]}{K_0 + [S_0]} \qquad (3)$$

This is the MM functional form [6] with $[E]=[E_f]+[ES_0]$ the constant total number of uptake sites. $V_{max}=K_2[E]$ is the (constant) maximum uptake rate and $K_0=K_2/K_1$ is the local half-saturation constant (i.e. the nutrient ion concentration in the vicinity of the cell when the uptake rate is 50% of $V_{max}$). They are the MM kinetic parameters, both considered invariant traits of the microbial populations [3] and used to characterize the species under study.

Eq. (3) recognizes that the rate of uptake of a nutrient by fully receptive cells is a function of the nutrient ion concentration up to a saturable limit of $V_{max}$. At low nutrient concentration uptake rate approaches $\alpha_0[S_0]$ where $\alpha_0=V_{max}/K_0$ is the local affinity of the cell, defined as the ratio of the kinetic parameters [7].

It is necessary a diffusion-limitation correction to the expression 2 in order to consider a more realistic situation in which microorganisms, due to their small size, can potentially develop a boundary layer with decreasing nutrient concentration toward the cell. That is, local nutrient concentration can be smaller than the ambient concentration caused by the difference in the fluxes owing to nutrient consumption by the organism and the diffusive transport of nutrient ions in the medium toward the cell [4,7,9]. By assuming stationary conditions and a spherical cell, we can write [4] the net flux of nutrient molecules toward the cell as $4\pi Dr([S_\infty]-[S_0])$ where D is the diffusion constant of the nutrient, r is the cell radius, $[S_\infty]$ is the nutrient concentration outside the boundary layer (which in practice corresponds to the ambient concentration measured in experiments) and $[S_0]$ is the nutrient concentration at the cell surface. The relative difference between $[S_0]$ and $[S_\infty]$ determines whether uptake is limited due to physical constraints imposed by nutrient diffusion (i.e., uptake rate faster than diffusion rate and, therefore, $[S_0]< [S_\infty]$) or due to the performance of the uptake machinery (uptake site limitation, $[S_0]= [S_\infty]$) [4,9].

The MM model, eq. (1), and diffusion-limited nutrient transport was coupled by Pasciak and Gavis [9] who obtained a quadratic (non-MM) model of V vs. $[S_\infty]$. Their approach was revisited by Armstrong [10], who derived a MM-approximation of the quadratic solution for the way in which V relates to $[S_\infty]$. Bonachela et al. [11] followed a different deduction based on the law of mass action and obtained an approximate solution valid for both the diffusion and uptake site limitation regimes:

$$V = \frac{V_{max}[S_\infty]}{K_0\left(1+\frac{V_{max}}{4\pi DrK_0}\right)+[S_\infty]} \qquad (4)$$

This generalized MM like function has the form of eq. (1) with an the effective half-saturation constant, $K_\infty$ [4] and takes into account how the possible presence of a boundary layer formed around the cell modifies the uptake rate of the organism. For cases where the organism is limited by diffusion (D or $[S_\infty]$ very small), the uptake rate will be given by

$$V=4\pi rD[S_\infty] \qquad (5)$$

This expression coincides with the pure diffusive flow of ions to the cell when it depletes completely the surrounding nutrient ($[S_0]=0$), i.e, when all nutrients encountering the cell surface are immediately absorbed [4,7]. As $[S_\infty]$ or D is increased, the uptake is limited solely by the transport through the membrane, i.e., uptake site limitation, reaching eventually the limit $V=V_{max}$ [4].

It is also possible to obtain a generalized form for the specific affinity of the cell. From its definition as the ratio of the kinetic parameters [8] the affinity is given, in this case, by

$$\alpha_\infty = \frac{V_{max}}{K_\infty} = \frac{4\pi rD\kappa_1[E]}{\kappa_1[E]+4\pi rD} \qquad (6)$$

For the case of uptake site limitation, affinity is reduced to $K_1[E]$ whereas for diffusion limitation it is given by $4\pi rD$ (which represents the maximum uptake affinity, $\alpha_{max}$, and is a theoretical upper limit for the uptake rate set by the rate of diffusion and the size of the cell, $V_{max}= \alpha_{max}$).

There is no way to predict the values of the kinetic parameters accurately save by experimental determination. Many measurements show close conformity to the predicted MM behavior, eq. (1), and, hence, to the generalized plot in Figure 1, showing the uptake rate of urea by *Ditrylum brightwellii*, as described by McCarthy [12].

A limitation of the MM-model is that no theoretical expectations on how the kinetic parameters scale with e.g. cell size, number of uptake sites, uptake site size, temperature, or external nutrient concentration are provided. This implies that, in an ecological context, it is often required additional parameterizations and coefficients that describe, e.g., how $V_{max}$ and $K_\infty$ depend on size and temperature. Such uncertainty in parameterizations can be reduced in models where these properties are embedded mechanistically [7].

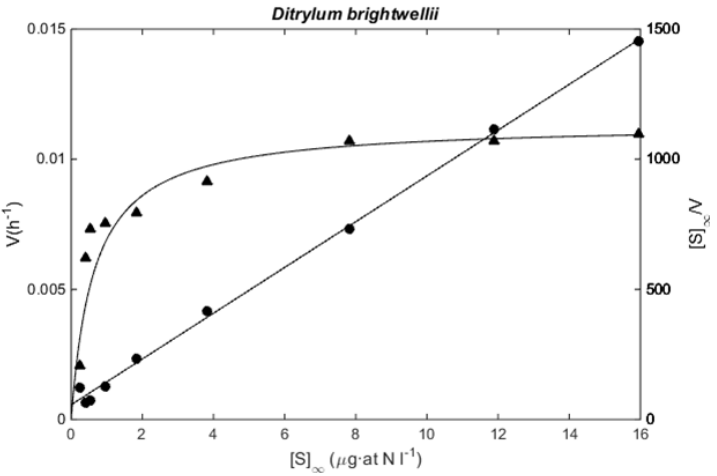


**Figure 1:** Urea uptake rate as a function of concentration for *Ditrylum brightwellii* (triangles) and the linear transformation of $[S_\infty]/V$ vs. $[S_\infty]$ (circles) in which the intercept is equal to $K_\infty/V_{max}$ and the slope equals to $1/V_{max}$ [11,12].

One of the first theoretical trait-based models for nutrient uptake was proposed by Aksnes and Egge [3]. Their approach is based on Holling's "disk" equation or functional response II [13], used to model predation in animals. They incorporated some new parameters in their model such as the number of uptake sites, n, introduced above, each with a nutrient catchment area at the cell surface, A, ion handling time, h, which corresponds to the time interval an uptake site is blocked due to the handling of nutrient ion from the outside to the inside of the cell, the number of encountered ions, m and mass transfer coefficient, v, interpreted as the velocity between ions and uptake sites.

Following their steps, the number of ions encountered by one uptake site during a finite time interval $T_1$ will be:

$$M = T_1 Av[S_0] \quad (7)$$

And as a result of ion handling, the time required for processing m encounters is $T_2$=mh. Therefore, the total time necessary for processing m encounters is $T_1+T_2$, so the uptake rate for one site becomes $m/(T_1+T_2)=nAv[S_0]/(1+hAv[S_0])$. Since the cell has n uptake sites, the uptake rate for the cell is:

$$V = \frac{nAv[S_0]}{1+hAv[S_0]} \quad (8)$$

Rearrangement of this equation into a MM form yields $V_{max}=n/h$, $K_0=1/Avh$ and $\alpha_0=nAv$. From these relationships we see that decreased handling time increases both half-saturation constant and maximum uptake rate, leading to opposite effects on the affinity and on the uptake rate at low nutrient concentrations. Note that we have used the subscript 0 instead of ∞ because this model doesn't address the boundary layer of the cell. The maximum nutrient uptake is limited by

handling time and number of uptake sites per cell at high nutrient concentrations, which can be interpreted as an exclusively biological limitation [3]. However, at low nutrient concentrations, the uptake rate approaches nAv[$S_0$], which represents the encounter limitation, and depends on both biological characteristics (such as the number of uptake sites and site area) and on the mobility (through the parameters v and [$S_0$]), which represents an environmental physical constraint. Note also that handling time is not part of uptake rate at low nutrient concentration neither affinity because these parameters reflect the response when the encounter is the rate-limiting step, not handling [3].

In 1977, Berg and Purcell [14] derived a relationship between uptake rate and the number of uptake sites (with S the site radius) for a spherical cell in the oligotrophic regime (i.e. at low nutrient concentrations, when the uptake rate is limited by diffusion). They have shown that the chance of capturing a nutrient molecule is a non-linear function of the uptake site number, and can be expressed as:

$$V = 4\pi D\left(\left[S_\infty\right]-\left[S_0\right]\right)\frac{ns}{ns+\pi r} \qquad (9)$$

This expression doesn't include the handling time idea, i.e. assumes that uptake sites are always receptive for uptake and therefore predicts no saturation uptake rate in uptake rate with increasing [$S_\infty$]. This is a reasonable assumption for low ambient concentrations, when the time interval between nutrient encounters at a porter is much longer than the time it takes to absorb the nutrient ion [15]. Critically, uptake is dependent on the number of uptake sites in the cell surface doing that uptake rate satures as the number of sites becomes larger [7]. Northrup [16] tested the model numerically and found some disagreement between the analytical model, eq. (9), and the numerical simulation at high site coverage [7], but this discrepancy was eliminated by Zwanzig [17] introducing a correction term (1-p) reflecting the interaction between sites:

$$V = 4\pi D\left(\left[S_\infty\right]-\left[S_0\right]\right)\frac{ns}{ns+\pi r(1-p)} \qquad (10)$$

Where *p* is the fraction of the surface area covered with uptake sites:

$$p = \frac{n\pi s^2}{4\pi r^2} \qquad (11)$$

As indicated by [15], when [$S_\infty$] increases, the uptake rate will be increasingly limited by the cellular processing rather than by diffusion-mediated transport, and eq. (9) becomes increasingly inaccurate. In high nutrient concentrations, not only the uptake site number, but also the handling time, will limit the uptake rate. In this regime, when all uptake sites are blocked, the uptake rate becomes independent of [$S_\infty$], but cannot exceed a maximum quantity, n/h [8,16], and this limit is not consider in the Berg and Purcell [14] and Zwanzig [17] models.

In order to consider this upper limit on the uptake rate as the nutrient concentration rises, Aksnes and Cao [15] applied the handling time of an uptake site idea into the result [9]. Their analytical expression for uptake rate of a spherical cell takes the form:

$$V = \frac{b}{2a}\left(1-\sqrt{1-\frac{4a}{b^2}}\right) \quad (12)$$

where

$$a = \frac{h}{4\pi Dr[S_\infty]n}\left(1-\frac{\pi rp}{ns}\right) \quad (13)$$

$$b = \frac{1}{\alpha_\infty[S_\infty]}+\frac{h}{n} \quad (14)$$

$$\alpha_\infty = 4D\pi r\frac{ns}{ns+\pi r(1-p)} \quad (15)$$

The uptake affinity is derived as the initial slope of the relationship v vs $[S_\infty]$ ($\lim_{[S_\infty]\to 0} V = \alpha_\infty[S_\infty]$), and therefore it is does not correspond to the MM affinity given by the ratio $V_{max}$: $K_\infty$. At low nutrient concentrations this uptake rate approaches eq. (10) and at high nutrient concentrations approaches the upper limit n/h. Therefore, this model is consistent with both oligotrophic and eutrophic regimes.

The derived eq. (12) is not of MM type but they proposed two alternative MM approximations. In the first approximation, they define the MM half-saturation constant as the ratio $V_{max}$: $K_\infty$, as commonly assumed within a MM framework. This provides:

$$K_\infty = \frac{\pi r(1-p)+ns}{4h\pi Drs} \quad (16)$$

In the second approximation, they used the analytical expression for the half-saturation constant of the uptake model, obtained as the nutrient concentration where uptake equals 50% of the maximum uptake rate (i.e. n/2h):

$$K_\infty = \frac{\pi r(2-p)+ns}{8h\pi Drs} \quad (17)$$

MM approximations are obtained by insertion of these expressions in the MM equation $V= V_{max}S/(K_\infty+S)$, with $V_{max}=n/h$. The errors of the two MM approximations relative to the solution provided by the model, eq. (12), are illustrated in [15] by using the *Vibrio splendidus* estimates. As they indicated, the error of both approximations increases with increased uptake site density.

This model suggest that, for an organism of a particular size, the benefit of increased uptake site number is very different for organisms living in oligotrophic (when $\alpha_\infty$ is rate limiting, $V= \alpha_\infty[S_\infty]$) and eutrophic (when $V_{max}$ is rate limiting, $V=V_{max}$) regimes. This is because $\alpha_\infty$ saturates for large n, and $V_{max}$ increases proportionally to n [15].

The effect of temperature is not explicitly expressed in this model, but temperature affects molecular diffusion (and thus affinity) and the cellular machinery through $V_{max}$, or equivalently through h [15]. Increasing the temperature causes a different increasing in $V_{max}$ [15,18] and

molecular diffusion [19]. This dual effect of temperature leads to the expectation that the uptake rate for an organism should be respond differently to temperature changes in oligotrophic and eutrophic regimes [15]. Such interactions between the temperature and the nutrient regime are not contained in the MM model, but it is phenomenologically assumed that $K_\infty$ varies with temperature in a different way than $V_{max}$ [15].

Experimental measurements show that many traits scale allometrically with cell volume, such as maximum uptake rate, the half-saturation constant for uptake, subsistence quotas, and uptake affinity [20-22]. Microbial traits can be estimated from some of these measurements, particularly, those concerning $V_{max}$, $K_\infty$ and $\alpha_\infty$. If the size of an organism and the value of the molecular diffusion of the solute are known, we are left with three unknowns, n, s, and h(p is given by n, s, r) and three equations that connect these traits to $V_{max}$, $K_\infty$ and $\alpha_\infty$ (eq. (15), eq. (17), and the relationship $V_{max}$=n/h) [7]. However, these estimations remain hypotheses today since they are still untested experimentally.

## PHYTOPLANKTON GROWTH

Monod [3] proposed in 1949 a model to relate microbial growth rates in an aqueous environment to the concentration of a limiting nutrient. The Monod equation has the same form as the MM equation, but differs in that it is empirical while the latter is based on theoretical considerations:

$$\mu = \mu_{max} \frac{S}{K + S} \qquad (18)$$

where μ is the specific growth rate of the microorganisms, $\mu_{max}$ is the maximum specific growth rate, S is the concentration of the limiting nutrient for growth and K is the half-saturation constant of growth rate.

It has been found that this model is not satisfactory for the description of nutrient-limited growth rates [11]. This may be attributed, in part, to inappropriate application and a misplaced assumption that growth rates are as rapid as the relevant materials can be assembled. In fact, growing cells may take up nutrients when they are abundant much more rapidly than they can deploy them, just as they can sustain growth at the expense of internal stores at times when the rate of uptake may be constrained by low external concentrations [11].

Droop [23], in 1973, adapted the Monod model to include a variable internal store in order to represent the impact of the cell quota on the rate of growth. As it is explained in [11], it is, firstly, quite plain that the intracellular content of the cell starved of a given particular resource will not just below (leaving the cell very responsive to new resource) but it will probably be close to the absolute minimum for the cell to stay alive. This is Droop's minimum cell quota, $Q_0$, and it is too small to be able to sustain any growth. Secondly, raising the actual internal content, Q, above the minimal threshold (essentially through uptake) makes resource available to deployment and growth. At low but steady rates of supply, some proportionality between the rates of growth and

resource is expected to be evident. With these considerations, the Droop equation becomes [11]:

$$\mu = \mu_{max}\left(\frac{Q-Q_0}{K+Q-Q_0}\right) \quad (19)$$

As it cannot be assumed that growth and uptake are half-saturated at the same concentrations, we must take account a half-saturation constant of growth.

## MODELS OF NUTRIENT-PHYTOPLANKTON-ZOOPLANKTON DYNAMICS

A full understanding of aquatic ecosystem dynamics requires knowledge of the influence of physical forcing on the abundance of plankton, and of the interaction between the different trophic levels: phytoplankton, zooplankton, and fishes. Models are becoming increasingly prevalent tools in ecosystem studies of any type. They can be used to gain understanding of how a system works or to make predictions of the future state of the ecosystem. Also, they can be used to perform simulations in ways it is impossible to do in a real environment. Physical or initial conditions and parameter characteristics of the models can be varied and the effects on the ecosystem examined [24,25].

While such simulations are not a substitute for the traditional observational approach, models do provide a valuable way of studying the details of the links between physical forces, nutrient uptake, and phytoplankton and zooplankton abundances. The ability to explore the impact of the influence of physical forces on phytoplankton and zooplankton communities provides valuable insights into aquatic ecosystem functionality, and contributes towards our understanding of observed spatial and temporal variations in ecosystem productivity.

There have been many approaches to aquatic ecosystem modeling [26]. However, dynamic models have proved to be the most common and successful approach for ecosystem understanding. Nutrient-Phytoplankton-Zooplankton (NPZ) models are composed of mathematical equations that describe the changes over time of quantities representing the system state variables [27,28].

An NPZ model has, by definition, three state variables: nutrients (N), phytoplankton (P) and zooplankton (Z). These are usually modeled in terms of their nitrogen content, g nitrogen/L, since nitrogen is often limiting to primary production in aquatic ecosystems. Another possibility is to refer them to the carbon content [29].

The differential equations that comprise an NPZ model describe the change in concentration of each of the state variables over time. For example, phytoplankton concentration changes over time as a result of phytoplankton growth, natural mortality, grazing by zooplankton, and advection and diffusion processes. A general set of NPZ model equations can be written [30]:

$$\frac{dP}{dt} = f(I)g(N)P - h(P)Z - i(P)P. \quad (20)$$

$$\frac{dZ}{dt} = \gamma h(P)Z - j(Z)Z \quad (21)$$

$$\frac{dN}{dt} = -f(I)g(N)P + (1-\gamma)h(P)Z + i(P)P + j(Z)Z \qquad (22)$$

In an NPZ model there are five transfer functions to consider: phytoplankton response to light f(I), phytoplankton nutrient uptake g(N), zooplankton grazing h(P), and phytoplankton i(P) and zooplankton j(Z) loss terms due to death, excretion, and predation by organisms not included in the model. Zooplankton assimilation γ may also be important, though it is typically modeled as a simple linear function of food ingested.

## Irradiance Function

Some of the functional forms that have been used to describe phytoplankton response to irradiance, f(I) (dimensionless), are the followings:

$$f(I) = \frac{I}{I_0} \qquad (23)$$

$$f(I) = \frac{I}{I_0 + I} \qquad (24)$$

$$f(I) = 1 - \exp\left(-\frac{I}{I_0}\right) \qquad (25)$$

$$f(I) = \tanh\left(-\frac{I}{I_0}\right) \qquad (26)$$

$$f(I) = \frac{I}{I_0}\exp\left(1 - \frac{I}{I_0}\right) \qquad (27)$$

where $I$ is the irradiance in the considered medium (W $m^{-2}$). As can be seen, eq (23) is a simple linear response to incident light, and eqs. (24-27) are nonlinear forms with a saturating and/or photoinhibiting response. Some forms are chosen for their ease of integration over a die period, while others are attempts to more accurately parameterize the nonlinear response of photosynthesis to irradiance. All the functional forms contain one only parameter, $I_0$. This parameter determines irradiance at photosynthesis maximum.

## Nutrient Uptake Function

As it noted in the previous section, nutrient uptake by phytoplankton, g(N)($d^{-1}$), is commonly modeled by MM functional form:

$$g(N) = \frac{V_{max} N}{K_0 + N} \qquad (28)$$

Where $V_{max}$ is the maximum uptake rate, $d^{-1}$, and $K_0$ is the local half-saturation constant, g nitrogen/L.

Droop [23,31] argued that phytoplankton show luxury uptake of nutrients, that is, they are stored in an internal pool before they are used for growth, allowing uptake to be uncoupled from growth. It has also been argued that only the most limiting process (photosynthesis or nutrient uptake) should determine the growth rate, allowing for switching between the two types of limitation depending on circumstances.

## Zooplankton Grazing Function

Unlike nutrient limitation, there is no such agreement on the best functional form to describe the rate of zooplankton grazing on phytoplankton despite much observational effort. A 'Michaelis-Menten' type formulation was traditionally a common choice [32,33]. This hyperbolic function is equivalent to the Monod equation for nutrient uptake, with the grazing rate (G) first increasing linearly with phytoplankton concentration (P) before becoming saturated. Several more complex grazing formulations have also been developed and are commonly used in NPZ models. The most common alternatives provide phytoplankton with a refuge from zooplankton grazing pressure when their concentrations are low. These formulations arose as a result of both observational studies and the desire of the modeler to prevent extinction of phytoplankton due to zooplankton grazing. The most notable of these modified grazing functions are the 'threshold' function [27,34,35], which incorporates a critical prey concentration below which grazing ceases, and the sigmoidal function, in which the grazing rate is reduced at low prey concentrations [36-38]. It is probable that no one equation is correct for all scenarios and the modeler will have to ascertain which is most appropriate for the situation of interest. This could depend on the key zooplankton species or stage of interest and the nature of the available prey.

Mathematical expressions for different functional forms of h(P)($d^{-1}$) are the followings:

$$h(P)=R_m P \quad (29)$$

$$h(P)=\frac{R_m\,(P-P_0)}{\lambda+(P-P_0)} \quad (30)$$

$$h(P)=\frac{R_m P^n}{\lambda+P^n},\ n=1 or\ 2 \quad (31)$$

$$h(P)=R_m[1-\exp(-\lambda P)] \quad (32)$$

$$h(P)=R_m[1-\exp(-\lambda(P-P_0))] \quad (33)$$

$$h(P)=R_m \lambda P[1-\exp(-\lambda P)] \quad (34)$$

As can be seen in eqs. (29-34), all h(P) functional forms contain one or more adjustable parameters ($R_m$, $P_0$, λ, n).

## Loss Phytoplankton and Zooplankton Functions

The death or loss terms of the phytoplankton, i(P)($d^{-1}$), and zooplankton, j(Z)($d^{-1}$), are the "closure" terms of the model. These functions allow nutrients in form of phytoplankton

or zooplankton to be recycled back, potentially to be taken up again during photosynthesis of phytoplankton. Phytoplankton death is almost always modeled as a linear or quadratic process [39]:

$$i(P) = \varepsilon \quad (35)$$

$$i(P) = \varepsilon P \quad (36)$$

Both functional forms contain one only adjustable parameter, ε.

In the case of zooplankton, death rate is sometimes more complicated. It has been proposed a non-linear death rate considering a density-dependent loss rate, that is, higher death rates at higher zooplankton densities. While there is little field evidence supporting the use of such a functional form [40], the use of a density-dependent loss rate has significant implications for the model behavior. Steele and Henderson [37] suggested that the NPZ model was stable with quadratic zooplankton mortality, but showed unforced oscillations with linear mortality. Edwards and Brindley [41,42] and Edwards and Yool [43] however, showed that both the linear and quadratic mortality terms allowed unforced oscillations, though the linear term allowed oscillations over a wider parameter range.

Mathematical expressions for different functional forms of j(Z)($d^{-1}$) are the followings:

$$j(Z) = \varepsilon' \quad (37)$$

$$j(Z) = \varepsilon' Z \quad (38)$$

$$j(Z) = \frac{\varepsilon' Z}{\varepsilon'' + Z} \quad (39)$$

As can be seen in eqs. (37-39), j(Z) functional forms contain one or two adjustable parameters (ε′, ε″).

The model previously developed is one of the most simple and intuitive in the group of the NPZ models. They have proposed more complex models that consider additional state variables. For example, bacteria [44], detritus (particulate organic nitrogen) [29], dissolved organic nitrogen [45], nitrate and ammonium ions separately [46], benthos [47] and fish [48]. Likewise, it was also considered the simultaneous presence of several types of phytoplankton and zooplankton, each with different characteristic parameters (nutrient uptake, growth, grazing, mortality, etc.) [49].

Moreover, an NPZ model must be always coupled to a physical model through the advection-diffusion equations. Each state variable of the NPZ model will have a separate equation describing its motion in space and time. These physical models range from one-dimensional models with biological dynamics averaged over a mixed layer [36,38,50] to three dimensional models with high turbulence [30,51].

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