

# Development Of A Simple Biological Model Of Vertical Phytoplankton Distribution

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## ABSTRACT

Phytoplankton in tropical waters aggregate and form a maxima below the surface where the common limiting materials for growth (light from the surface, nutrients from the depths) are at optimal levels. The location of optimum growth conditions is dependent on various physical, chemical and biological factors. The formation of phytoplankton maxima was simulated through a coupled physical and biological model for vertical chlorophyll distribution in Philippine waters. This paper evaluates biological models and the significance of 1) different forms of phytoplankton response to irradiance and nutrient uptake, 2) rate of nutrient uptake, and 3) light and/or nutrient limitation determining nutrient uptake. Phytoplankton response-to-irradiance form is less important than rate of light extinction in affecting the deep chlorophyll maximum (DCM) depth. The Michaelis-Menten form of nutrient uptake gives a bigger and deeper DCM but only under certain conditions. Temperature does not significantly affect nutrient uptake gives bigger and deeper DCMs. These findings will come in handy in future work of simulating empirical chlorophyll profiles.

## INTRODUCTION

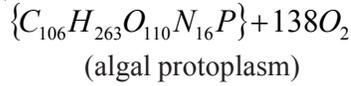
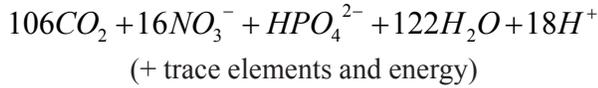
Phytoplankton is the base of the oceanic food web. These are consumed by bigger plankton, that are in turn eaten by organisms in the higher trophic levels. Phytoplankters, much like terrestrial plants, grow in biomass by utilizing carbon (in the form of carbon dioxide) through the process of photosynthesis. Although much smaller than their terrestrial counterparts, phytoplankton have greater surface area to volume ratios and much quicker turnover rates, making the amount of carbon dioxide that they consume quite significant. Thus they could play an important role in the sequestration of atmospheric carbon dioxide, the most significant greenhouse gas contributing to global warming.

Light is used as energy source in photosynthesis through the chlorophyll pigments, with chlorophyll  $\alpha$  as the principal photosynthetic pigment common to all phytoplankton. A high correlation of chlorophyll-a and phytoplankton biomass distributions (Akbulut, 2003) would then allow the use of chlorophyll  $\alpha$  as a measure of phytoplankton biomass (Parsons & Strickland, 1963; Engelsen et al., 2004; Cloern & Dufford, 2005). Any difference in the distribution of chlorophyll and phytoplankton biomass may be attributed to sinking velocity and increasing chlorophyll to biomass ratios at low light levels (Fennel and Boss, 2003).

Aside from light, nutrients are required in the photosynthetic reaction as shown by the equation below (Stumm & Morgan, 1995).

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Nutrients usually determine the rate of photosynthesis since their concentrations are found in limiting amounts (nitrogen for oceanic systems) compared to the abundance of light and carbon dioxide in surface waters (Falkowski, 1997). The amount of light available for photosynthesis decreases with depth due to attenuation (combined absorption and scattering) from particles in the water as well as the water itself. Inversely, nutrient gradients increase with depth. Somewhere in between is where a combination of both factors will be optimum for photosynthesis and phytoplankton growth. Phytoplankters tend to aggregate in this area giving rise to a phytoplankton maximum, commonly referred to as the deep chlorophyll maximum (DCM).

Models have been developed to explain phytoplankton dynamics. The NPZ (nutrient-phytoplankton-zooplankton) model by Franks (2002) is the simplest model that describes oceanic plankton dynamics.

$$\frac{\partial C}{\partial t} = K_H \left( \frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) + K_V \frac{\partial^2 C}{\partial z^2} - u \frac{\partial C}{\partial x} - v \frac{\partial C}{\partial y} - (w + w_s) \frac{\partial C}{\partial z}$$

+ biological dynamics (1)

$C$  is the concentration of the state variable (N, P or Z),  $K_H$  and  $K_V$  are the horizontal and vertical eddy diffusivities,  $u$ ,  $v$  and  $w$  are the horizontal and vertical water velocities, and  $w_s$  is the vertical sinking or swimming speed of the state variable. The biological dynamics of the NPZ model is shown as:

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

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

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

$f(I)$  is phytoplankton response to irradiance,  $g(N)$  is phytoplankton nutrient uptake,  $h(P)$  is zooplankton grazing,  $i(P)$  is phytoplankton loss,  $j(Z)$  is zooplankton loss, and the constant  $\gamma$  is the grazing assimilation efficiency of zooplankton.

The NPZ model is a very general form of ecosystem model and has been modified. Hadfield and Sharples (1996) and Sharples (1999) added an internal cell nutrient variable to account for chlorophyll to phytoplankton biomass ratio variations with depth. Zakardjian and Prieur (1994) included oxygen as to deal with oxidation of reduced forms of nitrogen. Fennel and Boss (2003) differentiated phytoplankton biomass maxima and chlorophyll maxima. Different parameterizations have also been added, such as effect of photoadaptation and sinking due to phytoplankton aggregation (Doney et al., 1996) and nutrient exudation during respiration (Bahamon and Cruzado, 2003). Varela et al. (1992) and Hodges and Rudnick (2004) focused on the DCM.

Varela et al. (1992) used several variables in his DCM model, these are 2 phytoplankton, 2 nutrients, and 2 heterotrophs. Although the model results were consistent with empirical data, Hodges and Rudnick (2004) noted that the fundamental constraint of nitrogen conservation was not satisfied in Varela et al.'s (1992) model. They then suggested a simple nutrient-phytoplankton model, where zooplankton grazing was factored into phytoplankton loss. Model results of Hodges and Rudnick (2004) showed that removal of nitrogen from the surface through surface boundary conditions and sinking of phytoplankton are necessary conditions in the formation of the DCM, and that addition of more variables do not significantly affect phytoplankton distribution.

Because of the advantage of having less variables and satisfying balance of nitrogen in the system, the model of Hodges and Rudnick (2004) was adapted in this study. The objective of the study is to examine the degree to which nutrients (specifically nitrate) determine the vertical distribution of chlorophyll a using a coupled physical-biological model, with

emphasis on the biological model. This could enhance understanding of phytoplankton dynamics and provide insights on fisheries potential of Philippine waters.

## MATERIALS AND METHODS

The biological model used in this study is based on the nutrient-phytoplankton model of Hodges and Rudnick (2004). The coupled physical-biological model is shown below.

$$\frac{\partial P}{\partial t} = K_z \left( \frac{\partial^2 P}{\partial z^2} \right) - w_s \left( \frac{\partial P}{\partial z} \right) - i(P)P + U_m f(I)g(N)P$$

$$\frac{\partial N}{\partial t} = K_z \left( \frac{\partial^2 P}{\partial z^2} \right) + i(P)P - U_m f(I)g(N)P$$

$U_m$  is the maximum nutrient uptake rate and  $K_z$  is the vertical eddy diffusion coefficient. The boundary conditions are:

$$\frac{\partial N}{\partial z} = w_s P - K_z \left( \frac{\partial P}{\partial z} \right) = 0, \quad \text{at the surface}$$

$$P = 0, N = \text{constant}, \quad \text{at the bottom}$$

Hodges and Rudnick (2004) used only basic mechanisms to demonstrate the formation of the DCM. In doing so, complex formulations of parameters and relationship of variables that may be necessary to reproduce empirical chlorophyll profiles were not considered. Since this study will eventually attempt to duplicate empirical chlorophyll data, related literature were reviewed to examine parameters for irradiance, nutrient uptake, and phytoplankton loss (Tables 1 and 2). In the model of Hodges and Rudnick (2004), the growth term (last term) for phytoplankton utilizes both nutrient and light influence at the same time. An alternative is Liebig's law, which uses either nutrient or light, or whichever is more limiting at a given time. Also, the maximum nutrient uptake rate can be either constant or variable. Eppley (1972) suggested a temperature-dependent maximum phytoplankton growth rate:

$$U_m(T) = U_m(T_0) q_{10}^{(T-T_0)/10}$$

$U_m(T)$  and  $U_m(T_0)$  are the maximum uptake rate at reference temperature  $T$  and reference temperature  $T_0$ , respectively.  $q_{10}$  is the factor by which the uptake rate changes with every 10°C change in temperature.

Response-to- irradiance, f(I)	Terms	Remarks	Source
1. $f(I)=I/I_0$		Linear; Not dependent on surface irradiance	Edwards et al. (2000), Franks (2002), Hodges & Rudnick (2004)
2. $f(I)=I/(I_0+I)$		Saturating	Franks (2002)
3. $f(I)=1-\exp(-I/I_0)$		Saturating; When photo-inhibition is insignificant	Franks (2002)
4. $f(I)=\tanh(I/I_0)$		Saturating	Franks (2002)
5. $f(I)= (I/I_0)/(\exp(1-I/I_0))$		Saturating; When photoinhibition is significant	Franks (2002), Steele (1962)
6. $f(I)=I/(k_1+I)$	$k_1$ =irradiance half-satn constant	Michaelis-Menten form; For multiple nutrients & phytoplankton models	Varela et al. (1992), Zakardjian & Prieur (1994), Gecek & Legovic (2001), Bahamon & Cruzado (2003)
7. $f(I)=q^{chl}(\alpha I - r_B)$	$\alpha$ =slope of photo- synthesis-irradiance curve; $q^{chl}$ =chlorophyll: biomass ratio; $r_B$ =respiration		Hadfield & Sharples (1996), Sharples (1999)

Table 1. List of functional forms for phytoplankton response-to-irradiance

Nutrient uptake, $g(N)$	Terms	Remarks	Source
1. $g(N)=N$	$N$ =nutrient concentration		Edwards et al. (2000), Hodges & Rudnick (2004)
2. $g(N)=N/(k_s+N)$	$k_s$ =nutrient uptake half-saturation constant	Michaelis-Menten uptake	Varela et al. (1992), Zakardjian & Prieur (1994), Gecek & Legovic (2001), Bahamon & Cruzado (2003)
3. $g(N)=1-(kQ/Q)$	$Q=N/chl$ =internal nutrient pool; $k_0$ =minimum $Q$ required by cell	Droop's internal cell quota model	Hadfield & Sharples (1996), Sharples (1999), Franks (2002)
Phytoplankton loss, $i(P)$	Terms	Remarks	Source
1. $i(P)=D/P$	$D$ =loss rate, constant	linear	Franks (2002)
2. $i(P)=D$		Non-linear; density-dependent	Doney et al. (1996), Edwards et al. (2000), Franks (2002), Hodges & Rudnick (2004)

Table 2. List of functional forms for nutrient uptake and phytoplankton loss

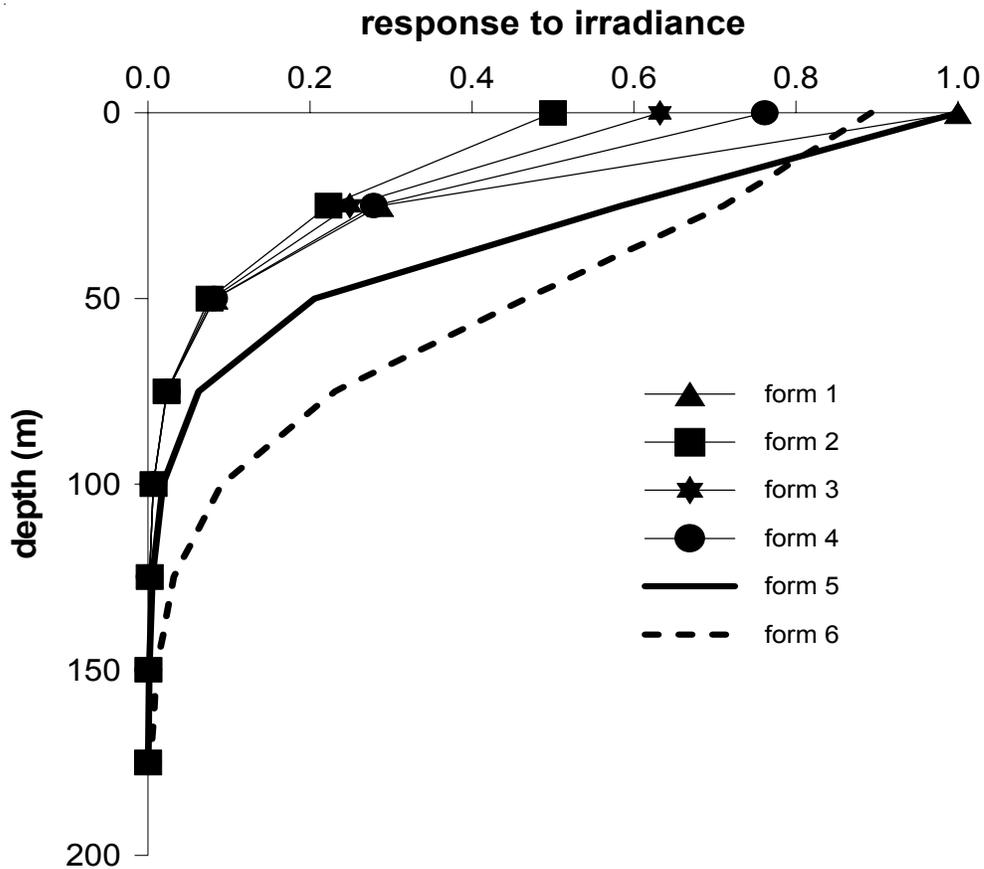


Figure 1. Phytoplankton profiles when nutrient uptake rate is constant (identical with profiles when nutrient uptake rate is variable).

The parameter forms in Tables 1 and 2 were tested on the model using the parameter values given in Table 3. Irradiance was calculated using Beer's law,  $I = I_0 e^{-\chi z}$  where  $I$  is irradiance at depth  $z$ ,  $I_0$  irradiance at the surface, and  $\chi$  the extinction coefficient. The first phytoplankton response-to-irradiance form in Table 1 is often used in very simple biological models where the magnitude of surface irradiance is not important. Forms # 2 - 4 are forms that have photosynthetically saturating response to irradiance. Form # 5 is also saturating but takes into account possible photo-inhibition by phytoplankton. The Michaelis-Menten response-to-irradiance form is often used in multiple nutrient and variable models. The profiles of these response-to-irradiance forms are shown in Figure 1. The last response-to-irradiance form was not used because it distinguishes phytoplankton chlorophyll and biomass.

Only two of the three forms of phytoplankton nutrient uptake in Table 2 were used since there was no empirical data available on internal nutrient pool that is required for the third form. The first form is commonly used in simple coupled models that only have one nutrient variable while the Michaelis-Menten form is often used in more complex models with multiple nutrient variables. The constant phytoplankton loss form (#2) in Table 2 was not used because it does not conform to the closed system suggested by Hodges and Rudnick (2004).

Thus the model runs for the study dealt primarily with 1) comparison of the different response-to-irradiance and nutrient uptake forms, 2) use of variable (temperature-dependent) nutrient uptake rate against a constant rate, and 3) application of Liebig's law compared to simultaneous light and nutrient influence in phytoplankton growth.

## RESULTS AND DISCUSSION

The model was run to determine response of phytoplankton to light and nutrients separately, and with simultaneous influence of these two parameters. Different parameter forms of irradiance response and nutrient uptake were examined. Variable and constant nutrient uptake rates were also tested. The resultant phytoplankton profiles when nutrient uptake rate is

constant are shown in Figure 2. As discussed below, Figure 2 can also represent phytoplankton profiles resulting from a variable nutrient uptake rate, making the figure representative of phytoplankton profiles for all runs.

### Comparison of parameter forms

#### *Response to irradiance*

Phytoplankton profiles using the different response to irradiance forms are differentiated among the columns in Figure 2. Model runs using the first four forms gave identical phytoplankton profiles (rows 1 - 4, Figure 1) even though response to irradiance profiles were different close to the surface (lines with solid blocks, Figure 1). The response to irradiance profiles converged at lower depths and could be the reason for the identical phytoplankton profiles. Profiles using response-to-irradiance forms # 5 and 6 have significantly slower light extinction rates thereby allowing for deeper light penetration (Figure 1) and thus the deeper DCM (rows 5 and 6, Figure 2).

#### Nutrient uptake

There is no significant difference in the phytoplankton profiles from the two nutrient uptake forms using Liebig's law (columns 3 and 4, Figure 2). In contrast, the DCM is bigger, deeper and more defined with the Michaelis-Menten nutrient uptake form when there is simultaneous nutrient and light influence on nutrient uptake (columns 1 and 2, Figure 2). Since nutrient concentration tends to be low ( $<1 \mu\text{M}$  nitrogen) due to model constraints and the half saturation constant  $k_s$  is small (0.05), nutrient uptake will increase when the Michaelis-Menten form is used. With the forms using Liebig's law, nutrient uptake increase occurs where light is limiting (below intersection of light factor and nutrient factor in Figure 3). Since the light factor (smaller than the nutrient factor) determines nutrient uptake in this region the increase in nutrient uptake is unable to influence the phytoplankton profile. When there is simultaneous influence of light and nutrients, the increase in nutrient uptake would result in a bigger, deeper and more defined DCM (columns 1 and 2, Figure 2).

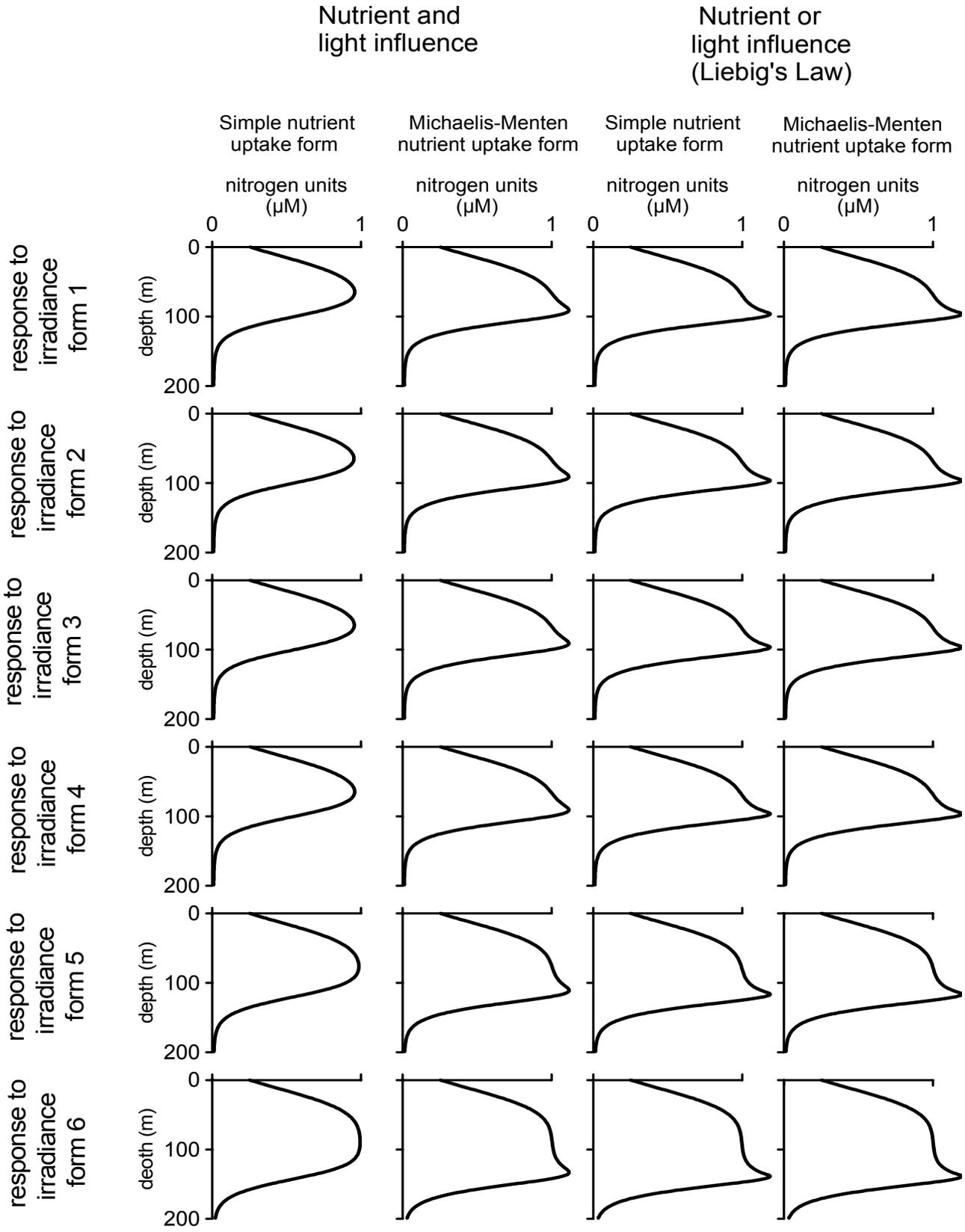


Figure 2. Response-to-irradiance profiles.

### Variable and constant nutrient uptake rate

The phytoplankton profile resulting from use of a temperature-dependent nutrient uptake rate did not differ significantly from the profile resulting from the use of a constant nutrient uptake rate. Although nutrient uptake rate is higher at higher temperature especially for the upper 100 m of the water column, there was no significant change in the DCM. This indicates that temperature variation does not affect phytoplankton growth based on the biological model and the nutrient uptake rate formula of Eppley (1972). Parsons et al. (1984) stated that photosynthesis of phytoplankton in tropical/sub-tropical communities is more likely to be limited by nutrients rather than temperature. Valiela (1984) also suggests that temperature is not a primary limiting factor in primary production in the sea and may have an effect only under certain situations.

### Nutrient uptake based on Liebig's law and simultaneous nutrient-light influence

The use of Liebig's law in phytoplankton nutrient uptake consistently gave bigger, deeper and more defined DCMs (columns 3 and 4, Figure 2) compared to using light and nutrient influence simultaneously (columns 1 and 2, Figure 2). This may be so because with Liebig's law nutrient available for uptake is situated deeper in the water column (Figure 4) and just below the nutricline nutrient availability is bigger, which could account for the bigger and deeper DCM.

### CONCLUSION

The light extinction rate inversely affects the depth of the DCM and is more important than the form of phytoplankton response-to-irradiance. Compared to the

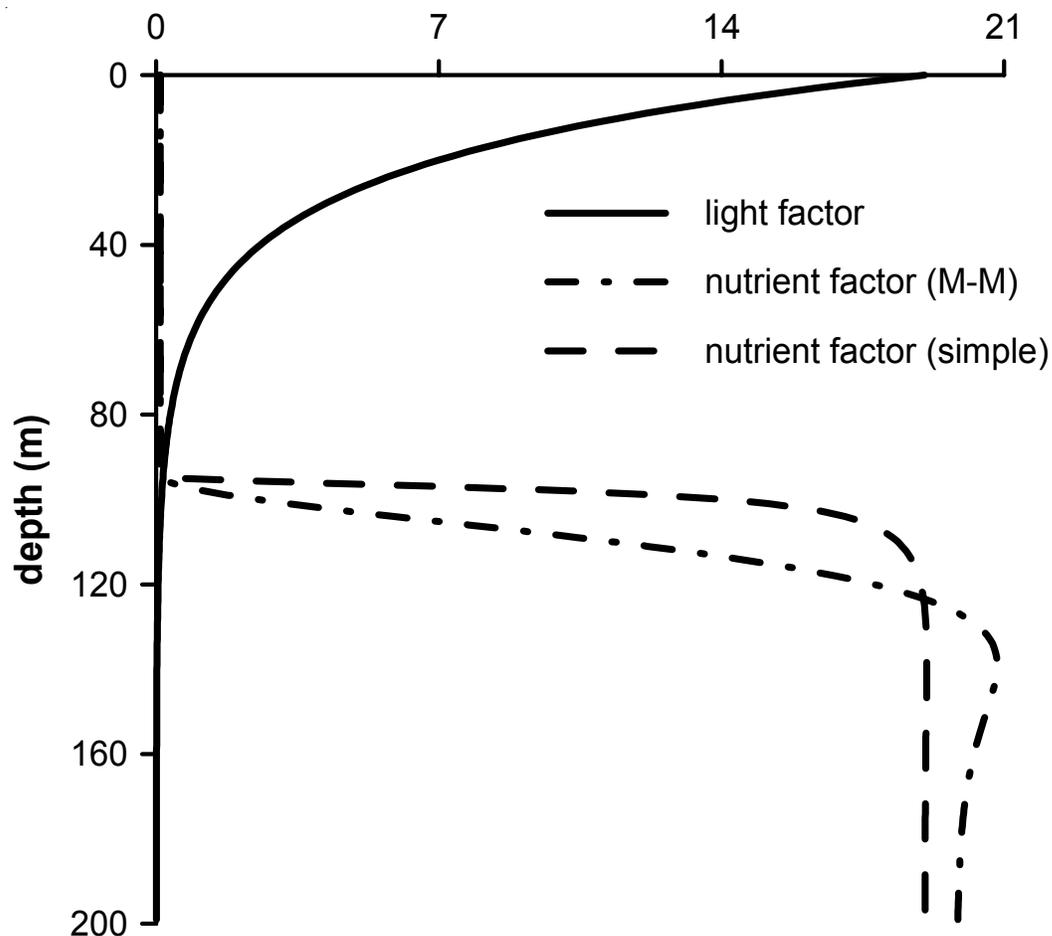


Figure 3. Nutrient and light factors when Liebig's law determines phytoplankton nutrient uptake.

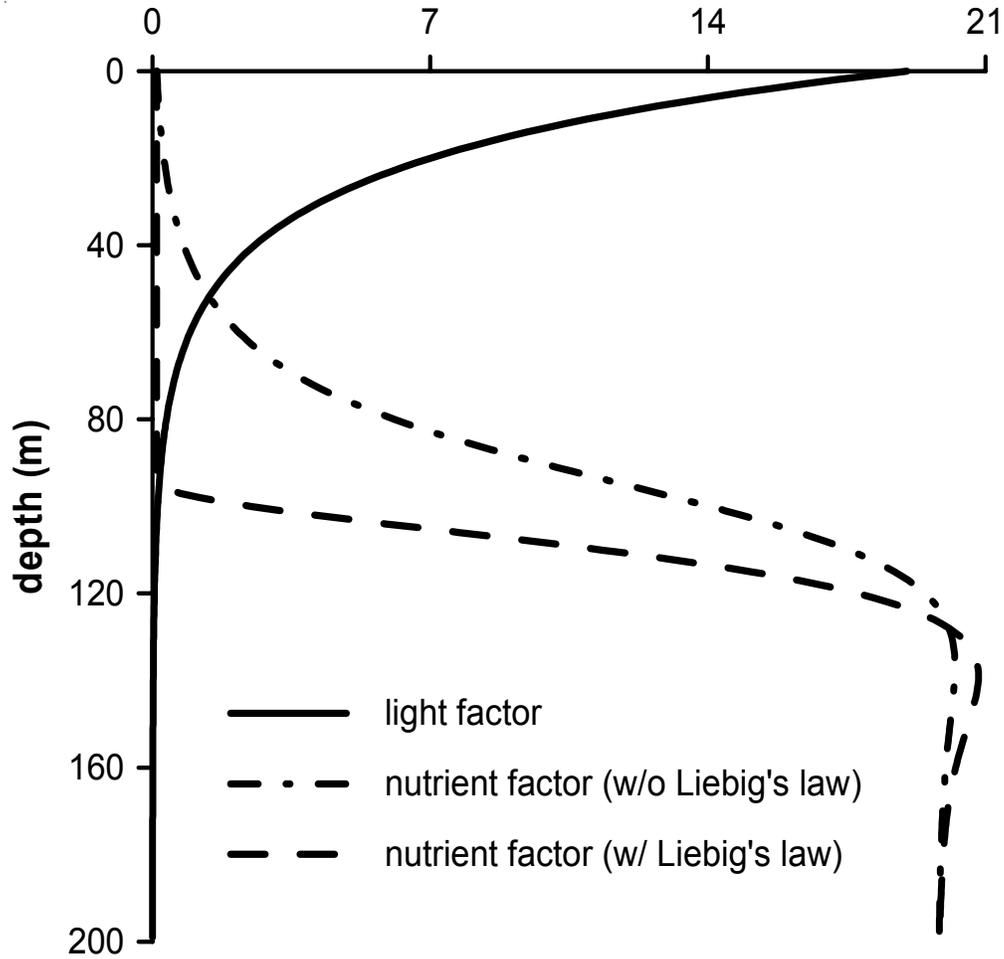


Figure 4. Nutrient and light factors when light and nutrient factors simultaneously influence phytoplankton nutrient uptake.

Parameter	Symbol	Value	Unit
Surface irradiance	$I_0$	100	$\mu\text{Em}^{-2}\text{s}^{-1}$
Irradiance half-saturation constant	$K_S$	12	$\mu\text{Em}^{-2}\text{s}^{-1}$
Light extinction coefficient	$c$	0.05	$\text{m}^{-1}$
Eddy diffusion coefficient	$K_Z$	$1 \times 10^{-4}$	$\text{m}^2\text{s}^{-1}$
Maximum nutrient uptake rate	$U_m$	20	$\text{d}^{-1}$
Sinking velocity	$w_s$	0.5	$\text{d}^{-1}$
Phytoplankton loss rate	$D$	0.1	$\text{d}^{-1}$
Maximum uptake rate at reference temperature (20°C)	$U_m(20)$	20	$\text{d}^{-1}$
Uptake rate change factor	$q_{10}$	1.884	no units

Table 3. Parameter constants used in all runs

simple nutrient uptake from the Michaelis-Menten form gives a bigger DCM depth and magnitude but only when there is simultaneous nutrient and light influence. Nutrient uptake rate does not seem to be temperature-dependent and might be due to temperature being less of a limiting factor in primary production especially in the tropics. The use of Liebig's law in phytoplankton nutrient uptake situates nutrients available for uptake deeper and results to deeper and bigger DCMs.

These findings will be most useful when the study will try to duplicate unique chlorophyll profiles among the different basins in Philippine waters as reported by Cordero et al. (unpublished report). Rate of light extinction and application of Liebig's law will be considered in differences in DCM depth while the Michaelis-Menten nutrient uptake form and Liebig's law may be useful when there are differences in DCM magnitude.

However, the need to increase the complexity of the biological model to include other nutrients, phytoplankton and zooplankton variables could arise. In which case the parameter forms used should be specific to such models (e.g. Greek and Legovic, 2001) and phytoplankton growth will follow Liebig's law, since this is typical of multiple-variable models (Varela et al., 1992; Zakardjian & Prieur, 1994; Gecek and Legovic, 2001; Bahamon & Cruzado, 2003).

Future work will be to find and develop a suitable physical model to couple with these biological models that will properly take into account the influence of hydrodynamics on the profiles of the variables studied.

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