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Steady-state solutions for subsurface chlorophyll maximum in stratified water columns with a bell-shape vertical profile of chlorophyll

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Abstract

A bell-shape vertical profile of chlorophyll a (Chl a) concentration, conventionally referred as Subsurface Chlorophyll Maximum (SCM) phenomenon, has frequently been observed in stratified oceans and lakes. This profile is assumed to be a general Gaussian distribution in this study. By substituting the general Gaussian function into ecosystem dynamical equations, the steady-state solutions for SCM characteristics (i.e. SCM layer depth, thickness, and intensity) in various scenarios are derived. These solutions indicate that: (1) The maximum in Chl a concentrations occurs at or below the depth with the maximum in growth rates of phytoplankton locating at the transition from nutrient limitation to light limitation, and the depth of SCM layer deepens logarithmically with an increase in surface light intensity; (2) The shape of SCM layer (thickness and intensity) is mainly influenced by nutrient supply, but independence of surface light intensity; (3) The intensity of SCM layer is proportional to the diffusive flux of nutrient from below, getting stronger as a result of this layer being shrank by a higher light attenuation coefficient or a larger sinking velocity of phytoplankton. The analytical solutions can be useful to estimate environmental parameters difficultly obtained from on-site observations.

1 Introduction

Vertical profiles of chlorophyll a (Chl a) concentration in lakes, coastal seas and open oceans are highly variable. However, a bell-shape vertical profile of Chl a, conventionally regarded as Subsurface Chlorophyll Maximum (SCM) phenomenon, has been frequently observed in stratified water columns, e.g., it occurred through the whole year in tropical and subtropical oceans while it existed only during summer in temperate and high latitude oceanic zones. SCM is commonly believed to be formed in a certain region of the water column where two opposing resource (light and nutrient) gradients combined with a vertically heterogeneous turbulent mixing is amenable for survival of

phytoplankton (Cullen, 1982). Fennel and Boss (2003) reported that the photoacclimation of phytoplankton can be another important reason forming SCM in oligotrophic waters.

The SCM phenomenon can be characterized by the thickness, depth, and intensity of SCM layer (SCML) (Beckmann and Hense, 2007). On-site observations (Platt et al., 1988; Sharples et al., 2001; Dekshenieks et al., 2001; Mellard et al., 2011) showed that the SCML occurred relatively shallow (1–50 m) and thin (several centimeters to a few meters) in lakes and coastal seas, but the concentration of Chl a was high (1–100 mg m^{-3}). In open oceans, the SCML was deeper (80–130 m) and thicker (tens of meters) while the concentration of Chl a is relatively low (< 1 mg m^{-3}) (Anderson, 1969; Platt et al., 1988).

SCM has been attracted much attention because of the significant contribution of SCML to the total biomass and primary production in the whole water column (Cullen and Eppley, 1981; Weston et al., 2005; Siswanto et al., 2005; Hanson et al., 2007; Sullivan et al., 2010). Pérez et al. (2006) showed that 65–75 % of the total Chl a in a water column of the Atlantic subtropical gyres was presented in SCML and the layer thickness was approximately 50 m. Weston et al. (2005) reported that the SCML accounted for 58 % of the water column primary production in the central North Sea, although the layer thickness was less than 5 m. Sullivan et al. (2010) found that the fraction of Chl a in the SCML (thickness < 3 m) out of the total water column ranged from 33 % to 47 % in Monterey Bay.

Many numerical studies have been conducted to link the thickness, depth and intensity of the SCML to various environmental parameters (Jamart et al., 1979; Varela et al., 1994; Klausmeier and Litchman, 2001; Hodges and Rudnick, 2004; Huisman et al., 2006; Beckmann and Hense, 2007). The thickness of SCML mainly depends on the degree of vertical mixing in lakes (Klausmeier and Litchman, 2001). In oligotrophic oceans, light attenuation coefficient is the key factor in determining the SCML depth (Varela et al., 1994; Hodges and Rudnick, 2004; Beckmann and Hense, 2007) and the intensity of the SCML depends strongly on sinking velocity of phytoplankton and

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vertical diffusivity rather than growth rate of phytoplankton (Hodges and Rudnick, 2004; Beckmann and Hense, 2007). However, the thickness, depth and intensity of SCML are very sensitive to variations of environment parameters. Therefore, the relationships obtained from a particular case may not be applicable for other cases. To understand the general relationships between SCM phenomenon and environmental parameters, the analytical solution for dynamic ecosystem equations is needed.

The algae game theoretical model, pioneered by Klausmeier and Litchmann (2001), was perhaps the first one to derive the depth and intensity of SCML, although the SCML is assumed to be infinitely thin. They adopted a delta function to approximate the phytoplankton distribution in this thin layer. Yoshiyama et al. (2009) used this model to examine more than one species competing for the limiting nutrient and light below the surface mixed layer. Mellard et al. (2011) included stratification into this model. However, the SCML was still confined to an infinitely thin layer. In fact, many observations showed that the thickness of SCML can reach as high as 100 m in oceans (Platt et al., 1988). For those cases, the infinite assumption is contradictory to the observations.

In this study, we assume that the vertical profile of Chl *a* can be approximately treated as a general Gaussian function, instead of a delta function under the infinite assumption. This parameterizing approach was proposed firstly by Lewis et al. (1983), and has been widely used to fit vertical profiles of Chl *a* (Platt et al., 1988; Weston et al., 2005; Ardyna et al., 2013). By incorporating the general Gaussian function into the ecosystem dynamical equations, we derive the steady-state solutions for the thickness, depth, and intensity of SCML in various scenarios and examine their dependence on environmental parameters, such as light attenuation coefficient, vertical diffusivity, sinking velocity of phytoplankton, etc.

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2 Methods

2.1 Models

The SCML occurs below the surface mixed layer, where the light attenuated from above and nutrients supplied from the deep water match best for phytoplankton growth (Fig. 1). The partial differential equations for phytoplankton and nutrient dynamics in which light and nutrient are two major limited factors (Eqs. 1 and 2) (Riley et al., 1949; Lewis et al., 1986; Gabric and Parslow, 1989; Huisman et al., 2006; Liccardo et al., 2013) were adopted in this study. Moreover, the photoacclimation of phytoplankton was not considered here and the Chl a distribution is supposed to represent the distribution of phytoplankton biomass. Although the equations are simple, they include the fundamental physical and biological processes that determine the vertical distribution of phytoplankton.

$$\frac{\partial P}{\partial t} = \mu_{m} \min(f(I), g(N))P - \varepsilon P - w\frac{\partial P}{\partial z} + \frac{\partial}{\partial z}\left(K_{v}\frac{\partial P}{\partial z}\right) \tag{1}$$

$$\frac{\partial N}{\partial t} = -\mu_{m} \min(f(I), g(N))P + \alpha\varepsilon P + \frac{\partial}{\partial z}\left(K_{v}\frac{\partial N}{\partial z}\right) \tag{2}$$

where P denotes the Chl a concentration, N is the limiting nutrient concentration, μ_{m} is the maximum growth rate of phytoplankton, ε is the loss rate of phytoplankton (including respiration, mortality, zooplankton grazing etc.), α is the recycling rate of dead phytoplankton ($0 \le \alpha \le 1$), and w is the sinking velocity of phytoplankton. K_{v} is the vertical turbulent diffusivity and it is much larger within the surface mixed layer than that beneath. Here, K_{v} links to different depth in the following way (Hodges and Rudnick, 2004; Mellard et al., 2011):

$$K_{v} = \begin{cases} K_{v1} & 0 < z \le z_{s} \\ K_{v2} & z_{s} < z < z_{b} \end{cases} \tag{3}$$

where z_s is the depth of surface mixed layer, z_b is the bottom of water column. We assume K_{v1}, K_{v2} are constant and K_{v1} is large enough to homogenize the Chl a and nutrient concentrations in the surface mixed layer.

The growth limitation function $\min(f(I), g(N))$ for light I and nutrient N is:

$$\min(f(I), g(N)) = \min\left(\frac{I(z)}{K_I + I(z)}, \frac{N(z)}{K_N + N(z)}\right) \tag{4}$$

where K_I and K_N denote the half-saturation constants of light and nutrient, respectively. The net growth rate, $\mu_m \min(f(I), g(N)) - \varepsilon$, is positive only if both light limiting term $\mu_m f(I)$ and nutrient limiting term $\mu_m g(N)$ are larger than the loss rate ε.

Owing to the absorption and self-shading, light intensity decreases exponentially with depth according to Lambert–Beer's law, i.e.,

$$I(z) = I_0 \exp(-K_d z) \tag{5}$$

where I_0 is the surface light intensity, K_d is the light attenuation coefficient of water, dissolved substances and phytoplankton.

The zero-flux boundary conditions for the phytoplankton at the surface and bottom of water column are used. Furthermore, we assume a zero-flux boundary condition for nutrient at the surface, while nutrient is replenished from below. That is,

$$\begin{cases} K_{v1}\frac{\partial P}{\partial z} - wP = 0, & K_{v1}\frac{\partial N}{\partial z} = 0, & \text{at } z = 0, \\ K_{v2}\frac{\partial P}{\partial z} - wP = 0, & K_{v2}\frac{\partial N}{\partial z} = K_{v2}\frac{\partial N}{\partial z}\Big|_{z=z_b}, & \text{at } z = z_b. \end{cases} \tag{6}$$

In addition, Lewis et al. (1983) first proposed a general Gaussian distribution function (Eq. 7) to model the nonlinear feature of observed vertical Chl a profiles. In this study, this function is adopted to represent the bell-shape vertical distribution of Chl a (Fig. 1).

$$P(z) = \frac{h}{\sigma\sqrt{2\pi}} e^{-\frac{(z-z_m)^2}{2\sigma^2}} \quad 0 \leq z \leq z_b \tag{7}$$

where $P(z)$ is Chl a concentration as a function of depth z. The three Gaussian parameters (h, z_m, σ) can vary to characterize the SCM phenomenon. Thus h is the vertical integrated Chl a over the entire water column, z_m is the depth of the maximum Chl a (the peak of the bell-shape), and σ is the standard deviation of Gaussian function, which controls the width of the SCML.

2.2 Three SCM characteristics

The thickness of SCML can characterize the vertical extent of Chl a distribution below the surface mixed layer. It is still debatable how to best define the thickness of SCML. One easy definition is to use the width between the two locations below and above the Chl a peak, where the Chl a is a certain fraction (e.g. 50 %, $100(e^{-1/2})$%) of the maximum Chl a (Platt et al., 1988; Pérez et al., 2006). Some studies bounded the layer by sharp vertical gradients in Chl a above and below the peak (Prairie et al., 2011). Others defined the upper and lower boundary of SCML by ad hoc choices, respectively. Pedrós-Alió et al. (1999) proposed the SCML from the depth of the surface mixed layer to the lower maximum gradient in the slope of the Chl a profile. Hanson et al. (2007) defined that the upper boundary of the SCML was the minimum gradient criterion of 0.02 mg Chl a m^{-1} and the lower was the base of the euphotic zone. Beckmann and Hense (2007) proposed to define the boundaries of SCML by the existence of two community compensation depths in the water column, which just locate at the depths of two maximum phytoplankton gradients in phytoplankton biomass. This is the first try to link the dynamics and the vertical distribution of phytoplankton.

Building on the study by Beckmann and Hense (2007), the locations of the maximum phytoplankton gradients are defined as the boundaries of SCML in this study. That is,

$$\left.\frac{d^2 P}{dz^2}\right|_{z=z_u, z_l} = 0 \tag{8}$$

where z_u and z_l are the upper and lower boundary of SCML, respectively.

By substituting Eq. (7) into this equality, we obtain $z_u = z_m - \sigma$, $z_l = z_m + \sigma$. Thus, the thickness of SCML can thereby be expressed as 2σ.

From Eq. (8) and the steady state of Eq. (1), one gets the following equality at the boundaries of SCML:

$$\left(\mu_m \min(f(I), g(N))P - \varepsilon P - w \frac{dP}{dz} \right) \Big|_{z=z_u, z_l} = 0 \qquad (9)$$

That is, the boundary of SCML locates at the community compensation depth (Ono et al., 2001), where is the balance between phytoplankton gains (gross growth) and losses (including respiration, mortality, and sinking). Thus, this definition can fully reflect the physical-biological ecosystem dynamics associated with SCML.

The depth of SCML is defined as the location where is the point-wise maximum value of the Chl a. In Eq. (7), z_m represents the term.

The third quantity, i.e. the intensity of SCML, refers to the maximum value of Chl a (P_{max}) in the water column. From Eq. (7) we can obtain $P_{max} = \frac{h}{\sqrt{2\pi}\sigma}$.

2.3 Approach used in this study

Numerical studies (Huisman et al., 2006; Ryabov et al., 2010) suggested that the ecosystem dynamical modeling (Eqs. 1 and 2) can approximately reproduce the bell-shape vertical profile of Chl a (Fig. 1). We substitute the general Gaussian function of vertical Chl a profile (Eq. 7) into Eqs. (1) and (2) to derive explicit relationships between three characteristics of SCM and the environmental parameters.

Firstly, by substituting the general Gaussian function of $P(z)$ with stead state of Eq. (1), we obtain that below the surface mixed layer the net growth rate of phytoplankton can be expressed as follow:

$$\mu_m \min(f(I), g(N)) - \varepsilon = -\frac{K_{v2}}{\sigma^2} \left(z - z_m + \frac{w\sigma^2}{2K_{v2}} \right)^2 + \frac{w^2}{4K_{v2}} + \frac{K_{v2}}{\sigma^2} \qquad (10)$$

Let $\mu_m \min(f(I), g(N)) - \varepsilon = 0$, we get the two compensation depths, z_{c1}, z_{c2}, by solving Eq. (10):

$$z_{c1} = z_m - \frac{w\sigma^2}{2K_{v2}} - \sqrt{\left(\frac{w\sigma^2}{2K_{v2}}\right)^2 + \sigma^2}, \quad z_{c2} = z_m - \frac{w\sigma^2}{2K_{v2}} + \sqrt{\left(\frac{w\sigma^2}{2K_{v2}}\right)^2 + \sigma^2} \tag{11}$$

Clearly, $z_{c1} > z_m - \sigma$ and $z_m < z_{c2} < z_m + \sigma$. This means the two compensation depths locate within the SCML. Hence, according to the property of quadratic function, there exists a depth z_0 within the SCML,

$$z_0 = z_m - \frac{w\sigma^2}{2K_{v2}} \tag{12}$$

such that the net growth rate of phytoplankton is at its maximum, i.e.,

$$\max(\mu_m \min(f(I), g(N)) - \varepsilon)\Big|_{z_0} = \frac{K_{v2}}{\sigma^2} + \frac{w^2}{4K_{v2}} \tag{13}$$

In other words, the maximum in net growth rates of phytoplankton occurs at the depth of z_0.

Let $L = 2K_{v2}/w$, it has been used to be the length scale, which determines the scale height of the phytoplankton distribution (Ghosal and Mandre, 2003). Let $T = \sigma^2/K_{v2}$, and define it as the characteristic vertical mixing time scale. Gabric and Parslow (1989) defined H^2/K to be the characteristic vertical mixing time scale, which is eight times of the vertical mixing time ($H^2/8K$) for neutrally buoyant tracers in waters of depth H with the mixing coefficient K (Bowdon, 1985). In other words, the maximum net growth rate of phytoplankton, $\max(\mu_m \min(f(I), g(N)) - \varepsilon)$, is determined by the vertical mixing time scale (T) and the time taken by a phytoplankton sinking (w) through lengths ($2L$).

Equation (12) also shows that $z_m \geq z_0$, that is, the depth of SCML must occur below or equal to the depth for phytoplankton having the maximum growth rate. Observations

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in the Southern California Bight supported this (Cullen and Eppley, 1981). Particularly, $z_m = z_0$ approximately holds when either the sinking velocity (w) or Gaussian parameter σ is very small. For non-sinking phytoplankton, i.e., $w \to 0$, the numerical modeling can support this equality (Beckmann and Hense, 2007). When parameter σ is assumed to be infinitely thin, the equality is obviously correct, which has been used to solve the equilibrium depth and intensity of an infinitely thin layer (Klausmeier and Litchman, 2001; Yoshiyama et al., 2009; Mellard et al., 2011).

In this special case ($z_m = z_0$), some studies found that the depth of SCML is at the equal limitation by nutrient and light (Klausmeier and Litchman, 2001; Yoshiyama et al., 2009; Mellard et al., 2011). In this study, we further infer that when $z_m > z_0$, the depth of SCML is at the limitation by light (Appendix A).

According to Eqs. (12) and (A2), the growth of phytoplankton is light-limited at and below the depth of SCML. Therefore, for $z = z_m$ and $z = z_m + \sigma$, the net growth rate of phytoplankton (Eq. 10) can be expressed as following, respectively:

$$\mu_m f(I)|_{z=z_m} - \varepsilon = K_{v2}/\sigma^2 \tag{14}$$

$$\mu_m f(I)|_{z=z_m+\sigma} - \varepsilon = -w/\sigma \tag{15}$$

At the depth of z_m, the net growth rate of phytoplankton (Eq. 14) is determined by the vertical mixing time, T, while the time taken by phytoplankton sinking through half-length of SCML, w/σ, controls the net growth rate of phytoplankton (Eq. 15) at the lower boundary of SCML ($z_m + \sigma$).

In addition, from Eq. (11) and (A2) we obtain that the upper compensation depth, z_{c1}, is the location where the growth limited by nutrient, $\mu_m g(N)$, equals to the loss rate, ε, including the respiration, mortality and grazing et al., while the lower compensation depth, z_{c2}, represents the depth where the growth limited by light, $\mu_m f(I)$, equals to the loss rate, ε. The lower compensation depth is the popular definition given by Sverdrup (1953), below which no net growth occurs. The popular compensation depth is physiologically and ecologically sound. However, it is hard to be observed in the field. By

incorporating the function of vertical Chl *a* profile in the ecosystem equations, we can obtain the compensation depth from Eq. (11).

3   Results

3.1   Analytic solutions of three SCM characteristics

By substituting the growth limitation function for light (Eqs. 4 and 5) to Eqs. (14) or (15), we obtain the expression of parameter z_m, i.e.,

$$z_m = \frac{1}{K_d} \ln \left[\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1 \right) \frac{I_0}{K_I} \right] \tag{16}$$

or

$$z_m = \frac{1}{K_d} \ln \left[\left(\frac{\mu_m}{\varepsilon - w/\sigma} - 1 \right) \frac{I_0}{K_I} \right] - \sigma \tag{17}$$

The occurrence for a SCM requires $z_m > 0$. According to the property of an logarithm function, from Eq. (16), we obtain $\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1 \right) \frac{I_0}{K_I} > 1$, i.e., $(\mu_m f(I_0) - \varepsilon) \sigma^2 > K_{v2}$. For any $\sigma > 0$, we get $\mu_m f(I_0) > \varepsilon$. That is, the necessary condition for the existence of SCM is $\mu_m f(I_0) > \varepsilon$.

Subtracting Eqs. (16) and (17), and rearranging, we obtain the expression of parameter σ:

$$\left(\frac{\mu_m}{\mu_m - \varepsilon + \frac{w}{\sigma}} - 1 \right) e^{K_d \sigma} = \frac{\mu_m}{\mu_m - \varepsilon - \frac{K_{v2}}{\sigma^2}} - 1 \tag{18}$$

Thus far, we have obtained the theoretical relationships between Gaussian parameter σ, z_m and environmental parameters (Eqs. 16–18). To derive the relationship between Gaussian parameter h and environmental parameters, we now return to Eqs. (1)

and (2). In steady state, adding these two equations leads to:

$$(1-\alpha)\varepsilon P + w\frac{dP}{dz} = \frac{d^2}{dz^2}(K_v(P+N)) \tag{19}$$

Note that this relationship holds irrespective of the form of growth limiting function. Integrating this equation from the surface to bottom boundary (z_b) and using boundary conditions (Eq. 6) gives:

$$(1-\alpha)\varepsilon \int_0^{z_b} P(z)dz = K_{v2}\frac{dN}{dz}\big|_{z=z_b} \tag{20}$$

When the recycling processes do not immediately convert dead phytoplankton back into dissolved nutrients below the surface mixed layer, i.e., $\alpha \neq 1$ (For $\alpha = 1$, the detailed derivation for the intensity of SCML is presented at Appendix B), one gets the total Chl a in the water column:

$$h = \frac{K_{v2}\frac{dN}{dz}\big|_{z=z_b}}{(1-\alpha)\varepsilon} \tag{21}$$

The intensity of SCML is

$$P_{max} = \frac{K_{v2}\frac{dN}{dz}\big|_{z=z_b}}{\sqrt{2\pi}\sigma(1-\alpha)\varepsilon} \tag{22}$$

Obviously, both the total Chl a in water column and the intensity of SCML are proportional to the flux of nutrients from below ($K_{v2}\frac{dN}{dz}\big|_{z=z_b}$), which is determined by the diffusivity below the surface mixed layer and the nutrient gradient at the bottom of water column. Varela et al. (1994) also found the similar result by simulations.

Equations (16) (or Eq. 17), (18), and (22) provided the possibility to predict the vertical profile of Chl a by remote sensing data (surface light intensity I_0, light attenuation

coefficient K_d) in conjunction with physical-biochemical modeling (such as sinking velocity of phytoplankton w, vertical diffusivity below the surface mixed layer K_{v2}, loss rate ε, etc.).

In addition, the relationships we derived (in this and the previous sections and in Appendixes A and B) can be used to compute missing environmental parameters (such as maximum growth rate μ_m, loss rate ε, recycling rate α, etc.) which are difficult to obtain by on-site observation, if estimates of others are available. For example, Eq. (B4) allows us to obtain an estimate of the sinking velocity of phytoplankton from the measurement of SCM thickness and intensity, the nutrient concentration at water column depth, and the vertical diffusivity below the surface mixed layer.

3.2 Influences of environmental parameters on SCM characteristics

We now investigate how the steady-state thickness, depth, and intensity of SCML depend on environmental parameters. Because the analytic solutions for SCML depth and intensity depend on Gaussian parameter σ and environmental parameters, we should first examine the influence of environmental parameters on parameter σ.

Equation (18) shows that the thickness of SCML is independent of sea surface light intensity (I_0). This is consistent with numerical simulations (Beckmann and Hense, 2007). This result also suggests that seasonal variation of SCML thickness has no relation with light intensity. Thus, it is not surprised that the empirical model poorly predicted parameter σ by using season as an important factor (Richardson et al., 2003).

The vertical diffusivity within the surface mixed layer (K_{v1}) has no influence on the parameter σ. Then we can infer that both the depth and intensity of SCML are independent of K_{v1}, which have already been pointed out by many numerical modeling (Varela et al., 1994; Beckmann and Hense, 2007; Lu et al., 2010).

To illustrate the effects of other environmental parameters (K_d, K_{v2}, μ_m, ε, w) on the parameter σ, we need to obtain informative algebraic expression of σ. To simplify, by

Taylor expanding $e^{K_d\sigma}$ at $\sigma = 0$, Eq. (18) can thereby be rewritten as

$$\sigma^3 - \frac{w}{\varepsilon}\sigma^2 - \frac{\varepsilon K_d K_{v2} + \mu_m w}{\varepsilon K_d(\mu_m - \varepsilon)}\sigma = \frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)} \tag{23}$$

According to the properties of a cubic function, we know that Eq. (23) has one and only one positive real root σ, when $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)} \geq 0$. Because $\mu_m f(I_0) > \varepsilon$ and $0 < f(I_0) < 1$, so $\mu_m > \varepsilon$. Thus, when phytoplankton growth rate (μ_m) within one penetration depth ($1/K_d$) is larger than sinking velocity of phytoplankton, i.e., $\mu_m/K_d - w \geq 0$, there exists a non-negative value of parameter σ, which increases with increasing $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}$.

Using dimensional analysis, Klausmeier and Litchman (2001) found that the degree of turbulence determines the thickness of SCML. Our analytical result shows that the thickness of SCML increases with increasing vertical diffusivity below the surface mixed layer (K_{v2}). In addition, the SCML thickness decreases with increasing sinking velocity of phytoplankton (w) and light attenuation coefficient (K_d).

The right hand term in Eq. (23), $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}$, can be rearranged as $\frac{K_{v2}(\mu_m/K_d - w)}{-(\varepsilon - \mu_m/2)^2 + \mu_m^2/4}$. Thus, the effect of loss rate (ε) on parameter σ should be identified by $\mu_m/2$. Note that $\mu_m f(I_0) > \varepsilon$ once the SCM occurs. When the surface light intensity I_0 is smaller than or equals to the half-saturate constant for light K_l, i.e., $f(I_0) \leq 0.5$, then $0 < \varepsilon < \mu_m f(I_0) \leq \mu_m/2$, thus, σ decreases with increasing ε. Conversely, when $f(I_0) > 0.5$, for $\varepsilon \geq \mu_m/2$, σ increases with increasing ε; for $\varepsilon < \mu_m/2$, σ decreases with increasing ε. In summarize, for smaller loss rates ($\varepsilon < \mu_m/2$), decreased ε leads to a thicker SCML, while for larger loss rates ($\varepsilon \geq \mu_m/2$), decreased ε leads to a thinner SCML.

Equation (16) can be rewritten as

$$z_m = \frac{1}{K_d}\ln(AI_0) \tag{24}$$

where $A = \frac{1}{K_l}\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1\right)$. Clearly, from Eq. (18) we know A is constant with varying surface light intensity (I), thus we infer that the depth of SCML increases logarithmically with increasing I. In other words, the SCML gets deeper dramatically due to the seasonal increase of I, and remains almost unchanged when the surface light intensity

5   increases to a certain degree. Observations at the HOT (Hawaii Ocean Time-series) site in the eastern Pacific and the SEATS (South East Asia Time-series Station) station in the South China Sea showed a significant seasonal variation of SCML depth (Chen et al., 2006; Hense and Beckmann, 2008). Hense and Beckmann (2008) explained the deepening of SCML depth in spring at HOT site by the seasonal increase of the light in-

10   tensity. Modeling sensitivity analyses also showed that an increase in the surface light intensity yields a deeper SCML (Jamart et al., 1979; Varela et al., 1994; Beckmann and Hense, 2007).

Determining the effect of vertical diffusivity below the surface mixed layer (K_{v2}) on the steady-state SCML intensity is more difficult. Increased K_{v2} increases parameter σ

15   (Eq. 23) and the diffusive flux of nutrient from below (Eq. 22), however, this parameter has opposite effects on P_{max} (Eq. 22). Rearranged Eq. (23) we obtain

$$\frac{K_{v2}}{\sigma} = \frac{(\mu_m - \varepsilon)\varepsilon}{(\mu_m/K_d - w)/\sigma^2 + \varepsilon/\sigma} + \frac{(\mu_m - \varepsilon)w}{(\mu_m/K_d - w)/\sigma + \varepsilon} - \frac{\mu_m w/K_d}{(\mu_m/K_d - w)/\sigma^2 + \varepsilon/\sigma} \qquad (25)$$

Clearly, all the three terms in the right hand of this equality increase due to the increasing σ by a higher K_{v2}. Therefore, it can be infered that increased vertical diffusivity

20   below the surface mixed layer (K_{v2}) leads to a stronger SCML intensity (P_{max}).

The influences of varying environmental parameters on SCM characteristics determined by Eqs. (16)–(18), (21) and (22) are summarized in Table 1. For example, increased light levels (increasing surface light intensity I_0, decreasing attenuation coefficient K_d) or increased light competitive ability (decreasing half-saturation constant for

25   light K_l) moves the SCML deeper; increased nutrient supply (increasing vertical diffusivity below the surface mixed layer K_{v2} and loss rate of phytoplankton ε) moves the

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layer toward the surface. The shape of SCML (thickness and intensity) is mainly influenced by nutrient supply (K_{v2} and ε). The intensity of SCML becomes weaker as a result of expanding the SCML by a lower sinking velocity of phytoplankton (w) and a smaller light attenuation coefficient (K_d).

4 Discussion

Equation (18) indicates that changes of parameter σ have an important relation with the vertical diffusivity below the surface mixed layer (K_{v2}), the sinking velocity of phytoplankton (w) and the light attenuation coefficient (K_d), which inversely affects depth and intensity of SCML (Eqs. 16, 17, and 22). Thus, three special situations of the theoretical solutions for SCM characteristics are discussed below.

Firstly, the term K_{v2}/σ^2 in the right hand of Eq. (18) is neglected. This special situation occurs either when the vertical diffusivity below the surface mixed layer is too small to be considered ($K_{v2} \rightarrow 0$), or when K_{v2}/σ^2 is much smaller than $\mu_m - \varepsilon$, i.e., the mixing time scale ($T = \sigma^2/K_{v2}$) below the surface mixed layer is much longer than the time taken by net growth of phytoplankton, $(\mu_m - \varepsilon)^{-1}$. Indeed, in the seasonal thermocline, vertical turbulent diffusive time scales can vary from weeks to months for phytoplankton displacements as small as several meters (Denman and Gargett, 1983). The value of $(\mu_m - \varepsilon)^{-1}$ used in many studies is usually from 0.1 to 5 days (Gabric and Parslow, 1989; Klausmeier and Litchman, 2001; Huisman et al., 2006).

In this situation, from Eq. (14), the growth rate at SCML depth can be expressed as:

$$\mu_m f(I)|_{z=z_m} = \varepsilon \tag{26}$$

In regions with a low vertical diffusivity, Fennel and Boss (2003) derived that, at the SCML depth, the growth rate of phytoplankton equals to the loss rate and the divergence of phytoplankton due to changes in the sinking velocity. Clearly, the form of their conclusion can be rewritten as Eq. (26) when the sinking velocity is constant.

In this situation, the depth of SCML can be derived from Eq. (16), i.e.,

$$z_\mathrm{m} = \frac{1}{K_\mathrm{d}} \ln \frac{(\mu_\mathrm{m} - \varepsilon) I_0}{\varepsilon K_\mathrm{l}} \tag{27}$$

It indicates the SCML depth is directly proportional to the light penetration depth ($1/K_\mathrm{d}$). Beckmann and Hense (2007) have found the similar result by statistical analysis of numerical modeling.

The right hand term of Eq. (27) can be rewritten as $\frac{1}{K_\mathrm{d}} \ln \frac{I_0}{I^*}$ by letting $I^* = \frac{\varepsilon K_\mathrm{l}}{\mu_\mathrm{m} - \varepsilon}$, where $\mu_\mathrm{m} f(I^*) = \varepsilon$. Under the assumption of infinitely thin SCML ($\sigma \to 0$), Klausmeier and Litchman (2001) also have derived Eq. (27) by setting the vertical diffusivity for phytoplankton as zero, i.e., $K_\mathrm{v} = 0$, in poorly mixed waters. Here, we go further to obtain the approximate expression of the thickness of SCML from Eq. (23), that is,

$$2\sigma = \frac{w}{\varepsilon} + \sqrt{\left(\frac{w}{\varepsilon}\right)^2 + \frac{w}{K_\mathrm{d}\left(\varepsilon - \varepsilon^2/\mu_\mathrm{m}\right)}} \tag{28}$$

Obviously, the thickness of SCML increases with an increase in the sinking velocity of phytoplankton (w), and with a decrease in the maximal growth rate (μ_m) and the light attenuation coefficient (K_d).

The second special situation refers to that the term w/σ in the left hand of Eq. (18) is neglected. This special case occurs in regions where phytoplankton sinking velocity is very low ($w \to 0$), or when w/σ is much smaller than $\mu_\mathrm{m} - \varepsilon$, i.e., the time taken by phytoplankton sinking through half-length of SCML, $(w/\sigma)^{-1}$, is much longer than the time taken by net growth of phytoplankton, $(\mu_\mathrm{m} - \varepsilon)^{-1}$. Phytoplankton sinking velocities exhibit a range of values depending on physical and physiological phenomena (e.g., size and shape of the cell). In the environment, estimates of sinking velocity vary from 0 to 9 m per day (Gabric and Parslow, 1989; Huisman and Sommeijer, 2002). Thus, the latter special scenarios (i.e., $w/\sigma \ll \mu_\mathrm{m} - \varepsilon$) can indeed occur.

In this situation, according to Eq. (15), the net growth rate at the lower boundary of SCML can be expressed as

$$\mu_m f(I)|_{z=z_m+\sigma} - \varepsilon = 0 \tag{29}$$

That is, the lower boundary of SCML, $z_m + \sigma$, locates at the compensation depth. In this situation, the depth of SCML can be derived from Eq. (17), i.e.,

$$z_m = \frac{1}{K_d} \ln \frac{(\mu_m - \varepsilon)I_0}{\varepsilon K_I} - \sigma \tag{30}$$

Compared with Eq. (27), we know that the depth of SCML is shallower in this special case than that in case of neglecting the influence of vertical diffusivity below the surface mixed layer on SCM. This result implies that the displacement (σ) of SCML depth is the result of combined influences of vertical diffusivity and sinking velocity of phytoplankton.

In this situation, from Eq. (23), we have

$$\sigma \left(\sigma + \sqrt{\frac{K_{v2}}{\mu_m - \varepsilon}} \right) \left(\sigma - \sqrt{\frac{K_{v2}}{\mu_m - \varepsilon}} \right) = \frac{\mu_m K_{v2}}{(\mu_m - \varepsilon)\varepsilon K_d} \tag{31}$$

The thickness of SCML thickens with a larger vertical diffusivity below the surface mixed layer (K_{v2}), a smaller growth rate (μ_m) or a lower light attenuation coefficient (K_d). Especially, when $K_{v2} = 0$, we have $\sigma = 0$. In other words, for non-sinking phytoplankton ($w \rightarrow 0$), when the vertical diffusivity below the surface mixed layer is very small ($K_{v2} \rightarrow 0$), the SCML disappears. This indicates that there must be a vertical diffusion window sustaining non-sinking phytoplankton species in deep waters.

The third special situation refers to $K_d\sigma$ (i.e., $\sigma/(K_d)^{-1}$) is too small to be considered in Eq. (18). This may occur in clear waters where the light attenuation coefficient is very small ($K_d \rightarrow 0$), or in regions where the light penetration depth ($1/K_d$) is much

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larger than a half-width of SCML (σ). Very narrow (from several to tens of centimeters) SCML has been observed in clear, stratified lakes where the light penetration depths were from several to tens of meters (Fee, 1976; Camacho, 2006).

In this situation, Eq. (18) can be modified to

$$w\sigma + K_{v2} = 0 \tag{32}$$

Clearly, when $K_{v2} = 0$, $w = 0$, this equation has infinitely many solutions. This means in stable, clear waters with a predominance of small cells, the deep SCML can occur with different thicknesses. For example, in the basin of South China Sea, $< 3\,\mu m$ phytoplankton (such as *Prochlorococcus*, *Synechococcus*, picoeukaryotes, etc.) are the dominant species in SCMLs (Takahashi and Hori, 1984; Liu et al., 2007) with variable thicknesses (Lee Chen, 2005; Chen et al., 2006).

5 Summary

A general Gaussian function is assumed to represent a bell-shape vertical distribution of Chl *a* in stratified water columns. The function is incorporated into the ecosystem dynamical equations to determine three steady-state SCM characteristics and examine their dependence on environmental parameters such as vertical diffusivity, sinking velocity of phytoplankton, light attenuation coefficient, etc.

The maximum in Chl *a* concentration occurs at or below the location of the maximum in growth rates of phytoplankton determined by the vertical mixing time scale and the time taken by a phytoplankton sinking through the length scale.

The depth of SCML in steady state deepens logarithmically with an increase in surface light intensity, but shoals with increasing light attenuation coefficient, increasing vertical diffusivity below the surface mixed layer, increasing loss rate of phytoplankton, and with decreasing sinking velocity of phytoplankton.

The shape of SCML (thickness and intensity) is mainly influenced by nutrient supply, but independence of sea surface light intensity. The SCML gets thicker and stronger

with a higher vertical diffusivity below the surface mixed layer. The intensity of SCML in steady state weakens as a result of expanding the SCML by a smaller sinking velocity of phytoplankton and a lower light attenuation coefficient.

In regions with a low vertical diffusivity, the SCML depth is inversely proportional to light attenuation coefficient, and is deeper than that in regions with a dominant of non-sinking phytoplankton. In clear and stable waters with a predominance of small cells, deeper SCMLs can occur with different thicknesses.

Upon potential risk on climate changes, it is critical to accurately estimate the global and regional SCML-related primary production. However, the SCM characteristics cannot be detected by remote sensing satellites, which will restrict the application of satellite data in estimating primary production in a large temporal and spatial scale. The relationships we derived might help to estimate depth-integrated primary production using available data from satellite observations (incident light and light attenuation coefficient) when appropriate vertical estimates of growth rate and loss rate of phytoplankton, sinking velocity of phytoplankton and vertical diffusivity were adopted based on observations or model results. The solutions could also help to compute environmental parameters difficultly obtained by on-site observation.

Appendix A:

In steady state, the net nutrient flux at any given depth (z) equals to the net nutrient consumption by phytoplankton, then we obtain Eq. (A1) below the surface mixed layer:

$$(\mu_m \min(f(I), g(N)) - \alpha \varepsilon) P(z) \approx K_{v2} \frac{dN(z)}{dz}\big|_z \qquad (A1)$$

If $\mu_m \min(f(I), g(N)) - \varepsilon > 0$, then $\mu_m \min(f(I), g(N)) - \alpha \varepsilon > 0$ for $0 < \alpha \leq 1$, we will have $\frac{dN}{dz} > 0$. That is, $N(z)$ will increase with depth below the surface mixed layer.

From the properties of the quadratic function in the right hand of Eq. (10), we have $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ on the interval (z_{c1}, z_{c2}). Hence, we have $\mu_m \min(f(I), g(N)) -$

$\alpha\varepsilon > 0$ for $0 < \alpha \leq 1$, then $dN/dz > 0$. In other words, $N(z)$ increases with depth on the interval (z_{c1}, z_{c2}).

According to Eq. (4), we know that $g(N)$ is a monotonic increasing function on interval (z_{c1}, z_{c2}), and $f(I)$ is a monotonic decreasing function on interval (z_{c1}, z_{c2}). Meanwhile, for the occurrence of SCM in stratified water column, the growth of phytoplankton in the surface mixed layer must be limited by nutrient (Mellard et al., 2011). In other words, the limitation by nutrient $g(N)$ is less than the limitation by light $f(I)$ within the surface mixed layer, i.e., $g(N) < f(I)$ for $0 \leq z \leq z_s$.

Because there is only one maximum in the growth rates of phytoplankton which occurs at the depth $z_0 = z_m - \frac{w\sigma^2}{2K_{v2}}$, and $z_{c1} < z_0 < z_{c2}$ (Eq. 11), we arrive at

$$\min(f(I), g(N)) = \begin{cases} g(N) & z_{c1} \leq z \leq z_0 \\ f(I) & z_0 \leq z \leq z_{c2} \end{cases} \tag{A2}$$

and

$$\max(\mu_m \min(f(I), g(N))) = \mu_m f(I)|_{z=z_0}. \tag{A3}$$

That is, the maximum growth rate occurs at the depth z_0 where is the transition from nutrient limitation to light limitation, and the growth of phytoplankton is light-limited below the depth z_0.

Appendix B:

The dead phytoplankton is entirely recycled ($\alpha = 1$), and thus the system is closed. In this case, at steady state Eq. (19) reduces to

$$w\frac{dP}{dz} = \frac{d^2}{dz^2}(K_v(P + N)) \tag{B1}$$

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Integrating this equation twice from the surface to bottom boundary (z_b) and using boundary conditions (Eq. 6) gives

$$w \int_0^{z_b} P(z)\mathrm{d}z = K_{v1}(P+N)\big|_0^{z_s} + K_{v2}(P+N)\big|_{z_s+0}^{z_b}. \tag{B2}$$

Note that we have known that the SCML occurs only when the growth of phytoplankton within the surface mixed layer is nutrient-limited, then we further assume the surface nutrient value is negligible. Using the assumption of small Chl a at the top and the bottom boundaries of the model domain, we obtain

$$h = \frac{K_{v2}}{w} N(z_b) \tag{B3}$$

and the intensity of SCML is

$$P_{\max} = \frac{K_{v2}}{\sqrt{2\pi}\sigma w} N(z_b) \tag{B4}$$

where $N(z_b)$ is the nutrient concentration at depth z_b. Therefore, with $\alpha = 1$, the intensity of SCML is affected by the ambient nutrient concentration below the surface mixed layer. The total Chl a in the water column depends on the sinking velocity of phytoplankton and the diffusivity, but it is independent on the growth rate and loss rate of phytoplankton. Analogous results have been obtained by Liccardo et al. (2013). Beckmann and Hense (2007) also found similar result by introducing an explicit compartment for the detritus in their models.

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Table 1. Influences of dynamic model parameters on the steady-state SCML thickness (2σ), depth (z_m), intensity (P_max), and the total Chl a in the water column (h).

Model parameters (↑)	2σ	z_m	P_max	h
I_0 (photosynthetically available radiation)	–	↑	–	–
K_I (half-saturation constant of light limited growth)	–	↓	–	–
K_v2 (vertical diffusivity below surface mixed layer)	↑	↓	↑	↑
w (sinking velocity of phytoplankton)	↓	↓	↑	–
K_d (light attenuation coefficient)	↓	↓	↑	–
ε (loss rate of phytoplankton)	↓*	↓	/	↓
	↑**	↓	↓	↓
α (nutrient recycling coefficient)	–	–	↑	↑
$\frac{\mathrm{d}N}{\mathrm{d}z}\big|_{z=z_\mathrm{b}}$ (nutrient gradient at the lower boundary of SCML)	–	–	↑	↑
K_N (half-saturation constant of nutrient limited growth)	–	–	–	–
K_v1 (vertical diffusivity in surface mixed layer)	–	–	–	–
μ_{max} (maximum growth rate of phytoplankton)	/	/	/	/

↑ indicates increase, ↓ indicates decrease, – indicates no effect, / indicates no straightforward result,
* indicates a result when $\varepsilon < \mu_{max}/2$, and ** indicates a result when $\varepsilon > \mu_{max}/2$.
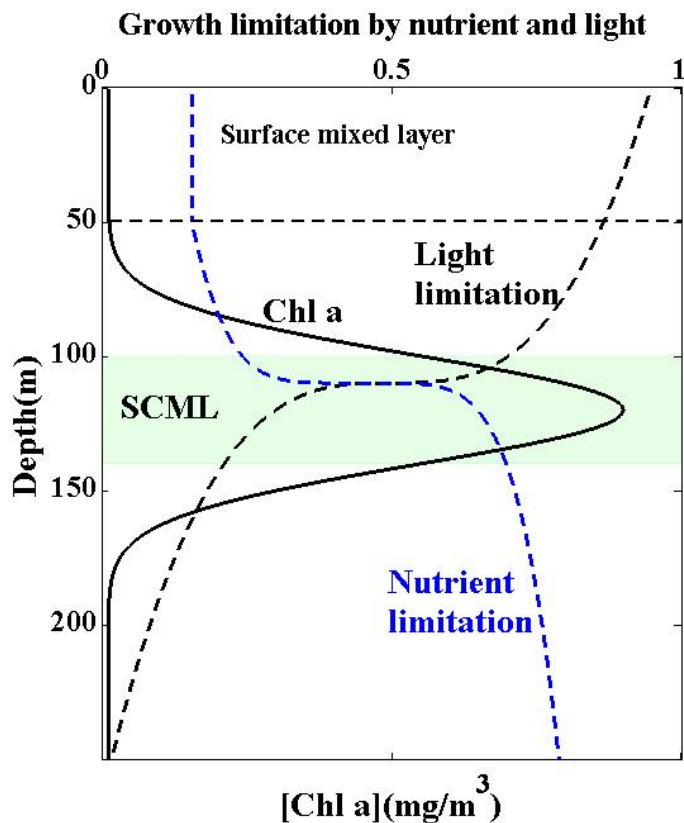
Figure 1. Schematic picture of Chl *a* distribution under the limitation by light and nutrient in stratified water column (black solid line is Chl *a* concentration as a function of depth; black dashed line is the growth limiting term with respect to light; blue dashed line is the growth limiting term with respect to nutrient; horizontal dashed lines represents the depth of surface mixed layer.)

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