Reviewer: E. Boss, UMaine

As I wrote before the topic of this paper is of importance and interest to oceanographers.

While the authors have done a significant job to improve the manuscript, there are still issues, that if addressed could improve the manuscript further.

Response: We are very grateful to the helpful comments and revise our manuscript accordingly.

I am returning and annotated PDF. My major concerns are:

1. The upper layer plays no role, as it seems that it is assumed to have no phytoplankton within it. This, obviously, is an approximation for the tail of the Gaussian which is not discussed.

Response: Thank you for this comment. We modified the discussion of Gaussian function and rewrite the second paragraph of Section 4.2, that is,

'Without considering nutrient input directly to the surface mixed layer, phytoplankton within it is assumed to be nearly zero. This assumption has been proved by Mellard et al. (2011). The SCML is assumed to occur significantly deeper than the base of surface mixed layer, and the vertical gradient of phytoplankton is assumed to be identically zero at the transition between the two layers. This vertical profile of phytoplankton (Fig. 1) is assumed to be fitted by a general Gaussian function (Eq. 7), in which phytoplankton within the surface mixed layer is an approximation for the tail of Gaussian function. The Gaussian assumption leads to the results that both phytoplankton concentration and vertical diffusivity within the surface mixed layer have no roles on the SCM. However, the assumption of a general Gaussian profile can be broken in several ways. If nutrient input directly to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, Chl a concentration within the surface mixed layer will be sustained, while a SCM by itself will be not possible (Mellard et al. 2011). If the depth of surface mixed layer z_s is large, this allows another way for the surface Chl a concentration being positive by extracting some of the Chl a from the SCML (Beckman and Hense, 2007), then the vertical gradient of Chl a may not be identically zero at the transition between the two layers. "

2. Most importantly, the BC for phytoplankton is not physical. Except at the ocean surface, phytoplankton can do a flux to depth. P->0 as z-> infinite would be more appropriate. The use of this BC is responsible to the fact that h and P_{max} are independent of the sinking velocity and also responsible to the large biomass when trying to fit data from the environment.

Response: We agree with you. Based on this suggestion, the bottom boundary condition ($K_v*dP/dz-wP=0$) was modified to P->0 as z-> z_b. z_b can be infinite (z->

infinite), in fact, only if z_b is located at a sufficiently deep water where phytoplankton vanishes together with flux, not necessarily infinite. For the BC, we get the same solutions to h and P_{max} (as shown in Eqs. 21-22), compared to the results by using the BC of $K_v*dP/dz-wP=0$. More importantly, this BC of P->0 as z-> z_b is more easily understood for less mathematically-inclined readers.

3. The author have to explain that they substituted a Gaussian into (1-2) even though this is NOT an exact solution (for example, it does not fit in layer 1 which is supposed to be homogenous in P).

Response: Thank you for this suggestion. We rewrite the paragraph from line 191 to 196 as:

Previous numerical studies (Huisman et al., 2006; Ryabov et al., 2010) showed that the ecosystem dynamical model (Eqs. 1 and 2) can approximately reproduce the bell-shape feature of the vertical Chl a profile (Fig. 1). If nutrient input to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, is considered in the ecosystem, the surface concentration of Chl a should be positive (Mellard et al. 2011). Thus, the general Gaussian function is not an exact solution, at best, an approximate solution of the dynamical Eqs. (1) and (2) by ignoring external nutrient input.

4. In the comparison with in-water data, if you increased K_v you are likely to fit better the thickness of the layer as well as the total biomass.

Response: Following the suggestion, we find that the thicknesses of the SCML can be increased by no more than 2% at the SEATS, HOT, and BATS stations when doubling the vertical diffusivity (K_v), though the SCML intensities (biomass) can increase by 83%, 88%, and 50%, respectively. It implies that we could not make a significant progress on estimations of the thicknesses only by increasing K_v. Therefore, we keep Fig. 2 unchanged.

Review of the revised version of Steady-state solutions for subsurface chlorophyll maximum in stratified water columns with a bell-shape vertical profile of chlorophyll by X. Gong et al.

The authors have responded adequately to the majority of my comments. Hence, the revised version is very much improved. A few (mostly minor) points, however, still require attention:

Response: We thank the helpful comments and revise our manuscript accordingly.

• *line 109 (Equation 2): The conversion factor 1.59 g Chl a per mol N needs to appear in the first two terms on the right hand side of equation 2 (and possibly other equations as well).*

Response: Agree. The conversion factor 1.59 g Chl a per mol N is added in Eq. (2) and (19-22).

• *line 530ff: and Figure 2: It seems that there is a systematic underestimation of the three quantities by the model. Is that something that can be explained?*

Response: As suggested by Prof. Boss, we doubled the vertical diffusivity (K_{v2}) and found that the SCML intensities can increase by 83%, 88%, and 50% at the SEATS, HOT, and BATS stations, respectively. Thus, in the revised version, we added "It should be noted that the estimation is sensitive to the used values of these environmental parameters. The values used in estimations above are representative for the averages over a large spatial or temporal scale, but they may not reflect the real values in a specific station."

• *line 18/19: "The shape of SCM layer (thickness and intensity) are ..." Thickness and intensity do not affect the shape (which is Gaussian in this study). It suffices to write "Thickness and intensity of the SCM are ..."*

• *line 23/24: "were also presented" should be "are also presented".*

• *line 30: "while it existed" should be "while it exists".*

• *line 38: the phrase "with vertically heterogeneous turbulent mixing" may be misleading. Turbulent mixing does not have to be heterogeneous, it is sufficient if there is a vertical profile that can be approximated by two layers of constant diffusivity (as this and other studies have shown).*

• *line 52: "SCM has attracted" should be "SCMs have attracted".*

• *line 70: "... depends strongly on sinking velocity of phytoplankton" the words "and/or detritus" should added, as Beckmann and Hense (2007) do not assume sinking phytoplankton.*

• *line 85: "of an infinite thickness" should be "of an infinitely small thickness".*

• *line 155: "controls the width of the SCML" should be "controls the thickness of the SCML"*

- *line 210: "Especially, ... " should be "In particular, ..."*

- *line 364/366: "sceneries" maybe better "scenarios".*

- *line 462: "Although these are important aspects that could be included ..." I don't see how these aspects could easily be included in this approach without making the system analytically intractable. Maybe just write "Although these are important aspects, their addition is unlikely to change our conclusions qualitatively."*

- *line 491: "... is the growth rate under the limitation of light intensity [...] is larger than ..." should be "... is that the growth rate under the limitation of light intensity [...] is larger than ..."*

- *line 527: Since BATS is spelled out, the same should be done for SEATS and HOTS.*

- *line 588: "Note that we have known ..." is unclear. Do you mean "It is well known that ..."?*

- *line 776: The description of colors in the figure caption is mixed up. In my copy, the red solid line refers to f(I) (not the Chl a concentration, which is green), and there is no black dashed line. Otherwise the figure is much improved.*

- *line 804: is the dN/dz value for HOTS from Beckmann and Hense (2007) or from Hense and Beckmann (2008). Please check again.*

Response: Many thanks for your detailed correction. We have revised them, please see the revised manuscript.

A List of what we changed in the revised version of manuscript:

Revised version 2	Revised version 3
Line 18-19	**Line 18-19**: Change "The shape of SCM layer (thickness and intensity) are ..." to "Thickness and intensity of the SCM are ..."
Line 70	**Line 69**: Change "... depends strongly on sinking velocity of phytoplankton" to "... depends strongly on sinking velocity of phytoplankton and/or detritus".
Line 85	**Line 84-85**: Change "... of an infinite thickness" to "... of an infinitely small thickness".
Line 99-100	**Line 98-99**: Change "... match best for phytoplankton growth" to "... result in the maximal value of phytoplankton growth rate"
Line 103-107	**Line 106-110**: The section from line 103 to 107 is placed at line 106-110, and the reference of Cullen, 1982 is added in line 110 off.
Line 109	**Line 105:** The conversion factor 1.59 g Chl a per mol N is added in the first two terms on the right hand side of Eq. (2).
Line 122-123	**Line 122-123**: Change "z_b is the bottom of water column or the location where the Chl a concentration reduces to nearly zero below the euphotic zone." to "z_b is the location where the Chl a concentration reduces to nearly zero in a sufficiently deep water column."
Line 142-143	**Line 142-145**: The boundary condition for phytoplankton "The zero-flux boundary conditions for the phytoplankton at the surface and bottom of the water column are used." was change to "The zero-flux boundary condition for the phytoplankton at the surface is used. Like the study reported by Ryabov et al. (2010), we also set the chlorophyll concentration approaches zero at the bottom boundary z_b, i.e., $P\rightarrow 0$ for $z\rightarrow z_b$. Fennel and Boss (2003) used an infinite depth as z_b."
Line 145	Equation (6) was modified as "$\begin{cases} K_{v1}\frac{\partial P}{\partial z}=0, \quad K_{v1}\frac{\partial N}{\partial z}=0, & at\ z=0, \\ P(z_b)=0, \quad K_{v2}\frac{\partial N}{\partial z}=K_{v2}\frac{\partial N}{\partial z}\Big\vert_{z=z_b}, & at\ z=z_b. \end{cases}$".
Line 191-196	**Line 196-203**: Add the explanation that we substituted a Gaussian into Eq. (1-2) even though this is NOT an exact

	solution, "We assume a general Gaussian function of $P(z)$ (Eq. 7) is the solution for the Eqs. (1) and (2) at steady-state to derive explicit relationships between three characteristics of SCM and the environmental parameters. If nutrient input to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, is considered in the ecosystem, the surface concentration of Chl a should be positive (Mellard et al. 2011). Thus, the general Gaussian function is not an exact solution, at best, an approximate solution of the dynamical Eqs. (1) and (2) by ignoring external nutrient input."
Line 204	**Line 211-213**: Rewrite this sentence "From the property of quadratic function with pointing downward (the right-hand terms in Eq. 10), we know that for $z_{c1} < z < z_{c2}$ the inequality $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ is satisfied."
Line 274, 278, 283, 285	**Line 282, 286, 291, 296:** The conversion factor 1.59 g Chl a per mol N is added in Eq. (19-22), respectively.
After line 283	**Line 292-294:** Add a new paragraph to interpret Eq. (21), **"**This equality indicates that the total Chl a in the water column (h) is independent of the sinking velocity of phytoplankton. Both Ryabov et al. (2010) and Mellard et al. (2011) obtained a similar result.**"**
Line 392	**Line 403-406:** Add an observed proof of the model result (Eq. 27), "Observations by four Bio-Argo floats in the North Pacific Subtropical Gyre, the South Pacific Subtropical Gyre, the Levantine Sea, and in the northwestern Mediterranean Sea showed a significant positive linear relationship between the two variables (Mignot et al. 2014)."
Line 462-464	**Line 476-478**: Modify the sentence "Although these are important aspects that could be included, their addition is unlikely to change our conclusions qualitatively (Fennel and Boss, 2003)" as "Although these are important aspects, their

	addition is unlikely to change our conclusions qualitatively under the boundary conditions chosen in this study (Fennel and Boss, 2003)."
Line 465-477	**Line 479-495:** Modify the discussion of Gaussian function and rewrite this paragraph "Without considering nutrient input directly to the surface mixed layer, phytoplankton within it is assumed to be nearly zero. This assumption has been proved by Mellard et al. (2011). The SCML is assumed to occur significantly deeper than the base of surface mixed layer, and the vertical gradient of phytoplankton is assumed to be identically zero at the transition between the two layers. This vertical profile of phytoplankton (Fig. 1) is assumed to be fitted by a general Gaussian function (Eq. 7), in which phytoplankton within the surface mixed layer is an approximation for the tail of Gaussian function. The Gaussian assumption leads to the results that both phytoplankton concentration and vertical diffusivity within the surface mixed layer have no roles on the SCM. However, the assumption of a general Gaussian profile can be broken in several ways. If nutrient input directly to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, Chl a concentration within the surface mixed layer will be sustained, while a SCM by itself will be not possible (Mellard et al. 2011). If the depth of surface mixed layer z_s is large, this allows another way for the surface Chl a concentration being positive by extracting some of the Chl a from the SCML (Beckman and Hense, 2007), then the vertical gradient of Chl a may not be identically zero at the transition between the two layers."
Line 486	**Line 504-505:** Change "---Chl a concentration" to "---phytoplankton and zooplankton concentrations".

Line 527-528	**Line 545-546 :** Change "---and the Bermuda Atlantic Time-Series Study (BATS)" to "--- and the BATS (Bermuda Atlantic Time-Series Study)".
Line 533	**Line 551 :** Add an example for nutrient supplement mechanism "--- (e.g., wind-driven nutrient pulse)---"
Line 536	**Line 554-558:** Add some explanations of the differences between modeled and observations in Fig. 2 "It should be noted that the estimation is sensitive to the used values of these environmental parameters. The values used in estimations above are representative for the averages over a large spatial or temporal scale, but they may not reflect the real values in a specific station."
References	Add 1 reference in **line 738-740.**
Tables	Table 2: modify the reference (18) as Hense and Beckmann, 2008.

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 to 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 concentration of Chl a occurs at or below the depth of maximum growth rates of phytoplankton located 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) Thickness and intensity of the SCM are mainly affected by nutrient supply, but independent of surface light intensity; 3) The intensity of SCM layer is proportional to the diffusive flux of nutrients from below, getting stronger as a result of this layer being shrunk by a higher light attenuation coefficient or a larger sinking velocity of phytoplankton. In addition, the limitation and potential application of the analytical solutions are also presented.

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 referred to as Subsurface Chlorophyll Maximum (SCM) phenomenon, has been frequently observed in stratified water columns, e.g., it occurs through the whole year in tropical and subtropical oceans while it exists only during summer in temperate and high latitude oceanic zones. The subsurface biomass maxima (SBMs) are also common in stratified water columns. The chlorophyll-to-biomass ratio generally increases with depth in the euphotic zone. Thus, SCMs may not necessarily represent SBMs (Cullen, 1982; Fennel and Boss, 2003) and are usually deeper than SBMs (Fennel and Boss, 2003; Hodges and Rudnick, 2004). However, both the subsurface maxima in chlorophyll and biomass are usually formed in certain regions of the water column where two opposing resource (light and nutrient) gradients combined with turbulent mixing is amenable for survival of phytoplankton. Thus, SCMs are approximately equal to SBMs in many studies (Klausmeier and Litchman, 2001; Sharples et al., 2001; Huisman et al., 2006; Raybov et al., 2010). Fennel and Boss (2003) reported that the photoacclimation of phytoplankton can be another important reason for forming a 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 was 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 was relatively low (<1 mg/m^3) (Anderson, 1969; Platt et al., 1988).

SCMs have 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 the 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 the 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/or detritus and 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 environmental 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 limiting nutrients 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 assumption of an infinitely small thickness of SCML 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. 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.

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 result in the maximal value of phytoplankton growth rate (Fig. 1). The partial differential equations for phytoplankton and nutrients dynamics in which light and nutrients are two major limiting 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.

$$\frac{\partial P}{\partial t}=\mu_m \min\left(f\left(I\right),g\left(N\right)\right)P-\varepsilon P-w\frac{\partial P}{\partial z}+\frac{\partial}{\partial z}\left(K_v\frac{\partial P}{\partial z}\right), \quad (1)$$

$$\frac{\partial N}{\partial t}=-1.59\mu_m \min\left(f\left(I\right),g\left(N\right)\right)P+1.59\alpha\varepsilon P+\frac{\partial}{\partial z}\left(K_v\frac{\partial N}{\partial z}\right), \quad (2)$$

where P denotes the Chl a concentration, N is the limiting nutrient concentration. The photo-acclimation of phytoplankton is not considered here and the Chl a distribution is supposed to represent the distribution of phytoplankton biomass. This is a significant simplification. In fact, phytoplankton increases inter-cellular pigment concentration when light level decreases (Cullen, 1982; Fennel and Boss, 2003). Usually, the unit of Chl a concentration is mg m^{-3}, the concentrations of phytoplankton and the limiting nutrients are in unit of mmol N m^{-3}. A ratio of 1.59 g chlorophyll per mol nitrogen (Cloern et al., 1995; Oschlies, 2001) is thereby used for unit conversion. μ_m is the maximum growth rate of phytoplankton, ε is the loss rate of phytoplankton (including respiration, mortality, zooplankton grazing), α is the recycling rate of dead phytoplankton ($0\le\alpha\le1$). w is the sinking velocity of phytoplankton, which is non-negative in the chosen coordinate system and assumed to be constant with depths. K_v is the vertical turbulent diffusivity and it is much larger within the surface mixed layer than that beneath. Here, K_v depends on depth in the following way (Hodges and Rudnick, 2004; Mellard et al., 2011):

$$K_v = \begin{cases} K_{v1} & 0 < z < z_s, \\ K_{v2} & z_s < z < z_b, \end{cases} \tag{3}$$

where z_s is the depth of surface mixed layer, z_b is the location where the Chl a concentration reduces to nearly zero in a sufficiently deep 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.

A gradual transition from the surface mixed layer to the deep one written in terms of a generalized Fermi function is adopted (Ryabov et al., 2010), that is, $K_v(z) = K_{v2} + \frac{K_{v1} - K_{v2}}{1+e^{(z-z_s)/l}}$, where parameter l characterizes the width of the transition layer. In our study, we assumed this transition layer is finitely thin.

The growth limited function $\min\left(f(I), g(N)\right)$ for light I and nutrients N is:

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

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

Light intensity is assumed to decrease exponentially with depth according to Lambert-Beer's law, i.e.,

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

where I_0 is the surface light intensity and K_d is the light attenuation coefficient (Morel, 1988). Assuming a constant K_d, we ignore the effects of the self-shading and the dissolved and particulate material on the attenuation coefficient.

The zero-flux boundary condition for the phytoplankton at the surface is used. Like the study reported by Ryabov et al. (2010), we also set the chlorophyll concentration approaches zero at the bottom boundary z_b, i.e., $P \rightarrow 0$ for $z \rightarrow z_b$. Fennel and Boss (2003) used an infinite depth as z_b. Furthermore, we assume a zero-flux boundary condition for nutrients at the surface, while nutrients are replenished from below. That is,

$$\begin{cases} K_{v1}\dfrac{\partial P}{\partial z}=0, \quad K_{v1}\dfrac{\partial N}{\partial z}=0, & at\ z=0, \\ P(z_b)=0, \quad K_{v2}\dfrac{\partial N}{\partial z}=K_{v2}\dfrac{\partial N}{\partial z}\Big|_{z=z_b}, & at\ z=z_b. \end{cases} \tag{6}$$

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).

$$P(z)=P_{\max}e^{-\frac{(z-z_m)^2}{2\sigma^2}} \qquad 0\le z\le z_b, \tag{7}$$

where $P(z)$ is Chl a concentration as a function of depth z, and $P_{\max}=\dfrac{h}{\sigma\sqrt{2\pi}}$. 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 thickness 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 two locations below and above the Chl a peak, where 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. 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 were located at the depths of two maximum phytoplankton gradients in phytoplankton biomass.

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,

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

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:

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

That is, the boundary of SCML is located at the depth where there is the balance between phytoplankton growth and all losses (including the divergence of the sinking flux $w\frac{dP}{dz}$ and the loss ε due to mortality, respiration, and grazing), named the community compensation depth (Ono et al., 2001). Thus, this definition reflects the physical-biological ecosystem dynamics associated with SCML.

As described in Eq. (7), the depth of the SCML is defined as z_m, that is, the location of the point-wise maximum value of Chl a.

The third quantity, i.e. the intensity of SCML, refers to the maximum value of Chl a ($P_{\max}$ in Eq. 7) in the water column.

2.3 Approach used in this study

Previous numerical studies (Huisman et al., 2006; Ryabov et al., 2010) showed that the ecosystem dynamical model (Eqs. 1 and 2) can approximately reproduce the bell-shape feature of the vertical Chl a profile (Fig. 1). We assume a general Gaussian function of $P(z)$ (Eq. 7) is the solution for the Eqs. (1) and (2) at steady-state to derive explicit relationships between three characteristics of SCM and the environmental parameters. If nutrient input to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, is considered in the ecosystem, the surface concentration of Chl a should be positive (Mellard et al. 2011). Thus, the general Gaussian function is not an exact solution, at best, an approximate solution of the dynamical Eqs. (1) and (2) by ignoring external nutrient input.

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

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

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

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

From the property of quadratic function with pointing downward (the right-hand terms in Eq. 10), we know that for $z_{c1} < z < z_{c2}$ the inequality $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ is satisfied. This indicates that the subsurface net production occurs only between the two compensation depths where the growth rate $\mu_m \min(f(I), g(N))$ equals the loss rate ε. Beckmann and Hense (2007) found similar results by numerical modeling and emphasized the often overlooked fact that an SCML has to have two compensation depths.

From Eq. (11), we obtain $z_{c1} \le z_m - \sigma$ and $z_m \le z_{c2} \le z_m + \sigma$ (Fig. 1). In particularly, $z_{c1} = z_m - \sigma$, and $z_{c2} = z_m + \sigma$ when the sinking velocity of phytoplankton w is too small to affect the chlorophyll profile significantly. This result is identical to that of Beckmann and Hense (2007) for neglecting sinking velocity of phytoplankton.

Hence, according to the property of quadratic function, there exists a depth z_0 between the two compensation depths,

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

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

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

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

We define $T=\sigma^2/K_{v2}$ as the characteristic vertical mixing time scale in the SCML of thickness σ (Bowdon, 1985; Gabric and Parslow, 1989). Let the length scale be $L=2K_{v2}/w$, which determines the scale height of the phytoplankton distribution (Ghosal and Mandre, 2003). Thus, the right hand terms of Eq. (13) can be rewritten as $1/T+w/(2L)$. 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 lies at or below the depth for phytoplankton having the maximum growth rate. Observations in the Southern California Bight have 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., $w \to 0$, 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 for 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 location of equal limitation by nutrients 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 located at where phytoplankton growth is limited 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 Eqs. (12) and (A2) we obtain that the upper compensation depth, z_{c1}, is the location where the growth limited by nutrients, $\mu_m g(N)$, equals the loss rate, ε, while the lower compensation depth, z_{c2}, represents the depth where the growth limited by light, $\mu_m f(I)$, equals the loss rate, ε.

3 Results

3.1 Analytic solutions of three SCM characteristics

By substituting the growth limitation function for light (Eqs. 4 and 5) into 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 $z_m>0$. Requiring a positive solution for Eq. (16), we obtain $\left(\frac{\mu_m}{\varepsilon+K_{v2}/\sigma^2}-1\right)\frac{I_0}{K_I}>1$, i.e., $\left(\mu_m f\left(I_0\right)-\varepsilon\right)\sigma^2>K_{v2}$. For any $\sigma>0$, we get $\mu_m f\left(I_0\right)>\varepsilon$. That is, the necessary condition for the existence of SCM is $\mu_m f\left(I_0\right)>\varepsilon$, which is identical with the result of Fennel and Boss (2003) when vertical sinking is constant as a function of depth in their model.

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

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

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:

$$(1-\alpha)\varepsilon P + w\frac{dP}{dz} = \frac{d^2(K_v P)}{dz^2} + \frac{1}{1.59}\frac{d^2(K_v N)}{dz^2} \quad (19)$$

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:

$$1.59(1-\alpha)\varepsilon\int_0^{z_b} P(z)dz = K_{v2}\frac{dN}{dz}\Big|_{z=z_b} \quad (20)$$

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:

$$h = \frac{K_{v2}\frac{dN}{dz}\Big|_{z=z_b}}{1.59(1-\alpha)\varepsilon} \quad (21)$$

This equality indicates that the total Chl a in the water column (h) is independent of the sinking velocity of phytoplankton. Both Ryabov et al. (2010) and Mellard et al. (2011) obtained a similar result.

The intensity of SCML is

$$P_{\max} = \frac{K_{v2}\frac{dN}{dz}\Big|_{z=z_b}}{1.59\sqrt{2\pi}\sigma(1-\alpha)\varepsilon} \quad (22)$$

Obviously, both the total Chl a in the 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 nutrients gradient at the bottom of water column. Varela et al. (1994) also found a similar result by simulations.

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 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 surprising that the empirical model poorly predicted parameter σ by using season as an important factor (Richardson et al., 2003).

To illustrate the effects of other model 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 $\sigma=0$ and truncating the Taylor series after the linear term, i.e., $e^{K_d\sigma}=1+K_d\sigma+o(\sigma^2)$, Eq. (18) can thereby be rewritten as:

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

According to the properties of a cubic function, we know that Eq. (23) has one and only one positive real root σ, when $\frac{K_{v2}\left(\mu_m/K_d-w\right)}{\varepsilon\left(\mu_m-\varepsilon\right)}\geq 0$. Because $\mu_m f\left(I_0\right)>\varepsilon$ and $0<f(I_0)<1$, so $\mu_m>\varepsilon$. Thus, when the maximum 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 $\frac{K_{v2}\left(\mu_m/K_d-w\right)}{\varepsilon\left(\mu_m-\varepsilon\right)}$.

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), $\frac{K_{v2}\left(\mu_m/K_d-w\right)}{\varepsilon\left(\mu_m-\varepsilon\right)}$, can be rearranged as $\frac{K_{v2}\left(\mu_m/K_d-w\right)}{-\left(\varepsilon-\mu_m/2\right)^2+\mu_m^2/4}$. Thus, the effect of loss rate (ε) on parameter σ depends on $\mu_m/2$.

Note that $\mu_{\mathrm{m}} f(I_0) > \varepsilon$ once the SCM occurs. When the surface light intensity I_0 is smaller than or equals to the half-saturation constant for light K_I, i.e., $f(I_0) \le 0.5$, then $0 < \varepsilon < \mu_{\mathrm{m}} f(I_0) \le \mu_{\mathrm{m}}/2$, thus, σ decreases with increasing ε. Conversely, when $f(I_0) > 0.5$, for $\varepsilon \ge \mu_{\mathrm{m}}/2$, σ increases with increasing ε; for $\varepsilon < \mu_{\mathrm{m}}/2$, σ decreases with increasing ε. In summary, for smaller loss rates ($\varepsilon < \mu_{\mathrm{m}}/2$), decreased ε leads to a thicker SCML, while for larger loss rates ($\varepsilon \ge \mu_{\mathrm{m}}/2$), decreased ε leads to a thinner SCML.

Equation (16) can be rewritten as:

$$z_m = \frac{1}{K_d} \ln\left(A I_0\right), \tag{24}$$

where $A = \frac{1}{K_I}\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1\right)$. Clearly, from Eq. (18) we know A does not depend on surface light intensity (I_0), thus we infer that the depth of SCML increases logarithmically with increasing I_0. In other words, the SCML gets deeper due to the seasonal increase of I_0, and remains almost unchanged when the surface light intensity 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 intensity. 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 (Eq. 23) and the diffusive flux of nutrients from below (Eq. 22), however, this parameter has opposite effects on $P_{\max}$ (Eq. 22). Rearranged Eq. (23) we obtain

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

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 inferred that increased vertical diffusivity below the surface mixed layer (K_{v2}) leads to a stronger SCML intensity ($P_{\max}$).

The influences of various 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 light K_I) moves the SCML deeper; increased nutrients supply (increasing vertical diffusivity below the surface mixed layer K_{v2} and loss rate of phytoplankton ε) moves the layer toward the surface. The shape of SCML (thickness and intensity) is mainly influenced by nutrients 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

Considering the two compartment system (nutrients and Chl a) in steady state and a general Gaussian function for vertical Chl a concentration, we derived the analytical solution for the fundamental relationships between SCM characteristics and various parameters. Three special scenarios, limitation and implications of this study were discussed below.

4.1 Three special scenarios

Equation (18) indicates that the parameter σ is affected by changes in 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 ($K_{v2}\to 0$), 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 is equal to the loss rate and the divergence of phytoplankton due to changes in the sinking velocity. Clearly, Eq. (26) is identical to that of Fennel and Boss (2003) for constant sinking velocity of phytoplankton.

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

$$z_m = \frac{1}{K_d} \ln \frac{(\mu_m - \varepsilon) I_0}{\varepsilon K_I}. \tag{27}$$

It indicates the SCML depth is directly proportional to the light penetration depth ($1/K_d$). Observations by four Bio-Argo floats in the North Pacific Subtropical Gyre, the South Pacific Subtropical Gyre, the Levantine Sea, and in the northwestern Mediterranean Sea showed a significant positive linear relationship between the two variables (Mignot et al. 2014). Beckmann and Hense (2007) also found a similar result by statistical analysis of numerical modeling.

The right hand term of Eq. (27) can be rewritten as $\frac{1}{K_d} \ln \frac{I_0}{I^*}$ by letting $I^* = \frac{\varepsilon K_I}{\mu_m - \varepsilon}$, where $\mu_m f(I^*) = \varepsilon$. 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., $K_v = 0$, in poorly mixed waters. Here, we go further to obtain the approximate expression of the thickness of SCML from Eq. (23), that is,

$$2\sigma = \frac{w}{\varepsilon} + \sqrt{\left(\frac{w}{\varepsilon}\right)^2 + \frac{w}{K_d\left(\varepsilon - \varepsilon^2/\mu_m\right)}}. \tag{28}$$

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 occurs when 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 ($w \rightarrow 0$), or when w/σ is much smaller than $\mu_m - \varepsilon$, 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, $(\mu_m - \varepsilon)^{-1}$. 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., $w/\sigma \ll \mu_m - \varepsilon$) 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, $z_m+\sigma$, is located 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 the 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

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

The 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 σ=0. In other words, for non-sinking phytoplankton (w→0), when the vertical diffusivity below the surface mixed layer is very small (K_{v2}→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 occurs when $K_d\sigma$ (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→0), or in regions where the light penetration depth ($1/K_d$) is much 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 μm 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).

4.2 Limitation and potential application

To make the complex problem (SCM phenomenon) tractable, the ecosystem dynamical equations adopted in this study are judiciously simplified. For example, a constant eddy diffusivity is assumed in the surface mixed layer and below this layer, respectively. Many processes (turbulence, internal waves, storms, slant-wise and vertical convection) in upper ocean dynamics are not captured in the model system. The assumption of steady state will be broken during episodic events of strong physical forcing, nutrient injection, or blooms (Fennel and Boss, 2003). Similarly the biological representation is also extremely limited. We neglect food-web and microbial loop dynamics (detritus, dissolved organic matter, and zooplankton are not included explicitly), and assume all loss processes, except sinking, to be linearly proportional to phytoplankton. The sinking velocity of phytoplankton is assumed to be constant with depths, excluding the effects of temperature and density gradients. Our model also neglects some feedback mechanisms, like the effect of phytoplankton on light attenuation. Although these are important aspects, their addition is unlikely to change our conclusions qualitatively under the boundary conditions chosen in this study (Fennel and Boss, 2003).

Without considering nutrient input directly to the surface mixed layer, phytoplankton within it is assumed to be nearly zero. This assumption has been proved by Mellard et al. (2011). The SCML is assumed to occur significantly deeper than the base of surface mixed layer, and the vertical gradient of phytoplankton is assumed to be identically zero at the transition between the two layers. This vertical profile of phytoplankton (Fig. 1) is assumed to be fitted by a general Gaussian function (Eq. 7), in which phytoplankton within the surface mixed layer is an approximation for the tail of Gaussian function. The Gaussian assumption leads to the results that both phytoplankton concentration and vertical diffusivity within the surface mixed layer have no roles on the SCM. However, the assumption of a general Gaussian profile can be broken in several ways. If nutrient input directly to the mixed layer due to riverine inputs, surface runoff, or atmospheric deposition, Chl a concentration within the surface mixed layer will be sustained, while a SCM by itself will be not possible (Mellard et al. 2011). If the depth of surface mixed layer z_s is large, this allows another way for the surface Chl a concentration being positive by extracting some of the Chl a from the SCML (Beckman and Hense, 2007), then the vertical gradient of Chl a may not be identically zero at the transition between the two layers.

Under the assumption of a constant loss rate, the lower compensation depth we got from Eq. (11), the location where the growth rate of phytoplankton limited by light equals the loss rate, is similar to the popular definition of compensation depth given by Sverdrup (1953), below which no net growth occurs. This assumption is in the heart of the Sverdrup's critical depth model and we now understand that it has significant limitations (Behrenfeld and Boss, 2014). Particularly, the treatment of grazing loss, is, in the least, an oversimplification, though many numerical models used a similar one (e.g., Klausmeier and Litchman, 2001; Fennel and Boss, 2003; Huisman et al., 2006). Grazing loss depends strongly on phytoplankton and zooplankton concentrations (it is an encounter based process) and, given that zooplankton can move, or, in the least, grow faster where more food is available, is unlikely to have a constant concentration distribution (Behrenfeld and Boss, 2014).

Our model suggests that the condition for the existence of a SCM is that the growth rate under the limitation of light intensity, $\mu_m f\left(I_0\right)$, is larger than the loss rate, ε, in stratified water columns. Fennel and Boss (2003) found a similar result and pointed out that this condition for a SCM is general. Many numerical studies have reproduced the SCM phenomenon, of which the condition of SCM occurrence met with variable values of the sinking velocity of phytoplankton and the mixing diffusivity (Klausmeier and Litchman, 2001; Huisman et al., 2006; Mellard et al., 2011).

Our two compartment system model reproduces some of the results of the more complex model with three compartments (phytoplankton, nutrients, and detritus, Beckmann and Hense, 2007). For example, our model predicts that with fully recycling of the dead phytoplankton, the total Chl a concentration in water columns depends on the sinking velocity of phytoplankton and the vertical diffusivity, but independents on the growth rate and the loss rate of phytoplankton. Beckmann and Hense (2007) found similar results. Here, we go further to point out an interesting finding that the derivations of the total Chl a are irrespective of the form of the growth limiting function. Since growth functional forms in phytoplankton models are still debated in the literature (Haney, 1996; Ayata et al., 2013), this will be most helpful to estimate the vertical integrated Chl a and primary production.

The relationships (in previous sections and in Appendices A and B) we derived can be used to compute missing model parameters (such as maximum growth rate μ_m, loss rate ε, recycling rate α) 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.

Our analytic solutions can in principle be tested through a comparison with observations: for example, the shape of profiles (the SCML thickness, depth, and intensity), expressed by the characteristic relationships (Eqs. 16-18, 22 and B4), the vertical integral of total subsurface Chl a concentration (Eqs. 21 and B3), the consistency of independent field estimates for sinking velocity, vertical diffusivity, recycling rate and loss rate (Eqs. 21-22 and B3-B4).

We retrieve the three SCM characteristics from Eqs. (16-18, and 22) by combining remote sensing data (annual averaged values of surface light intensity I_0 and light attenuation coefficient K_d) and some parameters from published field and numerical studies (e.g., sinking velocity of phytoplankton w, vertical diffusivity below the surface mixed layer K_{v2}, loss rate ε, maximum growth rate μ_m). Table 2 lists the values of model parameters at three time-series stations in different ocean regions, i.e., the SEATS station, the HOT station, and the BATS (Bermuda Atlantic Time-Series Study) site in the Sargasso Sea, and the corresponding references. The estimated results and the observed values of the SCML thickness, depth and intensity at the three stations are shown in Fig. 2.

The estimated depths and thicknesses of the SCML agree reasonably well with the observations at all three stations. However, the intensities of the SCML are poorly estimated, implying other mechanisms (e.g., wind-driven nutrient pulse) supplying nutrients for the SCML, except upward diffusivity, for phytoplankton growth (Williams et al., 2013). This is the first try to estimate the depth, thickness and intensity of the SCML using parameters from satellite data and field studies. It should be noted that the estimation is sensitive to the used values of these environmental parameters. The values used in estimations above are representative for the averages over a large spatial or temporal scale, but they may not reflect the real values in a specific station. Even though disagreements could be associated with uncertainties from several sources, this type of try would give some idea of how real-world data could be incorporated into the model and thus be applied to the field (Pitarch et al. 2014).

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.

The maximum Chl a concentration occurs at or below the location of the maximum 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 the 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 the SCML (thickness and intensity) is mainly influenced by nutrients supply, but independent 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 dominated by non-sinking phytoplankton. In clear and stable waters with a predominance of small cells, deeper SCMLs can occur with different thicknesses.

Upon potential risk of climate change, 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 Argo float equipped with optical sensor has been developed to measure the distribution of particles and chlorophyll in the world's ocean (Mignot et al., 2014), but the data are still limited. 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. Again, the solutions could also help to compute environmental parameters that are difficult to obtain from on-site observation.

Appendix A

In steady state, the net nutrient flux at any given depth (z) is equals to the net nutrients consumption by phytoplankton, then from steady-state of Eq. (2) we obtain Eq. (A1) below the surface mixed layer:

$$\int\left(\mu_m \min\left(f(I), g(N)\right) - \alpha\varepsilon\right)P(z)dz \approx K_{v2}\frac{dN(z)}{dz}\Big|_z \quad \text{(A1)}$$

If $\mu_m \min(f(I), g(N)) - \varepsilon > 0$, then $\mu_m \min(f(I), g(N)) - \alpha\varepsilon > 0$ for $0 < \alpha \le 1$, 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 $0 < \alpha \le 1$, 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}). It is well known that the stable SCML occurs in stratified water column only when the growth of phytoplankton in the surface mixed layer is nutrient-limited (Mellard et al., 2011; Ryabov et al., 2010). In other words, the limitation by nutrients $g(N)$ is less than the limitation by light $f(I)$ within the surface mixed layer, i.e., $g(N) < f(I)$ for $0 \le z \le z_s$.

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

$$\min\left(f(I), g(N)\right) = \begin{cases} g(N) & z_{c1} \le z \le z_0 \\ f(I) & z_0 \le z \le z_{c2} \end{cases} \quad \text{(A2)}$$

and

$$\max\left(\mu_m \min\left(f(I), g(N)\right)\right) = \mu_m f(I)\Big|_{z=z_0}. \quad \text{(A3)}$$

That is, the maximum growth rate occurs at the depth z_0 where is the transition from nutrients 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

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

Integrating this equation twice from the surface to bottom boundary (z_b) gives

$$w\int_0^{z_b} P(z)dz = K_{v1}\left(P+N\right)\Big|_0^{z_s} + K_{v2}\left(P+N\right)\Big|_{z_s+0}^{z_b} \tag{B2}$$

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 nutrients value is negligible. Using the assumption of small Chl a at the top and the bottom boundaries of the model domain, we obtain

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

and the intensity of SCML is

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

where $N(z_b)$ is the nutrients concentration at depth z_b. Therefore, with $\alpha = 1$, the intensity of SCML is affected by the ambient nutrients 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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References:

Anderson, G. C.: Subsurface chlorophyll maximum in the northeast Pacific Ocean, Limnol. Oceanogr., 14, 386-391, 1969.

Ardyna, M., Babin, M., Gosselin, M., Devred, E., Bélanger, S., Matsuoka, A., Tremblay, J. E.: Parameterization of vertical chlorophyll a in the Arctic Ocean: impact of the subsurface chlorophyll maximum on regional, seasonal and annual primary production estimates, Biogeosciences, 10, 4383-4404, doi: 10.5194/bg-10-4383-2013, 2013.

Ayata, S., Lévy, M., Aumont, O., Sciandra, A., Sainte-Marie, J., Tagliabue, A., Bernard, O.: Phytoplankton growth formulation in marine ecosystem models: should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas? J. Marine Syst., 125, 29-40, 2013.

Beckmann, A., Hense, I.: Beneath the surface: Characteristics of oceanic ecosystems under weak mixing conditions-A theoretical investigation, Prog. Oceanogr., 75, 771-796, 2007.

Behrenfeld, M. J., Boss, E. S.: Resurrecting the ecological underpinnings of ocean plankton blooms, Annu. Rev. Mar. Sci., 6, 167-194, 2014.

Bienfang, P. K., Harrison, P. J.: Sinking-rate response of natural assemblages of temperate and subtropical phytoplankton to nutrient depletion, Mar. Biol., 83, 293-300, 1984.

Bowdon, K. F.: Physical oceanography of coastal waters. Limnol. Oceanogr., 30, 449-450, 1985.

Cai Y. M., Ning X. R., Liu C. G.: Synechococcus and Prochlorococcus growth and mortality rates in the northern China Sea: range of variations and correlation with environmental factors. Acta Ecol. Sin. 7, 2237-2246, 2006.

Camacho, A.: On the occurrence and ecological features of deep chlorophyll maxima (DCM) in Spanish stratified lakes, Limnetica, 25, 453-478, 2006.

Chen, C. C., Shiah, F. K., Chung, S. W., Liu, K. K.: Winter phytoplankton blooms in the shallow mixed layer of the South China Sea enhanced by upwelling, J. Marine Syst., 59, 97-110, 2006.

Cianca, A., Godoy, J. M., Martin, J. M., Perez Marrero, J., Rueda, M. J., Llinás, O., Neuer, S.: Interannual variability of chlorophyll and the influence of low‐frequency climate models in the North Atlantic subtropical gyre, Global Biogeochem. Cy., 26, 2012.

Cianca, A., Helmke, P., Mouriño, B., Rueda, M. J., Llinás, O., Neuer, S.: Decadal analysis of hydrography and in situ nutrient budgets in the western and eastern North Atlantic subtropical gyre, J. Geophys. Res., 112, C07025, 1-18, 2007.

Cloern, J. E., Grenz, C., Vidergar-Lucas, L.: An empirical model of the phytoplankton chlorophyll: carbon ratio-the conservation factor between productivity and growth rate, Limnol. Oceanogr., 40, 1313-1321, 1995.

Cullen, J. J., Eppley, R. W.: Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance, Oceanol. Acta, 1, 23-32, 1981.

Cullen, J. J.: The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a, Can. J. Fish. Aquat. Sci., 39, 791-803, 1982.

Dekshenieks, M. M., Donaghay, P. L., Sullivan, J. M., Rines, J. E., Osborn, T. R., Twardowski, M. S.: Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes, Mar. Ecol-Prog. Ser., 223, 61-71, 2001.

Denman, K. L., Gargett, A. E.: Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean, Limnol. Oceanogr., 28, 801-815, 1983.

Fee, E. J.: The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. Limnol. Oceanogr., 26, 767-783, 1976.

Fennel, K., Boss, E.: Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions from a simple model, Limnol. Oceanogr.,, 48, 1521-1534, 2003.

Gabric, A. J., Parslow, J.: Effect of physical factors on the vertical distribution of phytoplankton in eutrophic coastal waters, Aust. J. Mar. Fishwater Res., 40, 559-569, 1989.

Ghosal, S., Mandre, S.: A simple model illustrating the role of turbulence on phytoplankton blooms, J. Math. Biol., 46, 333-346, 2003.

Haney, J. D.: Modeling phytoplankton growth rates, J. Plankton Res., 18, 63-85, 1996.

Hanson, C. E., Pesant, S., Waite, A. M., Pattiaratchi, C. B.: Assessing the magnitude and significance of deep chlorophyll maxima of the coastal eastern Indian Ocean, Deep-Sea Res. Pt. II, 54, 884-901, 2007.

Hense, I., Beckmann, A.: Revisiting subsurface chlorophyll and phytoplankton distributions, Deep-Sea Res. Pt. I, 55, 1193-1199, 2008.

Hodges, B. A., Rudnick, D. L.: Simple models of steady deep maxima in chlorophyll and biomass, Deep-Sea Res. Pt. I, 51, 999-1015, 2004.

Hood, R. R., Bates, N. R., Capone, D. G., Olson, D. B.: Modeling the effect of nitrogen fixation on carbon and nitrogen fluxes at BATS, Deep-Sea Res. Pt. II, 48, 1609-1648, 2001.

Huisman, J., Sommeijer, B.: Maximal sustainable sinking velocity of phytoplankton, Mar. Ecol-Prog. Ser., 244, 39-48, 2002.

Huisman, J., Thi, N., Karl, D. M., Sommeijer, B.: Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum, Nature, 439, 322-325, 2006.

Jamart, B. M., Winter, D. F., Banse, K.: Sensitivity analysis of a mathematical model of phytoplankton growth and nutrient distribution in the Pacific Ocean off the northwestern US coast, J. Plankton Res., 1, 267-290, 1979.

Klausmeier, C. A., Litchman, E.: Algal games: The vertical distribution of phytoplankton in poorly mixed water columns, Limnol. Oceanogr., 8, 1998-2007, 2001.

Lee Chen, Y.: Spatial and seasonal variations of nitrate-based new production and primary production in the South China Sea, Deep-Sea Res. Pt. I, 52, 319-340, 2005.

Lewis, M. R., Cullen, J. J., Platt, T.: Phytoplankton and thermal structure in the upper ocean: consequences of nonuniformity in chlorophyll profile, J. Geophys. Res., 88, 2565-2570, 1983.

Lewis, M. R., Harrison, W. G., Oakey, N. S., Hebert, D., Platt, T.: Vertical nitrate fluxes in the oligotrophic ocean, Science, 234, 870-873, 1986.

Liccardo, A., Fierro, A., Iudicone, D., Bouruet-Aubertot, P., Dubroca, L.: Response of the Deep Chlorophyll Maximum to fluctuations in vertical mixing intensity, Prog. Oceanogr., 2013, 33-46, 2013.

Liu, H., Chang, J., Tseng, C. M., Wen, L. S., Liu, K. K.: Seasonal variability of picoplankton in the Northern South China Sea at the SEATS station, Deep-Sea Res. Pt. II, 54, 1602-1616, 2007.

Lu, Z., Gan, J., Dai, M., Cheung, A.: The influence of coastal upwelling and a river plume on the subsurface chlorophyll maximum over the shelf of the northeastern South China Sea, J. Marine Syst., 82, 35-46, 2010.

Mara On, E., Holligan, P. M.: Photosynthetic parameters of phytoplankton from 50^{o} N to 50^{o} S in the Atlantic Ocean, Mar. Ecol.-Prog. Ser., 176, 191-203, 1999.

Mellard, J. P., Yoshiyama, K., Litchman, E., Klausmeier, C. A.: The vertical distribution of phytoplankton in stratified water columns, J. Theor. Biol., 269, 16-30, 2011.

Mignot, A., Claustre, H., Uitz, J., Poteau, A., D'Ortenzio, F., Xing, X.: Understanding the seasonal dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments: A Bio-Argo float investigation, Global Biogeochem. Cy., 28, 2013G-4781G, 2014.

Morel, A.: Optical modeling of the upper ocean in relation to its biogenous matter content (case I waters), J. Geophys. Res., 93, 749-768, 1988.

Ono, S., Ennyu, A., Najjar, R. G., Bates, N. R.: Shallow remineralization in the Sargasso Sea estimated from seasonal variations in oxygen, dissolved inorganic carbon and nitrate, Deep-Sea Res. Pt. II, 48, 1567-1582, 2001.

Oschlies, A.: Model-derived estimates of new production: New results point towards lower values, Deep-Sea Res. Pt. II, 48, 2173-2197, 2001.

Pedrós-Alió, C., Calderón-Paz, J. I., Guixa-Boixereu, N., Estrada, M., Gasol, J. M.: Bacterioplankton and phytoplankton biomass and production during summer stratification in the northwestern Mediterranean Sea, Deep-Sea Res. Pt. I, 46, 985-1019, 1999.

Pérez, V., Fernández, E., Mara Ón, E., Morán, X., Zubkov, M. V.: Vertical distribution of phytoplankton biomass, production and growth in the Atlantic subtropical gyres, Deep-Sea Res. Pt. I, 53, 1616-1634, 2006.

Pitarch, J., Odermatt, D., Kawka, M., Wüest, A.: Retrieval of vertical particle concentration profiles by optical remote sensing: a model study, Opt. Express, 22, A947-A959, 2014.

Platt, T., Sathyendranath, S., Caverhill, C. M., Lewis, M. R.: Ocean primary production and available light: further algorithms for remote sensing, Deep-Sea Res. Pt. I, 35, 855-879, 1988.

Prairie, J. C., Franks, P. J. S., Jaffe, J. S., Doubell, M. J., Yamazaki, H.: Physical and biological controls of vertical gradients in phytoplankton, Limnol. Oceanogr., 1, 75-90, 2011.

Raven, J. A., Richardson K.: Photosynthesis in marine environments. In: Topics in Photosynthesis, Elsevier, Edited by N. R. Baker and Long S., 7, 337-399, 1986.

Richardson, A. J., Silulwane, N. F., Mitchell-Innes, B. A., Shillington, F. A.: A dynamic quantitative approach for predicting the shape of phytoplankton profiles in the ocean, Prog. Oceanogr., 59, 301-319, 2003.

Riley, G. A., Stommel, H., Bumpus, D. F.: Quantitative ecology of the plankton of the western North Atlantic, Bulletin Bingham Oceanogra. Collect., 12, 1-69, 1949.

Ryabov, A. B., Rudolf, L., Blasius, B.: Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer, J. Theor. Biol., 263, 120-133, 2010.

Salihoglu, B., Garçon, V., Oschlies, A., Lomas, M. W.: Influence of nutrient utilization and remineralization stoichiometry on phytoplankton species and carbon export: A modeling study at BATS, Deep-Sea Res. Pt. I, 55, 73-107, 2008.

Sharples, J., Moore, C. M., Rippeth, T. P., Holligan, P. M., Hydes, D. J., Fisher, N. R., Simpson, J. H.: Phytoplankton distribution and survival in the thermocline, Limnol. Oceanogr., 46, 486-496, 2001.

Siswanto, E., Ishizaka, J., Yokouchi, K.: Estimating chlorophyll-a vertical profiles from satellite data and the implication for primary production in the Kuroshio front of the East China Sea, J. Oceanogr., 61, 575-589, 2005.

Sullivan, J. M., Donaghay, P. L., Rines, J. E.: Coastal thin layer dynamics: consequences to biology and optics, Cont. Shelf Res., 30, 50-65, 2010.

Sverdrup, H. U.: On conditions for the vernal blooming of phytoplankton, J. Cons. int. Explor. Mer., 18, 287-295, 1953.

Takahashi, M., Hori, T.: Abundance of picophytoplankton in the subsurface chlorophyll maximum layer in subtropical and tropical waters, Mar. Biol., 79, 177-186, 1984.

Tjiputra, J. F., Polzin, D., Winguth, A. M.: Assimilation of seasonal chlorophyll and nutrient data into an adjoint three‐dimensional ocean carbon cycle model: Sensitivity analysis and ecosystem parameter optimization, Global Biogeochem. Cy., 21, GB1001, 1-13, 2007.

Varela, R. A., Cruzado, A., Tintoré, J.: A simulation analysis of various biological and physical factors influencing the deep-chlorophyll maximum structure in oligotrophic areas, J. Marine Syst., 5, 143-157, 1994.

Weston, K., Fernand, L., Mills, D. K., Delahunty, R., Brown, J.: Primary production in the deep chlorophyll maximum of the central North Sea, J. Plankton Res., 27, 909-922, 2005.

Williams, C., Sharples, J., Mahaffey, C., Rippeth, T.: Wind‐driven nutrient pulses to the subsurface chlorophyll maximum in seasonally stratified shelf seas, Geophys. Res. Lett., 2013.

Wu Y. P., Gao K. S.: Photosynthetic response of surface water phytoplankton assemblages to different wavebands of UV radiation in the South China Sea, Acta Oceanol. Sin., 5, 146-151, 2011.

Yoshiyama, K., Mellard, J. P., Litchman, E., Klausmeier, C. A.: Phytoplankton competition for nutrients and light in a stratified water column, Am. Nat., 174, 190-203, 2009.

List of figures and tables

Figure 1

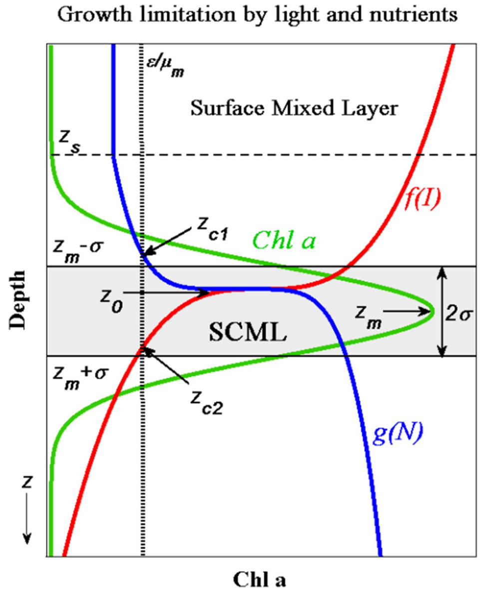

Fig. 1 Schematic picture of Chl a distribution under the limitation by light and nutrient in stratified water columns (green solid line is Chl a concentration as a function of depth; red solid line is the growth limiting term with respect to light, $f(I)$; blue solid line is the growth limiting term with respect to nutrients, $g(N)$; horizontal dashed line represents the depth of surface mixed layer, z_s; horizontal solid lines indicate the locations of the upper- and lower-SCML, z_m-σ, z_m+σ, respectively; vertical dotted line is the ratio of loss rate to maximum growth rate, ε/μ_m; z_{c1} *and* z_{c2} refer to the two compensation depths where $\mu_m g(N)=\varepsilon$ and $\mu_m f(I)=\varepsilon$, respectively; z_0 and z_m indicate the depths of maximum in growth rates and in Chl a concentrations, respectively; double arrow represents the thickness of the SCML, 2σ)

Figure 2

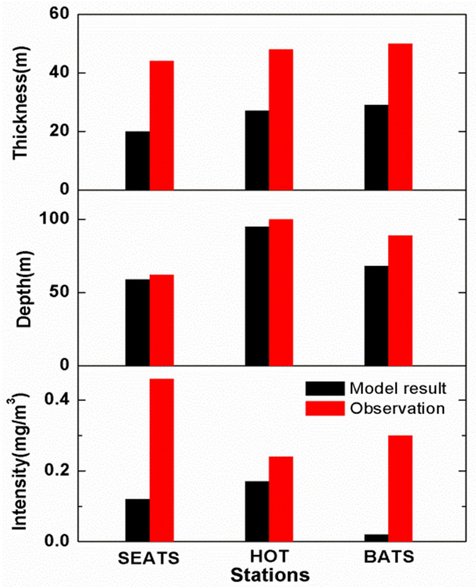

Fig. 2 Comparisons of the model results and observations (in terms of thickness, depth, and intensity of SCML) at SEATS, HOT, and BATS (black columns represent the model results, red columns are the observations at the three stations which were fitted by Gaussian function using annually averaged data obtained from http://www.odb.ntu.edu.tw/, http://hahana.soest.hawaii.edu/hot/hot-dogs/cextraction.html, and http://bats.bios.edu/, respectively)

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 (Surface light intensity)	-	↑	-	-
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)	-	-	↑	↑
$\frac{dN}{dz}\big\|_{z=z_b}$ 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 $\varepsilon>\mu_{max}/2$.

Table 2 Parameter values at SEATS, HOT, and BATS

Parameters	Units	Values at Stations		
		SEATS	HOT	BATS
I_0	$\mu mol\ photos\ m^{-2}\ s^{-1}$	700 [1, 2]	550 [1, 3]	448 [1, 4]
K_d	m^{-1}	0.052 [1, 5]	0.04 [1, 3]	0.042 [1, 4]
K_{v2}	$m^2\ s^{-1}$	$5*10^{-5}$ [6]	$5*10^{-5}$ [3]	$1*10^{-4}$ [7, 8]
μ_{max}	d^{-1}	1.2 [9, 10]	0.96 [3]	1 [11]
K_I	$\mu mol\ photos\ m^{-2}\ s^{-1}$	40 [12]	20 [3]	20 [3, 12, 13]
ε	d^{-1}	0.5 [9, 10]	0.24 [3]	0.5 [14]
α	-	0.3 [10]	0.5 [3]	0.16 [8]
w	$m\ d^{-1}$	1 [15]	1 [3, 15]	2 [8]
dN/dz at depth of z_b	$mmol\ N\ m^{-4}$	0.1 [16]	0.05 [17, 18]	0.02 [19, 20]
z_b	m	200	200	200

Superscripts refer to the references that provide the source for the parameter value and the citations are as follows: [1]http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Annual/9km/; [2]Wu and Gao, 2011; [3]Huisman et al., 2006; [4]Varela et al., 1994; [5]Lee Chen et al., 2005; [6]Lu et al., 2010; [7]Hood et al., 2001; [8]Salihoglu et al., 2008; [9]Cai et al., 2006; [10]Liu et al., 2007; [11]Ayata et al., 2013; [12]Raven and Richardson, 1986; [13]Mara On and Holligan, 1999; [14]Tjiputra et al., 2007; [15]Bienfang and Harrison, 1984; [16]Chen et al., 2006; [17]Fennel and Boss, 2003; [18]Hense and Beckmann, 2008; [19]Cianca et al., 2007; [20]Cianca et al., 2012.