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

X. Gong, J. Shi, H. W. Gao, X. H. Yao

Key Laboratory of Marine Environment and Ecology (Ministry of Education of
China), Ocean University of China, Qingdao 266100, China

7 Correspondence to: H. W. Gao (hwgao@ouc.edu.cn)

8 Abstract:

4

A bell-shape vertical profile of chlorophyll a (Chl a) concentration, conventionally 9 10 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 11 Gaussian distribution in this study. By substituting the general Gaussian function into 12 ecosystem dynamical equations, the steady-state solutions for SCM characteristics 13 (i.e., SCM layer depth, thickness, and intensity) in various scenarios are derived. 14 These solutions indicate that: 1) The maximum concentration of Chl a occurs at or 15 below the depth of maximum growth rates of phytoplankton located at the transition 16 from nutrient limitation to light limitation, and the depth of SCM layer deepens 17 logarithmically with an increase in surface light intensity; 2) The shape of SCM layer 18 (thickness and intensity) is mainly affected by nutrient supply, but independent of 19 surface light intensity; 3) The intensity of SCM layer is proportional to the diffusive 20 flux of nutrients from below, getting stronger as a result of this layer being shrunk by 21 a higher light attenuation coefficient or a larger sinking velocity of phytoplankton. In 22 23 addition, the limitation and potential application of the analytical solutions were also presented. 24

25 **1 Introduction**

Vertical profiles of chlorophyll a (Chl a) concentration in lakes, coastal seas and open 26 oceans are highly variable. However, a bell-shape vertical profile of Chl a, 27 conventionally referred to as Subsurface Chlorophyll Maximum (SCM) phenomenon, 28 has been frequently observed in stratified water columns, e.g., it occurred through the 29 whole year in tropical and subtropical oceans while it existed only during summer in 30 temperate and high latitude oceanic zones. The subsurface biomass maxima (SBMs) 31 are also common in stratified water columns. The chlorophyll-to-biomass ratio 32 generally increases with depth in the euphotic zone. Thus, SCMs may not necessarily 33 34 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 35 subsurface maxima in chlorophyll and biomass are usually formed in certain regions 36 of the water column where two opposing resource (light and nutrient) gradients 37 38 combined with vertically heterogeneous turbulent mixing is amenable for survival of phytoplankton. Thus, SCMs are approximately equal to SBMs in many studies 39 40 (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 41 42 phytoplankton can be another important reason for forming a SCM in oligotrophic 43 waters.

The SCM phenomenon can be characterized by the thickness, depth, and intensity of 44 SCM layer (SCML) (Beckmann and Hense, 2007). On-site observations (Platt et al., 45 1988; Sharples et al., 2001; Dekshenieks et al., 2001; Mellard et al., 2011) showed 46 that the SCML occurred relatively shallow (1-50 m) and was thin (several centimeters 47 to a few meters) in lakes and coastal seas, but the concentration of Chl a was high 48 $(1-100 \text{ mg/m}^3)$. In open oceans, the SCML was deeper (80-130 m) and thicker (tens 49 of meters) while the concentration of Chl a was relatively low ($<1 \text{ mg/m}^3$) (Anderson, 50 1969; Platt et al., 1988). 51

SCM has 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.</p>

Many numerical studies have been conducted to link the thickness, depth and 62 intensity of the SCML to various environmental parameters (Jamart et al., 1979; 63 Varela et al., 1994; Klausmeier and Litchman, 2001; Hodges and Rudnick, 2004; 64 Huisman et al., 2006; Beckmann and Hense, 2007). The thickness of the SCML 65 mainly depends on the degree of vertical mixing in lakes (Klausmeier and Litchman, 66 2001). In oligotrophic oceans, light attenuation coefficient is the key factor in 67 determining the SCML depth (Varela et al., 1994; Hodges and Rudnick, 2004; 68 Beckmann and Hense, 2007) and the intensity of the SCML depends strongly on 69 sinking velocity of phytoplankton and vertical diffusivity rather than growth rate of 70 phytoplankton (Hodges and Rudnick, 2004; Beckmann and Hense, 2007). However, 71 the thickness, depth and intensity of SCML are very sensitive to variations of 72 environmental parameters. Therefore, the relationships obtained from a particular 73 case may not be applicable for other cases. To understand the general relationships 74 75 between SCM phenomenon and environmental parameters, the analytical solution for dynamic ecosystem equations is needed. 76

The algae game theoretical model, pioneered by Klausmeier and Litchmann (2001), 77 was perhaps the first one to derive the depth and intensity of SCML, although the 78 SCML is assumed to be infinitely thin. They adopted a delta function to approximate 79 the phytoplankton distribution in this thin layer. Yoshiyama et al. (2009) used this 80 model to examine more than one species competing for limiting nutrients and light 81 below the surface mixed layer. Mellard et al. (2011) included stratification into this 82 model. However, the SCML was still confined to an infinitely thin layer. In fact, 83 84 many observations showed that the thickness of SCML can reach as high as 100 m in 85 oceans (Platt et al., 1988). For those cases, the assumption of an infinite thickness of SCML is contradictory to the observations. 86

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.

96 2 Methods

97 *2.1 Models*

109

98 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 99 100 growth (Fig. 1). The partial differential equations for phytoplankton and nutrients dynamics in which light and nutrients are two major limited factors (Eqs. 1, 2) (Riley 101 102 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 103 phytoplankton was not considered here and the Chl a distribution is supposed to 104 represent the distribution of phytoplankton biomass. This is a significant 105 simplification. In fact, phytoplankton increases inter-cellular pigment concentration 106 when light level decreases (Fennel and Boss, 2003). 107

108
$$\frac{\partial P}{\partial t} = \mu_m \min(f(I), g(N)) P - \varepsilon P - w \frac{\partial P}{\partial z} + \frac{\partial}{\partial z} \left(K_v \frac{\partial P}{\partial z} \right), \tag{1}$$

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

where P denotes the Chl a concentration, N is the limiting nutrient concentration. 110 Usually, the unit of Chl a concentration is mg m⁻³, the concentrations of 111 phytoplankton and the limiting nutrients are in unit of mmol N m⁻³. A ratio of 1.59 g 112 chlorophyll per mol nitrogen (Cloern et al., 1995; Oschlies, 2001) is thereby used for 113 unit conversion. μ_m is the maximum growth rate of phytoplankton, ε is the loss 114 rate of phytoplankton (including respiration, mortality, zooplankton grazing), α is 115 the recycling rate of dead phytoplankton ($0 \le \alpha \le 1$). w is the sinking velocity of 116 phytoplankton, which is non-negative in the chosen coordinate system and assumed 117 to be constant with depths. K_{y} is the vertical turbulent diffusivity and it is much 118

119 larger within the surface mixed layer than that beneath. Here, K_v depends on depth 120 in the following way (Hodges and Rudnick, 2004; Mellard et al., 2011):

121
$$K_{v} = \begin{cases} K_{v1} & 0 < z < z_{s}, \\ K_{v2} & z_{s} < z < z_{b}, \end{cases}$$
(3)

where z_s is the depth of surface mixed layer, z_b is the bottom of water column or the location where the Chl a concentration reduces to nearly zero below the euphotic zone. 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 transient layer. In our study, we assumed this transient layer is finitely thin.

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

131
$$\min(f(I),g(N)) = \min\left(\frac{I(z)}{K_I + I(z)}, \frac{N(z)}{K_N + N(z)}\right), \tag{4}$$

where K_I and K_N denote the half-saturation constants of light and nutrients, respectively. The net growth rate, $\mu_m \min(f(I), g(N)) - \varepsilon$, 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 toLambert-Beer's law, i.e.,

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

where I_0 is the surface light intensity and K_d is the light attenuation coefficient (Morel, 140 1988). Assuming a constant K_d , we ignore the effects of the self-shading and the 141 dissolved and particulate material on the attenuation coefficient.

142 The zero-flux boundary conditions for the phytoplankton at the surface and bottom of 143 the water column are used. Furthermore, we assume a zero-flux boundary condition 144 for nutrients at the surface, while nutrients are replenished from below. That is,

145
$$\begin{cases} K_{v1} \frac{\partial P}{\partial z} - wP = 0, \quad K_{v1} \frac{\partial N}{\partial z} = 0, & at \ z = 0, \\ K_{v2} \frac{\partial P}{\partial z} - wP = 0, \quad K_{v2} \frac{\partial N}{\partial z} = K_{v2} \frac{\partial N}{\partial z} \Big|_{z=z_b}, & at \ z = z_b. \end{cases}$$
(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).

150
$$P(z) = P_{\max} e^{-\frac{(z-z_m)^2}{2\sigma^2}} \quad 0 \le z \le z_b,$$
(7)

151 where P(z) is Chl a concentration as a function of depth z, and $P_{\text{max}} = \frac{h}{\sigma\sqrt{2\pi}}$. 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

155 Gaussian function, which controls the width of the SCML.

156 2.2 Three SCM characteristics

The thickness of SCML can characterize the vertical extent of Chl a distribution 157 below the surface mixed layer. It is still debatable how to best define the thickness of 158 SCML. One easy definition is to use the width between two locations below and 159 above the Chl a peak, where Chl a is a certain fraction (e.g. 50%, $100(e^{-1/2})\%$) of the 160 maximum Chl a (Platt et al., 1988; Pérez et al., 2006). Some studies bounded the 161 layer by sharp vertical gradients in Chl a above and below the peak (Prairie et al., 162 2011). Others defined the upper and lower boundary of SCML by ad hoc choices. 163 Pedrós-Alió et al. (1999) proposed the SCML from the depth of the surface mixed 164 layer to the lower maximum gradient in the slope of the Chl a profile. Hanson et al. 165 (2007) defined that the upper boundary of the SCML was the minimum gradient 166 criterion of 0.02 mg Chl a m⁻¹ and the lower was the base of the euphotic zone. 167 Beckmann and Hense (2007) proposed to define the boundaries of SCML by the 168 existence of two community compensation depths in the water column, which were 169 located at the depths of two maximum phytoplankton gradients in phytoplankton 170 171 biomass.

Building on the study by Beckmann and Hense (2007), the locations of the maximum

173 phytoplankton gradients are defined as the boundaries of SCML in this study. That is,

$$\frac{d^2 P}{dz^2}\Big|_{z=z_u, z_l} = 0,$$
(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:

180
$$\left(\mu_{m}\min(f(I),g(N))P-\varepsilon P-w\frac{dP}{dz}\right)\Big|_{z=z_{u},z_{l}}=0.$$
 (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 (D_{11}, D_{12}, D_{13})

189 (P_{max} in Eq. 7) in the water column.

190 *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 substitute the general Gaussian function of the vertical Chl a profile (Eq. 7) into Eqs. (1) and (2) to derive explicit relationships between three characteristics of SCM and the environmental parameters.

197 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

199 phytoplankton can be expressed as follows

200
$$\mu_{m} \min(f(I), g(N)) - \varepsilon = -\frac{K_{\nu 2}}{\sigma^{4}} \left(z - z_{m} + \frac{w\sigma^{2}}{2K_{\nu 2}}\right)^{2} + \frac{w^{2}}{4K_{\nu 2}} + \frac{K_{\nu 2}}{\sigma^{2}}.$$
 (10)

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

203
$$z_{c1} = z_m - \frac{w\sigma^2}{2K_{v2}} - \sqrt{\left(\frac{w\sigma^2}{2K_{v2}}\right)^2 + \sigma^2}, \ z_{c2} = z_m - \frac{w\sigma^2}{2K_{v2}} + \sqrt{\left(\frac{w\sigma^2}{2K_{v2}}\right)^2 + \sigma^2}.$$
 (11)

Clearly, the inequality $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ is satisfied in the interval (z_{c1}, z_{c2}) . 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). Especially, $z_{c1} = z_m - \sigma$, and $z_{c2} = z_m + \sigma$ when the sinking velocity of phytoplankton *w* is too small to be considered. 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 within the two compensation depths,

216
$$z_0 = z_m - \frac{w\sigma^2}{2K_{v2}},$$
 (12)

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

218
$$\max\left(\mu_{m}\min(f(I),g(N))-\varepsilon\right)\Big|_{z_{0}} = \frac{K_{v_{2}}}{\sigma^{2}} + \frac{w^{2}}{4K_{v_{2}}}.$$
 (13)

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

We define $T=\sigma^2/K_{\nu 2}$ as the characteristic vertical mixing time scale in the SCML of thickness σ (Bowdon, 1985; Gabric and Parslow, 1989). Let the length scale be $L=2K_{\nu 2}/w$, 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 (2*L*).

Equation (12) also shows that $z_m \ge z_0$, that is, the depth of SCML lies at or below 228 the depth for phytoplankton having the maximum growth rate. Observations in the 229 Southern California Bight have supported this (Cullen and Eppley, 1981). 230 Particularly, $z_m = z_0$ approximately holds when either the sinking velocity (w) or 231 Gaussian parameter σ is very small. For non-sinking phytoplankton, i.e., $w \rightarrow 0$, 232 numerical modeling can support this equality (Beckmann and Hense, 2007). When 233 234 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 235 layer (Klausmeier and Litchman, 2001; Yoshiyama et al., 2009; Mellard et al., 2011). 236

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:

245

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

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

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, 253 ε , while the lower compensation depth, z_{c2} , represents the depth where the growth 254 limited by light, $\mu_m f(I)$, equals the loss rate, ε .

255 **3 Results**

256 *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.,

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

260 or

261
$$z_m = \frac{1}{K_d} \ln \left[\left(\frac{\mu_m}{\varepsilon - w/\sigma} - 1 \right) \frac{I_0}{K_I} \right] - \sigma.$$
(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., $\left(\mu_m f(I_0) - \varepsilon\right) \sigma^2 > K_{v2}$. For any $\sigma > 0$, we

get $\mu_m f(I_0) > \varepsilon$. That is, the necessary condition for the existence of SCM is $\mu_m f(I_0) > \varepsilon$, 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 :

269
$$\left(\frac{\mu_m}{\mu_m - \varepsilon + \frac{W}{\sigma}} - 1\right) e^{K_d \sigma} = \frac{\mu_m}{\mu_m - \varepsilon - \frac{K_{\nu 2}}{\sigma^2}} - 1$$
(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:

274
$$(1-\alpha)\varepsilon P + w\frac{dP}{dz} = \frac{d^2}{dz^2} (K_v(P+N))$$
(19)

275 Note that this relationship holds irrespective of the form of growth limiting function.

276 Integrating this equation from the surface to bottom boundary (z_b) and using 277 boundary conditions (Eq. 6) gives:

278
$$(1-\alpha)\varepsilon \int_0^{z_b} P(z)dz = K_{\nu 2} \frac{dN}{dz}\Big|_{z=z_b}$$
(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:

283
$$h = \frac{K_{v2} \frac{dN}{dz}|_{z=z_b}}{(1-\alpha)\varepsilon}$$
(21)

284 The intensity of SCML is

285
$$P_{\max} = \frac{K_{v2} \frac{dN}{dz} \Big|_{z=z_b}}{\sqrt{2\pi}\sigma(1-\alpha)\varepsilon}$$
(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 $(K_{v2} \frac{dN}{dz}|_{z=z_b})$, 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.

291 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 $(K_d, K_{v2}, \mu_m, \varepsilon, w)$ 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:

306
$$\sigma^{3} - \frac{w}{\varepsilon} \sigma^{2} - \frac{\varepsilon K_{d} K_{v2} + \mu_{m} w}{\varepsilon K_{d} (\mu_{m} - \varepsilon)} \sigma = \frac{K_{v2} (\mu_{m} / K_{d} - w)}{\varepsilon (\mu_{m} - \varepsilon)}.$$
 (23)

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

309 $0 \le f(I_0) \le 1$, so $\mu_m > \varepsilon$. Thus, when the maximum phytoplankton growth rate (μ_m) 310 within one penetration depth $(1/K_d)$ is larger than sinking velocity of phytoplankton, 311 i.e., $\mu_m/K_d - w \ge 0$, there exists a non-negative value of parameter σ , which

312 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).

318 The right hand term in Eq. (23),
$$\frac{K_{\nu 2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}$$
, can be rearranged as

319
$$\frac{K_{v2}(\mu_m/K_d - w)}{-(\varepsilon - \mu_m/2)^2 + \mu_m^2/4}$$
. Thus, the effect of loss rate (ε) on parameter σ depends on $\mu_m/2$

Note that $\mu_{\rm m} f(I_0) > \varepsilon$ 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 $0 < \varepsilon < \mu_{\rm m} f(I_0) \le \mu_{\rm m}/2$, thus, σ decreases with increasing ε . Conversely, when $f(I_0) > 0.5$, for $\varepsilon \ge \mu_{\rm m}/2$, σ increases with increasing ε ; for $\varepsilon < \mu_{\rm m}/2$, σ decreases with increasing ε . In summary, for smaller loss rates ($\varepsilon < \mu_{\rm m}/2$), decreased ε leads to a thicker SCML, while for larger loss rates ($\varepsilon \ge \mu_{\rm m}/2$), decreased ε leads to a thinner SCML.

327 Equation (16) can be rewritten as:

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

329 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

328

surface light intensity (I_0) , thus we infer that the depth of SCML increases 330 logarithmically with increasing I_0 . In other words, the SCML gets deeper due to the 331 seasonal increase of I_0 , and remains almost unchanged when the surface light 332 intensity increases to a certain degree. Observations at the HOT (Hawaii Ocean 333 Time-series) site in the eastern Pacific and the SEATS (South East Asia Time-series 334 Station) station in the South China Sea showed a significant seasonal variation of 335 SCML depth (Chen et al., 2006; Hense and Beckmann, 2008). Hense and Beckmann 336 (2008) explained the deepening of SCML depth in spring at HOT site by the seasonal 337 increase of the light intensity. Modeling sensitivity analyses also showed that an 338 increase in the surface light intensity yields a deeper SCML (Jamart et al., 1979; 339 Varela et al., 1994; Beckmann and Hense, 2007). 340

Determining the effect of vertical diffusivity below the surface mixed layer ($K_{\nu 2}$) on the steady-state SCML intensity is more difficult. Increased $K_{\nu 2}$ 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

345
$$\frac{K_{v2}}{\sigma} = \frac{(\mu_m - \varepsilon)\varepsilon}{(\mu_m/K_d - w)/\sigma^2 + \varepsilon/\sigma} + \frac{(\mu_m - \varepsilon)w}{(\mu_m/K_d - w)/\sigma + \varepsilon} - \frac{\mu_m w/K_d}{\mu_m/K_d - w + \varepsilon\sigma}.$$
 (25)

Clearly, all the three terms in the right hand of this equality increase due to the increasing σ by a higher $K_{\nu 2}$. Therefore, it can be inferred that increased vertical diffusivity below the surface mixed layer ($K_{\nu 2}$) 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_l) moves the SCML deeper; increased nutrients supply (increasing vertical diffusivity below the surface mixed layer $K_{\nu 2}$ 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).

360 **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 sceneries, limitation and implications of this study were discussed below.

366 *4.1 Three special sceneries*

Equation (18) indicates that the parameter σ is affected by changes in the vertical diffusivity below the surface mixed layer ($K_{\nu 2}$), 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.

372 Firstly, the term K_{2}/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 373 too small to be considered $(K_{\nu 2} \rightarrow 0)$, or when $K_{\nu 2}/\sigma^2$ is much smaller than $\mu_m - \varepsilon$, 374 i.e., the mixing time scale $(T = \sigma^2/K_{v_2})$ below the surface mixed layer is much longer 375 than the time taken by net growth of phytoplankton, $(\mu_m - \varepsilon)^{-1}$. Indeed, in the 376 377 seasonal thermocline, vertical turbulent diffusive time scales can vary from weeks to months for phytoplankton displacements as small as several meters (Denman and 378 Gargett, 1983). The value of $(\mu_m - \varepsilon)^{-1}$ used in many studies is usually from 0.1 to 5 379 days (Gabric and Parslow, 1989; Klausmeier and Litchman, 2001; Huisman et al., 380 2006). 381

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

383

$$\mu_m f(I)|_{z=z_m} = \varepsilon.$$
(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 ofphytoplankton.

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

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

It indicates the SCML depth is directly proportional to the light penetration depth ($1/K_d$). Beckmann and Hense (2007) have 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 ($\sigma \rightarrow 0$), 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,

$$2\sigma = \frac{w}{\varepsilon} + \sqrt{\left(\frac{w}{\varepsilon}\right)^2 + \frac{w}{K_d \left(\varepsilon - \varepsilon^2 / \mu_{\rm m}\right)}}.$$
(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).

400

The second special situation occurs when the term w/σ in the left hand of Eq. (18) is 404 neglected. This special case occurs in regions where phytoplankton sinking velocity 405 is very low $(w \rightarrow 0)$, or when w/σ is much smaller than $\mu_m - \varepsilon$, i.e., the time taken by 406 phytoplankton sinking through half-length of SCML, $(w/\sigma)^{-1}$, is much longer than the 407 time taken by net growth of phytoplankton, $(\mu_m - \varepsilon)^{-1}$. Phytoplankton sinking 408 velocities exhibit a range of values depending on physical and physiological 409 phenomena (e.g., size and shape of the cell). In the environment, estimates of sinking 410 411 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 412 413 occur.

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

416
$$\mu_m f(I)|_{z=z_m+\sigma} -\varepsilon = 0.$$
(29)

417 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.,

419
$$z_m = \frac{1}{K_d} \ln \frac{(\mu_m - \varepsilon) I_0}{\varepsilon K_I} - \sigma.$$
(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.

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

426
$$\sigma \left(\sigma + \sqrt{\frac{K_{\nu 2}}{\mu_{\rm m} - \varepsilon}} \right) \left(\sigma - \sqrt{\frac{K_{\nu 2}}{\mu_{\rm m} - \varepsilon}} \right) = \frac{\mu_{\rm m} K_{\nu 2}}{(\mu_{\rm m} - \varepsilon) \varepsilon K_d}.$$
(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 $\sigma = 0$. 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 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 $(K_d \rightarrow 0)$, 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).

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

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

Clearly, when $K_{\nu 2} = 0$, 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).

448 *4.2 Limitation and potential application*

To make the complex problem (SCM phenomenon) tractable, the ecosystem 449 dynamical equations adopted in this study are judiciously simplified. For example, a 450 constant eddy diffusivity is assumed in the surface mixed layer and below this layer, 451 respectively. Many processes (turbulence, internal waves, storms, slant-wise and 452 vertical convection) in upper ocean dynamics are not captured in the model system. 453 The assumption of steady state will be broken during episodic events of strong 454 physical forcing, nutrient injection, or blooms (Fennel and Boss, 2003). Similarly the 455 456 biological representation is also extremely limited. We neglect food-web and microbial loop dynamics (detritus, dissolved organic matter, and zooplankton are not 457 included explicitly), and assume all loss processes, except sinking, to be linearly 458 proportional to phytoplankton. The sinking velocity of phytoplankton is assumed to 459 460 be constant with depths, excluding the effects of temperature and density gradients. Our model also neglects some feedback mechanisms, like the effect of phytoplankton 461 462 on light attenuation. Although these are important aspects that could be included, their addition is unlikely to change our conclusions qualitatively (Fennel and Boss, 463 2003). 464

In a stratified water column with a well-mixed surface layer on top of a poorly mixed 465 subsurface layer, a general Gaussian function of vertical Chl a profile represents the 466 distribution of which the surface Chl a concentration is nearly zero, the maximum of 467 Chl a is significantly deeper than the base of surface mixed layer, and the vertical 468 gradient of Chl a is identically zero at the transition between the two layers. The 469 470 assumption of a general Gaussian profile can be broken in several ways. If nutrient input to the mixed layer due to riverine inputs, surface runoff, or atmospheric 471 deposition, was considered in the ecosystem, then the surface concentration of Chl a 472

441

should be positive (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 478 from Eq. (11), the location where the growth rate of phytoplankton limited by light 479 equals the loss rate, is similar to the popular definition of compensation depth given 480 by Sverdrup (1953), below which no net growth occurs. This assumption is in the 481 heart of the Sverdrup's critical depth model and we now understand that it has 482 significant limitations (Behrenfeld and Boss, 2014). Particularly, the treatment of 483 grazing loss, is, in the least, an oversimplification, though many numerical models 484 used a similar one (e.g., Klausmeier and Litchman, 2001; Fennel and Boss, 2003; 485 486 Huisman et al., 2006). Grazing loss depends strongly on Chl a concentration (it is an encounter based process) and, given that zooplankton can move, or, in the least, grow 487 faster where more food is available, is unlikely to have a constant concentration 488 489 distribution (Behrenfeld and Boss, 2014).

Our model suggests that the condition for the existence of a SCM is the growth rate under the limitation of light intensity, $\mu_m f(I_0)$, 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 497 complex model with three compartments (phytoplankton, nutrients, and detritus, 498 499 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 500 501 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 502 Hense (2007) found similar results. Here, we go further to point out an interesting 503 finding that the derivations of the total Chl a are irrespective of the form of the 504

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.

515 Our analytic solutions can in principle be tested through a comparison with 516 observations: for example, the shape of profiles (the SCML thickness, depth, and 517 intensity), expressed by the characteristic relationships (Eqs. 16-18, 22 and B4), the 518 vertical integral of total subsurface Chl a concentration (Eqs. 21 and B3), the 519 consistency of independent field estimates for sinking velocity, vertical diffusivity, 520 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 521 remote sensing data (annual averaged values of surface light intensity I_0 and light 522 attenuation coefficient K_d) and some parameters from published field and numerical 523 studies (e.g., sinking velocity of phytoplankton w, vertical diffusivity below the 524 surface mixed layer $K_{\nu 2}$, loss rate ε , maximum growth rate μ_m). Table 2 lists the 525 values of model parameters at three time-series stations in different ocean regions, i.e., 526 the SEATS station, the HOT station, and the Bermuda Atlantic Time-Series Study 527 528 (BATS) 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 529 three stations are shown in Fig. 2. 530

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 that other mechanisms 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. We note that the kinematic solution assumed (Eq. 7) is, at best, an approximate solution of the dynamical Eqs. (1-2). 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).

541 **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.
- 563 Upon potential risk of climate change, it is critical to accurately estimate the global 564 and regional SCML-related primary production. However, the SCM characteristics 565 cannot be detected by remote sensing satellites, which will restrict the application of 566 satellite data in estimating primary production in a large temporal and spatial scale. 567 The relationships we derived might help to estimate depth-integrated primary 568 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.

574

575 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:

579
$$\int \left(\mu_m \min(f(I), g(N)) - \alpha \varepsilon \right) P(z) dz \approx K_{v2} \frac{dN(z)}{dz} |_z$$
(A1)

580 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}) . Note that we have 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

595
$$\min(f(I), g(N)) = \begin{cases} g(N) & z_{c1} \le z \le z_0 \\ f(I) & z_0 \le z \le z_{c2} \end{cases}$$
(A2)

596 and

597
$$\max\left(\mu_{m}\min(f(I),g(N))\right) = \mu_{m}f(I)\Big|_{z=z_{0}}.$$
 (A3)

598 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 .

601 Appendix B

604

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) and using boundary conditions (Eq. 6) gives

607
$$w \int_{0}^{z_{b}} P(z) dz = K_{v1} (P+N) \Big|_{0}^{z_{s}} + K_{v2} (P+N) \Big|_{z_{s}+0}^{z_{b}}$$
(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

$$h = \frac{K_{\nu 2}}{W} N(z_b)$$
(B3)

and the intensity of SCML is

614
$$P_{\max} = \frac{K_{\nu 2}}{\sqrt{2\pi}\sigma w} N(z_b)$$
(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.

Acknowledgements. We gratefully acknowledge E. Boss, J. Pitarch, and two
anonymous reviewers for constructive and insightful reviews. We also thank
particularly X. H. Liu and Z. Y. Cai for programming assistance and precious advice.
This work is funded in part by the National Key Basic Research Program of China
under the contract 2014CB953700, the National Nature Science Foundation of China
under the contract (41406010, 41210008, 41106007), and the China Postdoctoral
Science Foundation under the contract 2013M541958.

References:

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

632 Ardyna, M., Babin, M., Gosselin, M., Devred, E., Bélanger, S., Matsuoka, A., Tremblay, J. E.:

633 Parameterization of vertical chlorophyll a in the Arctic Ocean: impact of the subsurface chlorophyll

634 maximum on regional, seasonal and annual primary production estimates, Biogeosciences, 10,

635 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.

646 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.
- 649 Camacho, A.: On the occurrence and ecological features of deep chlorophyll maxima (DCM) in
 650 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.
- 653 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.
- 656 Cianca, A., Helmke, P., Mouriño, B., Rueda, M. J., Llinás, O., Neuer, S.: Decadal analysis of 657 hydrography and in situ nutrient budgets in the western and eastern North Atlantic subtropical gyre, J.
- 658 Geophys. Res., 112, C07025, 1-18, 2007.
- 659 Cloern, J. E., Grenz, C., Vidergar-Lucas, L.: An empirical model of the phytoplankton chlorophyll:
- 660 carbon ratio-the conservation factor between productivity and growth rate, Limnol. Oceanogr., 40,661 1313-1321, 1995.
- 662 Cullen, J. J., Eppley, R. W.: Chlorophyll maximum layers of the Southern California Bight and
 663 possible mechanisms of their formation and maintenance, Oceanol. Acta, 1, 23-32, 1981.
- 664 Cullen, J. J.: The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a, Can. J. Fish.
 665 Aquat. Sci., 39, 791-803, 1982.
- 666 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.
- 671 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.
- 674 Fennel, K., Boss, E.: Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions
- 675 from a simple model, Limnol. Oceanogr., 48, 1521-1534, 2003.

629

- 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.
- 678 Ghosal, S., Mandre, S.: A simple model illustrating the role of turbulence on phytoplankton blooms, J.

679 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,
- 683 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 productionin 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.
- 707 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° N to 50° 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.
- 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.
- 718 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.
- 723 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.
- 735 Raven, J. A., Richardson K.: Photosynthesis in marine environments. In: Topics in Photosynthesis,
- 736 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.
- 744 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.
- 749 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 biologyand 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.
- 758 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.
- 761 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.
- 770 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.

772 List of figures and tables

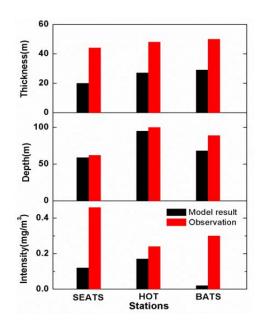
Figure 1

Growth limitation by light and nutrients ε/µ m Surface Mixed Layer Z _<u>s</u>_ \mathcal{T} c1 Chl a $z_m^{-\sigma}$ Depth z_o z_m SCML $z_m + \sigma$ z_{c2} g(N) Chl a

774

775 Fig. 1 Schematic picture of Chl a distribution under the limitation by light and nutrient in stratified water column (red solid line is Chl a concentration as a function of depth; black dashed 776 777 line is the growth limiting term with respect to light, f(I); blue dashed line is the growth limiting 778 term with respect to nutrients, g(N); horizontal dashed line represents the depth of surface mixed 779 layer, z_s ; horizontal solid lines indicate the locations of the upper- and lower-SCML, z_m - σ , z_m + σ , 780 respectively; vertical dotted line is the ratio of loss rate to maximum growth rate, ε/μ_m ; z_{c1} and z_{c2} 781 refer to the two compensation depths where $\mu_m g(N) = \varepsilon$ and $\mu_m f(I) = \varepsilon$, respectively; z_0 and z_m 782 indicate the depths of maximum in growth rates and in Chl a concentrations, respectively; double 783 arrow represents the thickness of the SCML, 2σ)

Figure 2



785

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)

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

Model parameters (↑)	2σ	Z_m	P_{max}	k
I_0 (Surface light intensity)	-	Ţ	-	-
K_I (Half-saturation constant of light limited growth)	-	Ļ	-	-
$K_{\nu 2}$ (Vertical diffusivity below surface mixed layer)	¢	Ļ	Ţ	1
w (Sinking velocity of phytoplankton)	\downarrow	\downarrow	Ť	-
K_d (Light attenuation coefficient)	Ļ	Ļ	¢	-
	↓*	\downarrow	/	
(Loss rate of phytoplankton) ε	1**	Ļ	Ļ	
α (Nutrient recycling coefficient)	-	-	ţ	
$\frac{dN}{dz}\Big _{z=z_b}$ Nutrient gradient at the lower boundary of SCML	-	-	Ţ	
K_N (Half-saturation constant of nutrient limited growth)	-	-	-	
K_{vI} (Vertical diffusivity in surface mixed layer)	-	-	-	-
μ_{max} (Maximum growth rate of phytoplankton)	/	/	/	,

 \uparrow indicates increase, \downarrow indicates decrease, - indicates no effect, / indicates no straightforward

result, * indicates a result when $\varepsilon < \mu_{max}/2$, and ** indicates a result when $\varepsilon > \mu_{max}/2$.

	Units		Values at Stations	
Parameters		SEATS	НОТ	BATS
I_0	μ 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	μ mol photos m ⁻² s ⁻¹	40 (12)	20 ⁽³⁾	20 (3, 12, 13)
Э	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	т	200	200	200

Table 2 Parameter values at SEATS, HOT, and BATS

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⁾Beckmann and Hense, 2007; ⁽¹⁹⁾Cianca et al., 2007; ⁽²⁰⁾Cianca et al., 2012.