

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

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

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

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

8 **Abstract:**

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

25 **1 Introduction**

26 Vertical profiles of chlorophyll a (Chl a) concentration in lakes, coastal seas and open
27 oceans are highly variable. However, a bell-shape vertical profile of Chl a,
28 conventionally referred to as Subsurface Chlorophyll Maximum (SCM) phenomenon,
29 has been frequently observed in stratified water columns, e.g., it occurs through the
30 whole year in tropical and subtropical oceans while it exists only during summer in
31 temperate and high latitude oceanic zones. The subsurface biomass maxima (SBMs)
32 are also common in stratified water columns. The chlorophyll-to-biomass ratio
33 generally increases with depth in the euphotic zone. Thus, SCMs may not necessarily
34 represent SBMs (Cullen, 1982; Fennel and Boss, 2003) and are usually deeper than
35 SBMs (Fennel and Boss, 2003; Hodges and Rudnick, 2004). However, both the
36 subsurface maxima in chlorophyll and biomass are usually formed in certain regions
37 of the water column where two opposing resource (light and nutrient) gradients
38 combined with turbulent mixing is amenable for survival of phytoplankton. Thus,
39 SCMs are approximately equal to SBMs in many studies (Klausmeier and Litchman,
40 2001; Sharples et al., 2001; Huisman et al., 2006; Raybov et al., 2010). Fennel and
41 Boss (2003) reported that the photoacclimation of phytoplankton can be another
42 important reason for forming a SCM in oligotrophic waters.

43 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; Deksheniaks 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 SCMs have attracted much attention because of the significant contribution of SCML
52 to the total biomass and primary production in the whole water column (Cullen and
53 Eppley, 1981; Weston et al., 2005; Siswanto et al., 2005; Hanson et al., 2007;
54 Sullivan et al., 2010). Pérez et al. (2006) showed that 65-75% of the total Chl a in a
55 water column of the Atlantic subtropical gyres was presented in SCML and the layer
56 thickness was approximately 50 m. Weston et al. (2005) reported that the SCML

57 accounted for 58% of the water column primary production in the central North Sea,
58 although the layer thickness was less than 5 m. Sullivan et al. (2010) found that the
59 fraction of Chl a in the SCML (thickness <3 m) out of the total water column ranged
60 from 33% to 47% in the Monterey Bay.

61 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/or detritus and vertical diffusivity rather than
70 growth rate of phytoplankton (Hodges and Rudnick, 2004; Beckmann and Hense,
71 2007). However, the thickness, depth and intensity of SCML are very sensitive to
72 variations of environmental parameters. Therefore, the relationships obtained from a
73 particular case may not be applicable for other cases. To understand the general
74 relationships between SCM phenomenon and environmental parameters, the
75 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 many observations showed that the thickness of SCML can reach as high as 100 m in
84 oceans (Platt et al., 1988). For those cases, the assumption of an infinitely small
85 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
87 as a general Gaussian function, instead of a delta function. This parameterizing
88 approach was proposed firstly by Lewis et al. (1983), and has been widely used to fit
89 vertical profiles of Chl a (Platt et al., 1988; Weston et al., 2005; Ardyna et al., 2013).

90 By incorporating the general Gaussian function into the ecosystem dynamical
 91 equations, we derive the steady-state solutions for the thickness, depth, and intensity
 92 of SCML in various scenarios and examine their dependence on environmental
 93 parameters, such as light attenuation coefficient, vertical diffusivity, sinking velocity
 94 of phytoplankton.

95 **2 Methods**

96 *2.1 Models*

97 The SCML occurs below the surface mixed layer, where the light attenuated from
 98 above and nutrients supplied from the deep water result in the maximal value of
 99 phytoplankton growth rate (Fig. 1). The partial differential equations for
 100 phytoplankton and nutrients dynamics in which light and nutrients are two major
 101 limiting factors (Eqs. 1 and 2) (Riley et al., 1949; Lewis et al., 1986; Gabric and
 102 Parslow, 1989; Huisman et al., 2006; Liccardo et al., 2013) were adopted in this
 103 study.

$$104 \quad \frac{\partial P}{\partial t} = \mu_m \min(f(I), g(N))P - \varepsilon P - w \frac{\partial P}{\partial z} + \frac{\partial}{\partial z} \left(K_v \frac{\partial P}{\partial z} \right), \quad (1)$$

$$105 \quad \frac{\partial N}{\partial t} = -1.59 \mu_m \min(f(I), g(N))P + 1.59 \alpha \varepsilon P + \frac{\partial}{\partial z} \left(K_v \frac{\partial N}{\partial z} \right), \quad (2)$$

106 where P denotes the Chl a concentration, N is the limiting nutrient concentration. The
 107 photo-acclimation of phytoplankton is not considered here and the Chl a distribution
 108 is supposed to represent the distribution of phytoplankton biomass. This is a
 109 significant simplification. In fact, phytoplankton increases inter-cellular pigment
 110 concentration when light level decreases (Cullen, 1982; Fennel and Boss, 2003).
 111 Usually, the unit of Chl a concentration is mg m^{-3} , the concentrations of
 112 phytoplankton and the limiting nutrients are in unit of mmol N m^{-3} . A ratio of 1.59 g
 113 chlorophyll per mol nitrogen (Cloern et al., 1995; Oschlies, 2001) is thereby used for
 114 unit conversion. μ_m is the maximum growth rate of phytoplankton, ε is the loss
 115 rate of phytoplankton (including respiration, mortality, zooplankton grazing), α is
 116 the recycling rate of dead phytoplankton ($0 \leq \alpha \leq 1$). w is the sinking velocity of
 117 phytoplankton, which is non-negative in the chosen coordinate system and assumed
 118 to be constant with depths. K_v is the vertical turbulent diffusivity and it is much

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):

$$121 \quad K_v = \begin{cases} K_{v1} & 0 < z < z_s, \\ K_{v2} & z_s < z < z_b, \end{cases} \quad (3)$$

122 where z_s is the depth of surface mixed layer, z_b is the location where the Chl a
 123 concentration reduces to nearly zero in a sufficiently deep water column. We assume
 124 K_{v1} , K_{v2} are constant and K_{v1} is large enough to homogenize the Chl a and nutrient
 125 concentrations in the surface mixed layer.

126 A gradual transition from the surface mixed layer to the deep one written in terms of a
 127 generalized Fermi function is adopted (Ryabov et al., 2010), that is, $K_v(z) = K_{v2} +$
 128 $\frac{K_{v1}-K_{v2}}{1+e^{(z-z_s)/l}}$, where parameter l characterizes the width of the transition layer. In our
 129 study, we assumed this transition layer is finitely thin.

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

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

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

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

$$138 \quad I(z) = I_0 \exp(-K_d z), \quad (5)$$

139 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 condition for the phytoplankton at the surface is used. Like
 143 the study reported by Ryabov et al. (2010), we also set the chlorophyll concentration
 144 approaches zero at the bottom boundary z_b , i.e., $P \rightarrow 0$ for $z \rightarrow z_b$. Fennel and Boss
 145 (2003) used an infinite depth as z_b . Furthermore, we assume a zero-flux boundary

146 condition for nutrients at the surface, while nutrients are replenished from below.

147 That is,

$$148 \quad \begin{cases} K_{v1} \frac{\partial P}{\partial z} = 0, & K_{v1} \frac{\partial N}{\partial z} = 0, & \text{at } z = 0, \\ P(z_b) = 0, & K_{v2} \frac{\partial N}{\partial z} = K_{v2} \frac{\partial N}{\partial z} \Big|_{z=z_b}, & \text{at } z = z_b. \end{cases} \quad (6)$$

149 In addition, Lewis et al. (1983) first proposed a general Gaussian distribution function
150 (Eq. 7) to model the nonlinear feature of observed vertical Chl a profiles. In this study,
151 this function is adopted to represent the bell-shape vertical distribution of Chl a (Fig.
152 1).

$$153 \quad P(z) = P_{\max} e^{-\frac{(z-z_m)^2}{2\sigma^2}} \quad 0 \leq z \leq z_b, \quad (7)$$

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

155 three Gaussian parameters (h , z_m , σ) can vary to characterize the SCM phenomenon.
156 Thus h is the vertical integrated Chl a over the entire water column, z_m is the depth of
157 the maximum Chl a (the peak of the bell-shape), and σ is the standard deviation of
158 Gaussian function, which controls the thickness of the SCML.

159 2.2 Three SCM characteristics

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

174 biomass.

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

177
$$\left. \frac{d^2 P}{dz^2} \right|_{z=z_u, z_l} = 0, \quad (8)$$

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

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

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

183
$$\left(\mu_m \min(f(I), g(N))P - \varepsilon P - w \frac{dP}{dz} \right) \Big|_{z=z_u, z_l} = 0. \quad (9)$$

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

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

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

193 *2.3 Approach used in this study*

194 Previous numerical studies (Huisman et al., 2006; Ryabov et al., 2010) showed that
195 the ecosystem dynamical model (Eqs. 1 and 2) can approximately reproduce the
196 bell-shape feature of the vertical Chl a profile (Fig. 1). We assume a general
197 Gaussian function of $P(z)$ (Eq. 7) is the solution for the Eqs. (1) and (2) at
198 steady-state to derive explicit relationships between three characteristics of SCM and
199 the environmental parameters. If nutrient input to the mixed layer due to riverine
200 inputs, surface runoff, or atmospheric deposition, is considered in the ecosystem, the
201 surface concentration of Chl a should be positive (Mellard et al. 2011). Thus, the

202 general Gaussian function is not an exact solution, at best, an approximate solution of
 203 the dynamical Eqs. (1) and (2) by ignoring external nutrient input.

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

$$207 \quad \mu_m \min(f(I), g(N)) - \varepsilon = -\frac{K_{v2}}{\sigma^4} \left(z - z_m + \frac{w\sigma^2}{2K_{v2}} \right)^2 + \frac{w^2}{4K_{v2}} + \frac{K_{v2}}{\sigma^2}. \quad (10)$$

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

$$210 \quad z_{c1} = z_m - \frac{w\sigma^2}{2K_{v2}} - \sqrt{\left(\frac{w\sigma^2}{2K_{v2}} \right)^2 + \sigma^2}, \quad z_{c2} = z_m - \frac{w\sigma^2}{2K_{v2}} + \sqrt{\left(\frac{w\sigma^2}{2K_{v2}} \right)^2 + \sigma^2}. \quad (11)$$

211 From the property of quadratic function with pointing downward (the right-hand
 212 terms in Eq. 10), we know that for $z_{c1} < z < z_{c2}$ the inequality
 213 $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ is satisfied. This indicates that the subsurface net
 214 production occurs only between the two compensation depths where the growth rate
 215 $\mu_m \min(f(I), g(N))$ equals the loss rate ε . Beckmann and Hense (2007) found similar
 216 results by numerical modeling and emphasized the often overlooked fact that an
 217 SCML has to have two compensation depths.

218 From Eq. (11), we obtain $z_{c1} \leq z_m - \sigma$ and $z_m \leq z_{c2} \leq z_m + \sigma$ (Fig. 1). In particularly,
 219 $z_{c1} = z_m - \sigma$, and $z_{c2} = z_m + \sigma$ when the sinking velocity of phytoplankton w is too
 220 small to affect the chlorophyll profile significantly. This result is identical to that of
 221 Beckmann and Hense (2007) for neglecting sinking velocity of phytoplankton.

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

$$224 \quad z_0 = z_m - \frac{w\sigma^2}{2K_{v2}}, \quad (12)$$

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

$$226 \quad \max\left(\mu_m \min(f(I), g(N)) - \varepsilon\right)\Big|_{z_0} = \frac{K_{v2}}{\sigma^2} + \frac{w^2}{4K_{v2}}. \quad (13)$$

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

229 We define $T=\sigma^2/K_{v2}$ as the characteristic vertical mixing time scale in the SCML of
230 thickness σ (Bowdon, 1985; Gabric and Parslow, 1989). Let the length scale be
231 $L=2K_{v2}/w$, which determines the scale height of the phytoplankton distribution
232 (Ghosal and Mandre, 2003). Thus, the right hand terms of Eq. (13) can be rewritten
233 as $1/T+w/(2L)$. In other words, the maximum net growth rate of phytoplankton,
234 $\max(\mu_m \min(f(I), g(N)) - \varepsilon)$, is determined by the vertical mixing time scale (T) and the
235 time taken by a phytoplankton sinking (w) through lengths ($2L$).

236 Equation (12) also shows that $z_m \geq z_0$, that is, the depth of SCML lies at or below
237 the depth for phytoplankton having the maximum growth rate. Observations in the
238 Southern California Bight have supported this (Cullen and Eppley, 1981).
239 Particularly, $z_m = z_0$ approximately holds when either the sinking velocity (w) or
240 Gaussian parameter σ is very small. For non-sinking phytoplankton, i.e., $w \rightarrow 0$,
241 numerical modeling can support this equality (Beckmann and Hense, 2007). When
242 parameter σ is assumed to be infinitely thin, the equality is obviously correct, which
243 has been used to solve for the equilibrium depth and intensity of an infinitely thin
244 layer (Klausmeier and Litchman, 2001; Yoshiyama et al., 2009; Mellard et al., 2011).

245 In this special case ($z_m = z_0$), some studies found that the depth of SCML is at the
246 location of equal limitation by nutrients and light (Klausmeier and Litchman, 2001;
247 Yoshiyama et al., 2009; Mellard et al., 2011). In this study, we further infer that when
248 $z_m > z_0$, the depth of SCML is located at where phytoplankton growth is limited by
249 light (Appendix A).

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

$$253 \quad \mu_m f(I)|_{z=z_m} - \varepsilon = K_{v2}/\sigma^2 \quad (14)$$

$$254 \quad \mu_m f(I)|_{z=z_m+\sigma} - \varepsilon = -w/\sigma \quad (15)$$

255 At the depth of z_m , the net growth rate of phytoplankton (Eq. 14) is determined by

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

259 In addition, from Eqs. (12) and (A2) we obtain that the upper compensation depth, z_{c1} ,
 260 is the location where the growth limited by nutrients, $\mu_m g(N)$, equals the loss rate, ε ,
 261 while the lower compensation depth, z_{c2} , represents the depth where the growth
 262 limited by light, $\mu_m f(I)$, equals the loss rate, ε .

263 **3 Results**

264 *3.1 Analytic solutions of three SCM characteristics*

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

$$267 \quad z_m = \frac{1}{K_d} \ln \left[\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1 \right) \frac{I_0}{K_I} \right] \quad (16)$$

268 or

$$269 \quad z_m = \frac{1}{K_d} \ln \left[\left(\frac{\mu_m}{\varepsilon - w/\sigma} - 1 \right) \frac{I_0}{K_I} \right] - \sigma. \quad (17)$$

270 The occurrence for a SCM requires $z_m > 0$. Requiring a positive solution for Eq.

271 (16), we obtain $\left(\frac{\mu_m}{\varepsilon + K_{v2}/\sigma^2} - 1 \right) \frac{I_0}{K_I} > 1$, i.e., $(\mu_m f(I_0) - \varepsilon) \sigma^2 > K_{v2}$. For any $\sigma > 0$, we

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

273 $\mu_m f(I_0) > \varepsilon$, which is identical with the result of Fennel and Boss (2003) when

274 vertical sinking is constant as a function of depth in their model.

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

$$277 \quad \left(\frac{\mu_m}{\mu_m - \varepsilon + \frac{w}{\sigma}} - 1 \right) e^{K_d \sigma} = \frac{\mu_m}{\mu_m - \varepsilon - \frac{K_{v2}}{\sigma^2}} - 1 \quad (18)$$

278 Thus far, we have obtained the theoretical relationships between Gaussian parameter
 279 σ , z_m and environmental parameters (Eqs. 16-18). To derive the relationship between

280 Gaussian parameter h and environmental parameters, we now return to Eqs. (1) and
 281 (2). In steady state, adding these two equations leads to:

$$282 \quad (1-\alpha)\varepsilon P + w \frac{dP}{dz} = \frac{d^2(K_v P)}{dz^2} + \frac{1}{1.59} \frac{d^2(K_v N)}{dz^2} \quad (19)$$

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

$$286 \quad 1.59(1-\alpha)\varepsilon \int_0^{z_b} P(z) dz = K_{v2} \frac{dN}{dz} \Big|_{z=z_b} \quad (20)$$

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

$$291 \quad h = \frac{K_{v2} \frac{dN}{dz} \Big|_{z=z_b}}{1.59(1-\alpha)\varepsilon} \quad (21)$$

292 This equality indicates that the total Chl a in the water column (h) is independent of
 293 the sinking velocity of phytoplankton. Both Ryabov et al. (2010) and Mellard et al.
 294 (2011) obtained a similar result.

295 The intensity of SCML is

$$296 \quad P_{\max} = \frac{K_{v2} \frac{dN}{dz} \Big|_{z=z_b}}{1.59\sqrt{2\pi\sigma}(1-\alpha)\varepsilon} \quad (22)$$

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

302 *3.2 Influences of environmental parameters on SCM characteristics*

303 We now investigate how the steady-state thickness, depth, and intensity of SCML
 304 depend on environmental parameters. Because the analytic solutions for SCML depth

305 and intensity depend on Gaussian parameter σ and environmental parameters, we first
 306 examine the influence of environmental parameters on parameter σ .

307 Equation (18) shows that the thickness of SCML is independent of sea surface light
 308 intensity (I_0). This is consistent with numerical simulations (Beckmann and Hense,
 309 2007). This result also suggests that seasonal variation of SCML thickness has no
 310 relation with light intensity. Thus, it is not surprising that the empirical model poorly
 311 predicted parameter σ by using season as an important factor (Richardson et al.,
 312 2003).

313 To illustrate the effects of other model parameters (K_d , K_{v2} , μ_m , ε , w) on the parameter
 314 σ , we need to obtain informative algebraic expression of σ . To simplify, by Taylor
 315 expanding $e^{K_d\sigma}$ at $\sigma=0$ and truncating the Taylor series after the linear term, i.e.,
 316 $e^{K_d\sigma} = 1 + K_d\sigma + o(\sigma^2)$, Eq. (18) can thereby be rewritten as:

$$317 \quad \sigma^3 - \frac{w}{\varepsilon}\sigma^2 - \frac{\varepsilon K_d K_{v2} + \mu_m w}{\varepsilon K_d (\mu_m - \varepsilon)}\sigma = \frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}. \quad (23)$$

318 According to the properties of a cubic function, we know that Eq. (23) has one and
 319 only one positive real root σ , when $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)} \geq 0$. Because $\mu_m f(I_0) > \varepsilon$ and
 320 $0 < f(I_0) < 1$, so $\mu_m > \varepsilon$. Thus, when the maximum phytoplankton growth rate (μ_m)
 321 within one penetration depth ($1/K_d$) is larger than sinking velocity of phytoplankton,
 322 i.e., $\mu_m/K_d - w \geq 0$, there exists a non-negative value of parameter σ , which
 323 increases with increasing $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}$.

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

329 The right hand term in Eq. (23), $\frac{K_{v2}(\mu_m/K_d - w)}{\varepsilon(\mu_m - \varepsilon)}$, can be rearranged as

$$330 \quad \frac{K_{v2}(\mu_m/K_d - w)}{-(\varepsilon - \mu_m/2)^2 + \mu_m^2/4}. \text{ Thus, the effect of loss rate } (\varepsilon) \text{ on parameter } \sigma \text{ depends on } \mu_m/2.$$

331 Note that $\mu_m f(I_0) > \varepsilon$ once the SCM occurs. When the surface light intensity I_0 is
 332 smaller than or equals to the half-saturation constant for light K_I , i.e., $f(I_0) \leq 0.5$,
 333 then $0 < \varepsilon < \mu_m f(I_0) \leq \mu_m/2$, thus, σ decreases with increasing ε . Conversely, when
 334 $f(I_0) > 0.5$, for $\varepsilon \geq \mu_m/2$, σ increases with increasing ε ; for $\varepsilon < \mu_m/2$, σ decreases
 335 with increasing ε . In summary, for smaller loss rates ($\varepsilon < \mu_m/2$), decreased ε leads to
 336 a thicker SCML, while for larger loss rates ($\varepsilon \geq \mu_m/2$), decreased ε leads to a thinner
 337 SCML.

338 Equation (16) can be rewritten as:

$$339 \quad z_m = \frac{1}{K_d} \ln(AI_0), \quad (24)$$

340 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
 341 surface light intensity (I_0), thus we infer that the depth of SCML increases
 342 logarithmically with increasing I_0 . In other words, the SCML gets deeper due to the
 343 seasonal increase of I_0 , and remains almost unchanged when the surface light
 344 intensity increases to a certain degree. Observations at the HOT (Hawaii Ocean
 345 Time-series) site in the eastern Pacific and the SEATS (South East Asia Time-series
 346 Station) station in the South China Sea showed a significant seasonal variation of
 347 SCML depth (Chen et al., 2006; Hense and Beckmann, 2008). Hense and Beckmann
 348 (2008) explained the deepening of SCML depth in spring at HOT site by the seasonal
 349 increase of the light intensity. Modeling sensitivity analyses also showed that an
 350 increase in the surface light intensity yields a deeper SCML (Jamart et al., 1979;
 351 Varela et al., 1994; Beckmann and Hense, 2007).

352 Determining the effect of vertical diffusivity below the surface mixed layer (K_{v2}) on
 353 the steady-state SCML intensity is more difficult. Increased K_{v2} increases parameter
 354 σ (Eq. 23) and the diffusive flux of nutrients from below (Eq. 22), however, this
 355 parameter has opposite effects on P_{\max} (Eq. 22). Rearranged Eq. (23) we obtain

$$356 \quad \frac{K_{v2}}{\sigma} = \frac{(\mu_m - \varepsilon)\varepsilon}{(\mu_m/K_d - w)/\sigma^2 + \varepsilon/\sigma} + \frac{(\mu_m - \varepsilon)w}{(\mu_m/K_d - w)/\sigma + \varepsilon} - \frac{\mu_m w/K_d}{\mu_m/K_d - w + \varepsilon\sigma}. \quad (25)$$

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

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

361 The influences of various parameters on SCM characteristics determined by Eqs.
362 (16)-(18), (21) and (22) are summarized in Table 1. For example, increased light
363 levels (increasing surface light intensity I_0 , decreasing attenuation coefficient K_d) or
364 increased light competitive ability (decreasing half-saturation constant for light K_I)
365 moves the SCML deeper; increased nutrients supply (increasing vertical diffusivity
366 below the surface mixed layer K_{v2} and loss rate of phytoplankton ε) moves the layer
367 toward the surface. The shape of SCML (thickness and intensity) is mainly
368 influenced by nutrients supply (K_{v2} and ε). The intensity of SCML becomes weaker
369 as a result of expanding the SCML by a lower sinking velocity of phytoplankton (w)
370 and a smaller light attenuation coefficient (K_d).

371 **4 Discussion**

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

377 *4.1 Three special scenarios*

378 Equation (18) indicates that the parameter σ is affected by changes in the vertical
379 diffusivity below the surface mixed layer (K_{v2}), the sinking velocity of phytoplankton
380 (w) and the light attenuation coefficient (K_d), which inversely affects depth and
381 intensity of SCML (Eqs. 16, 17, and 22). Thus, three special situations of the
382 theoretical solutions for SCM characteristics are discussed below.

383 Firstly, the term K_{v2}/σ^2 in the right hand of Eq. (18) is neglected. This special
384 situation occurs either when the vertical diffusivity below the surface mixed layer is
385 too small to be considered ($K_{v2} \rightarrow 0$), or when K_{v2}/σ^2 is much smaller than $\mu_m - \varepsilon$,
386 i.e., the mixing time scale ($T = \sigma^2/K_{v2}$) below the surface mixed layer is much longer
387 than the time taken by net growth of phytoplankton, $(\mu_m - \varepsilon)^{-1}$. Indeed, in the
388 seasonal thermocline, vertical turbulent diffusive time scales can vary from weeks to
389 months for phytoplankton displacements as small as several meters (Denman and

390 Gargett, 1983). The value of $(\mu_m - \varepsilon)^{-1}$ used in many studies is usually from 0.1 to 5
 391 days (Gabric and Parslow, 1989; Klausmeier and Litchman, 2001; Huisman et al.,
 392 2006).

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

$$394 \quad \mu_m f(I)|_{z=z_m} = \varepsilon. \quad (26)$$

395 In regions with a low vertical diffusivity, Fennel and Boss (2003) derived that, at the
 396 SCML depth, the growth rate of phytoplankton is equal to the loss rate and the
 397 divergence of phytoplankton due to changes in the sinking velocity. Clearly, Eq. (26)
 398 is identical to that of Fennel and Boss (2003) for constant sinking velocity of
 399 phytoplankton.

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

$$401 \quad z_m = \frac{1}{K_d} \ln \frac{(\mu_m - \varepsilon) I_0}{\varepsilon K_l}. \quad (27)$$

402 It indicates the SCML depth is directly proportional to the light penetration depth
 403 ($1/K_d$). Observations by four Bio-Argo floats in the North Pacific Subtropical Gyre,
 404 the South Pacific Subtropical Gyre, the Levantine Sea, and in the northwestern
 405 Mediterranean Sea showed a significant positive linear relationship between the two
 406 variables (Mignot et al. 2014). Beckmann and Hense (2007) also found a similar
 407 result by statistical analysis of numerical modeling.

408 The right hand term of Eq. (27) can be rewritten as $\frac{1}{K_d} \ln \frac{I_0}{I^*}$ by letting $I^* = \frac{\varepsilon K_l}{\mu_m - \varepsilon}$,

409 where $\mu_m f(I^*) = \varepsilon$. Under the assumption of infinitely thin SCML ($\sigma \rightarrow 0$),
 410 Klausmeier and Litchman (2001) also have derived Eq. (27) by setting the vertical
 411 diffusivity for phytoplankton as zero, i.e., $K_v = 0$, in poorly mixed waters. Here, we
 412 go further to obtain the approximate expression of the thickness of SCML from Eq.
 413 (23), that is,

$$414 \quad 2\sigma = \frac{w}{\varepsilon} + \sqrt{\left(\frac{w}{\varepsilon}\right)^2 + \frac{w}{K_d(\varepsilon - \varepsilon^2/\mu_m)}}. \quad (28)$$

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

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

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

$$430 \quad \mu_m f(I)|_{z=z_m+\sigma} - \varepsilon = 0. \quad (29)$$

431 That is, the lower boundary of SCML, $z_m + \sigma$, is located at the compensation depth.

432 In this situation, the depth of SCML can be derived from Eq. (17), i.e.,

$$433 \quad z_m = \frac{1}{K_d} \ln \frac{(\mu_m - \varepsilon) I_0}{\varepsilon K_l} - \sigma. \quad (30)$$

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

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

$$440 \quad \sigma \left(\sigma + \sqrt{\frac{K_{v2}}{\mu_m - \varepsilon}} \right) \left(\sigma - \sqrt{\frac{K_{v2}}{\mu_m - \varepsilon}} \right) = \frac{\mu_m K_{v2}}{(\mu_m - \varepsilon) \varepsilon K_d}. \quad (31)$$

441 The SCML thickens with a larger vertical diffusivity below the surface mixed layer
 442 (K_{v2}), a smaller growth rate (μ_m) or a lower light attenuation coefficient (K_d).

443 Especially, when $K_{v2} = 0$, we have $\sigma = 0$. In other words, for non-sinking
444 phytoplankton ($w \rightarrow 0$), when the vertical diffusivity below the surface mixed layer is
445 very small ($K_{v2} \rightarrow 0$), the SCML disappears. This indicates that there must be a
446 vertical diffusion window sustaining non-sinking phytoplankton species in deep
447 waters.

448 The third special situation occurs when $K_d \sigma$ (i.e., $\sigma / (K_d)^{-1}$) is too small to be
449 considered in Eq. (18). This may occur in clear waters where the light attenuation
450 coefficient is very small ($K_d \rightarrow 0$), or in regions where the light penetration depth
451 ($1/K_d$) is much larger than a half-width of SCML (σ). Very narrow (from several to
452 tens of centimeters) SCML has been observed in clear, stratified lakes where the light
453 penetration depths were from several to tens of meters (Fee, 1976; Camacho, 2006).

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

$$455 \quad w\sigma + K_{v2} = 0. \quad (32)$$

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

462 *4.2 Limitation and potential application*

463 To make the complex problem (SCM phenomenon) tractable, the ecosystem
464 dynamical equations adopted in this study are judiciously simplified. For example, a
465 constant eddy diffusivity is assumed in the surface mixed layer and below this layer,
466 respectively. Many processes (turbulence, internal waves, storms, slant-wise and
467 vertical convection) in upper ocean dynamics are not captured in the model system.
468 The assumption of steady state will be broken during episodic events of strong
469 physical forcing, nutrient injection, or blooms (Fennel and Boss, 2003). Similarly the
470 biological representation is also extremely limited. We neglect food-web and
471 microbial loop dynamics (detritus, dissolved organic matter, and zooplankton are not
472 included explicitly), and assume all loss processes, except sinking, to be linearly
473 proportional to phytoplankton. The sinking velocity of phytoplankton is assumed to

474 be constant with depths, excluding the effects of temperature and density gradients.
475 Our model also neglects some feedback mechanisms, like the effect of phytoplankton
476 on light attenuation. Although these are important aspects, their addition is unlikely to
477 change our conclusions qualitatively under the boundary conditions chosen in this
478 study (Fennel and Boss, 2003).

479 Without considering nutrient input directly to the surface mixed layer, Chl a
480 concentration within it is assumed to be nearly zero. The SCML is assumed to occur
481 significantly deeper than the base of surface mixed layer, and the vertical gradient of
482 Chl a is assumed to be identically zero at the transition between the two layers. This
483 vertical profile of Chl a (Fig. 1) is assumed to be well fitted by a general Gaussian
484 function (Eq. 7), in which Chl a within the surface mixed layer is an approximation
485 for the tail of Gaussian function. The Gaussian assumption leads to the results that
486 the vertical diffusivity within the surface mixed layer has no roles on the SCM.
487 However, the assumption of a general Gaussian profile can be broken in several ways.
488 If nutrient input directly to the mixed layer due to riverine inputs, surface runoff, or
489 atmospheric deposition, a positive Chl a concentration within the surface mixed layer
490 will be sustained (Mellard et al., 2011). In this case, the general Gaussian function
491 can be modified with a superimposition of a background which is either a constant
492 (Platt et al., 1988; Richardson et al., 2003) or a function of water depth (Uitz et al.,
493 2006; Mignot et al., 2011). If the depth of surface mixed layer z_s is large, this allows
494 another way for the surface Chl a concentration being positive by extracting some of
495 the Chl a from the SCML (Beckman and Hense, 2007), then the vertical gradient of
496 Chl a may not be identically zero at the transition between the two layers.

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

507 zooplankton can move, or, in the least, grow faster where more food is available, is
508 unlikely to have a constant concentration distribution (Behrenfeld and Boss, 2014).

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

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

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

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

539 recycling rate and loss rate (Eqs. 21-22 and B3-B4).

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

550 The estimated depths and thicknesses of the SCML agree reasonably well with the
551 observations at all three stations. However, the intensities of the SCML are poorly
552 estimated, implying other mechanisms (e.g., wind-driven nutrient pulse) supplying
553 nutrients for the SCML, except upward diffusivity, for phytoplankton growth
554 (Williams et al., 2013). This is the first try to estimate the depth, thickness and
555 intensity of the SCML using parameters from satellite data and field studies. It should
556 be noted that the estimation is sensitive to the used values of these environmental
557 parameters. The values used in estimations above are representative for the averages
558 over a large spatial or temporal scale, but they may not reflect the real values in a
559 specific station. Even though disagreements could be associated with uncertainties
560 from several sources, this type of try would give some idea of how real-world data
561 could be incorporated into the model and thus be applied to the field (Pitarch et al.
562 2014).

563 **5 Summary**

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

569 The maximum Chl a concentration occurs at or below the location of the maximum
570 growth rates of phytoplankton determined by the vertical mixing time scale and the

571 time taken by a phytoplankton sinking through the length scale.

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

576 The thickness and intensity of the SCML are mainly influenced by nutrients supply,
577 but independent of sea surface light intensity. The SCML gets thicker and stronger
578 with a higher vertical diffusivity below the surface mixed layer. The intensity of
579 SCML in steady state weakens as a result of expanding the SCML by a smaller
580 sinking velocity of phytoplankton and a lower light attenuation coefficient.

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

585 Upon potential risk of climate change, it is critical to accurately estimate the global
586 and regional SCML-related primary production. However, the SCM characteristics
587 cannot be detected by remote sensing satellites, which will restrict the application of
588 satellite data in estimating primary production in a large temporal and spatial scale.
589 The Argo float equipped with optical sensor has been developed to measure the
590 distribution of particles and chlorophyll in the world's ocean (Mignot et al., 2014),
591 but the data are still limited. The relationships we derived might help to estimate
592 depth-integrated primary production using available data from satellite observations
593 (incident light and light attenuation coefficient) when appropriate vertical estimates
594 of growth rate and loss rate of phytoplankton, sinking velocity of phytoplankton and
595 vertical diffusivity were adopted based on observations or model results. Again, the
596 solutions could also help to compute environmental parameters that are difficult to
597 obtain from on-site observation.

598

599 **Appendix A**

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

$$603 \quad \int (\mu_m \min(f(I), g(N)) - \alpha \varepsilon) P(z) dz \approx K_{v2} \frac{dN(z)}{dz} \Big|_z \quad (\text{A1})$$

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

606 From the properties of the quadratic function in the right hand of Eq. (10), we have
 607 $\mu_m \min(f(I), g(N)) - \varepsilon > 0$ on the interval (z_{c1}, z_{c2}) . Hence, we have
 608 $\mu_m \min(f(I), g(N)) - \alpha \varepsilon > 0$ for $0 < \alpha \leq 1$, then $dN/dz > 0$. In other words, $N(z)$
 609 increases with depth on the interval (z_{c1}, z_{c2}) .

610 According to Eq. (4), we know that $g(N)$ is a monotonic increasing function on
 611 interval (z_{c1}, z_{c2}) , and $f(I)$ is a monotonic decreasing function on interval (z_{c1}, z_{c2}) .
 612 It is well known that the stable SCML occurs in stratified water column only when
 613 the growth of phytoplankton in the surface mixed layer is nutrient-limited (Mellard et
 614 al., 2011; Ryabov et al., 2010). In other words, the limitation by nutrients $g(N)$ is less
 615 than the limitation by light $f(I)$ within the surface mixed layer, i.e., $g(N) < f(I)$ for
 616 $0 \leq z \leq z_s$.

617 Because there is only one maximum in the growth rates of phytoplankton which
 618 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

$$619 \quad \min(f(I), g(N)) = \begin{cases} g(N) & z_{c1} \leq z \leq z_0 \\ f(I) & z_0 \leq z \leq z_{c2} \end{cases} \quad (\text{A2})$$

620 and

$$621 \quad \max(\mu_m \min(f(I), g(N))) = \mu_m f(I) \Big|_{z=z_0} \quad (\text{A3})$$

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

623 from nutrients limitation to light limitation, and the growth of phytoplankton is
624 light-limited below the depth z_0 .

625 **Appendix B**

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

628
$$w \frac{dP}{dz} = \frac{d^2}{dz^2} (K_v (P + N)) \quad (\text{B1})$$

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

630
$$w \int_0^{z_b} P(z) dz = K_{v1} (P + N) \Big|_0^{z_s} + K_{v2} (P + N) \Big|_{z_s}^{z_b} \quad (\text{B2})$$

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

635
$$h = \frac{K_{v2}}{w} N(z_b) \quad (\text{B3})$$

636 and the intensity of SCML is

637
$$P_{\max} = \frac{K_{v2}}{\sqrt{2\pi\sigma w}} N(z_b) \quad (\text{B4})$$

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

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

References:

- 653 Anderson, G. C.: Subsurface chlorophyll maximum in the northeast Pacific Ocean, *Limnol. Oceanogr.*,
654 14, 386-391, 1969.
- 655 Ardyna, M., Babin, M., Gosselin, M., Devred, E., Bélanger, S., Matsuoka, A., Tremblay, J. E.:
656 Parameterization of vertical chlorophyll a in the Arctic Ocean: impact of the subsurface chlorophyll
657 maximum on regional, seasonal and annual primary production estimates, *Biogeosciences*, 10,
658 4383-4404, doi: 10.5194/bg-10-4383-2013, 2013.
- 659 Ayata, S., Lévy, M., Aumont, O., Sciandra, A., Sainte-Marie, J., Tagliabue, A., Bernard, O.:
660 Phytoplankton growth formulation in marine ecosystem models: should we take into account
661 photo-acclimation and variable stoichiometry in oligotrophic areas? *J. Marine Syst.*, 125, 29-40, 2013.
- 662 Beckmann, A., Hense, I.: Beneath the surface: Characteristics of oceanic ecosystems under weak
663 mixing conditions-A theoretical investigation, *Prog. Oceanogr.*, 75, 771-796, 2007.
- 664 Behrenfeld, M. J., Boss, E. S.: Resurrecting the ecological underpinnings of ocean plankton blooms,
665 *Annu. Rev. Mar. Sci.*, 6, 167-194, 2014.
- 666 Bienfang, P. K., Harrison, P. J.: Sinking-rate response of natural assemblages of temperate and
667 subtropical phytoplankton to nutrient depletion, *Mar. Biol.*, 83, 293-300, 1984.
- 668 Bowdon, K. F.: Physical oceanography of coastal waters. *Limnol. Oceanogr.*, 30, 449-450, 1985.
- 669 Cai Y. M., Ning X. R., Liu C. G.: *Synechococcus* and *Prochlorococcus* growth and mortality rates in
670 the northern China Sea: range of variations and correlation with environmental factors. *Acta Ecol. Sin.*
671 7, 2237-2246, 2006.
- 672 Camacho, A.: On the occurrence and ecological features of deep chlorophyll maxima (DCM) in
673 Spanish stratified lakes, *Limnetica*, 25, 453-478, 2006.
- 674 Chen, C. C., Shiah, F. K., Chung, S. W., Liu, K. K.: Winter phytoplankton blooms in the shallow
675 mixed layer of the South China Sea enhanced by upwelling, *J. Marine Syst.*, 59, 97-110, 2006.
- 676 Cianca, A., Godoy, J. M., Martin, J. M., Perez Marrero, J., Rueda, M. J., Llinás, O., Neuer, S.:
677 Interannual variability of chlorophyll and the influence of low - frequency climate models in the North
678 Atlantic subtropical gyre, *Global Biogeochem. Cy.*, 26, 2012.
- 679 Cianca, A., Helmke, P., Mouriño, B., Rueda, M. J., Llinás, O., Neuer, S.: Decadal analysis of
680 hydrography and in situ nutrient budgets in the western and eastern North Atlantic subtropical gyre, *J.*
681 *Geophys. Res.*, 112, C07025, 1-18, 2007.
- 682 Cloern, J. E., Grenz, C., Vidregar-Lucas, L.: An empirical model of the phytoplankton chlorophyll:
683 carbon ratio-the conservation factor between productivity and growth rate, *Limnol. Oceanogr.*, 40,
684 1313-1321, 1995.
- 685 Cullen, J. J., Eppley, R. W.: Chlorophyll maximum layers of the Southern California Bight and
686 possible mechanisms of their formation and maintenance, *Oceanol. Acta*, 1, 23-32, 1981.
- 687 Cullen, J. J.: The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a, *Can. J. Fish.*
688 *Aquat. Sci.*, 39, 791-803, 1982.
- 689 Deksheniaks, M. M., Donaghay, P. L., Sullivan, J. M., Rines, J. E., Osborn, T. R., Twardowski, M. S.:
690 Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes, *Mar.*
691 *Ecol-Prog. Ser.*, 223, 61-71, 2001.
- 692 Denman, K. L., Gargett, A. E.: Time and space scales of vertical mixing and advection of
693 phytoplankton in the upper ocean, *Limnol. Oceanogr.*, 28, 801-815, 1983.
- 694 Fee, E. J.: The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area,
695 northwestern Ontario: Implications for primary production estimates. *Limnol. Oceanogr.*, 26, 767-783,
696 1976.
- 697 Fennel, K., Boss, E.: Subsurface maxima of phytoplankton and chlorophyll: Steady-state solutions
698 from a simple model, *Limnol. Oceanogr.*, 48, 1521-1534, 2003.

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

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

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

704 Hanson, C. E., Pesant, S., Waite, A. M., Pattiaratchi, C. B.: Assessing the magnitude and significance
705 of deep chlorophyll maxima of the coastal eastern Indian Ocean, *Deep-Sea Res. Pt. II*, 54, 884-901,
706 2007.

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

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

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

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

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

717 Jamart, B. M., Winter, D. F., Banse, K.: Sensitivity analysis of a mathematical model of phytoplankton
718 growth and nutrient distribution in the Pacific Ocean off the northwestern US coast, *J. Plankton Res.*, 1,
719 267-290, 1979.

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

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

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

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

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

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

732 Lu, Z., Gan, J., Dai, M., Cheung, A.: The influence of coastal upwelling and a river plume on the
733 subsurface chlorophyll maximum over the shelf of the northeastern South China Sea, *J. Marine Syst.*,
734 82, 35-46, 2010.

735 Mara On, E., Holligan, P. M.: Photosynthetic parameters of phytoplankton from 50° N to 50° S in the
736 Atlantic Ocean, *Mar. Ecol.-Prog. Ser.*, 176, 191-203, 1999.

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

739 Mignot, A., Claustre, H., D'Ortenzio, F., Xing, X., Poteau, A., Ras, J.: From the shape of the vertical
740 profile of in vivo fluorescence to Chlorophyll-a concentration, *Biogeosciences*, 8, 2391-2406,
741 doi:10.5194/bg-8-2391-2011, 2011.

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

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

747 Ono, S., Ennyu, A., Najjar, R. G., Bates, N. R.: Shallow remineralization in the Sargasso Sea estimated
748 from seasonal variations in oxygen, dissolved inorganic carbon and nitrate, *Deep-Sea Res. Pt. II*, 48,
749 1567-1582, 2001.

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

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

755 Pérez, V., Fernández, E., Mara Ón, E., Morán, X., Zubkov, M. V.: Vertical distribution of
756 phytoplankton biomass, production and growth in the Atlantic subtropical gyres, *Deep-Sea Res. Pt. I*,
757 53, 1616-1634, 2006.

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

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

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

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

766 Richardson, A. J., Silulwane, N. F., Mitchell-Innes, B. A., Shillington, F. A.: A dynamic quantitative
767 approach for predicting the shape of phytoplankton profiles in the ocean, *Prog. Oceanogr.*, 59, 301-319,
768 2003.

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

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

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

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

778 Siswanto, E., Ishizaka, J., Yokouchi, K.: Estimating chlorophyll-a vertical profiles from satellite data
779 and the implication for primary production in the Kuroshio front of the East China Sea, *J. Oceanogr.*,
780 61, 575-589, 2005.

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

783 Sverdrup, H. U.: On conditions for the vernal blooming of phytoplankton, *J. Cons. int. Explor. Mer.*, 18,
784 287-295, 1953.

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

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

790 Uitz, J., Claustre, H., Morel, A., Hooker, S. B.: Vertical distribution of phytoplankton communities in
791 open ocean: An assessment based on surface chlorophyll, *J. Geophys. Res.*, 111, C8005, 2006.

792 Varela, R. A., Cruzado, A., Tintoré, J.: A simulation analysis of various biological and physical factors
793 influencing the deep-chlorophyll maximum structure in oligotrophic areas, *J. Marine Syst.*, 5, 143-157,
794 1994.

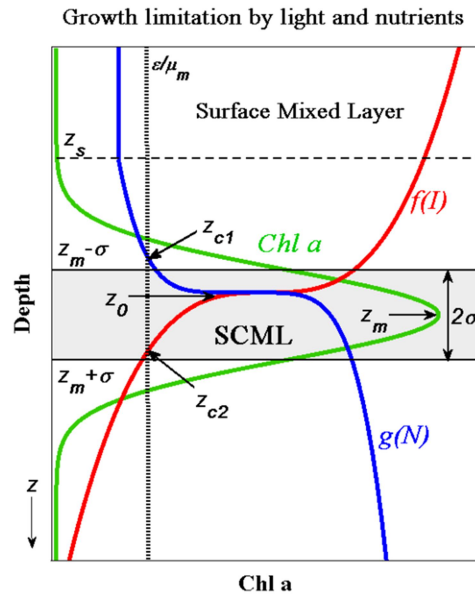
795 Weston, K., Fernand, L., Mills, D. K., Delahunty, R., Brown, J.: Primary production in the deep
796 chlorophyll maximum of the central North Sea, *J. Plankton Res.*, 27, 909-922, 2005.

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

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

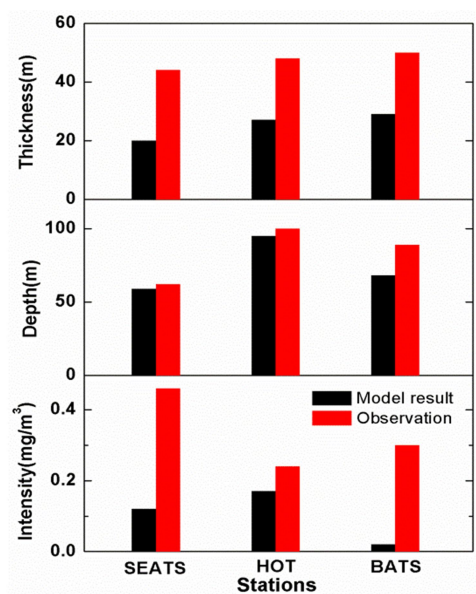
801 Yoshiyama, K., Mellard, J. P., Litchman, E., Klausmeier, C. A.: Phytoplankton competition for
802 nutrients and light in a stratified water column, *Am. Nat.*, 174, 190-203, 2009.

803 List of figures and tables
 804 Figure 1



805
 806 Fig. 1 Schematic picture of Chl a distribution under the limitation by light and nutrient in
 807 stratified water columns (green solid line is Chl a concentration as a function of depth; red solid
 808 line is the growth limiting term with respect to light, $f(I)$; blue solid line is the growth limiting
 809 term with respect to nutrients, $g(N)$; horizontal dashed line represents the depth of surface mixed
 810 layer, z_s ; horizontal solid lines indicate the locations of the upper- and lower-SCML, $z_m-\sigma$, $z_m+\sigma$,
 811 respectively; vertical dotted line is the ratio of loss rate to maximum growth rate, ϵ/μ_m ; z_{c1} and z_{c2}
 812 refer to the two compensation depths where $\mu_m g(N)=\epsilon$ and $\mu_m f(I)=\epsilon$, respectively; z_0 and z_m
 813 indicate the depths of maximum in growth rates and in Chl a concentrations, respectively; double
 814 arrow represents the thickness of the SCML, 2σ)

815 Figure 2



816

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

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

| Model parameters (\uparrow) | 2σ | z_m | P_{max} | h |
|--|-----------------|--------------|--------------|--------------|
| I_0 (Surface light intensity) | - | \uparrow | - | - |
| K_I (Half-saturation constant of light limited growth) | - | \downarrow | - | - |
| K_{v2} (Vertical diffusivity below surface mixed layer) | \uparrow | \downarrow | \uparrow | \uparrow |
| w (Sinking velocity of phytoplankton) | \downarrow | \downarrow | \uparrow | - |
| K_d (Light attenuation coefficient) | \downarrow | \downarrow | \uparrow | - |
| ε (Loss rate of phytoplankton) | \downarrow^* | \downarrow | / | \downarrow |
| | \uparrow^{**} | \downarrow | \downarrow | \downarrow |
| α (Nutrient recycling coefficient) | - | - | \uparrow | \uparrow |
| $\frac{dN}{dz} \Big _{z=z_b}$ Nutrient gradient at the lower boundary of SCML | - | - | \uparrow | \uparrow |
| K_N (Half-saturation constant of nutrient limited growth) | - | - | - | - |
| K_{v1} (Vertical diffusivity in surface mixed layer) | - | - | - | - |
| μ_{max} (Maximum growth rate of phytoplankton) | / | / | / | / |

825 \uparrow indicates increase, \downarrow indicates decrease, - indicates no effect, / indicates no straightforward
 826 result, * indicates a result when $\varepsilon < \mu_{max}/2$, and ** indicates a result when $\varepsilon > \mu_{max}/2$.

827

Table 2 Parameter values at SEATS, HOT, and BATS

| Parameters | Units | Values at Stations | | |
|---------------------------|---------------------------------------|----------------------------------|----------------------------------|-------------------------------------|
| | | SEATS | HOT | BATS |
| I_0 | $\mu\text{mol photos } m^{-2} s^{-1}$ | 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} | $m^2 s^{-1}$ | $5 \cdot 10^{-5}$ ⁽⁶⁾ | $5 \cdot 10^{-5}$ ⁽³⁾ | $1 \cdot 10^{-4}$ ^(7, 8) |
| μ_{max} | d^{-1} | 1.2 ^(9, 10) | 0.96 ⁽³⁾ | 1 ⁽¹¹⁾ |
| K_I | $\mu\text{mol photos } m^{-2} s^{-1}$ | 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.