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Experiments in optimizing simulations of the subsurface chlorophyll maximum in the South China Sea

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ABSTRACT

The subsurface chlorophyll maximum (SCM) is widespread in the oligotrophic ocean and significantly contributes to primary production. One reason for the SCM formation is believed to be the rapid export of phytoplankton from surface layers, which might be caused by aggregation, faster sinking rates under nutrient limitation, or the formation of a resting stage. In this study, these three processes were included in a biological model to investigate their contributions to subsurface chlorophyll. To further identify their individual effects on SCM formation, four modeling experiments were carried out. Three used a simple approach with either (a) density-dependent aggregation, (b) accelerated sinking rate of phytoplankton, or (c) a resting stage. The other experiment combined all three approaches (a–c). A set of observations in the South China Sea was used to optimize the four experiments and compare their abilities to replicate observed values. The results of the experiments with the resting stage showed the best fit to the field observations. All experiments were able to capture major features of the chlorophyll field (e.g. surface bloom and SCM). The experiment with accelerated sinking rate failed to reproduce the observed profile of particulate organic carbon. The experiment with only aggregation predicted lower chlorophyll concentrations in summer than those measured in the field, while experiments with the resting stage reproduced more accurate chlorophyll concentrations. Formulas including the resting stage more successfully captured the timing of phytoplankton export than did those including aggregation and accelerated sinking rate. The processes of aggregation and accelerated sinking rate made small contributions to the SCM formation in the last experiment. Overall, these results show that introducing the resting stage improves SCM simulations of the South China Sea. The results of the experiment with only the resting stage showed that the resting cells shift rapidly from the surface water, encounter better nutrient conditions in nutricline layers, partially germinate into vegetative cells, become shade-adapted, and increase subsurface chlorophyll concentrations during summer, which contributes to SCM formation.

1. Introduction

The subsurface chlorophyll maximum (SCM) phenomenon has attracted substantial attention (Cullen, 1982; Parslow et al., 2001; Williams et al., 2013). The SCM contributes significantly to phytoplankton stocks and primary production (Fernand et al., 2013; Macías et al., 2014; Siswanto et al., 2005) and is believed to be an important food reservoir for herbivores in the marine ecosystem. Approximately 66% of new production in the North Sea was found in the SCM layer (Fernand et al., 2013).

The South China Sea (SCS) is a semi-enclosed and oligotrophic water body in the subtropical and tropical western Pacific. In the central SCS, surface layers are nutrient depleted because stratification prevents vertical transport of nutrients. Phytoplankton are believed to penetrate the nutrient-rich water of the photic zone (Richardson et al., 2000) or adapt to low light levels (Anderson, 1969). The maximum chlorophyll content is usually found near the nutricline in a stratified water column. Takahashi and Hori (1984) reported that almost 55% of total chlorophyll in the entire water column was in the SCM layer in the SCS. Through a physical–biological model, Liu et al. (2007b) found that photoadaptation was critical for the development of the SCM in the SCS. However, the modeled SCM was at shallower depths than the observed SCM. There was a similar deficiency in another biological model of the SCS (Gan et al., 2010). Liu et al. (2007b) pointed out that further modifications of both physical and biogeochemical models were needed to improve their performance.

The faster sinking of phytoplanktonic cells in nutrient-depleted surface layers is believed to be another reason for the formation of the SCM (Bienfang, 1980; Parslow et al., 2001). Phytoplankton can enhance their vertical sinking rates via aggregation of cells into large detrital particles,

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or by increasing their stickiness and predisposition to aggregation (Fernández-Méndez et al., 2014; Kiørboe et al., 1990; Pinel-Alloul et al., 1996; Richardson and Jackson, 2007). Resting-stage cells sink much faster than do vegetative cells (Bienfang, 1981; Eppley et al., 1967). Under unfavorable conditions (nutrient stress, light limitation, temperature changes, bacterial or allelopathic attack), many phytoplankton groups produce thick-walled resting cells, such as cysts (in dinoflagellates), resting spores (in diatoms) and akinetes (in cyanophyta) to tolerate adverse environmental conditions (Agrawal, 2012). When conditions become suitable for vegetative growth, the resting-stage cells germinate into new vegetative cells. Resting stages generally form near the end of a planktonic bloom when resources such as nitrogen become limiting. The faster sinking of resting cells from nutrient-depleted surface layers may be one reason for the SCM formation.

The resting stage may be an important process in the SCS. Species with a resting stage are abundant in the SCS basin. Ning et al. (2004) researched primary production and coupled physical–chemical–biological processes in the SCS. They found that diatoms were the most abundant group in the basin, followed by dinoflagellates and cyanobacteria. Takahashi and Hori (1984) reported that more than 70% of chlorophyll was contained in picoplankton in the SCS. The cyanobacteria *Prochlorococcus* and *Synechococcus* were reported to be the most abundant picoplankton at the Southeast Asia Time-Series Station (SEATS) (Liu et al., 2007a). Cyanobacteria and many planktonic diatoms and dinoflagellates form resting-stage cells as part of their life cycle. There are many resting cells in the coastal bottom sediments of the SCS (Chen et al., 2009; Wang et al., 2013).

The resting stage is considered an important stage of phytoplankton in the model of harmful algal blooms (HABs) (He et al., 2008; Hense, 2010). However, only a few Nutrient–Phytoplankton–Zooplankton–Detritus (NPZD)-type models have taken resting stages into account. Bagniewski et al. (2011) established an NPZD-type model that included diatom aggregation triggered by low silicate concentrations in the North Atlantic. This model successfully simulated an observed collapse of a diatom bloom by this mechanism, and also simulated the resulting observed rapid export of carbon to lower depths. This model combined the effects of resting stage and aggregation. Models with a full predictive life cycle have been developed for coastal areas (Hense and Burchard, 2010; Warns et al., 2013). Their results suggested that resting stages are important for the timing and duration of algal blooms.

In this study, we compared the effects of aggregation, variable sinking rate, and resting stage on simulations of the SCM in the SCS. These three processes were included in a biological model, which was coupled with a one-dimensional physical model. Four experiments were run and optimized to achieve the best fit to the observed results. Our aim was to compare the three processes in terms of their ability to simulate the SCM, and to investigate how the modeled processes affected the formation of the SCM. The study area and models are described in Section 2. The method of parameter optimization is described in Section 3. The results of the four optimized experiments and several numerical experiments are shown in Section 4, and are discussed and summarized in Sections 5 and 6.

2. Model descriptions

2.1. Model setup

The biological model was developed based on an NPZD-type model explored by Fennel et al. (2006), which has been used for the northern SCS (Gan et al., 2010). The basic model includes one phytoplankton group, two nutrient groups, two types of detritus, and one zooplankton group. Processes of growth, mortality, grazing, aggregation, and sinking are modeled to determine phytoplankton concentration. We added processes of accelerated sinking rate (Fizpartick, 2004) and resting stage to the original model. The formulas for resting stage were based on the existing knowledge of this stage. We carried out the following four experiments to compare the effects of the three processes on the simulation of the SCM in the SCS:

(a) Original NPZD model with simple density-dependent aggregation (hereafter, NPZD-τ)
(b) NPZD model with accelerated sinking rate under low-nitrogen conditions and without aggregation (hereafter, NPZD-W)
(c) NPZD model with resting stage and without aggregation (hereafter, NPZD-R)
(d) NPZD model with all the three processes (hereafter, NPZD-ALL)

The processes of aggregation, variable sinking rate, and resting stage were easily removed by setting the corresponding parameters to zero. The following description concerns the construction of NPZD-ALL. The original model included seven state variables: phytoplankton, *Phy*; zooplankton, *Zoo*; nitrate, *NO3*; ammonium, *NH4*; small and large detritus, *SDet* and *LDet*; and phytoplankton chlorophyll, *Chl*. To represent quiescent stages responding to adverse environmental conditions such as resting spores for diatoms, cysts for dinoflagellates, and others, a new state variable, *Cyst*, was added to the original model (Fig. 1). In the model, chlorophyll is expressed in units of mg chl m^{-3}. All other biogeochemical state variables are expressed in terms of nitrogen concentration (mmol N m^{-3}).

The times of the rate of change of *Phy* and *Chl* caused by biological sources and sinks are given by the following equations:

$$\frac{\partial Phy}{\partial t} = \mu Phy - gZoo - m_P Phy - \tau(SDet + Phy)Phy - \left[w_{Phy} + w_N(1-L_N)\right]\frac{\partial Phy}{\partial z} + \sigma_g F_g Cyst - EnPhy, \tag{1}$$

$$\frac{\partial Chl}{\partial t} = \rho_{Chl}\mu Chl - gZoo\frac{Chl}{Phy} - m_P Chl - \tau(SDet + Phy)Chl + \sigma_g F_g Cyst\frac{Chl}{Phy} - EnChl, \tag{2}$$

where rates μ, g, and m represent growth, grazing, and mortality rates, respectively. Rate τ represents aggregation and was set to 0 in NPZD-W and NPZD-R. w_{Phy} is the base sinking rate of phytoplankton, w_N is the nutrient-dependent sinking rate, and L_N is nutrient limitation defined in the original model. w_N represents the accelerated sinking rate and was set to 0 in NPZD-τ and NPZD-R. *En* is the rate of resting

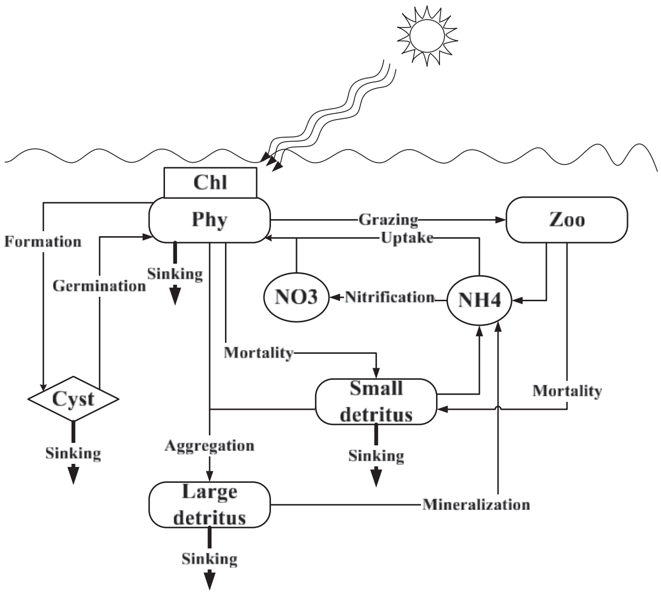

Fig. 1. Schematic of biological model.