

Research Article

Numerical Mesocosm Experimental Study on Harmful Algal Blooms of Two Algal Species in the East China Sea

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From the results of algal culture and mesocosm experiments, a numerical mesocosm experiment is designed that accounts for the effect of the marine environment (sea currents, nutrient levels, and temperature) on the harmful algal bloom (HAB) processes of *Skeletonema costatum* and *Prorocentrum donghaiense*, two of the most frequent HAB-associated species in the East China Sea. Physical and ecological environment of the waters is simulated numerically by applying a hydrodynamic-ecological-one-way-coupled marine culture box model, which is semienclosed. The algal growth rate is digitalized by a temperature-factor-optimization Droop equation. A 90-mode-day numerical mesocosm experiment for the above two species is conducted. The species were found to alternately trigger algal blooms in the experimental waters, replicating the population succession phenomenon observed in the field and confirming that the two HAB species compete for nutrients. Deductively, the numerical result shows that both the Taiwan Warm Current and the eutrophication in the adjacent water of the Yangtze River Estuary contribute to the northward movement of algal concentration centers during HAB and also suggests that the lack of nutritious supplements in the open sea limits HAB occurrences in coastal waters.

1. Introduction

As a disaster phenomenon causing huge losses, harmful algal bloom (HAB) has significantly restricted coastal economic sustainable development in China and has become of great public and governmental concern [1–3]. Being characterized by seasonal and location-concentrated occurrence, HABs in certain sea areas frequently arise from only two or three causative species. In the East China Sea (ECS), *Skeletonema costatum* and *Prorocentrum donghaiense* appear to dominate HAB processes [4]. Primary ecophysiological characteristics have been described in culture experiments of both species. *P. donghaiense* belongs to a group of algae with specific nutritional needs, and its growth depends on the levels and ratios of nitrate and phosphate [5]. A high nitrogen to phosphorus ratio will significantly limit the multiplication of *P. donghaiense* [6, 7] and its particular phosphorus requirements ensure a long incubation period before *P. donghaiense* can bloom [8]. Nutrients exert a similarly large impact on the growth of *S. costatum* [9], as does light, temperature, salinity,

and suspended matter [10, 11]. Compared with *P. donghaiense*, *S. costatum* has a better capacity for adapting to temperature changes and storing nutrients for later absorption [12–14]. Culture experiments on the above-mentioned species confirm that both species enjoy a physiological advantage in an artificial ideal environment. Mesocosm experiments performed at specified marine locations provide a more realistic description of the algal growth characteristics and the interspecific competition mechanism in the nonideal environment. Field mesocosm experiments show that the temperature, salinity, nutrient concentrations, and light conditions in seawater exert varying degrees of impact on the growth of *P. donghaiense* and *S. costatum*, which to some extent reflects the competitive advantage of these red tide algae in different environments. Further mesocosm experiments [11, 15, 16], showing how seawater temperature, salinity, nutrient, light, and other field factors affect the growth of both species, essentially reveal a competitive advantage for either species under a particular marine condition. Clearly, most of the local marine environmental factors are inherently included in mesocosm

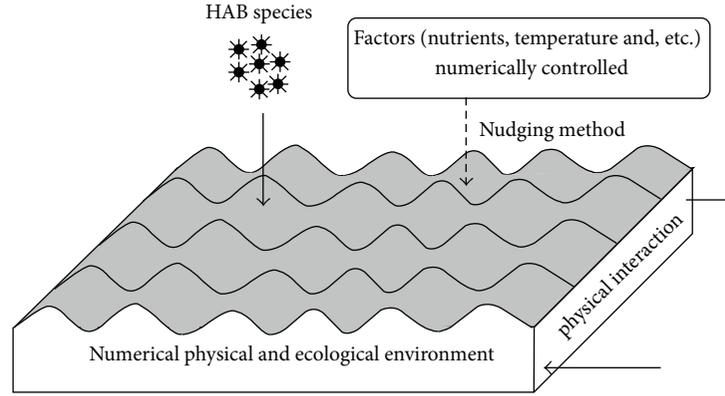


FIGURE 1: Framework of the numerical mesocosm experiment.

experiments, from which more realistic conclusions can be drawn regarding the HAB mechanism. However, the single fixed locality of the experimental site, the limited mesocosm range, and the isolating nature of the device will largely restrict the impact of surrounding environment factors such as currents, nutrients, and temperature. Here, guided by the results of culture and mesocosm experiments [17, 18], a numerical mesocosm experiment on harmful algal blooms of two algal species in the ECS is conducted to account for multiple impacting factors on the process and dynamics of HAB. To achieve this, we apply a hydrodynamic-ecological coupled model combined with an improved algal growth model.

2. Scheme Design

A coupled hydrodynamical ecological model for regional shelf seas (COHERENS) [19] is used to construct the environmental background of this experiment.

The physical part, including seawater temperature, salinity, light, and current, is simulated by the physical module of COHERENS. This physical module is a baroclinic prognostic model [20] with complete forcing at sea surface and is governed by a general set of equations describing the momentum, the continuity, the thermohaline, and the density of the ambient seawater. The physical equations are discretized horizontally on a C-grid and adopt the level 2.5 turbulence closure model (for details see [19]).

The biological module of COHERENS provides the ecological background in which organic carbon and nitrogen cycling is carried out within microplankton and detrital compartments, with associated changes in concentrations of dissolved nitrate, ammonium, and oxygen. The coupling between these two modules is rendered unidirectional by inputting the physical variable field calculations into the biological module for running the biochemical process and by outputting the distribution of each ecological state variable. In this one-way coupling mode, hydrodynamic conditions influence the distribution of ecological variables, while the ecosystem by no means affects the movement of sea water within or outside the mesocosm boundary. Such a semi-enclosed marine culture box mode is essentially equivalent to

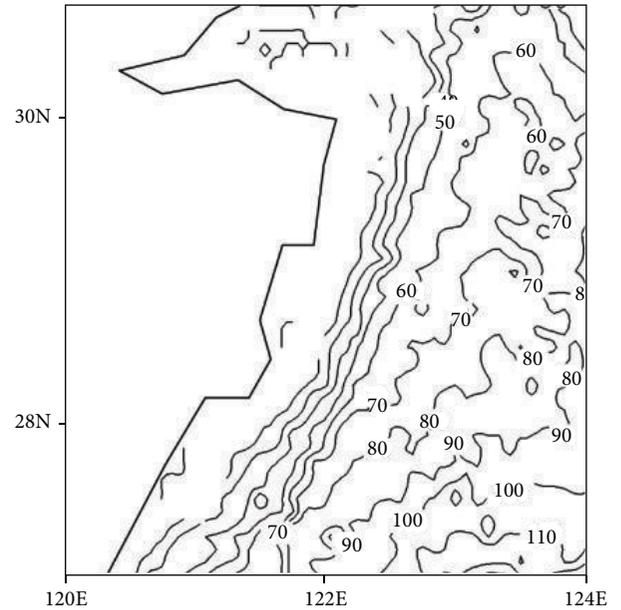


FIGURE 2: Bathymetry (m) of the numerical experimental region.

the marine environmental background of field mesocosm experiments.

The concentration of HAB algae added to the experimental waters is modeled by a general scalar convection-diffusion equation:

$$\frac{dAX}{dt} - \text{diff}(AX) = \beta(AX), \quad (1)$$

where AX is the algal concentration (mmol m^{-3}) and the algal source/sink process $\beta(AX)$ is considered as biomass variation caused by the algal net growth and grazing pressure. The algal growth is described by the Droop equation [21] modified by a temperature factor $f(T)$:

$$\mu_{AX} = \mu_{AX \max} \min \left(\frac{C_{Nj} - C_{Nj \min}}{C_{Nj}} \right) f(T), \quad (2)$$

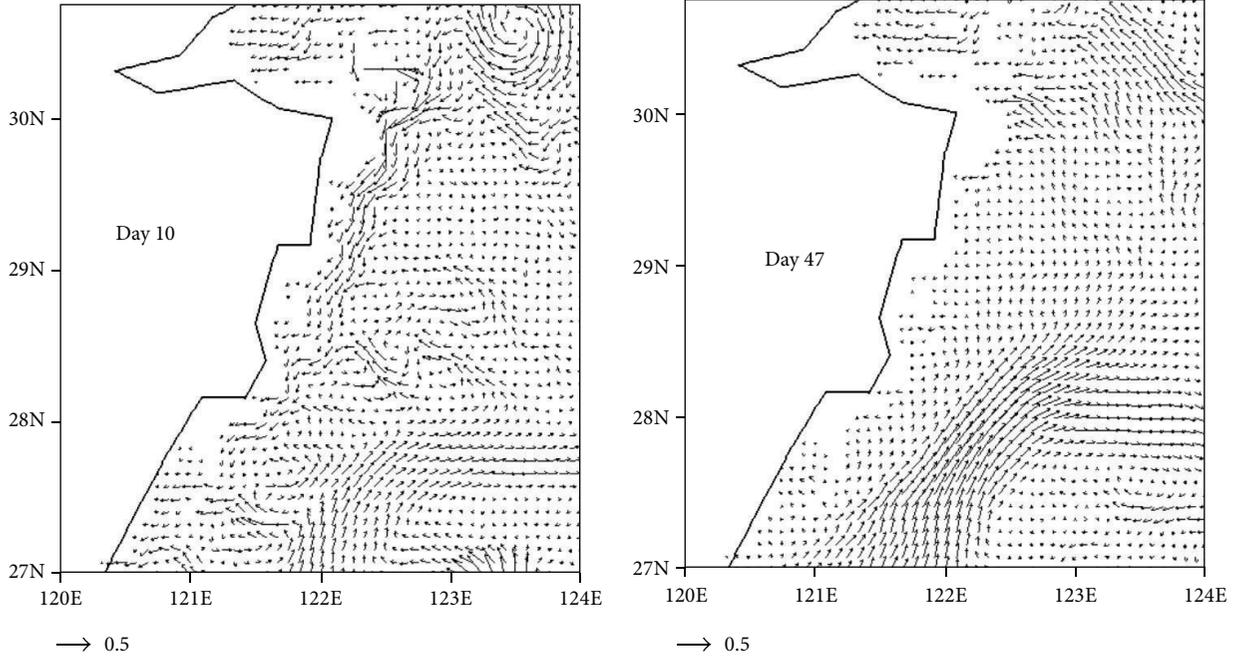


FIGURE 3: Surface current fields in the experimental region (m/s).

where $\mu_{AX\max}$ is the algal maximum growth rate, C_{Nj} is the concentration of nutrient j , and $C_{Nj\min}$ is the nutrient threshold required for algal growth. The temperature factor is parameterized by an improved form of the empirical formula specified in [22] as follows:

$$f(T) = e^{-q_T|T-T_r|}, \quad (3)$$

where q_T is an empirically determined coefficient, T is the sea water temperature, and T_r is the reference temperature. A simple nudging method [23] is introduced to configure the temperature and surface concentrations of nitrate, phosphate, and silicate in this numerical marine incubator. The default value of basal respiration rate for autotrophs is 0.05 day^{-1} . It is a crucial assumption of this version of microplankton that the value of the heterotroph fraction does not change during a simulation and the default ratio of microheterotroph to microplankton carbon biomass is 0.3. A schematic of the numerical mesocosm experiment based on the above theory is shown in Figure 1.

To reduce the limitations on local conditions, the range of the numerical mesocosm experiment is extended from a specified locality to the Yangtze River Estuary and its adjacent waters ($120^{\circ}00'E-124^{\circ}00'E$, $27^{\circ}00'N-30^{\circ}45'N$), where HABs occur frequently. The numerical resolution is set at $5' \times 5'$ in the horizontal and 11 sigma levels in the vertical. The bathymetry of the experimental region is shown in Figure 2.

The initial and open physical boundary conditions are obtained from baroclinic diagnostic simulations of a wider range of spring circulation encompassing the entire ESC, which is performed as described in [24], except that open boundary flux conditions are imposed on the spring in the COHERENS physical module [25]. The initial ecological variable fields are distributed according to a subset of

chlorophyll data archived in the 2001 World Ocean Atlas [26]. Wind stress and surface fluxes of heat, salinity, and dissolved oxygen are input as sea surface forcing. A zero-flux condition is imposed on land boundary, but a certain amount of ecological exchange is allowed at the sea bottom. At the open boundary, a radiation condition is applied for horizontal currents and a zero gradient condition is chosen for scalar variables (for details see [19]). The latter is a feasible option given the lack of complete and continuous ecological survey data in the ESC, which also makes the values of each nutrient threshold and grazing pressure adjustable. The algal parameters are valued according to related research as follows: the maximum growth rate of *P. donghaiense* and *S. costatum* is separately 1.88 day^{-1} and 4.21 day^{-1} [17]; the reference temperature of *P. donghaiense* and *S. costatum* is separately 20°C and 17°C .

Over time, surface concentrations of nitrate, phosphate, and silicate are nudged towards their observed concentrations [27] during the process of HAB. The algal species cultured in this experiment are specified as *S. costatum* and *P. donghaiense*. From estimates of HAB sources [28] these two species are assumed initially to be located in the Zhejiang offshore area ($121^{\circ}30'E-123^{\circ}00'E$, $27^{\circ}00'N-28^{\circ}00'N$), and the initial algal concentrations are distributed according to the tracking observations [29, 30]. The numerical mesocosm experimental period is set to 90 mode days.

3. Results and Discussion

Since the HAB in the ESC generally occurs in the coastal upper water column between 30 m and 60 m isobaths [31],

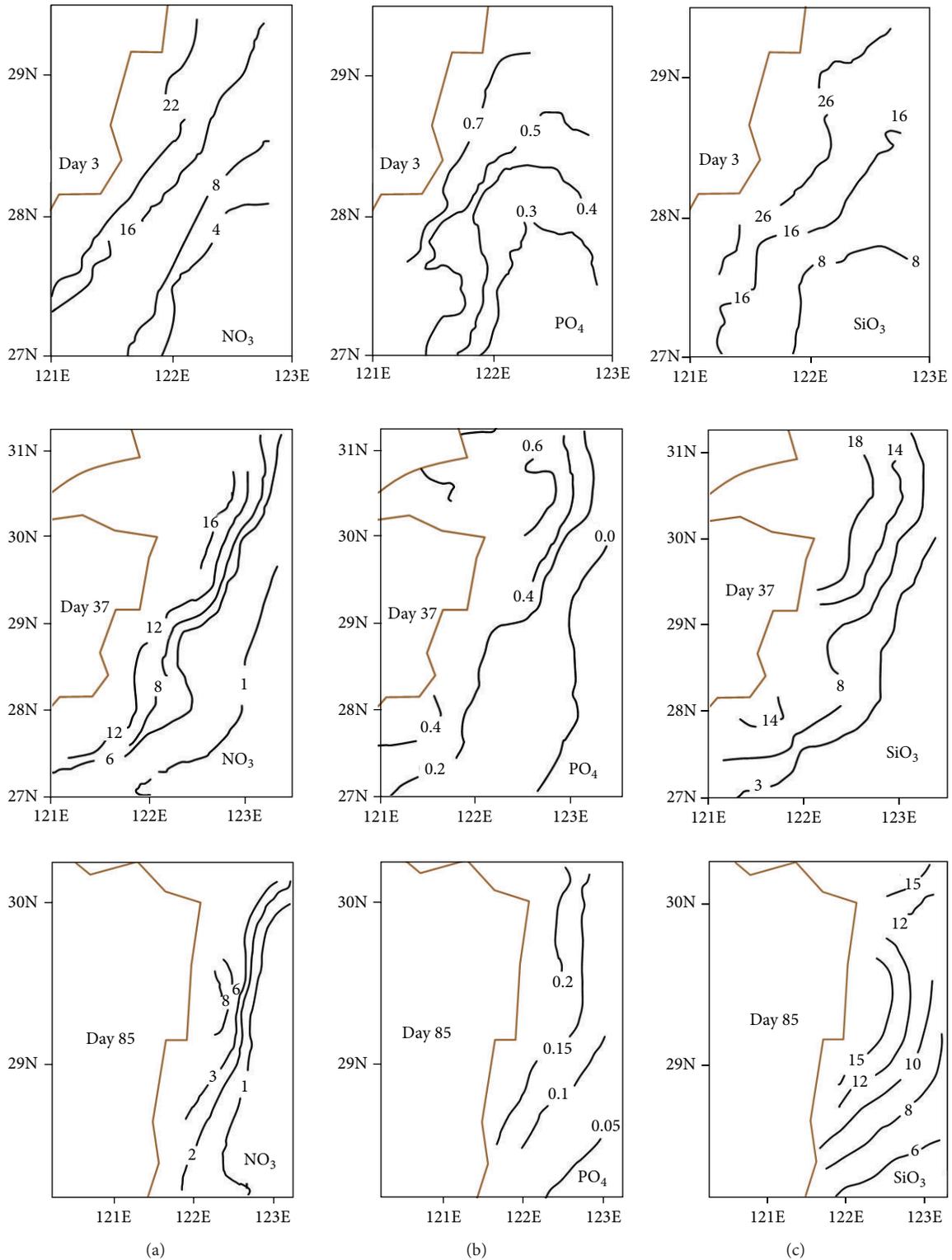


FIGURE 4: Surface nutrient concentration (mmol/m^3) of nitrate (a), phosphate (b), and silicate (c) in the experimental region.

the surface data alone from the mesocosm experimental results were used in the analysis. The physical fields were plotted at specified time intervals to view their dynamics throughout the experiment.

3.1. Currents. The surface currents plotted in Figure 3 indicate that the Kuroshio intrusion little affected the experimental region, while the southward Zhejiang coastal current (usually driven by northerly winds) gradually retreated

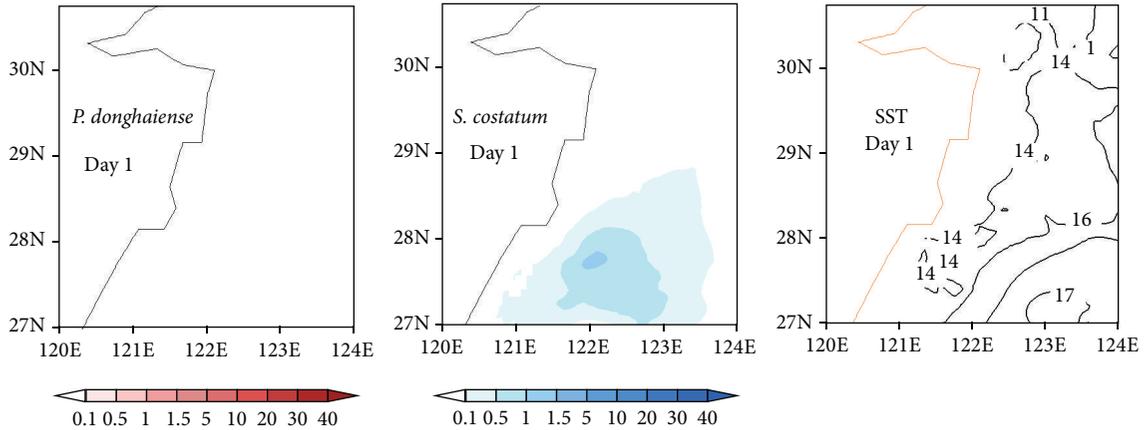


FIGURE 5: Surface concentrations (mmol/m^3) of *P. donghaiense* and *S. costatum* algae and SST ($^{\circ}\text{C}$) on day 1.

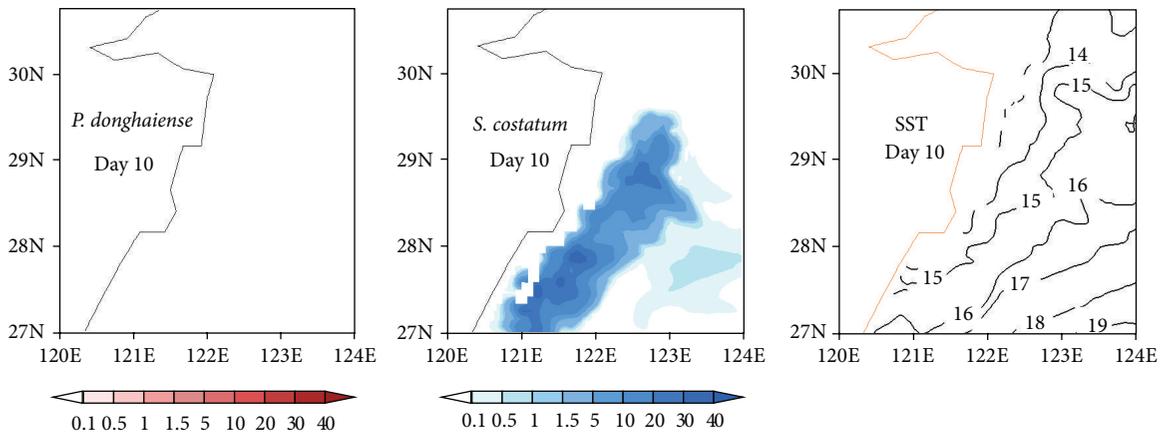


FIGURE 6: Surface algal concentration (mmol/m^3) of *P. donghaiense* and *S. costatum* algae and SST ($^{\circ}\text{C}$) on day 10.

northward, even tending directly towards north at late times. The Taiwan Warm Current, however, retained a northern flow throughout. The gradual strengthening of this flow over time was possibly the main reason for the northward migration of the HAB center.

3.2. Nutrients. Initially (Figure 4, Day 3), the specified high level of nutrient provided substantial sustenance for the blooming of numerically incubated *S. costatum* and *P. donghaiense*. More than half of the nutrients had been consumed within the first 37 days of the experiment, providing indirect evidence of an algal bloom, probably *S. costatum* one. Another algal bloom could be tracked by the nearly 50% reduction of nitrate and phosphate (but not silicate) during the next 48 days. Because *P. donghaiense* does not usually absorb silicate, this second bloom, with less nutrient consumption than the first, was assumed to be caused by *P. donghaiense*. By the final phase of the experiment, the phosphate concentration had descended to a very low level while the silicate concentration was raised, which suggests that the nudging approach had achieved moderate success.

3.3. Algal Concentration and Sea Surface Temperature. The initial concentration of *S. costatum* was set at twenty times that of *P. donghaiense* in accordance with previous analysis [29, 30], in which the concentration of *P. donghaiense* was apparently less than 0.1 mmol/m^3 (Figure 5). The sea surface temperature (SST) on day 1 ranged from 13 to 17°C .

With a strong competition advantage in eutrophic waters, *S. costatum* reproduced at a high rate within the first few days of the experiment, culminating in a large-scale bloom on day 10 with maximum concentration exceeding 30 mmol/m^3 . The bloom center visibly moved northward, along the flow direction of the Taiwan Warm Current. Now the SST ranged from 15 to 19°C , consistent with the adaptive temperature range ($15\text{--}25^{\circ}\text{C}$) of exponential growth in *S. costatum* [18]. Meanwhile, the surface concentration of *P. donghaiense* had remained below 0.1 mmol/m^3 , possibly because the SST was outside the adaptive temperature range of this organism.

The *S. costatum* bloom, which lasted for approximately 22 days, consumed a large quantity of nutrients in the experimental region. Eventually, the reduced nutrient levels could no longer sustain rapid *S. costatum* growth and, by day 33, the bloom had dissipated under the default pressures of respiration and grazing (Figure 6). However, *P. donghaiense*,

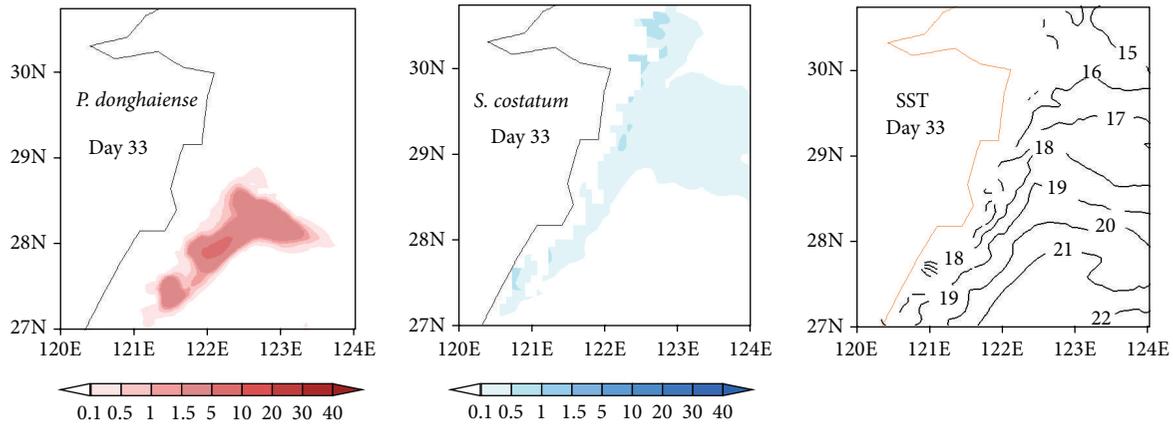


FIGURE 7: Surface algal concentration (mmol/m^3) of *P. donghaiense* and *S. costatum* algae and SST ($^{\circ}\text{C}$) on day 33.

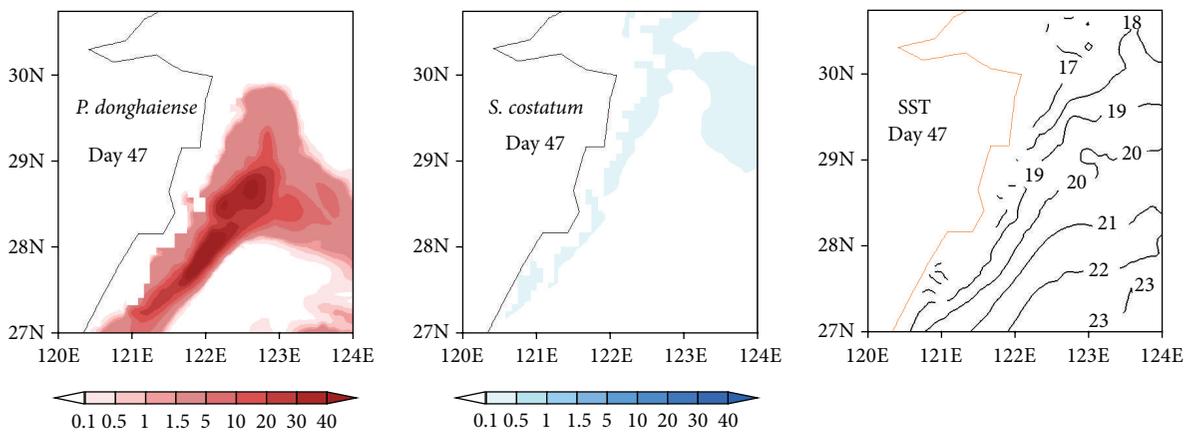


FIGURE 8: Surface algal concentration (mmol/m^3) of *P. donghaiense* and *S. costatum* algae and SST ($^{\circ}\text{C}$) on day 47.

with lower nutrient requirements than *S. costatum*, began to fill the depleted niche as the SST approached the *P. donghaiense* adaptive range (Figure 7).

When the SST had risen to between 19°C and 23°C inclusively (day 47), *P. donghaiense* bloomed within a wide-ranging area with maximum concentration exceeding $40 \text{ mmol}/\text{m}^3$ (Figure 8). This was accompanied by an obvious northward migration of its bloom center. *S. costatum* declined rapidly in most areas, persisting at low levels solely around the Yangtze River Estuary, consistent with its strong dependence on nutrient availability.

The *P. donghaiense* bloom was sustained for 40 days, fading away on day 88 to concentrations below $0.5 \text{ mmol}/\text{m}^3$ in most areas (Figure 9). Multiplication of both algal species was not further increased by ascending concentration of silicate. The decay of the *P. donghaiense* bloom and the further reduction in *S. costatum* concentration were both influenced by the increasing SST, indicating that this numerical experiment is relatively sensitive to temperature.

4. Conclusions and Discussion

4.1. Conclusions. Results from indoor culture [18] and field mesocosm experiments [17] show that *S. costatum* has

a competitive advantage in a rich nutrient environment; it proliferates rapidly and thus blooms within a shorter period than its competitor. Conversely, *P. donghaiense* can survive in a low nutrient environment and maintains a long bloom period if sea temperature is favorable. The mechanism by which *S. costatum* and *P. donghaiense* compete was unveiled in the numerical mesocosm experiment. This experiment confirmed that both the Taiwan Warm Current and the eutrophication in the adjacent water of Yangtze River Estuary contribute to the northward moving of the HAB center and also suggested that the lack of nutrient supplement in the open sea limits HAB occurrences in coastal waters.

4.2. Discussion. By comparing the three types of experiment (Table 1), we note that some ecological parameters in the numerical mesocosm can be directly determined from the results of indoor culture and field mesocosm, which are represented in turn by those of the numerical experiment. The equivalency between them confirms that the parameters of bioexperiments, whether indoor or field, are the preconditions and the important bases of numerical ones.

Although the numerical mesocosm is less restricted by temporal and spatial constraints than physical systems, large

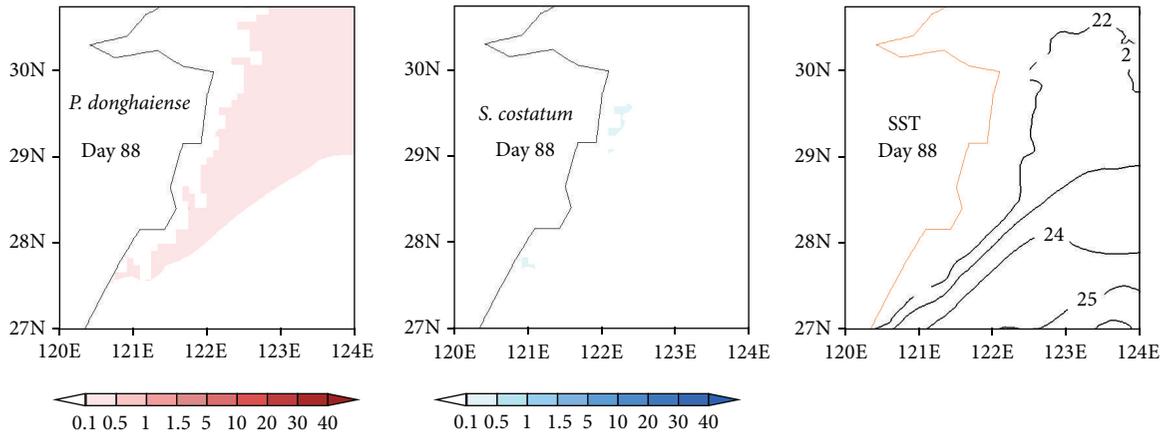


FIGURE 9: Surface algal concentration (mmol/m^3) of *P. donghaiense* and *S. costatum* algae and SST ($^{\circ}\text{C}$) on day 88.

TABLE 1: Comparison between indoor culture, field mesocosm, and numerical mesocosm.

Mode	Indoor culture	Field mesocosm	Numerical mesocosm
Location	Culture dishes	30°50.5'N, 122°6.7'E	~120°00'E–124°00'E, ~27°00'N–30°45'N
Species	<i>S. costatum</i> and <i>P. donghaiense</i>	<i>S. costatum</i> and <i>P. donghaiense</i>	<i>S. costatum</i> and <i>P. donghaiense</i>
Physical environment	Artificial light source Fixed thermohaline value Still water	Natural light Local water temperature and salinity No current impact	Parameterized irradiance Simulated thermohaline value Simulated current
Nutrient condition	Artificially added culture medium	Artificially added nutrients	Simulated nutrient concentration nudged towards observations
Exchange with outside	None	Artificial circulation	Numerical boundary conditions
Results	(a) Adaptive temperature range of exponential growth phase for these two species (b) <i>S. costatum</i> is more competitive in a rich nutrient environment (c) <i>P. donghaiense</i> can live in low nutrient environment	(a) Maximum growth rates of these two species (b) <i>S. costatum</i> can proliferate rapidly under high nutrient conditions and has a shorter duration of bloom (c) <i>P. donghaiense</i> can survive under nutrient-limited conditions and its blooms persist over a longer period	(a) Simulation of the algal blooms caused in turn by these two species further confirms the competition mechanism between them (b) The current contribution to the northward migration of the bloom center (c) The lack of nutrient supplement in the open sea limits HAB occurrences in the coastal waters

calculation errors arise because of the incomplete understanding of marine ecological mechanisms and the uncertainty of ecological parameters. Consequently, the numerical experiment results cannot be quantitatively validated in this study. More accurate results of the numerical mesocosm experiment can be obtained only through a complete marine ecological investigation and a thorough understanding of the marine ecosystem.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

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