

The 18th Biennial Conference of International Society for Ecological Modelling

Investigating the roles of intrinsic and extrinsic factors in the blooms of *Pyrodinium bahamense* var. *compressum* using an individual-based model

A. T. Yñiguez^{*}, A. Cayetano, C. L. Villanoy, I. Alabia, I. Fernandez, J. D. Palermo, G. A. Benico, F. P. Siringan, R. V. Azanza

Marine Science Institute, Velasquez St., University of the Philippines, Diliman, Quezon City 1101, Philippines

Abstract

Harmful algal blooms are a recurrent, expensive and at times fatal problem plaguing the Philippines. In particular, Sorsogon Bay in the Bicol region has experienced prolonged shellfish bans due to blooms by the Paralytic Shellfish Poisoning causative species *Pyrodinium bahamense* var. *compressum* (Pbc). In order to help explore and understand the population dynamics of Pbc in Sorsogon Bay in relation to environmental factors, an individual-based model has been developed. This model accounts for key life history processes (reproduction, mortality, encystment, excystment) in a spatially-explicit setting. Vegetative cells and resting cysts are separately represented. Movement is due to advection rates from a 3D hydrodynamic model, as well as sinking rates. Asexual reproduction (population growth) occurs in response to light, temperature, salinity and nutrient conditions where the cells are spatially situated. Encystment and excystment processes are also spatially-explicit based on intrinsic factors, and environmental factors. Grazing effects on blooms are also being explored in the model. Results from field studies in the past years indicate that Pbc blooms develop a few months after the onset of rains, relatively lower temperature, and stratification of the water column. Pronounced blooms are observed at a particular time of the year and in certain areas of the Bay. Bloom formation patterns in the model are compared with these field results. This model will be used to further investigate the conditions leading to blooms and their decline, specifically the roles of transport, stratification, nutrients, cyst dynamics, and grazing on Pbc blooms in Sorsogon Bay.

© 2011 Published by Elsevier B.V. Selection and/or peer-review under responsibility of School of Environment, Beijing Normal University.

Keywords: harmful algal blooms, *Pyrodinium*, Philippines, biophysical model, individual based model

^{*} Corresponding author. Tel.: +63-2-393-7567; fax: +63-2-922-3963.
E-mail address: atyniguez@gmail.com, atyniguez@upmsi.ph.

1. Introduction

Harmful algal blooms have plagued various areas in the Philippines for decades. In particular, the cyst-forming dinoflagellate *Pyrodinium bahamense* var. *compressum* has been responsible for many toxic blooms that have led to fatalities and economic impacts [1]. *Pyrodinium bahamense* var. *compressum*, as with other cyst-forming dinoflagellates, have a complex life cycle that involves an alternation between benthic cysts and motile cells. This alternation between stages, the factors influencing each stage and the transition in between are important in bloom formation [2-5]. Physical (e.g., tides and waves) and biological (bioturbation) are necessary for cyst resuspension which give rise to the opportunity for germination, and if conditions for growth are appropriate, blooms could then develop. Light, temperature, salinity and nutrient conditions are significant biological requirements for phytoplankton growth and reproduction (e.g., [5-9]). The horizontal and vertical distributions of these factors are thus important determinants of bloom development [10]. Water mass stratification has also been observed to play a significant role in bloom development. This is due to the dinoflagellates' intolerance to increased shear-stress associated with water column mixing, high velocity coastal currents and turbulence [11]. In Manila Bay, blooms of Pbc in the late 80s and early 90s coincided with the onset of the southwest monsoon where warm water temperatures and freshwater flux resulted in strong water column stratification [12]. Similarly, the seasonal fluctuation of temperature and salinity in the bay shows the compounded effect of convection and water column stability regulating the vertical movement of plankton and the resources necessary for its growth [13]. HABs appear to occur in areas where stratification is strong [14].

Exploring the interactions of the HAB species' life history events with physical factors and particularly conditions leading to re-suspension, good growth conditions and stratification are thus necessary for obtaining a better understanding of bloom formation, development and decline in coastal waters in the Philippines. This paper presents an integrated biophysical model that captures the life history dynamics of *Pyrodinium bahamense* var. *compressum* in a spatially-explicit individual-based model. Initial results from the model are compared with observed data from Sorsogon Bay, Philippines.

2. Model Description

2.1. Physical model

The hydrodynamic model for Sorsogon Bay was simulated using the DELFT-3D platform for a total duration of one year (January-December 2009) with a two-month spin up period from November-December 2008. The model is initially forced by tides, winds and heat flux data. The resulting velocities as well as temperature values were used as part of the environmental conditions and hydrodynamic forcing for the biological model described below.

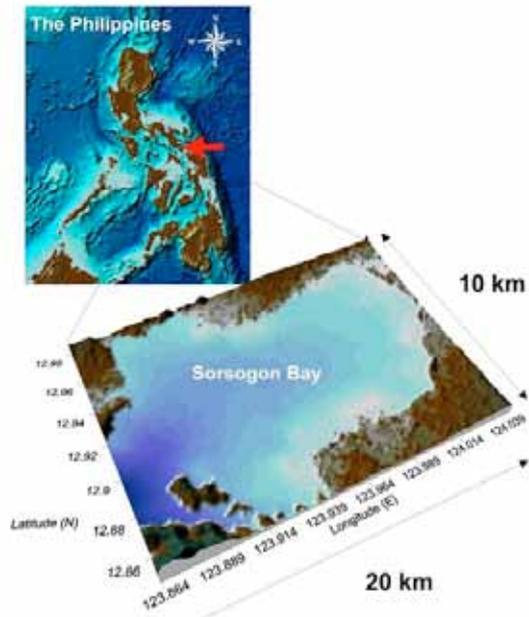


Figure 1. Map of Sorsogon Bay in the northeast of the Philippines.

2.2. Biological model

The biological model is described below in detail using the standardized Overview, Design Concepts, Details (ODD) structure promulgated by [15, 16] in order to facilitate an organized and comprehensive discussion of the model.

2.2.1. Overview

2.2.1.1. Purpose

A 3-dimensional individual-based model was constructed in order to study the bloom dynamics of *Pyrodinium bahamense* var. *compressum* (Pbc). Through individual-based modelling, the events necessary for bloom occurrence or decline were represented as mechanistically as possible. Such individual or bottom-level representations will then give rise to certain global (system-wide) emergent behaviours which could then be used as basis for identifying patterns and crucial factors such as cyst beds, stratification and nutrient input, and potentially making predictions regarding the occurrence of harmful algal blooms.

2.2.1.2. Entities, state variables and scales

The model separately represents the vegetative cell and cyst (hypnozygote) life stages of Pbc. Cells can move through advection and has a particular buoyancy rate. They also reproduce asexually, senesce and encyst depending on environmental conditions. Upon encystment, cysts are advected and have a sinking rate until they reach and settle on the sea floor. They can be resuspended depending on a certain

bottom current velocity threshold, and can only excyst if they have finished their mandatory dormancy period and environmental conditions are appropriate.

The 3D model was designed to represent the area of Sorsogon Bay starting at the mouth of the bay up to the head including the ocean floor (Figure 2). Overall, the covered length is about 10 km, the covered width is about 20 km and the maximum depth covered is around 26 m. To minimize computation complexity while maximizing the accuracy of representation, the dimensions of the bay were represented using different scales. The length and width of Sorsogon Bay were represented using a coarser scale namely 100 m: 1 unit model distance (or cell) while the depth was represented at a finer scale equal to 0.52 m: 1 unit model distance. Hence, the entire model dimensions or grid is 100 units long, 200 units wide and 50 units deep.

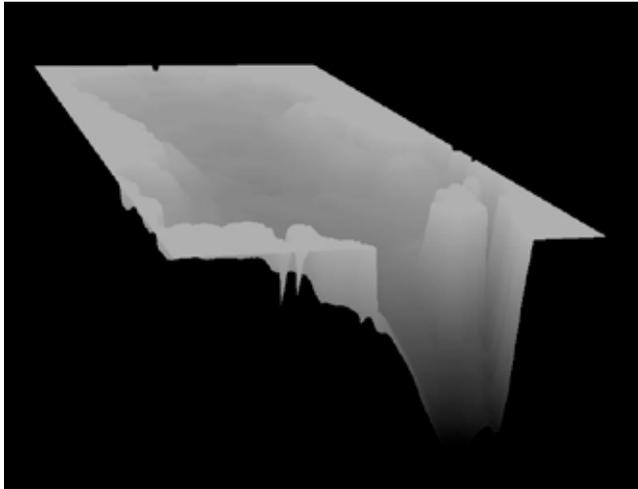


Figure 2. The model simulation space.

2.2.1.3. Process overview and scheduling

Each time step in the model is equivalent to one day. As a consequence, each event in the environment or action that an agent undergoes works as if it is a discrete whole day event. Updates of the model occur sequentially per event class or category. That is, the changes in the environment (light, temperature, salinity and nutrients) occur first followed by the behaviours of the cells and cysts. For a Pbc cell, there are four distinct events that could possibly occur within each time step (i.e. within a day). First, cells are transported based on the prevailing water velocities in three directions, diffusivity and buoyancy values. They then undergo asexual reproduction as a function of the environmental conditions in its location. The cell may then die or encyst which are processes also dependent on environmental conditions. Pbc cysts, being a dormant stage, perform only two main biological events. Depending on its current state cysts can either be transported as a function of water velocities, diffusivity and sinking values if it is still in the water column and unable to excyst. If the cyst is on the sea floor and has already undergone its mandatory dormancy period, then it can excyst depending on its being resuspended in the water column and the conditions it then encounters. Water velocities for the following day are then processed. Lastly, the abundances and densities of cells and cysts (comparable to actual *in situ* data) from virtual sampling stations are obtained.

2.2.2. Design Concepts

2.2.2.1. Emergence

The global properties observable in the model are the rise and fall of Pyrodinium population representing periods of bloom and decline. The pattern of distribution of the Pbc cells and Pbc cysts throughout the area of the bay and especially with depth is also a good emergent property to be observed. Lastly, time-dependent variations of Pbc cell and cyst populations are also valuable pieces of information that could be derived from the model.

2.2.2.2. Adaptation/Objectives

The cells and cysts are able to respond to their changing environment. Cells asexually reproduce as a function of their environment. The alternation between cell and cyst stages is also an adaptive response to their environment. However, this is an implicit adaptive mechanism since this is assumed to reflect an inherent adaptive mechanism in this species life cycle that allows its population to survive unfavourable conditions [17].

2.2.2.3. Learning/Prediction

The agents have no way of predicting the future events that would occur within themselves or the environment. The agents perceive only their current condition as well as that of the environment. They also do not take note of their history hence they have no learning mechanisms.

2.2.2.4. Sensing

Sensing is simulated by simple variable checking. Cells and cysts are able to sense only the local environment. The farthest they can sense is the distance that advection, diffusivity and buoyancy/sinking rate could take them at one time step. In that way, they would know whether they would fall near or at the shore, above the surface or below the floor of the bay. In those cases, they try other possible locations several times and if there is still no feasible location found, they stay where they are currently located. Hence, the incorporation of such sensing capability gives the agents the ability to evaluate boundary conditions. Cells and cysts are able to assess the environmental conditions in their local environment and use this as information for the processes they undergo (i.e., reproduction, encystment and excystment).

2.2.2.5. Interaction

At the moment, agents do not interact. Their behaviour is independent of each other. There is also no form of relationship (such as predator-prey) happening between the agents.

2.2.2.6. Stochasticity

Numerous rules imposed in the model are governed by stochastic events. For instance, the mortality and the proliferative capacity of an agent involve some elements of chance (to be discussed in Section Details).

2.2.2.7. Collectives

No social groupings occur among the agents. Only implied groups exist such as the distinct population of Pbc cell and Pbc cyst although such grouping does not have any influence on the behavior of the agents involved.

2.2.2.8. Observation

The model output would be the population of cells and cysts at a specific area at a given time. Currently, the model is capable of taking the latitude-longitude of the sampling stations in a text file and converting such value into the corresponding model coordinates. In that way, field sampling is simulated.

2.2.3. Details

2.2.3.1. 2.2.3.1 Initialization

Currently, the model can be initialized by specifying the initial population of Pbc cells and cysts and how they are distributed throughout the bay (e.g., Figure 3). Once specific areas have been selected, Pbc cells can be seeded at any depth while Pbc cysts are automatically situated at the bottom. Also, the starting date for simulation can also be specified during initialization. Lastly, the model also obtains the specific areas of interest (i.e. sampling sites) where the model output will be obtained.

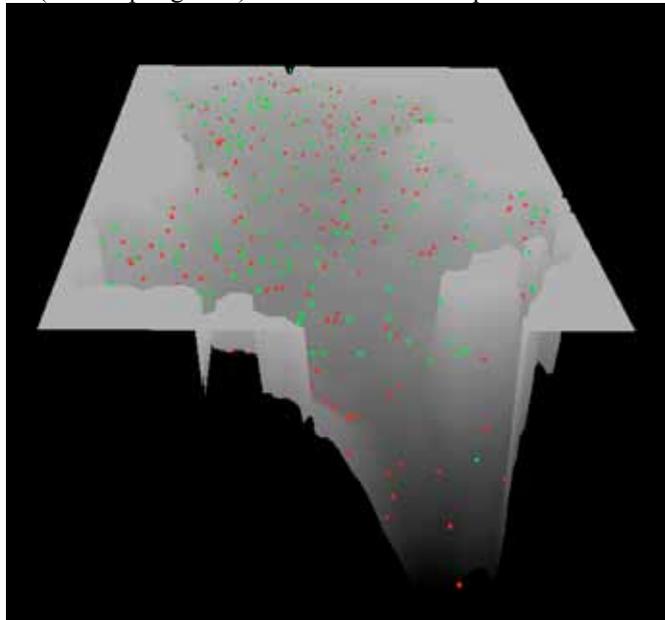


Figure 3. Initial distribution of Pbc cells and cysts.

2.2.3.2. Input data

The model requires the input of the bathymetry and hydrodynamic circulation of the study area, and the environmental factors of light, temperature, salinity, nutrients.

2.2.3.3. Bathymetry and Circulation

The bathymetry of Sorsogon Bay was obtained from digitized charts and bathymetric surveys. This 20 km x 10 km area covering from 123.86372°-124.04385° E longitude and 12.8489°-12.9817° N latitude was gridded and represented using a 200 x 100 x 50 cells grid with a resolution of 100m x 100m x 2m per cell. Below is a screenshot of the model with the bathymetry placed beside the contour of the actual bathymetry data.

The physical model discussed above provides the water velocity vectors in three dimensions and diffusivity rates, which are then used to calculate advection of cells and cysts as discussed in Section 2.2.3.5 Movement (Pbc cell and Pbc cyst) below.

The velocity data is spatially-specific according to the granularity set-up of the hydrodynamic DELFT-3D model. Also, depth-specificity was achieved by defining 5 layers for the depth of the bay where velocity quantities are distinct. Lastly, since the granularity of the agent-based model grid is finer, linear interpolation was performed to obtain a finer resolution for the velocities.

2.2.3.4. Light

Irradiance was modeled using the Beer-Lambert law:

$$I_{depth} = I_0 e^{-k(depth)} \quad (1)$$

This calculates irradiance at a particular depth, I_{depth} , in $\mu\text{Einstein}/\text{m}^2/\text{sec}$ as a function of I_0 , the surface irradiance, k (attenuation coefficient) and the depth.

The surface irradiance was obtained from satellite data available from Giovanni (MODIS-Aqua 4km). The resolution of such data made it possible to divide the bay into 25 pixels each having a particular value for surface irradiance in the form of photosynthetically available radiation (PAR). Also, the data have monthly temporal resolution allowing the model to have a different value of surface irradiation depending on the month.

2.2.3.5. Temperature and Salinity

Temperature data was obtained as part of the output of the hydrodynamic model of Sorsogon Bay from DELFT-3D. The values obtained are specific for each location in the bay depending on the granularity of the model grid initialized on DELFT-3D. Also, similar to the velocity data, the values of temperature are depth-specific such that depth of the bay was divided into 5 thermally-distinct layers. Lastly, to scale the grid size of temperature values from the DELFT-3D model with respect to the grid of the agent-based model, linear interpolation was done.

For the salinity, the data came from field studies on 3 months representing the 3 seasons. To obtain spatially-specific values for salinity, nearest-neighbor interpolation was performed using such field data.

2.2.3.6. Nutrients

Data for nutrients came from field studies by Project 4 of the Philippine HABs Program (Gil S. Jacinto, Project Leader) involving 3 months covering the 3 seasons. However, since the actual data is only at specific sampling sites, nearest-neighbor interpolation was done to obtain the corresponding values for other locations.

2.2.3.7. Submodels

The behaviour of the agents in response to internal and external factors follows particular mathematical formulations. A meta-analysis of available information on *Pyrodinium bahamense* var. *compressum* was conducted and the growth responses derived using known biological equations for phytoplankton [18].

2.2.3.7.1. Reproduction

Below is the equation used in determining the probability for asexual reproduction of a cell as a function of the light, temperature, salinity and nutrient values, respectively, in its current location. The

specific growth rate is calculated based on Leibig's law of minimum, such that the maximum growth rate is regulated by the most limiting factor.

$$\mu = \mu_{\max} \min[f(I)f(T)f(S)f(N)] \quad (2)$$

The influence of the individual factors light, temperature, salinity and nutrients are shown below. These equations are based on results of the non-linear regressions of all known available information on *Pbc* as affected by each of these factors. These functions give values from 0 to 1 and are then scaled by the maximum growth rate (μ_{\max}). Table 1 lists and describes the specific parameters used in the submodels.

The growth response to light is calculated as a saturating function:

$$f(I) = 1 - e^{-\alpha(I - I_{\text{comp}})} \quad (3)$$

The growth response to temperature follows the form of [19] wherein there is a temperature range where *Pyrodinium bahamense* var. *compressum* can grow and a higher growth rate at the optimum growth temperature (T_0):

$$f(T) = \frac{1}{\tau_1} (A^T e^{-B(T-T_0)^C} - \tau_2) \quad (4)$$

The growth response to salinity was derived from data fitted to a quadratic polynomial equation normalized to give non-dimensional values ranging from 0 to 1:

$$f(S) = (\beta_0 + \beta_1 S + \beta_2 S^2) / 0.7003 \quad (5)$$

The growth response to nutrients uses the Michaelis-Menton formulation. Nutrients considered here are in terms of Dissolved Inorganic Nitrogen (DIN):

$$f(N) = (N / (N + k_{SAT})) \quad (6)$$

Table 1. Description and values of parameters used in the biological submodels.

Symbol	Description	Unit	Values	Source
μ_{\max}	Maximum specific growth rate of <i>Pyrodinium bahamense</i> var. <i>compressum</i>	NA	0.4	[5, 20]
α	Light growth response coefficient	NA	0.014	Best fit through non-linear regression
I_{comp}	Irradiance at light compensation point	$\mu\text{Einstein m}^{-2} \text{s}^{-1}$	-11.143	Best fit through non-linear regression
τ_1	Temperature normalizing coefficient	NA	1.38	Best fit through non-linear regression
τ_2	Temperature normalizing coefficient	NA	-0.402	Best fit through non-linear regression
A	Temperature curve coefficient	NA	0.9333	Best fit through non-linear regression
B	Temperature range coefficient	NA	0.047	Best fit through non-linear regression
C	Temperature decay coefficient	NA	4	Best fit through non-linear regression
T_0	Optimum growth temperature	$^{\circ}\text{C}$	29.218	[5] and best fit through

β_0	Salinity growth coefficient	NA	-0.286	non-linear regression Best fit through non-linear regression
β_1	Salinity growth coefficient	NA	0.024	Best fit through non-linear regression
β_2	Salinity growth coefficient	NA	-0.000146	Best fit through non-linear regression
k_{sat}	Half-saturation constant for DIN	NA	3	Exploratory. Initially based on studies on dinoflagellates [21-23]
d_{cell}	Vegetative cell mortality probability		0.05	Exploratory
d_{cyst}	Cyst mortality probability		0.005	Exploratory

2.2.3.8. Mortality (*Pbc cell and Pbc cyst*)

Currently, assumed mortality probabilities (d_{cell} and d_{cyst}) are used for both cells and cysts. A spatially-explicit mortality grazing potential map will eventually be overlaid as an indication of mortality probability.

2.2.3.9. Encystment

The encystment probability is based on the light, temperature and salinity conditions. A vegetative cell will encyst if two of the following conditions are met: if irradiance is lower than 15 PAR [5], or temperature is lower than 22 oC or warmer than 36 oC [24], or salinity is less than 20 ppt or greater than 36 ppt [24].

2.2.3.10. Resuspension and Excystment

Cysts need to be re-suspended from the sediments first through bottom velocities exceeding 0.0003 m/s [13], after which water column conditions are evaluated if they can excyst. If light, temperature and salinity conditions are within its range [5, 13, 24] then they will excyst.

2.2.3.11. Movement (*Pbc cell and Pbc cyst*)

Movement of cells and cysts occur through advection by the prevailing water velocities in three dimensions calculated using the following equations:

$$X_i^{n+1} = X_i^n + U\Delta t + \gamma\sqrt{2\Delta tD_H} \tag{7}$$

$$Y_i^{n+1} = Y_i^n + V\Delta t + \gamma\sqrt{2\Delta tD_H} \tag{8}$$

$$Z_i^{n+1} = Z_i^n + W\Delta t + \gamma\sqrt{2\Delta tD_V} \tag{9}$$

where, X_i^{n+1} and Y_i^{n+1} and Z_i^{n+1} are the next position at X, Y and Z coordinates

X_i^n and Y_i^n and Z_i^n are the current position at X, Y and Z coordinates

U, V, W are daily-averaged velocities at x, y and z directions

D_H and D_V are horizontal and vertical diffusivities with values 5 and 0.001, respectively

Δt is the time interval (currently a tweakable parameter in order to scale the effect of the very coarse daily-averaged velocity approximations)

γ is a coefficient (random number between 0 and 1)

3. Model implementation and performance

The model was implemented in Java using the MASON multi-agent simulation toolkit. A whole year simulation run takes only several minutes to finish on an Intel Core i3 desktop computer.

Currently, one of the most valuable information that can be extracted from the model is the abundance of the population of Pbc cells and cysts through space and time. Such data allows the user to monitor during each time step the pattern of bloom and decline of Pbc. Also, the monitoring of populations can be bay-wide or only at user-specified sampling sites.

The role of cysts in bloom formation has been highlighted in the intensively studied Gulf of Maine blooms of *Alexandrium fundyense* [2, 25], as well as locally in Manila Bay blooms of *Pyrodinium bahamense* var. *compressum* [3, 13, 26]. In Manila Bay, a mainly physical model tracked the re-suspension and germination of cysts, and consequent transport of passive cells. The transport of the cells from identified cyst beds coincided with the pattern of past shellfish ban patterns. The advection of or the in situ growth of cells due to enhanced growth conditions (e.g., release from nutrient limitation) have also been implicated in bloom formation [7, 27]. In this paper, we more directly test the role of cysts in bloom initiation. Two initial questions were investigated with the model:

- 1) Can blooms be initiated and emerge from a purely cyst population?
- 2) Does the distribution of cysts affect the patterns observed?

To answer these questions, two scenarios were set-up by varying the initial distribution of a fixed population of Pbc cysts (i.e., a total of 1000 initial cysts) and using the default parameters in Table 1. The first scenario distributes the initial population of cysts in specific areas (Figure 4a) based on actual observations of surface cysts (Project 5 of Philippine HABS Program, FP Siringan Project Leader). The second scenario also starts the simulation with only cysts; however these were distributed randomly throughout the bay (Figure 4b).

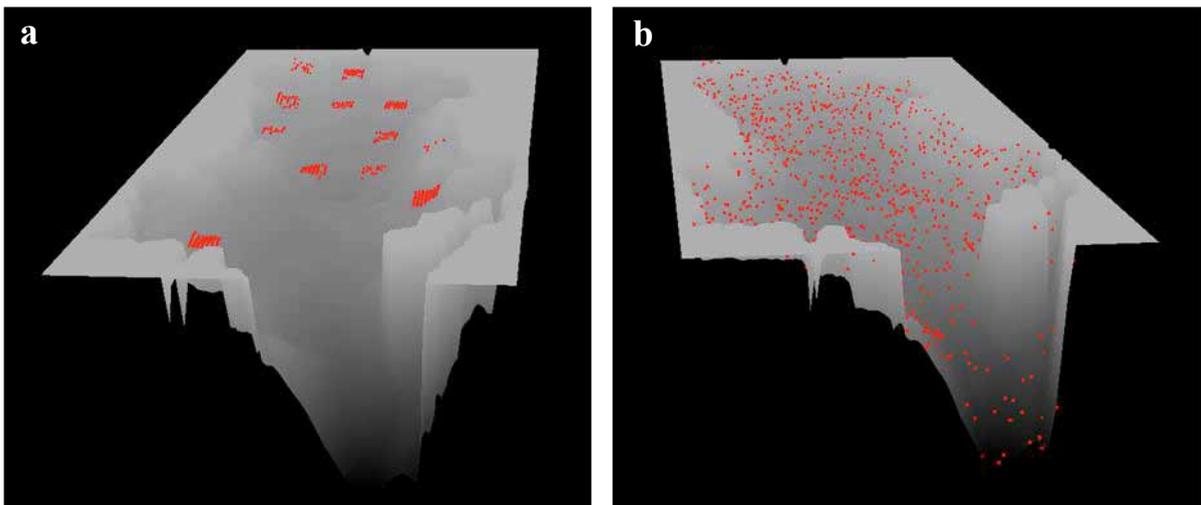


Figure 4. Initial distribution of Pbc cysts at the start of the simulation runs representing scenarios where a) cysts are initially distributed in specific areas; and, b) cysts are randomly distributed.

Results from the simulation runs (average of 5 trials) produced year-long time-series of the vegetative Pbc cell population. The simulations showed that the model can capture variations in the Pbc cell abundances, and bloom-like increases and distributions were observed even with just cysts (and no cells) used to initialize the model. The first scenario resulted in a small increase in March, with a big pulse in cell abundance around June followed by a rapid decline until the end of the simulated year (Figure 5). Spatially, the cells were relatively more abundant in the areas of the cyst beds, except for those towards the mouth of the bay (Figure 6a). The area towards the mouth of the bay is deeper and may not present as favorable conditions as the shallower areas in the current configuration.

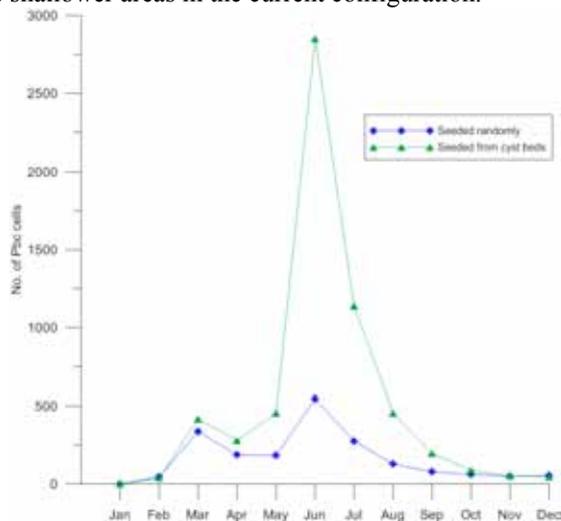


Figure 5. *Pyrodinium bahamense* var. *compressum* (Pbc) abundance (no. of cells) per month from the two scenarios run.

The second scenario where cysts were randomly distributed showed a similar small peak in March, and a relatively bigger cell abundance peak in June after which the population declined till the end of the simulated year. However, unlike the first scenario, the second peak was more similar to the first peak in cell abundance (Figure 5). For the spatial distribution, even if the cysts had been randomly distributed, pockets of relatively higher cell abundances developed in areas that were similar to the first scenario (Figure 6b). Interestingly, the scenario with cysts seeded using seed beds yielded higher numbers of cells compared to just randomly distributing the cysts. The environmental conditions and/or advective processes could be filtering the areas where cells can increase and/or accumulate.

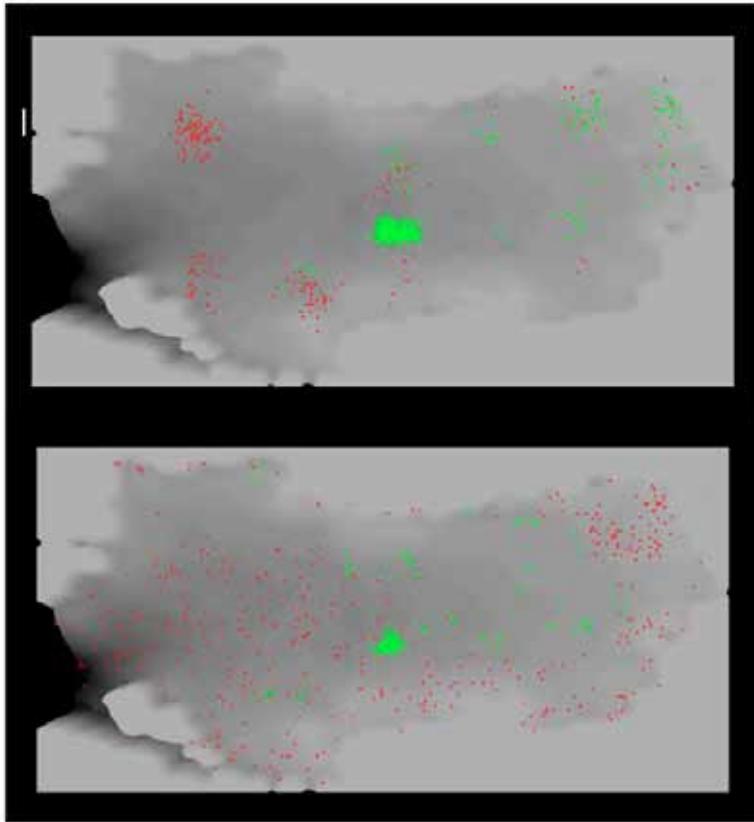


Figure 6. Top view of the spatial distribution of Pbc cells and cysts resulting from the (a) scenario with cysts distributed in certain cyst beds, and (b) randomly distributed cysts.

4. Comparison with field data

Field studies have already been conducted in Sorsogon Bay where the population of Pbc cells was monitored during specific months [28]. The trends emerging from the model were compared with this data from 2009 and used to help evaluate the model (Figure 7).

Figure 7 shows the normalized trend for both the model outputs and field data on the abundance of Pbc cells throughout the bay in different months. The model, in particular the scenario wherein cyst beds were initialized, was able to capture a bloom and decline pattern seen in the observed data. However, the peak cell abundance occurred later (September) in the actual data. The pattern from the model exhibiting two peaks was not seen in the actual data, however it is difficult to be definitive that there was only one peak abundance and when this peak occurred within the year since there was discontinuous monthly sampling.

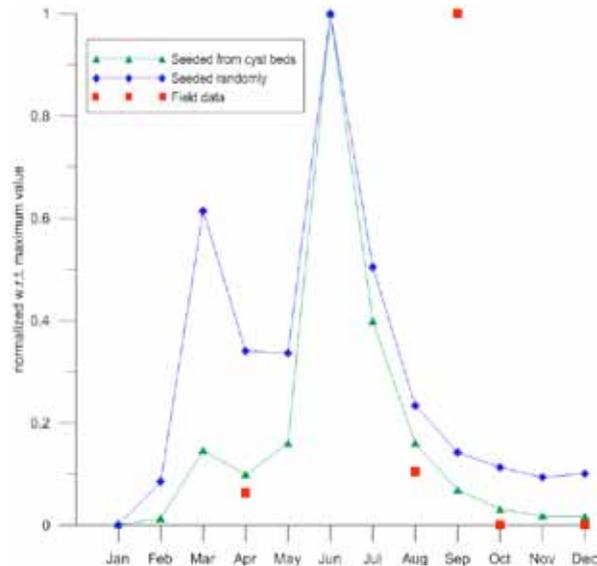


Figure 7. Comparison of normalized abundances of Pbc cells through time from the two simulated scenarios and the observed abundances in Sorsogon Bay.

5. Next steps

The model is currently still being improved on, in particular the hydrodynamic and environmental inputs are still being refined to reflect known conditions more realistically (e.g., capturing freshwater influx since salinity effects on stratification seem to be an important process in blooms), as well as to increase resolution. Grazing potentials will also still be incorporated. However, the model is promising in its use to investigate the details on mechanisms and factors of bloom initiation, maintenance and decline as shown in the initial scenarios that were done testing the role of various cyst configurations in bloom formation patterns through time and in a spatially-explicit manner.

Acknowledgments

We would like to acknowledge the Department of Science and Technology of the Philippines through the Philippine Council for Aquatic and Marine Research and Development for funding this study.

References

- [1] Azanza RV, Taylor MFJR. Are *Pyrodinium* blooms in the Southeast Asian region recurring and spreading? A view at the end of the millennium. *AMBIO: A Journal of the Human Environment* 2001; **30**(6): 356-64.
- [2] Anderson DM, Stock CA, Keafer BA, Bronzino Nelson A, Thompson B, McGillicuddy JDJ, Keller M, Matrai PA, Martin J. *Alexandrium fundyense* cyst dynamics in the Gulf of Maine. *Deep Sea Research Part II: Topical Studies in Oceanography* 2005; **52**(19-21): 2522.

- [3] Azanza RV, Siringan FP, Diego-Mcglone MLS, Yñiguez AT, Macalalad NH, Zamora PB, Agustin MB, Matsuoka K. Horizontal dinoflagellate cyst distribution, sediment characteristics and benthic flux in Manila Bay, Philippines. *Phycol Res* 2004; **52**(4): 376-86.
- [4] Azanza RV. Contributions to the understanding of the bloom dynamics of *Pyrodinium bahamense* var. *compressum*: a toxic tide causative organism. *Science Diliman* 1997; **9**(1&2): 1-6.
- [5] Usup G, Azanza RV. Physiology and bloom dynamics of the tropical dinoflagellate *Pyrodinium bahamense*, in *Physiological Ecology of Harmful Algal Blooms*, DM Anderson, AD Cembella, and GM Hallegraeff, Editors. 1998, Springer-Verlag Berlin Heidelberg.
- [6] Etheridge SM, Roesler CS. Effects of temperature, irradiance, and salinity on photosynthesis, growth rates, total toxicity, and toxin composition for *Alexandrium fundyense* isolates from the Gulf of Maine and Bay of Fundy. *Deep Sea Research Part II: Topical Studies in Oceanography* 2005; **52**(19-21): 2491.
- [7] Heisler J, Glibert PM, Burkholder JM, Anderson DM, Cochlan W, Dennison WC, Dortch Q, Gobler CJ, Heil CA, Humphries E, Lewitus A, Magnien R, Marshall HG, Sellner K, Stockwell DA, Stoecker DK, Suddleson M. Eutrophication and harmful algal blooms: A scientific consensus. *Harmful Algae* 2008; **8**(1): 3.
- [8] Lim P-T, Leaw C-P, Usup G, Kobiyama A, Koike K, Ogata T. Effects of light and temperature on growth, nitrate uptake, and toxin production of two tropical dinoflagellates: *Alexandrium tamiyavanichii* and *Alexandrium minutum*. *J Phycol* 2006; **42**(4): 786-99.
- [9] Philips EJ, Badylak S, Bledsoe E, Cichra M. Factors affecting the distribution of *Pyrodinium bahamense* var. *bahamense* in coastal waters of Florida. *Mar Ecol Prog Ser* 2006; **322**: 99-115.
- [10] Klausmeier C, Litchman E. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. *Limnol Oceanogr* 2001; **46**(8): 1998-2007.
- [11] Smayda T. Adaptive Ecology, Growth Strategies and the Global Bloom Expansion of Dinoflagellates. *Journal of Oceanography* 2002; **58**(2): 281.
- [12] Villanoy CL, Corrales RA, Jacinto GS, Cuaresma Jr. NT, Crisostomo R. Towards the development of a cyst-based model for *Pyrodinium* red tides in Manila Bay, Philippines. In: T Yasumoto, Y Oshima, and Y Fukuyo, editors. *Harmful and Toxic Algal Blooms: Intergovernmental Oceanographic Commission of UNESCO*; 1996, p. 189-92.
- [13] Villanoy CL, Azanza RV, Altemerano A, Casil AL. Attempts to model the bloom dynamics of *Pyrodinium*, a tropical toxic dinoflagellate. *Harmful Algae* 2006; **5**: 156-83.
- [14] GEOHAB. Global ecology and oceanography of harmful algal blooms, GEOHAB Core research project: HABs in stratified systems, P Gentien, et al., Editors. 2008. p. 59.
- [15] Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jorgensen C, Mooij WM, Muller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Ruger N, Strand E, Souissi S, Stillman RA, Vabo R, Visser U, DeAngelis DL. A standard protocol for describing individual-based and agent-based models. *Ecol Model* 2006; **198**(1-2): 115-26.
- [16] Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF. The ODD protocol: A review and first update. *Ecol Model* 2010; **221**(23): 2760-8.
- [17] Nehring S. Mechanisms for recurrent nuisance algal blooms in coastal zones: resting cyst formation as life-strategy of dinoflagellates. In: H Sterr, J Hofstade, and H-P Plag, editors. *Interdisciplinary Discussion of Coastal Research and Coastal Management Issues and Problems*. Lang, Frankfurt/M; 1993, p. 454-67.
- [18] Yñiguez AT, Villanoy CL, David LT, Siringan FP, Palermo JD, Alabia I, Almo A, Fernandez I, Peñaflor E, Bornilla Jr. E, Cayetano A, Quevedo JM. Project 7. Stratification and Algal Blooms in the Tropics Year 2 Technical Annual Report. 2011, Marine Science Institute, University of the Philippines: Quezon City. p. 36.
- [19] Follows M, Dutkiewicz S, Grant S, Chisholm SW. Emergent biogeography of microbial communities in a model ocean. *Science* 2007; **315**: 1843-6.
- [20] Camoying M, Yñiguez AT, Azanza RV, Palermo JD. Effects of irradiance on the growth of the harmful algal bloom forming species *Pyrodinium bahamense* var. *compressum*, in *10th National Symposium in Marine Science*. 2009: Eden Resort, Davao City.

- [21] Eppley RW, Thomas WH. Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. *J Phycol* 1969; **5**(4): 375-9.
- [22] Carpenter EJ, Guillard RRL. Intraspecific Differences in Nitrate Half-Saturation Constants for Three Species of Marine Phytoplankton. *Ecology* 1971; **52**(1): 183-5.
- [23] Lomas MW, Glibert PM. Comparisons of nitrate uptake, storage, and reduction in marine diatoms and flagellates. *J Phycol* 2000; **36**(5): 903-13.
- [24] Gedaria AI, Luckas B, Reinhardt K, Azanza RV. Growth response and toxin concentration of cultured *Pyrodinium bahamense* var. *compressum* to varying salinity and temperature conditions. *Toxicon* 2007; **50**(4): 518-29.
- [25] Stock CA, McGillicuddy JDJ, Solow AR, Anderson DM. Evaluating hypotheses for the initiation and development of *Alexandrium fundyense* blooms in the western Gulf of Maine using a coupled physical-biological model. *Deep Sea Research Part II: Topical Studies in Oceanography* 2005; **52**(19-21): 2715.
- [26] Siringan FP, Azanza RV, Macalalad NJH, Zamora PB, Maria M. Temporal changes in the cyst densities of *Pyrodinium bahamense* var. *compressum* and other dinoflagellates in Manila Bay, Philippines. *Harmful Algae* 2008; **7**(4): 523-31.
- [27] Fauchot J, Saucier FJ, Levasseur M, Roy S, Zakardjian B. Wind-driven river plume dynamics and toxic *Alexandrium tamarense* blooms in the St. Lawrence estuary (Canada): A modeling study. *Harmful Algae* 2008; **7**(2): 214-27.
- [28] Azanza RV, Benico G, Baula IU. *Pyrodinium bahamense* var. *compressum* toxic blooms in Sorsogon Bay, Philippines, in *14th International Conference on Harmful Algae*. 2010: Hersonissos-Crete, Greece.