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Identifying bloom origins of the toxic dinoflagellate *Karenia brevis* in the western Gulf of Mexico using a spatially explicit individual-based model

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ABSTRACT

Harmful algal blooms caused by *Karenia brevis* result in large fish kills, human respiratory irritation, and shellfishing closures in affected areas. Most previous work on bloom formation in the Gulf of Mexico has focused on the west coast of Florida. To investigate the origin of bloom-forming cells along the coast of Texas, potential distributions of cells during two bloom years (2009, 2011) and one non-bloom year (2010) were examined using a spatially explicit, individual-based model of *K. brevis*. The model incorporates a previously developed model of dinoflagellate vertical migration and utilizes observed data (field samples of cell concentrations, photosynthetically active radiation) and modeled environmental output (salinity, temperature, current velocities) from a hydrodynamic model. Running the model in reverse showed that cells near the coast of Texas during early fall originate from the southern Gulf of Mexico in bloom years and from the northern Gulf of Mexico in the non-bloom year for the three years studied. Identification of a southern origin for bloom-forming cells provides a target area for increased sampling in order to provide early warning of potentially harmful algal blooms of *K. brevis*.

1. Introduction

Harmful algal blooms formed by the dinoflagellate *Karenia brevis* have occurred in the Gulf of Mexico (hereafter Gulf) for at least several hundred years and likely longer (Magaña et al., 2003). Blooms of *K. brevis* occur almost every year on the west coast of Florida, but infrequently near the coast of Texas. The factor(s) responsible for this difference are not known. The harmful impacts of blooms (i.e., fish kills, respiratory irritation, and shellfish toxicity resulting in closures of shellfishing) can result in millions of dollars of lost revenue for local economies (Hoagland et al., 2002). *K. brevis* is a species tolerant of a wide range of light intensities, salinities, and temperatures (Brand et al., 2012) and has been found throughout the Gulf at low background concentrations (1–1000 cells L^{-1}; Tester and Steidinger, 1997). In contrast to other dinoflagellates (e.g., *Alexandrium* spp.), there is no known seed bed of *K. brevis* and resting stages (e.g., cysts) have not been conclusively identified, raising the question: where do bloom-forming cells off the coast of Texas originate?

On the west Florida shelf, initiation of blooms typically begins ~18–74 km offshore and at depth (Steidinger et al., 1998). These offshore blooms can then be concentrated onshore where their harmful effects are often observed. The frequency with which blooms occur near Florida has resulted in extensive research on blooms and bloom development in this region (e.g. Hu et al., 2008; Milroy et al., 2008; Robbins et al., 2006; Vargo et al., 2004) but research into the development of blooms near Texas has remained minimal (Hetland and Campbell, 2007; Stumpf et al., 2008; Thyng et al., 2013). Previous work revealed no genetic differentiation among blooms from Florida and blooms from Texas and it was hypothesized that bloom-forming cells in Florida and Texas originate from the same source yet the location of the source population remained unknown (Henrichs et al., 2013). Blooms of *K. brevis* off the coast of Texas appear to be the product of widely dispersed cells accumulating by physical concentration (Hetland and Campbell, 2007; Stumpf et al., 2008). The combination of low background cell concentrations and the physical accumulation of cells suggests blooms could occur randomly throughout the year; however, this is not the case. Blooms of *K. brevis* typically initiate from late summer through fall and cells are often not observed above background levels during the rest of the year (Campbell et al., 2013; Magaña et al., 2003; Tester and Steidinger, 1997). Stumpf et al. (2008) hypothesized that blooms of *K. brevis* occurring off the coast of Texas might

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have initiated in Mexican waters near the southwestern side of the Bay of Campeche and been advected northward. Further support for a southern origin of *K. brevis* cells was given by Thyng et al. (2013), who found modeled surface drifters released in the region near Port Aransas, TX predominantly originated from the southern region of the Texas coast in years when blooms of *K. brevis* occurred. However, surface drifters may not capture critical aspects of bloom distributions. Like many dinoflagellate species, *K. brevis* vertically migrates and blooms of *K. brevis* are known to form at depth (Steidinger et al., 1998). Janowitz et al. (2008) used the behavioral model of Liu et al. (2001a,b) in a three-dimensional simulation of vertically migrating cells of *K. brevis* and demonstrated that wind-driven currents could drive a single column of cells to become spatially distinct populations depending on their initial vertical distribution. Inclusion of vertical migration behavior into models of *K. brevis* distributions could provide more insight into bloom origins and formation. Identification of a region where cells are known to originate is important for early warning systems and would permit further study of the life history stages of this species (including a cyst stage, if any). To investigate the origin of blooms along the coast of Texas, we developed a spatially explicit, individual-based model (IBM) of *K. brevis* that combines modeled output from a hydrodynamic model with a behavioral model of vertical migration for *K. brevis* (Liu et al., 2001a,b). The model can be run forward or backward in time. By running the IBM backwards in time and inserting cells into the model based on field observations from actual bloom events off the coast of Texas, we identified a region from which bloom-forming cells are likely to originate.

2. Methods

2.1. Input data acquisition and preprocessing

2.1.1. Hydrodynamic model

Hourly snapshot files from the 1/25° Gulf of Mexico analysis of the hybrid coordinate ocean model (HYCOM) for the years 2009, 2010, and 2011 were downloaded from the FTP data server (ftp://ftp.hycom.org/datasets/GOMl0.04/expt_31.0/data/). The model outputs for temperature, salinity, u, v, and mixed layer depth were utilized from all grid points between 18.09 and 30.76°N (latitude) and −98.00 to −86.03°W (longitude) in the top 17 depth layers (0, 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100, 125, 150, 200 m) of the HYCOM output (Fig. 1).

2.1.2. MODIS data

Daily photosynthetically active radiation (PAR) data (~4 km resolution) from the MODIS sensor on NASA's Aqua and Terra satellites was downloaded (http://oceandata.sci.gsfc.nasa.gov/) and combined into a single input file for each year (2009, 2010, 2011). If PAR data for a grid point were available from both satellite files, the PAR values were averaged together. Because the locations of the grid points from the HYCOM data and MODIS data differed, the MODIS data were re-gridded based on latitude and longitude to match the model grid from HYCOM. Data for the new grid points were linearly interpolated from the data at the original grid points.

2.1.3. K. brevis *sample data*

Information about the location, cell concentrations, and date/time of sample collection was obtained from Texas Parks and Wildlife Department (TPWD) and the Imaging FlowCytobot (IFCB) deployed at Port Aransas, TX (Campbell et al., 2013). When depth information was unavailable, it was assumed the sample was taken near the surface and a depth of one meter was used.

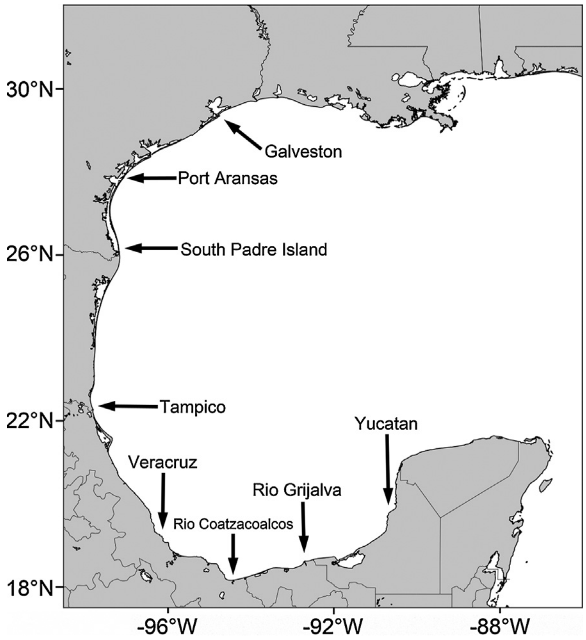

Fig. 1. Western Gulf of Mexico model domain. Arrows indicate locations where blooms of *Karenia brevis* have been known to occur historically.

2.1.4. Nutrient concentration

The only nutrient considered in the model was nitrate. Field measurements of nitrate concentrations throughout the Gulf of Mexico are few and instead, a simple nutrient gradient increasing with depth was used throughout the model domain. The nutrient concentration equation of Liu et al. (Eq. 12, 2001b) was modified so that the nutricline depth at a given location in the model was set to be the depth of the mixed layer (see Section 2.1.1 above) at that same location. The nutrient concentration at the surface was set to a background level of 0.05 μM, a similar background level used by Liu et al. (0.10 μM, 2001b) in their model and within the range observed off the coast of Texas during cruises in the summer of 2013 and 2014 (S. DiMarco pers. comm.), and increased with depth. Nitrate concentration at a given location was fixed during a time step and nutrient uptake by individuals did not reduce nitrate concentration in the environment.

2.2. Individual-based model

A very brief description of the model used for vertical migration of the individuals is given below. A fully detailed description of the IBM following the ODD protocol (Grimm et al., 2010), including model equations, can be found in the Appendix.

2.2.1. Movement of individuals

Movement of individuals in the vertical (z) domain is driven solely by the vertical migration of the individuals while movements in the horizontal (x,y) domains are driven solely by the current velocities provided by the hydrodynamic model (i.e. individuals do not 'swim' horizontally but are instead passively carried by currents). This model simplification was made to highlight the role of diel vertical migration (DVM) on the distribution of individuals. A discrete, three minute time step was used in all model runs (i.e. individuals' locations were updated 480 times per model day). Equations were processed following the Euler method and the values of an individual's internal variables at each time step were determined only by the internal and external (environmental) variables from the previous time step. During forward runs, individuals were stepped forward in time according to the current velocities