A scoping and consensus building model of a toxic blue-green algae bloom

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Abstract

Nuisance blooms of *Lyngbya majuscula* have been occurring with increasing frequency in tropical coastal waters around the world. Outbreaks of this cyanobacterium (blue-green algae) threaten water quality, coastal ecosystems, and can be harmful in instances of human contact. While scientific and popular theories abound regarding Lyngbya bloom initiation and growth, a clear research agenda has not emerged. This article offers a scoping and consensus building model for the development of research directions. The model is based on the hypothesis that Lyngbya is iron limited and that blooms are initiated and perpetuated in response to increased bioavailable iron concentrations. Interacting model sectors for Lyngbya, bioavailable iron, dissolved oxygen, and seagrass have been developed. Simulations show that the occurrence of Lyngbya bloom is sensitive to a number of uncertain parameters and model structures, including inflows and decay times of organically complexed iron, Lyngbya maximum growth rate and half-saturation constant for bioavailable iron, and bioturbation. Development of the first stage scoping model is reported here, as are simulation results that are instrumental in setting priorities for empirical investigations and future simulation-based research. It is expected that this model, after additional empirical work is completed, will lead to research and management models that will help set policy for community response to Lyngbya blooms. Copyright © 2004 John Wiley & Sons, Ltd.

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Costanza and Ruth (1997) propose a three-stage modeling process for improving understanding and management of complex environmental systems. These three modeling stages include a *scoping and consensus building model* of low information resolution and high generality, a *research model* incorporating detailed historical or empirical data, and a *management model* building on the first two stages and used to examine the implications of management actions. We have adopted this three-step modeling approach to address harmful blooms of *Lyngbya majuscula*, a toxic cyanobacterium (blue-green algae), which have been occurring with increasing frequency over the past decade in coastal Queensland, Australia and in tropical and sub-tropical coastal marine waters world wide. The purpose of this article is to describe the development and application of our first-stage scoping and consensus building model. It is our hope that a description of our work at its present stage will demonstrate a useful approach to environmental problem solving through iterative hypothesis development and consensus building.

Lyngbya is normally present in trace amounts in the coastal marine sediments but can bloom explosively under certain conditions. Blooms have been observed

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in Morton Bay, Queensland, Australia to cover an area of over 8 km^2 within a period of several days. Lyngbya is biphasic in nature, exhibiting both benthic (bottom dwelling) and surface floating phases. During bloom episodes Lyngbya biomass forms thick mats on the seafloor, often overgrowing seagrass beds. The blooms have been observed to persist for periods of three to six months and are typically followed by rapid decline (Dennison *et al.* 1999). The cause of bloom collapse is unknown; however there is some evidence that viral attack may contribute (Hewson *et al.* 2001).

Lyngbya blooms can have adverse impacts on human health, coastal eco-systems, and local economies. Lyngbya has been associated with acute contact dermatitis and eye and respiratory infections in humans (Osborne *et al.* 2001). Three toxins isolated in Lyngbya are known tumor promoters (Beer *et al.* 1986). There is also evidence that Lyngbya causes seagrass loss when seagrass beds are overgrown (Dennison *et al.* 1999). Seagrass beds are a key habitat for many marine species including dugongs and green sea turtles, both rare and endangered species. Lyngbya blooms have damaged commercial and recrea-tional fisheries and diminished the recreational value of affected areas as a result of perceived health risks and loss of aesthetic appeal. Floating Lyngbya mats washed ashore befoul beaches and necessitate cleanup programs. State and local governments are investing in expensive programs to physically remove Lyngbya from the environment and are now prompted to invest in research programs to learn why Lyngbya blooms occur and how they may be controlled or eliminated.

Possible causes of the blooms are poorly understood. Researchers have suggested that combined effects of temperature, light, and nutrient availability may trigger the blooms (Dennison *et al.* 1999; Thacker and Paul 2001; Watkinson 2000). However, to our knowledge no formal hypothesis has yet been put forward. Our objective for the first-stage model is to develop and communicate a formal hypothesis of Lyngbya bloom causation based on literature and the field and laboratory work of researchers focused on the Lyngbya problem. The first-stage model is intended to provide a forum for debate and consensus building and to help guide a strategic research agenda through the identi-fication of uncertain parameters and structures that are influential on bloom occurrence, thus establishing the foundation for a second-stage research model.

The development of our model has drawn on Anderson's (1973) classic system dynamics model of eutrophication of lakes. Anderson modeled the fundamental processes of cultural (human-induced) eutrophication of lakes through accelerated carbon loading and examined the implications of a number of mitigative management actions. Anderson suggested that his model could be modified to examine the influences of other limiting nutrients. More recently Moline *et al.* (2002) have developed a Stella model to examine the effects of limiting factors, including light and nutrients, on marine phytoplankton abundance and community structure. A Stella model by Grzymski *et al.* (2002)

considers the limiting effects of iron on nitrogen uptake and carbon fixation by marine phytoplankton and the effects on the global carbon balance. In addition to the above mentioned system dynamics and Stella models, we have drawn on a large body of mathematical models of algae growth developed over the past three decades (EPA 1985).

The next section presents a dynamic hypothesis of Lyngbya bloom causation, which provides the conceptual framework for the first-stage model. This is followed by a detailed description of the model structure and a discussion of model behavior. Model implementation is then discussed. We conclude with a discussion of the implications of model behavior for setting a strategic research agenda and developing a second-stage research model. A glossary is given as an Appendix.

Dynamic hypothesis

Growing evidence indicates that Lyngbya growth may be iron limited, and that increases in bioavailable iron are linked to the blooms (Dennison *et al.* 1999). The case for iron limitation is based on the following:

- Iron is often a limiting nutrient for cyanobacteria. Cyanobacteria have a high requirement for iron for nitrogenase, an enzyme essential for nitrogen fixation (Geider 1999). However, bioavailable iron is normally present in minute concentrations in marine waters.
- The study area, in Morton Bay, Australia, is considered by some researchers to be a nitrogen-limited ecosystem (Dennison *et al.* 1999). Lyngbya is capable of fixing atmospheric nitrogen and thus should not be subject to nitrogen limitation.
- Field investigations have found that water-column iron concentrations during early stages of Lyngbya blooms were significantly elevated (Watkinson 2000).
- Phosphorus (PO_4) is often considered a limiting nutrient for cyanobacteria growth (Paerl *et al.* 1987). Field research undertaken by Thacker and Paul (2001) suggests that Lyngbya may be limited by phosphorus in waters near Guam. Water quality surveys conducted in Morton Bay during Lyngbya blooms, however, found PO_4 concentrations to be low (Dennison *et al.* 1999).
- Many cyanobacteria are able to produce and release siderophores, iron-specific chelating agents that aid in the solubilization and assimilation of iron in environments where iron availability is growth limiting (Geider 1999). Laboratory investigations have found no evidence of siderophore production by Lyngbya (Gross and Martin 1996).
- Bioassays undertaken by Gross and Martin (1996) demonstrate that Lyngbya growth is distinctly dependent on bioavailable iron.

Iron is one of the most abundant elements on earth, however its bioavailability is strongly dependent on its speciation (Matsunaga *et al.* 1998). Ferrous iron, Fe^{2+}, which exists under anoxic conditions, is bioavailable and is found in the anoxic layers of coastal marine sediments. Ferrous iron can efflux into the water column from the sediment porewater when the overlying water becomes anoxic. Under oxic conditions ferrous iron rapidly oxidizes to insoluble oxyhydroxides that are not bioavailable, effectively blocking efflux into the water column (DiToro 2001). A second category of bioavailable iron comprises organically bound iron complexes associated with humic or fulvic acids (Matsunaga *et al.* 1998; Kuma *et al.* 1999). These organically bound iron complexes originate on land and enter the coastal marine environment through surface runoff and possibly groundwater discharge. The organically bound iron complexes remain bioavailable under oxic conditions and have been shown to be important sources of iron for planktonic algae (Matsunaga *et al.* 1998; Kuma *et al.* 1999).

A preliminary hypothesis has emerged that suggests that Lyngbya blooms occur in response to a pulse of bioavailable iron entering the coastal marine environment during periods when conditions of light and temperature are in the optimal range for Lyngbya growth (Dennison *et al.* 1999; Watkinson 2000). The pulse originates from anthropogenic land cover alterations, such as forest felling in areas of humic soils, which cause runoff of organically bound iron complexes during heavy rain events. The pulse of bioavailable iron overrides the normal iron limitation on Lyngbya growth and induces Lyngbya to grow at an exponential rate. As Lyngbya biomass increases, respiration and detritus decay also increase. The dual influence of respiration and detrital decay cause the lower water column to become anoxic during nights. Fe^{2+} then enters the water column from the sediment porewater, providing the bioavailable iron that allows the bloom to persist for a period of months after the initial pulse of organically bound iron has been depleted (Watkinson 2000). Figure 1 expresses the hypothesis in terms of a feedback structure.

We hypothesize that Lyngbya bloom is caused by the interaction of three major reinforcing feedback loops indicated in Figure 1. Loop R1 causes exponential growth of Lyngbya. As Lyngbya biomass increases, its absolute growth rate also increases, creating a spiral of accelerating growth. Loops R2 and R3 increase the availability of Lyngbya's limiting resource, bioavailable iron. A balancing feedback loop, Loop B1, limits the growth of Lyngbya through the influence of the environmental carrying capacity. The carrying capacity is based on field observations and is considered to be the maximum density of Lyngbya possible in the study area due to limiting effects of other nutrients, self-shading, disease, etc. A shift in dominance from the positive feedback loops causing bloom to the negative loop linked to the carrying capacity creates a pattern of s-shaped growth. We do not concern ourselves at this point with the eventual collapse of the blooms.

Fig. 1. Hypothetical feedback structure causing Lyngbya bloom. The bloom is initiated by an exogenous pulse of the limiting nutrient. As Lyngbya biomass approaches its carrying capacity, dominance shifts from the reinforcing growth-generating feedback loops to the balancing, controlling loop
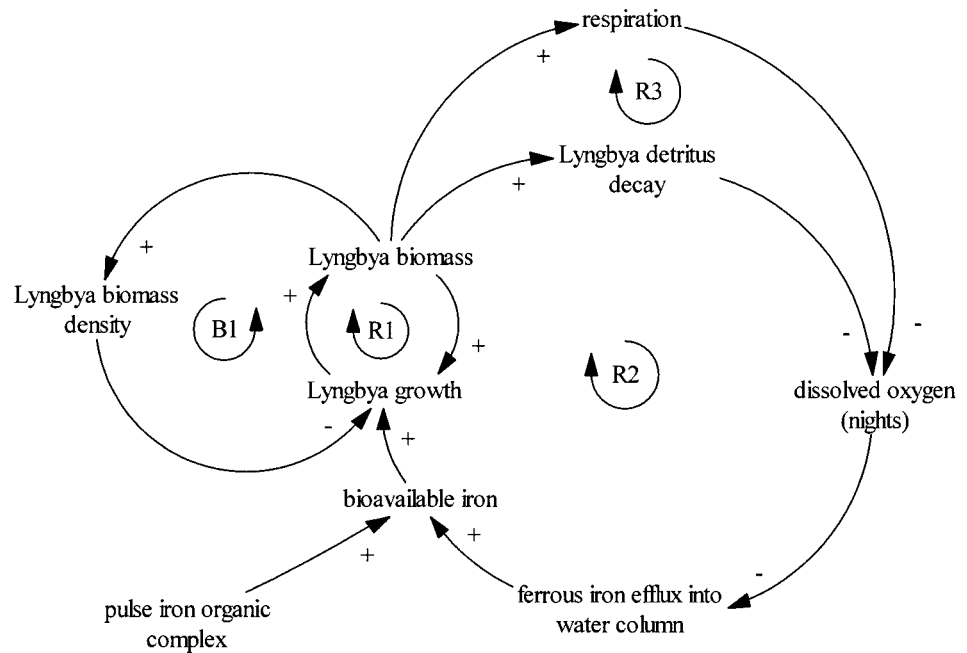
Model structure

General structure

The model consists of four interacting sectors, the Lyngbya Sector, the Iron Sector, the Dissolved Oxygen Sector, and the Seagrass Sector. The Seagrass Sector has been included because of the role of seagrass in the dissolved oxygen balance of the ecosystem and because seagrass meadows are the foundation of a diverse ecological community adversely impacted upon by Lyngbya blooms. Figure 2 shows the sector interactions of the model.

The model is generic but parameterized to correspond roughly to study areas in Morton Bay, Australia, where Lyngbya blooms have been observed. The generic study area is 10 km^2 with an average water column depth of 2 m. The water column is divided into upper and lower sections to allow modeling of benthic and floating Lyngbya and dissolved oxygen and iron regimes in the upper and lower water columns. No distinction is made for areal spatial distribution; we assume that the stocks of Lyngbya, iron, dissolved oxygen, and seagrass are evenly distributed across the study area.

The time unit is one half-day to allow representation of the diurnal processes of carbon uptake and respiration and the key influences of these on the patterns of dissolved oxygen and bioavailable iron. A sine wave function
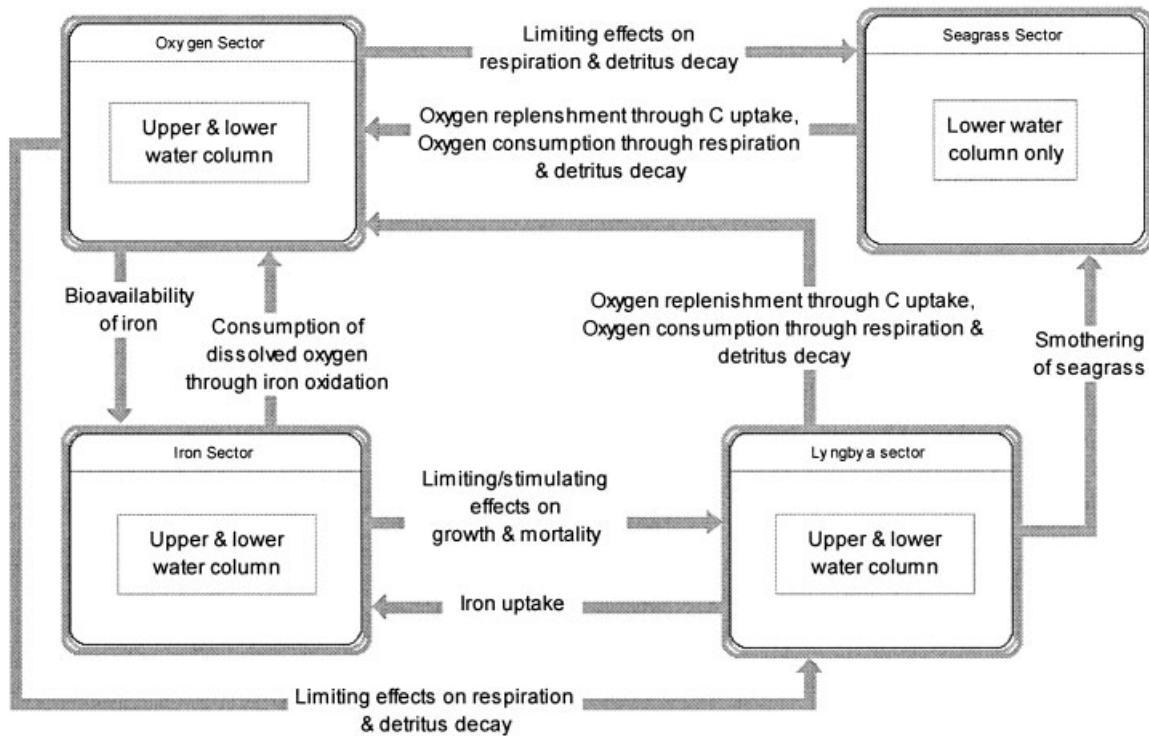
Fig. 2. Subsector diagram showing linkages between model sectors for Lyngbya, dissolved oxygen, iron, and seagrass

switches day and night processes, i.e., carbon uptake and respiration, on and off. The simulation time horizon is 180 half days, or three months. The model is an example of a stiff system, the shortest time constant is 0.1 half days (for the decay time of ferrous iron) yet the system behavior unfolds over a period of several months. To accommodate the short time constant we have set DT to 0.03125. Runge–Kutta fourth order was selected as the integration method to minimize cumulative error associated with rapidly changing rates (Sterman 2000, p. 908). The modeling platform is STELLA Research version 7.0.2. A table of parametric and initial values is appended in the longer version of this paper available on the Special Issue website (http://www.wsu.edu/~forda). The simplified stock and flow diagrams in Figures 3, 4, and 5, show approximately 40 percent of the total number of base model variables.

Lyngbya Sector

Figure 3 shows the stock and flow structure of the Lyngbya Sector. The sector has four stocks representing benthic and floating Lyngbya biomass and detritus with units in grams dry weight.
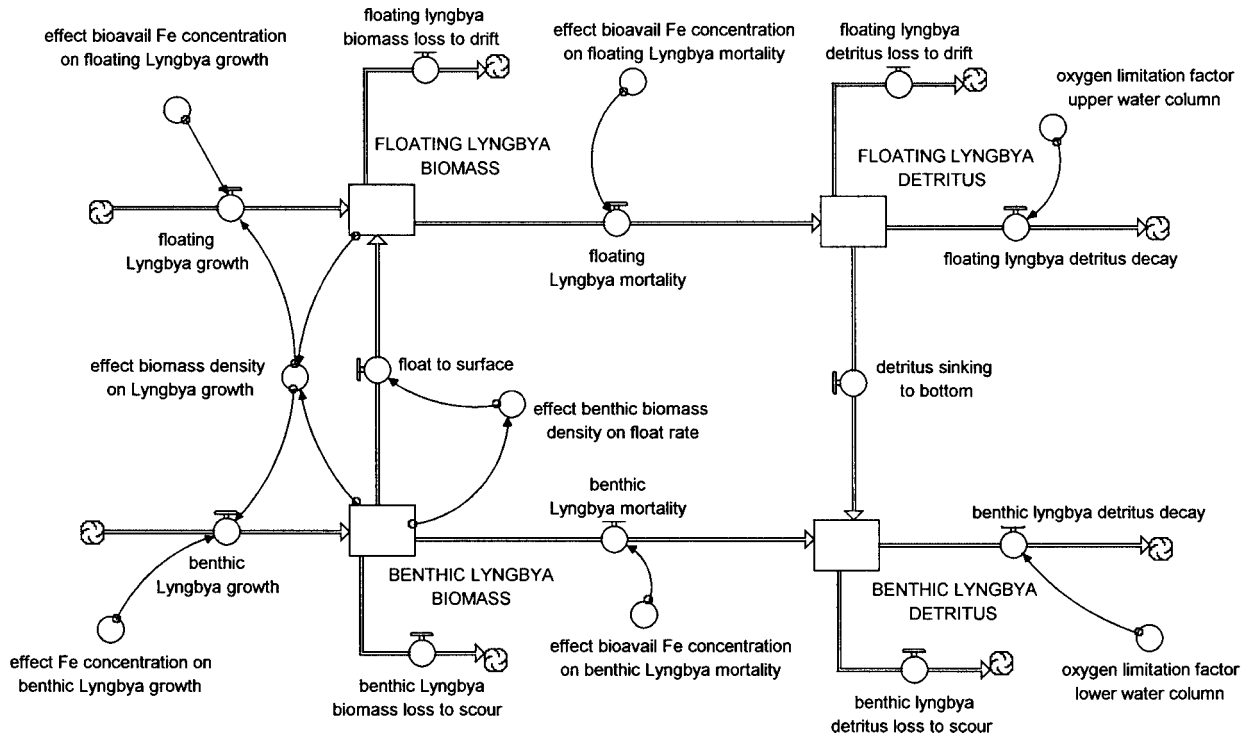
Fig. 3. Simplified stock and flow structure of Lyngbya Sector. Names of stocks are capitalized. Key influences on flows are indicated

The growth rate of Lyngbya is modeled as the product of the Lyngbya biomass stock, a maximum fractional growth rate and the effects of two limiting factors, bioavailable iron concentration and Lyngbya biomass density. The effect of bioavailable iron on Lyngbya growth is expressed through a Michaelis–Menton formulation $c/(c + k)$, where c is the external concentration of the limiting nutrient, in this case bioavailable iron, and k is the half-saturation constant, i.e., the concentration of limiting nutrient at which one half of maximum growth is attained. Research by Gross and Martin (1996) suggests that the relationship between bioavailable iron concentration and Lyngbya growth response follows a Michaelis–Menton pattern. We have followed Ford's (1999, p. 61) recommendations on modeling density-dependent relationships to capture the self-limiting effect of Lyngbya density.

We assume that the Lyngbya mortality rate will decrease as bioavailable iron concentration increases, contributing to the net growth of the bloom. The Lyngbya mortality rate is the product of Lyngbya biomass, the normal fractional mortality rate, and the effect of bioavailable iron concentration on mortality. The effect of bioavailable iron concentration on morality is formulated
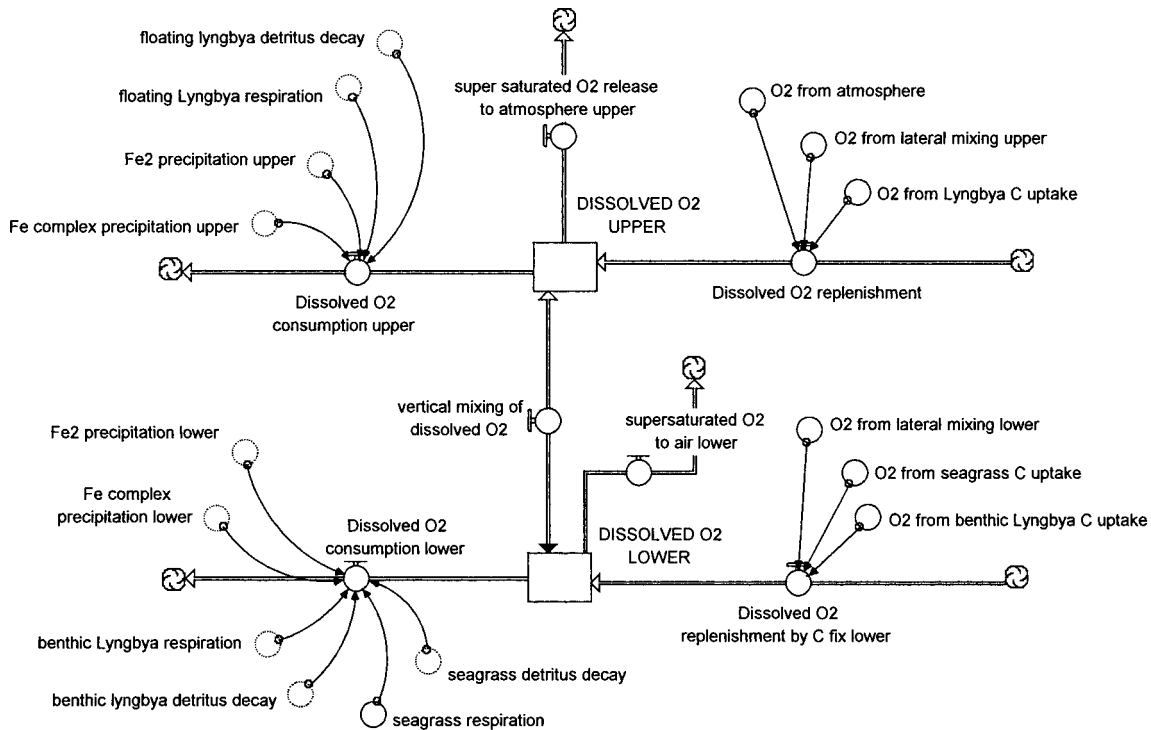
Fig. 4. Simplified stock and flow structure of Dissolved Oxygen Sector

as one minus the effect on growth, $1 - [c/(c + k)]$ (EPA 1985). The mortality rate is assumed to account for both non-predaceous and predaceous mortality. Research findings indicate that toxins produced by Lyngbya effectively deter grazing by zooplankton and macro predators (Thacker and Paul 2001). Hence we do not explicitly model a grazing population. Detritus decay is assumed to be aerobic only and is modeled as first-order decay multiplied by an oxygen limitation factor, which is the ratio of the dissolved oxygen concentration to the concentration of dissolved oxygen at saturation (Anderson 1973). Anaerobic detritus decay is a much slower process than aerobic decay and, more importantly for our purposes, does not contribute to dissolved oxygen consumption. The transition of Lyngbya biomass to the floating phase is mimicked with a maximum float to surface fractional rate multiplied by a graph function expressing the effect of benthic Lyngbya density on the float to surface rate. The structure is based on research by Beer *et al.* (1986) that demonstrates that Lyngbya biomass floats to the surface when a critical benthic density is reached. We assume that floating Lyngbya biomass does not settle or reattach to the benthic surface. Settling of floating Lyngbya detritus, losses of floating Lyngbya
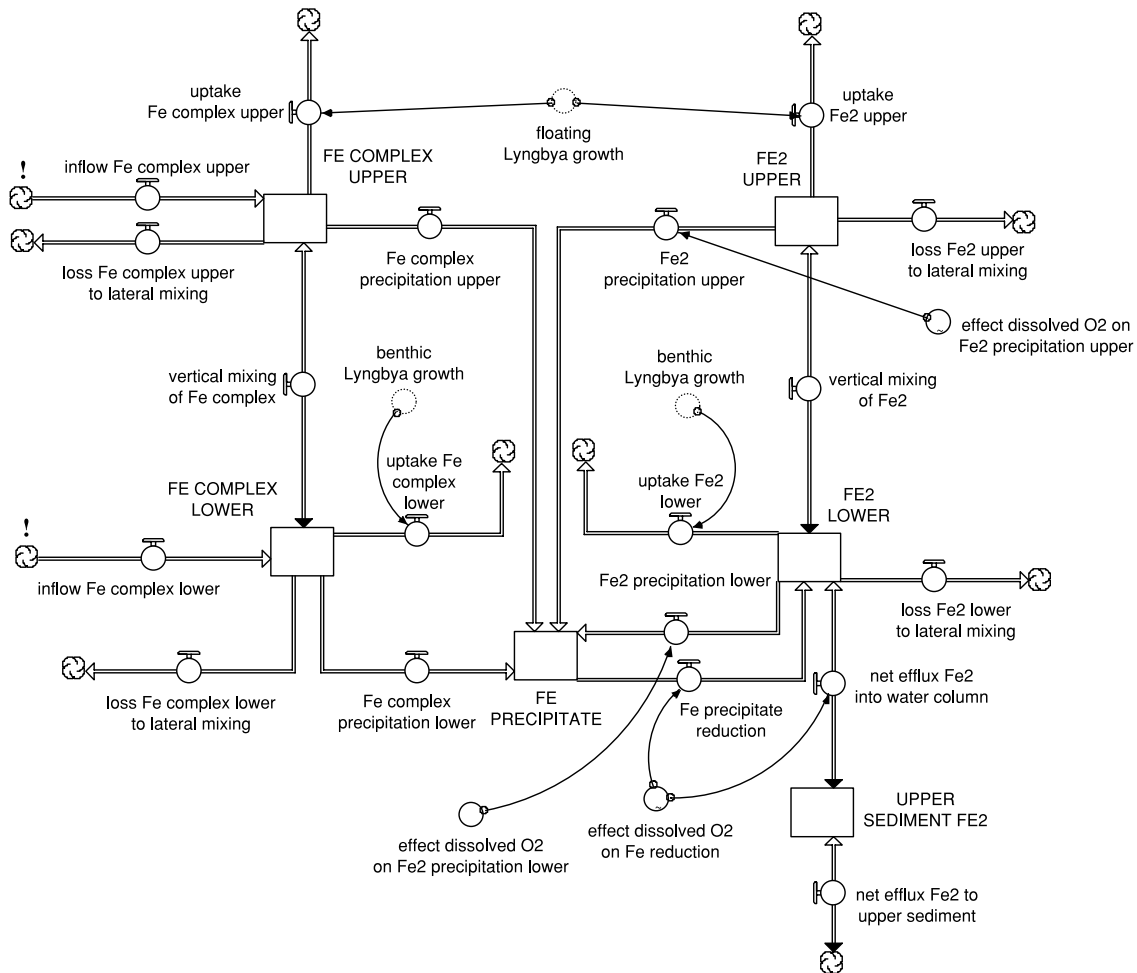
Fig. 5. Simplified stock and flow structure of Iron Sector. Effects of dissolved oxygen concentrations on Fe^{2+} precipitation, sediment efflux, and precipitate reduction are indicated. Co-flow relationships between Lyngbya growth and iron uptake are indicated

biomass and detritus through drift, and losses of benthic biomass and detritus through tidal scour are represented as first-order outflows.

The Lyngbya Sector influences dissolved oxygen through carbon (as CO_2) uptake and release of carbon through respiration and detritus decay. Detritus decay is converted to grams carbon based on an assumed fixed ratio of carbon mass to Lyngbya dry weight. Respiration is calculated with a fractional respiration rate multiplied by carbon in Lyngbya biomass and by the oxygen limitation factor (Anderson 1973). Carbon uptake is calculated as Lyngbya biomass

growth converted to carbon plus respiration. To convert carbon uptake, respiration, and detritus decay from carbon to oxygen terms, we use the ratio 2.67 grams oxygen to one gram carbon.

Dissolved Oxygen Sector

Figure 4 shows the stock and flow diagram for the Dissolved Oxygen Sector. The sector contains two stocks representing dissolved oxygen (O_2) in the lower and upper water column. The units are grams of oxygen per square meter.

Dissolved oxygen in the upper layer is replenished by carbon uptake and corresponding oxygen release by Lyngbya, by atmospheric exchange, and through mixing with oxygenated waters from outside the study area. Oxygen in the lower water column is replenished by carbon uptake of Lyngbya and seagrass and through mixing with outside waters. We assume that seawater outside the study area is saturated with oxygen and that both upper and lower layers tend toward oxygen saturation at a rate based on lateral mixing times and the difference between the dissolved oxygen concentrations in the upper and lower water column and the oxygen saturation concentration. A similar formulation is used for reoxygenation from the atmosphere.

Dissolved oxygen in the upper water column is consumed through respiration and detrital decay of Lyngbya and through oxidation of Fe^{2+} to iron oxyhydroxide (FeOOH). When one gram of Fe^{2+} is oxidized we assume that 0.57 grams of dissolved oxygen are removed from the water column. Dissolved oxygen in the lower water column is consumed by respiration and detrital decay of Lyngbya and seagrass and by Fe^{2+} oxidation. The outflows *super saturated O2 release to atmosphere upper* and *lower* allow rapid release of oxygen when dissolved oxygen becomes supersaturated. The upper and lower stocks of dissolved oxygen tend to equilibrate through a biflow based on the concentration gradient and a vertical mixing time.

The growth of thick Lyngbya mats on the benthic surface restricts water exchange at the sediment–water interface. To mimic this effect we have linked the density of benthic Lyngbya to the vertical mixing time and to the lateral mixing time for the lower water column. As Lyngbya biomass increases, mixing in the lower water column slows. Slower mixing leads to lower dissolved oxygen in the lower water column and, consequently, greater efflux of Fe^{2+} from the sediment porewater.

Iron Sector

Figure 5 shows the stock and flow diagram of the Iron Sector. The sector contains stocks representing two classes of bioavailable iron, iron (Fe) complex and ferrous iron (Fe^{2+}) in the upper and lower water column. A single stock represents Fe^{2+} in the sediment porewater. A single stock represents non-bioavailable iron precipitate that accumulates from decay and oxidation

of the bioavailable iron species. The units of the stocks are grams of iron per square meter.

The source of iron complex is runoff from the land. *Inflow Fe complex upper* and *lower* include a normal flow of iron complex, and a pulse of iron complex associated with a heavy rain event. The normal flow supplies the bioavailable iron that sustains Lyngbya under non-bloom conditions. The pulse is the primer that initiates the bloom. In Figure 5 the flows containing the pulse inputs that initiate Lyngbya bloom are designated with the "!" symbol.

Fe^{2+} enters the water column from two sources, Fe^{2+} in the sediment porewater and iron precipitate. Fe^{2+} will flow from the sediment porewater into the water column only when the dissolved oxygen concentration in the lower water column approaches anoxic levels. When the water column is oxygenated, porewater Fe^{2+} is rapidly oxidized at the sediment–water interface, blocking efflux into the overlying water column. The flows *net efflux into water column* and *net efflux into upper sediment* represent efflux by molecular diffusion in accordance with Fick's Law (DiToro 2000) and influenced by the effect of bioturbation, the collective sediment churning action of benthic fauna (DiToro 2000; Boudreau 1997). Efflux between adjacent layers can flow in either direction depending on the concentration gradient, and are modeled with biflows. The stock of iron precipitate represents the accumulation of non-bioavailable iron precipitate from decay and oxidation of Fe complex and Fe^{2+} and released through the decay of Lyngbya detritus. Fe complex has a lifetime that varies widely depending on the form of organic complexation, water temperature and sunlight intensity (Barbeau *et al.* 2001). The lifetime of Fe^{2+} is dependent on the concentration of dissolved oxygen. Under anoxic or reducing conditions its lifetime is indefinite; in oxygenated water Fe^{2+} will oxidize and precipitate within minutes (DiToro 2000). Under anoxic conditions the iron precipitate is reduced to Fe^{2+} and flows into the stock of lower water column Fe^{2+}, thus recycling a portion of the bioavailable iron lost through oxidation and Lyngbya uptake. The uptake rates of bioavailable iron species are determined by the Lyngbya growth rate multiplied by a fixed ratio of iron to biomass dry weight. We assume that Lyngbya has no uptake preference between Fe complex and Fe^{2+}.

Seagrass Sector

The Seagrass Sector (not shown) contains structure for growth, mortality and detritus decay similar to the Lyngbya Sector. The sector contains two stocks representing the total dry weights of seagrass biomass and detritus.

The limiting factors on seagrass growth are the effect of Lyngbya smothering and the self-limiting effect of seagrass density. We do not consider iron to be a limiting factor for seagrass and hence do not include the effect of bioavailable iron concentration in the seagrass sector. We assume that seagrass obtains its iron requirements from the sediments through its root system (Hemminga and Duarte 2000) and therefore does not compete with Lyngbya for bioavailable

iron in the water column (Lyngbya has no root system and absorbs bioavailable iron from the water column). Seagrass influences the dissolved oxygen level through carbon uptake, respiration and detritus decay. Its influence, however, is not as strong as that of Lyngbya under bloom conditions owing to smaller fractional rates of growth, respiration, and detritus decay.

Model behavior

Figure 6 shows the base simulation with time horizon of 180 half days, or 3 months. The variables simulated are total Lyngbya biomass (including benthic and surface floating phases), and the concentrations of iron complex, Fe^{2+}, and dissolved oxygen in the lower water column. Figure 7 shows the same variables simulated over a time horizon of 720 half days.
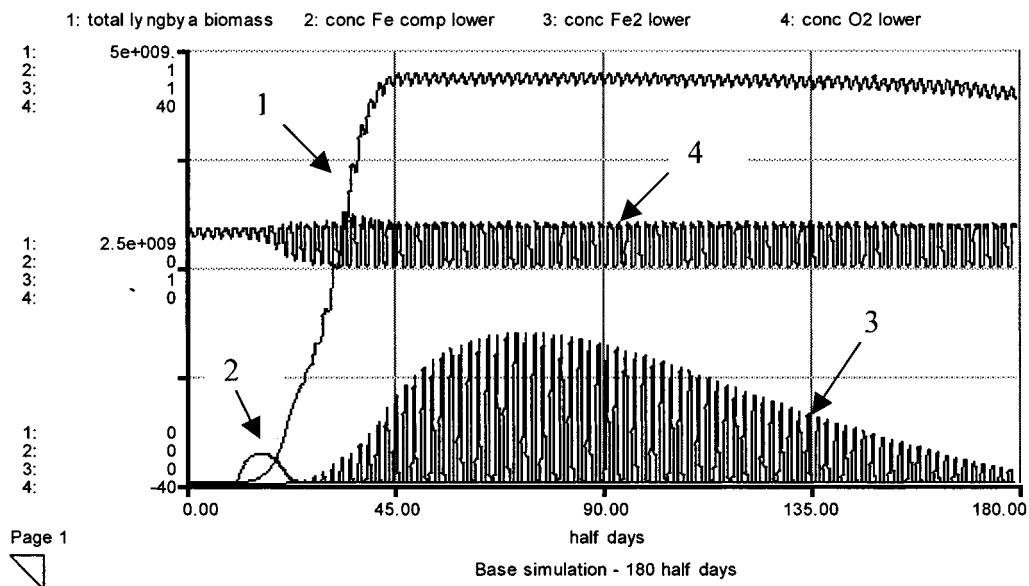

Fig. 6. Base simulation exhibiting pattern of Lyngbya bloom with time horizon of 180 half days. Time paths: 1 = total Lyngbya biomass; 2 = concentration of Fe complex in lower water column; 3 = concentration of Fe^{2+} in lower water column; 4 = dissolved oxygen concentration in lower water column

The base simulation can be broken down into four intervals exhibiting distinct behavior modes:

1. *Pre bloom interval, from time zero to 10 half days (Figure 6).* Lyngbya biomass is in equilibrium at its normal low density. Its iron requirement is

Fig. 7. Base simulation with time horizon of 720 half days exhibiting a pattern of Lyngbya bloom and decline. The decline is caused by depletion of porewater Fe^{2+}. Time paths: 1 = total Lyngbya biomass; 2 = concentration of Fe complex in lower water column; 3 = concentration of Fe^{2+} in lower water column; 4 = dissolved oxygen concentration in lower water column
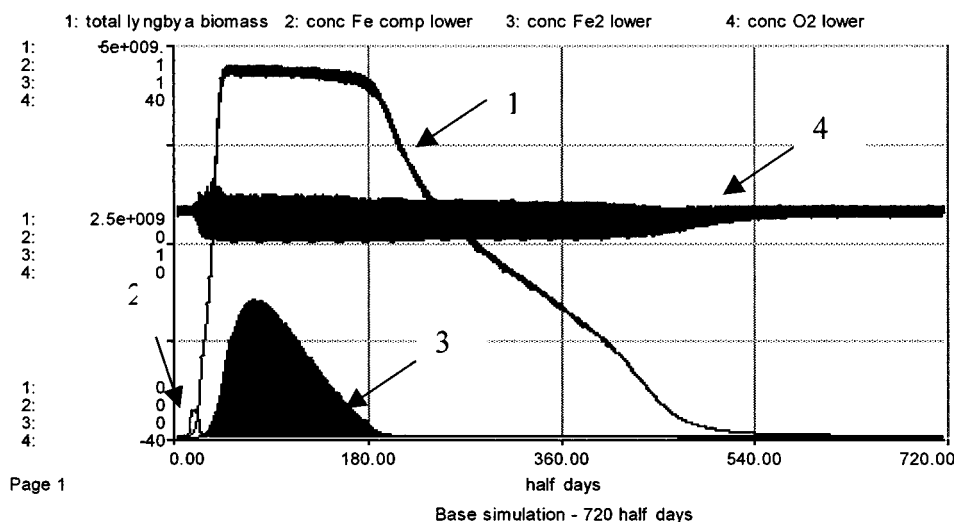
supplied by the normal inflow of Fe complex. Dissolved oxygen in the lower layer fluctuates between 5 and 7 g/m^2 on the diurnal cycle.

2. *Interval of exponential growth (bloom), from 10 to approximately 45 half days.* At time 10 half days a pulse of Fe complex enters the coastal waters, initiating the bloom of Lyngbya biomass. Oxygen levels are driven to zero at night-time by Lyngbya respiration, allowing Fe^{2+} to efflux into the water column from the sediment porewater. The Fe^{2+} concentration shows a pulsating pattern because Fe^{2+} rapidly precipitates when the water is oxygenated during daylight hours. As the Fe complex is depleted, Fe^{2+} becomes the principal source of bioavailable iron, causing Lyngbya to continue to bloom until approaching the exogenously specified carrying capacity (5 billion grams, which is the upper limit of the display). Lyngbya biomass exhibits a slight but distinct oscillating pattern that reflects its growth response to the diurnal availability of Fe^{2+}.

3. *Interval of sustained bloom, from 45 to approximately 180 half days.* During this period of approximately 2.25 months Lyngbya is sustained by Fe^{2+} from sediment porewater and from the reduction of accumulated iron oxide precipitate. Fe^{2+} water column concentrations steadily decline, however, due to depletion of porewater Fe^{2+}. By 180 half days Lyngbya biomass begins to decline as water column Fe^{2+} concentrations approach zero.

4. *Interval of bloom decline, from 180 to approximately 550 half days (Figure 7).* During this approximate six month interval Lyngbya biomass steadily declines as a result of insufficient bioavailable iron. As the normal concentration of biomass is approached, the diurnal oxygen fluctuations return to the pattern seen before the bloom.

Lyngbya blooms observed at the study areas in Morton Bay, Australia have exhibited patterns of explosive growth, reaching maximum density within one week, and persisting for three to six months before sharply declining (Dennison *et al.* 1999; Watkinson 2000). Blooms have been observed to disintegrate within one to six weeks after the onset of decay symptoms (Hewson *et al.* 2001). Our base simulation appears to generally correspond to observed patterns of growth and persistence; however, the simulated decline period is significantly longer than field observations. The simulations suggest that, while depletion of porewater iron storage may be a contributing factor to bloom decline, other causes such as viral attack may be responsible for more sudden collapse.

Interestingly, a number of other environmental problems are characterized by a similar dynamic pattern as described above. In our hypothesis, Lyngbya blooms in response to a pulse increase of a limiting resource, bioavailable iron as Fe complex. As Lyngbya biomass grows it alters the environment in such a way that a second source of bioavailable iron, Fe^{2+}, emerges and sustains continued growth. An analogous dynamic pattern, albeit on a vastly greater time and spatial scale, is seen in global warming. Global warming is caused in part by heat absorption by elevated atmospheric CO_2 (carbon dioxide) resulting from the burning of fossil fuels. As global temperatures increase in the polar regions, thawing of permafrost may release large quantities of methane, another greenhouse gas, through decay of organic matter, thus causing further warming (Ford 1999, p. 93; Sterman 2000, p. 247).

Sensitivity analyses and identification of research priorities

Many of the parametric and structural assumptions in the model are highly uncertain. In the simulations discussed below we investigate the sensitivity of Lyngbya bloom to changes in some of these uncertain assumptions. Assumptions that are both uncertain and influential on the model's behavior are then identified as areas for more detailed empirical investigation (Sterman 2000, p. 884).

Supply of organic iron complex

The supply of iron complex available for Lyngbya growth is heavily dependent on the pulse volume and decay rate of iron complex. Estimates for both parameters are highly uncertain. The inflowing pulse of iron complex will vary with the intensity and duration of the associated rain event. Also, the concentration and speciation of iron complex in runoff water will vary depending on land cover characteristics. Some estimates of iron complex decay rates have been found in the literature (Kuma *et al.* 1999). Decay rates, however, vary significantly with speciation and are probably influenced by water temperature and sunlight intensity (Barbeau *et al.* 2001).
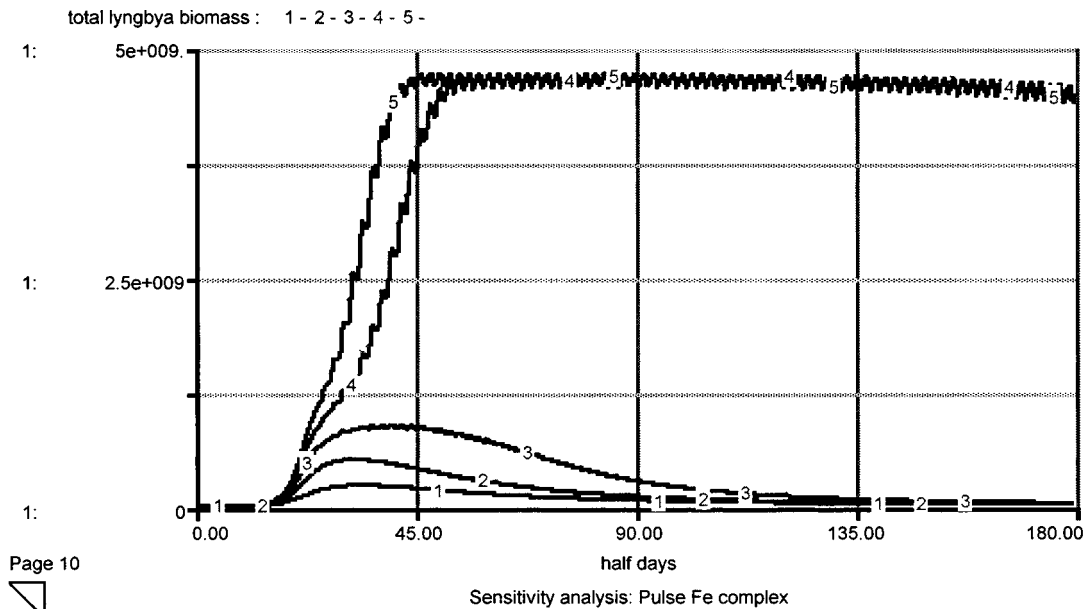
Fig. 8. Sensitivity analysis indicating response of Lyngbya biomass to varying amounts of Fe complex pulse inflow. The time paths indicate a distinct tipping point for bloom occurrence. Settings: 1 = Fe complex pulse set to 1 MT (metric tons); 2 = 2 MT; 3 = 3 MT; 4 = 4 MT; 5 = 5 MT (base value)

Figure 8 compares five simulations of Lyngbya biomass with differing values for the pulse of iron complex. All other parameters are the same as with the base simulation.

The simulations were run with the Fe complex pulse set to 1, 2, 3, 4, and 5 metric tons respectively. The resulting patterns of Lyngbya biomass indicate that a tipping point occurs between 3 and 4 metric tons to which the bloom response is sensitive.

Lyngbya researchers have expressed interest in understanding the sensitivity of Lyngbya bloom to differing combinations of iron complex pulse and decay rate. Figure 9 summarizes the results of simulations with differing values of pulse and decay time in two-dimensional parameter space.

The curve in Figure 9 represents a continuum of tipping points to which the occurrence of sustained bloom is sensitive. The area to the right of the curve represents values of Fe complex pulse and Fe complex decay time that initiate sustained blooms. The area to the left represents values that lead to non-sustained growth response. For decay times ranging from 10 to two days the Fe complex pulse required for sustained bloom initiation increases gradually. However, below decay times of around two days the pulse requirement increases exponentially. The rapid decay rates associated with very short decay times necessitate large pulse inflows to maintain sufficient Fe complex for the

Fig. 9. Parameter space diagram summarizing combined influences of iron complex pulse and iron complex decay time on Lyngbya bloom. The curve represents a suggested continuum of tipping points. The encircled B indicates the values used in the base simulation. The T indicates a suggested tipping point based on the simulations in Figure 8
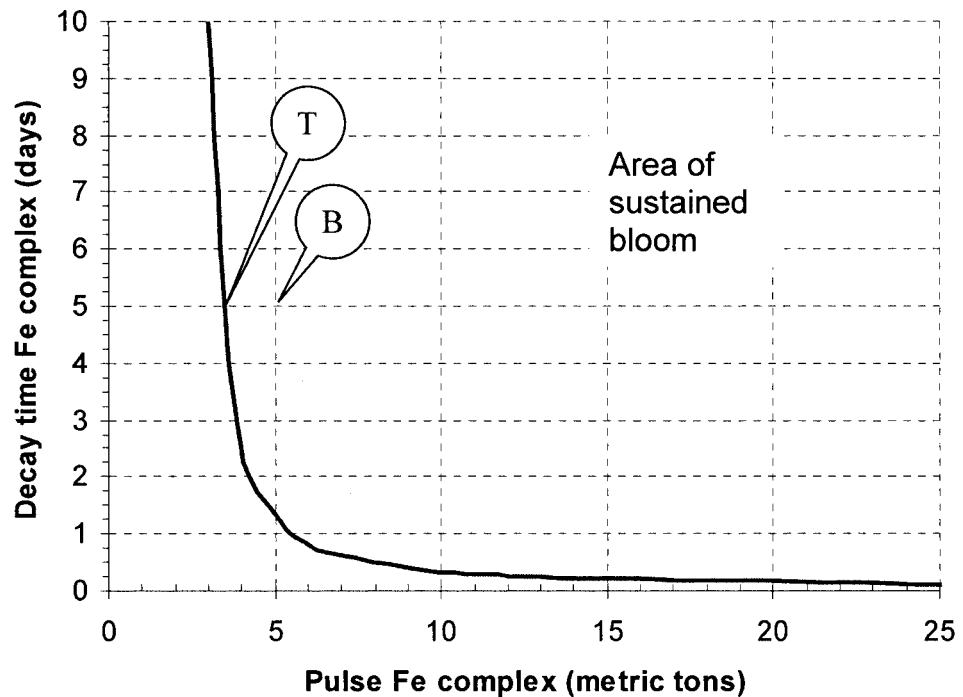
initiation of a sustained bloom. Obtaining estimates of these parameters through field and laboratory research would be valuable for assessing the explanatory power of the current hypothesis. Parameter estimates falling within the area to the right of the curve would lend support to the hypothesis and model. Estimates falling to the left of the curve would indicate the need to reassess the hypothesis or some other aspects of the model.

In similar fashion we have made an analysis of the growth response of Lyngbya to bioavailable iron by comparing ranges of half saturation concentrations of bioavailable iron and maximum Lyngbya growth rates in two-dimensional parameter space. A description of this analysis, and a structural sensitivity analysis of the effect of bioturbation are presented in a longer version of this paper available on the Special Issue website (http://www.wsu.edu/~forda).

Model implementation

The model is intended to work in conjunction with the existing institutional framework established in response to the Lyngbya bloom problem. The Environmental Protection Agency (EPA) of Queensland, Australia has established a committee of stakeholders from government departments, academic

institutions, and community organizations to identify causes and implement management actions to reduce the risk of future blooms.

The scoping model was presented at a series of workshops attended by members of the stakeholder committee. The purposes of the workshops were to assess the current state of knowledge of Lyngbya bloom and to outline a proposed research agenda for a new round of government funding for Lyngbya research. Scientists, engineers, and modelers involved with research on Lyngbya bloom gave presentations of their work and findings. Mathematical models of catchment runoff, groundwater flow, hydrodynamics and Lyngbya iron uptake kinetics were presented as well as the Lyngbya scoping model. Participants were asked to propose future research activities, and specify the information inputs needed to progress their work.

We proposed an iterative modeling process to facilitate participatory hypothesis building. In this proposed process, simulation aids in the identification of influential parametric and structural assumptions that then become foci for empirical investigations. The hypothesis is then tested through simulations with a model updated with more realistic assumptions. Insights gained from testing lead to revisions of the hypothesis and model, leading to a new iterative cycle of hypothesis building.

Workshop participants pointed out that outputs from refined catchment and groundwater models could be used to parameterize the iron pulse inputs in the scoping model, and that the scoping model's structure for Lyngbya growth response to iron could be refined by the iron uptake kinetics modeling work in progress. Participants expressed interest in extending the existing scoping model to include other potentially important limiting factors such as phosphorus, light, and temperature. The proposal for government funding later put forward requested support for refinement of the scoping model, including field and bioassay investigations into important model parameters. Also proposed was a series of workshops in which the model and hypothesis could be further developed through direct participation with researchers and other stakeholders.

Conclusions

The first-stage model has helped identify specific research questions for hypothesis development, which may in some instances be addressed through field or laboratory work. Examples are the quantity of iron complex entering the coastal waters in association with rainstorms and the decay times of the iron complex species. These parameters are not known with accuracy yet they are very influential on the model's behavior and may have important implications in the development of a hypothesis of Lyngbya bloom. As we move into the second stage of modeling it is likely that aspects of our current hypothesis will be refuted and alternative explanations adopted. Developing the research model will be an ongoing, iterative process as new information and ideas

become available through empirical investigation. Our goal is improved management of the Lyngbya bloom problem through the development of a third–stage management model that is well grounded scientifically and generally accepted by stakeholders.

Acknowledgement

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Appendix
Glossary

Anoxic Conditions characterized by an absence of oxygen.

Benthic Referring to the sediment surface, e.g., the sea floor.

Bioassay A method of determining the effect of a compound by quantifying its effect on living organisms or their component parts.

Bioturbation The collective sediment churning actions of bottom dwelling organisms.

Chelator an organic compound that has the ability to bind trace metals and hold them in soluble form. In this article we are primarily concerned with two groups of chelators, humic and fulvic acids.

Cyanobacteria A photosynthetic bacterium, generally blue-green in color and in some species capable of nitrogen fixation.

Detritus Non-living organic debris from tissue mortality, secretions, and excretion.

Diffusion Net transport due to random motion of solute particles.

Diurnal a recurrent daily cycle. For example, carbon uptake occurs during daylight hours on a daily cycle.

Efflux The process of flowing, in this paper due to the action of molecular diffusion, possibly accelerated by bioturbation.

Ferrous iron Iron in the form of Fe^{2+}. Ferrous iron is bioavailable but rapidly oxidizes and precipitates into non-bioavailable forms under oxygenated conditions.

Fick's Law Fick's Law states that the flux of solute mass crossing a unit area, per unit time, in a given direction, is proportional to the gradient of concentration in that direction, and is counter-gradient, i.e., the net flux moves from a region of higher solute concentration to one of lower concentration.

Hypoxic Conditions characterized oxygen deficiency.

Iron complex In this paper refers to bioavailable organically chelated iron.

Lyngbya majuscula (Lyngbya pronounced similarly to "India") a toxic filamentous marine cyanobacterium (blue green algae) inhabiting tropical and sub-tropical estuarine and coastal waters.

Oxidation A chemical process in which electrons are removed from an atom, ion or compound. The addition of oxygen is a specific form of oxidation. Always occurs accompanied by reduction of the oxidizing agent.

Porewater The water found in the spaces between particles in submerged sediments.

Precipitate a substance separated from a solution into solid form that may then accumulate in a layer.

Reduction Any process in which electrons are added to an atom or ion (as by removing oxygen or adding hydrogen); always occurs accompanied by oxidation of the reducing agent.

Respiration Energy yielding reactions in living matter, which typically involve oxygen consumption and release of carbon dioxide and water as end products.

Sediment Any mineral or organic material accumulating in a loose unconsolidated form. May be precipitated chemically or produced biologically in situ, or transported by wind or water and deposited on the bottom.