A TURBULENT

DIATOM VS. DINOFLAGELLATE

PHYTOPLANKTON BIOMASS MODEL

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Kristen Kennedy

Supervised by Coleen Moloney

A TURBULENT DIATOM VS DINOFLAGELLATE PHYTOPLANKTON BIOMASS MODEL

Phytoplankton blooms play an important role in global primary productivity and the dynamics of blooms are of interest to modellers. Diatom dominated phytoplankton blooms followed by dinoflagellate blooms are common in the Southern Benguela, and are often associated with Harmful Algal Blooms. A well-known ecological explanation for the succession of diatoms to dinoflagellates is given by Margalef's Mandala which attributes the successional change to the interaction between turbulence and available nutrient concentration. This study introduced a simple variable accounting for the effects of turbulence to a numerical model describing diatom and dinoflagellate growth in order to emulate the common successional pattern. Succession was successfully modelled by reducing the maximum growth rate of diatoms in stratified conditions. The model was then used to investigate the predictions of Margalef's Mandala. This study unpicks the relationship between nutrients, turbulence, diatoms and dinoflagellates through a simple 0D phytoplankton model with interesting insight into the role of turbulence in phytoplankton dynamics.

INTRODUCTION

Phytoplankton are assemblages of photoautotrophic microorganisms which play an important role in macroscopic systems. A significant portion of global production occurs in the coastal ocean (Chavez and Toggweiler 1995) with oceanic phytoplankton responsible for more than 45% of global net primary productivity (Field *et al.* 1998), and up to one third of primary production in the marine food web (Moloney 1992). It is therefore important to understand the ecology of phytoplankton and the associated blooms. Phytoplankton are prone to blooms which have impacts on a range of spatial and temporal scales and which influence food webs and industries. Impacts of blooms can be beneficial, allowing for efficient energy supply along the pelagic food web (Moloney 1992), or harmful, in the case of toxic red tides (Smayda 1997).

Phytoplankton photosynthesise and are therefore constrained by many of the same variables which influence terrestrial plant growth such as light, nutrient availability, temperature and grazing by heterotrophs. In addition to these factors, phytoplankton exist in a 3-dimensional space, in a viscous medium and at scales which are often difficult to grasp (Smayda 1997). These variables and factors further complicate the understanding of phytoplankton dynamics. Phytoplankton community structure varies according to environmental conditions and the characteristics of the species assemblages (Pitcher *et al.* 1991; Reynolds 1997). Phytoplankton cover a broad range of shapes and cell sizes which result in a relationship between morphology, function and ecology (Lewis 1976). There are an estimated 3400 – 4100 species of phytoplankton (Sournja 1995), these are often divided into functional groups (Litchman *et al.* 2006), which are not necessarily phylogenetically related but rather related based on common biogeochemical processes and responses (Iglesias-Rodriguez *et al.* 2002). Natural assemblages of phytoplankton are the complex result of the species present and their reactions to the environmental variables (Di Toro *et al.* 1975).

Models have become popular tools to understand the complexity of phytoplankton communities and the factors influencing population dynamics, with numerical models providing tools to study mesoscale dynamics of marine ecosystems (Franks 2002).Complexity is dismissed with models which focus on key relationships governing population dynamics. Simple planktonic ecosystem models were pioneered by Gordon Riley as early as 1947 (Riley 1947), and expanded upon over the following decades. The basic structure of the model has stayed remarkably similar over the years (Steele 1958; Walsh 1976; Koné *et al.* 2005). Models mostly follow a “nutrient-phytoplankton-zooplankton” (NPZ) structure, in which nutrients are taken up by phytoplankton which are in turn grazed upon by zooplankton, and nutrients are recycled through both plankton forms back into the dissolved nutrient pool (Franks 2002). This structure has been expanded and built upon to include additional nutrients, multiple phytoplankton functional types, light attenuation and the effect of depth, temperature and diel migration (daily movement into and out of the euphotic zone), and coupled to physical models (Koné *et al.* 2005; Franks 2009).

Phytoplankton models are typically forced by nutrient concentration (most commonly nitrate) and based on a carbon or nutrient currency (Fasham *et al.* 1990). Phytoplankton depend on the uptake of dissolved nutrients for growth and this relationship is commonly described using Michaelis-Menten uptake kinetics (Eppley *et al.*1969). The dependence of models on this functional relationship has received some criticism but is generally accepted (Franks 2009). State variables are linked by functions such as uptake rates, growth and mortality rates (Franks 2002). The Michaelis-Menten model has two parameters which differ for the different organisms modelled. Different species, or functional types, of phytoplankton can be represented in models through specific individual (more accurately – community) rates of growth, uptake and mortality and average values for each taxon are commonly accepted as representative for modelling purposes (Litchman *et al.* 2006). General relationships between growth rates, metabolic rates and size of organism has been widely studied (Banse 1967). Many rates for functional types are accepted and allometric relationships have been discovered between cell mass, maximum growth rates and half saturation constants (K_s) (Moloney and Field 1989; 1991).

Phytoplankton blooms typically occur in the euphotic layer of water bodies where light is sufficient for photosynthesis, they occur when incoming nutrients from deeper layers or surface runoff are sufficient to support exponential growth rates (Sverdrup 1953). These conditions are met by upwelling events which are mesoscale (~10km) phenomena forced by wind blowing along continental shelves and resulting in surface waters rich in nutrients. Some of the world’s major fishing industries depend on upwelling systems (Schumann *et al.* 1982). The literature on phytoplankton blooms in upwelling regions is extensive and is largely summarized and explained by Wilkerson and Dugdale (2008). The most important upwelling zones are located on the west coast of North and South America and West Africa. The Benguela upwelling system off the west coast of southern Africa is one of the four major coastal upwelling regions of the world (Cushing 1975) and this system is a popular subject for modellers (Shannon *et al.* 2003). Many blooms progress through a sequence of phytoplankton development which varies mainly with water column stability associated with upwelled water (Brown 1986). A succession of phytoplankton cell size has been seen to predictably follow upwelling events (Sprules and Munawar 1986).

The Benguela upwelling system experiences high phytoplankton biomass during late summer and autumn (Pitcher *et al.* 1992). Barlow (1982) described phytoplankton blooms in this region as a sequence of three water types. Type I corresponds to cold (<10°C) nutrient rich, newly upwelled water with low phytoplankton abundance and high nitrate concentrations; Type II water is considered maturing upwelled water which is warmer (>10°C), with nitrate concentrations between 2 and $15\mu M.L^{-1}$, and high plankton biomass; Type III water is considered aged upwelled water with low nitrate concentrations ($<2\ \mu M.L^{-1}$) and high phytoplankton biomass. Blooms are typically dominated by diatoms although species succession from diatoms to dinoflagellates is common (Pitcher *et al.* 2005), the shift is associated with spatial and temporal transitions from turbulent to stratified water conditions and a shift in production from dependence on new nitrogen (diatoms dependent on upwelled nitrate) to regenerated nitrogen (dinoflagellates dependent on excreted ammonium and urea) (Hutchings *et al.* 1995). The change in phytoplankton community structure in the Southern Benguela is proposed to be strongly influenced by hydrodynamic processes with the sequence of populations resulting from an orderly shift in the environment as turbulence dissipates and diatoms are succeeded by dinoflagellates (Pitcher *et al.* 1991).

A conceptual model outlining these successional changes was proposed by Margalef (1978), in which nutrient concentrations and turbulence are the main factors determining the functional type or species composition of a bloom. Margalef’s Mandala outlines a succession of phytoplankton assemblages dominated by diatoms during the early high nutrient high turbulence period, and succeeded by dinoflagellates in later stratified conditions. This model has important implications for the formation of red tides. Red tides or Harmful Algal Blooms (HABs) are formed by about 2% of phytoplankton species (Sournja 1995) which are toxic and may dominate a bloom under specific conditions, the majority of this 2% is made up of dinoflagellates (Smayda 1997). Harmful blooms have drastic consequences for fishing industries and are therefore economically important subjects. It is often suggested that a reduction in vertical mixing is a precondition for HAB outbreaks (Smayda

1997). Margalef's Mandala accounts for this by focusing on the interactions between turbulence and nutrient concentrations (Margalef *et al.* 1979). Turbulence in the marine environment spans several orders of magnitude (Peters and Marrasé 2000) and influences biological activity spanning a variety of spatio-temporal scales from kilometres to microns (Lévy *et al.* 2009).

Margalef's Mandala takes the form of a plane with turbulence on one axis and nutrient concentration on the other; major phytoplankton groups occupy different spaces within the plane (Figure 1). Large, fast growing, non-motile diatoms thrive in high turbulence, high nutrient conditions while dinoflagelattes which are relatively small (compared to many diatom species) are able to grow and survive in relatively nutrient poor conditions. The r-K axis, parallel to the direction of successional change, describes the trade-off between reproduction and growth and maintenance and the strategies adopted by different functional types existing in varying conditions (Wyatt 2012). Diatoms with fast growth rates are considered r strategists while the slower growing longer living dinoflagellates are categorized as K strategists (Cavalier-Smith 1980).

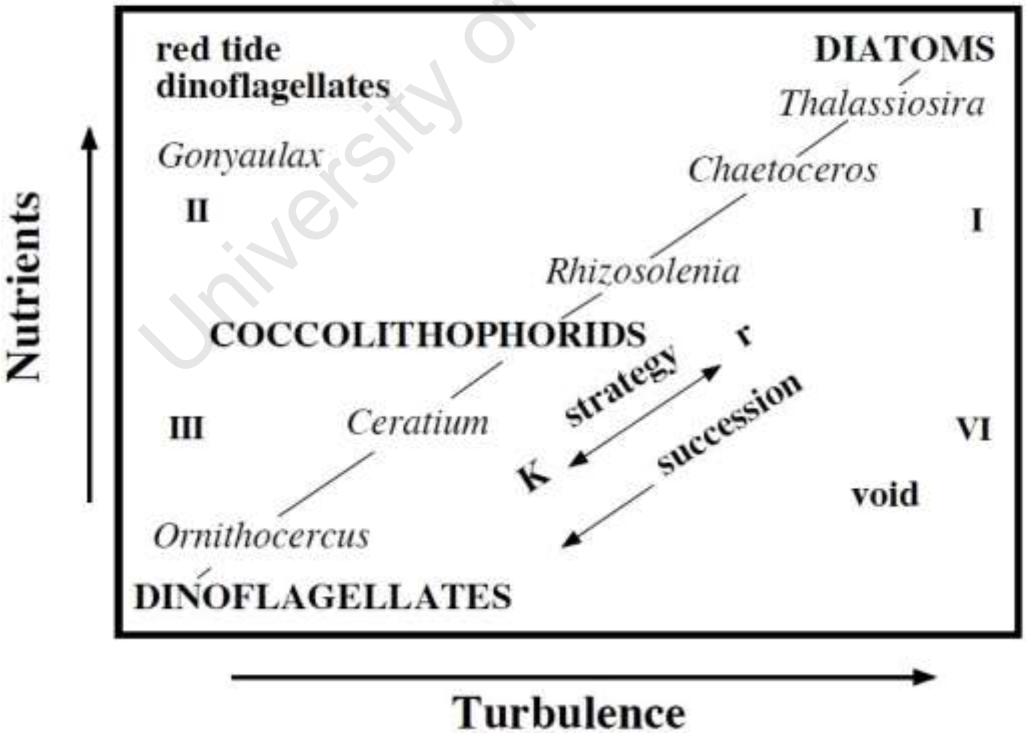


Figure 1. Graphical representation of Margalef's Mandala showing the main phytoplankton life forms in an ecological space defined by nutrient concentration and turbulence. Redrawn from Margalef (1978).

Turbulence in the marine environment spans several orders of magnitude (Peters and Marrasé 2000) and influences biological activity spanning a variety of spatio-temporal scales from kilometres to microns (Lévy *et al.* 2009). Turbulence can affect phytoplankton on two main scales, simplified to meso- and micro-scales. Mesoscale (from a few metres to tens of kilometres) effects mainly result in the passive movement of cells through space. This level of turbulence is based on gyres, upwelling events and fronts (Estrada and Berdalet 1997). Microscale (a few centimetres) turbulence results from motion such as thermohaline intrusions and wind forced convection. Phytoplankton niches are largely determined by sub-mesoscale phenomena (d'Ovidio *et al.* 2010) and phytoplankton exist at scales below the Kolmogorov length scale; this means that turbulence is experienced variably depending on cell size, with most phytoplankton experiencing turbulence as a uniform straining force that is continually changing in magnitude and direction (Lazier and Mann 1989). Karp-Boss *et al.* (1996) found that cell size greater than 60µm is necessary for significantly increased nutrient uptake in turbulent conditions. As phytoplankton take up nutrients, a depleted zone is formed around them (Kiørboe 1993), the relative movement of water to the diffusive layer surrounding a cell is therefore important in order to maximize nutrient uptake and growth. Non-motile diatoms are dependent on some level of water movement to achieve sufficient growth to overcome diffusion. Application of a turbulence parameter which lowers the maximum nitrogen specific growth rate in conditions where water movement is low is therefore a realistic way in which to model the effect of turbulence on diatom growth and abundance.

Turbulence is known to affect the growth and nutrient uptake rates of phytoplankton (Estrada and Berdalet 1997); however the effect on community composition is confounded by the many ways in which this occurs (Peters and Marrasé 2000). Turbulence has been shown to inhibit dinoflagellate growth (White 1976; Berdalet 1992; Peters and Marrasé 2000). Dinoflagellates possess flagella which increase motility in the water column and facilitate their retention in the euphotic zone in the absence of turbulence while allowing for migration to deeper nutrient rich water (Fraga *et al.* 1989). Diatoms on the other hand, especially those which form chains, may be unable to remain buoyant and will therefore sink in the absence of turbulence enhanced suspension (Jackson 1990). Schöne (1970) showed that turbulence inhibited chain formation in several colony forming diatoms. Diatoms additionally rely on water movement to obtain maximum uptake rates, and thus maximum growth rates (Estrada and Berdalet 1997). Diatoms are therefore disadvantaged by stratified waters.

Turbulence is incorporated into more complex models through biophysical coupling but is not commonly included in simple plankton models. This is possibly due to the complexity of turbulence which is seen as one of the yet to be conquered frontiers of physics (Nelkin 1992). Therefore there is much to learn about the role turbulence plays in the succession of phytoplankton types commonly seen in bloom events (Pitcher *et al.* 1991). Given the prevalence and importance of HABs and the role of the relationship between nutrients and turbulence, Margalef's Mandala is examined in this study in the light of a simple phytoplankton biomass model. This is done through the introduction of a term which accounts for the effects of turbulence on the growth rate of diatoms and dinoflagellates. Furthermore, the interplay between turbulence and nutrients is investigated through the testing of the model.

The Global Ecology and Oceanography of Harmful Algal Blooms Research Project (Pitcher *et al.* 2005) posed a key research question regarding HAB: "To what extent is the growth rate of HAB species determined by turbulence through its influence on the transport if nutrients, the mixing of phytoplankton through gradients of light, and by direct impairment of growth?" This study investigates an aspect of this question by focusing on the importance of maximum growth rate in modelling diatom-dinoflagellate succession.

METHOD

Model Construction

The model follows a basic NPZ structure altered to include two phytoplankton functional types and with a general loss term accounting for grazing by zooplankton, sinking and other loss of nitrogen from the system. Nitrogen is the currency of each component, as nitrogen often limits primary production in the ocean (Franks 2002). The model has four state variables, included in these is a variable accounting for the effect of turbulence on phytoplankton growth rates; however the

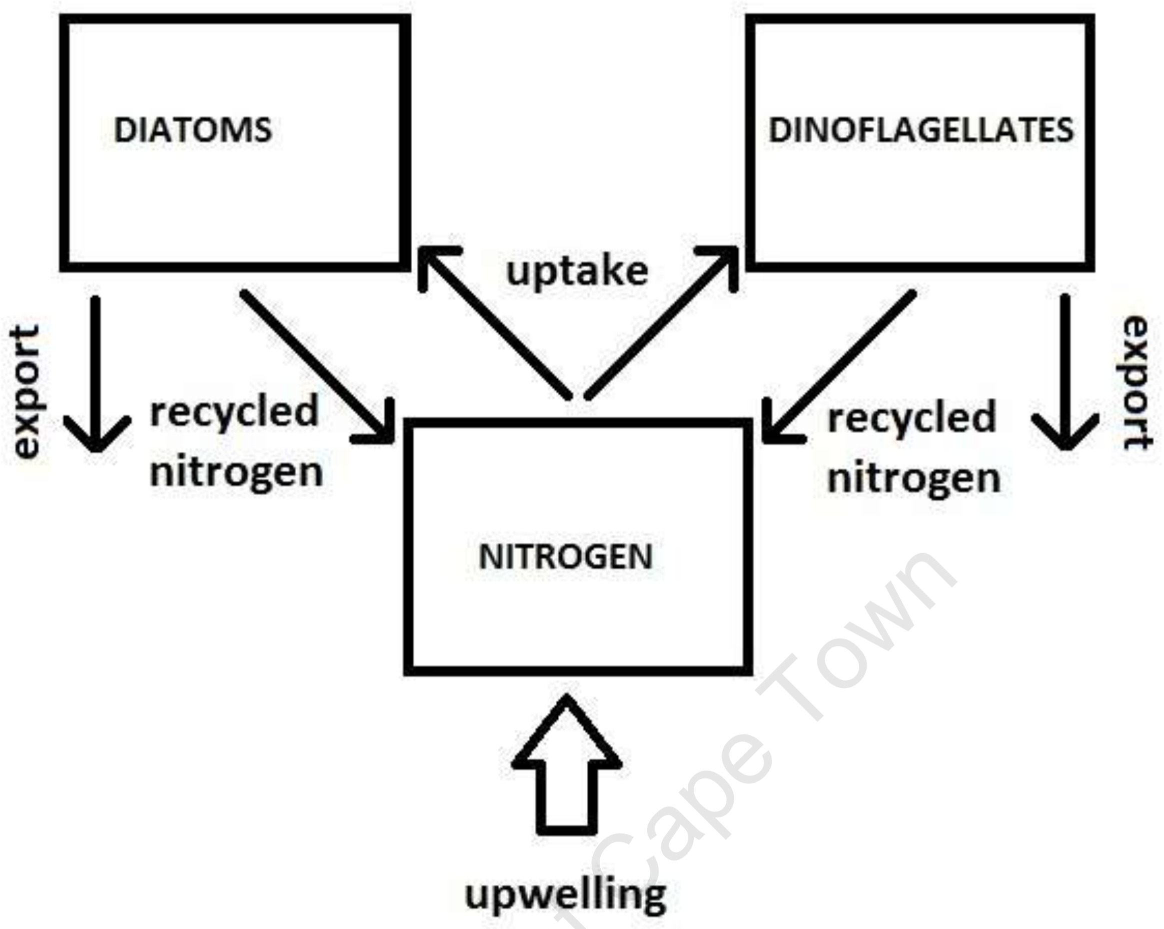


Figure 2. Basic conceptual model of two phytoplankton functional types competing for a shared nitrogen resource which is forced by an upwelling event.

remaining three variables are not the usual NPZ, but rather nitrogen and two phytoplankton types representing diatoms and dinoflagellates (Figure 2). Replacing the Zooplankton grazer is a general density dependent term for mortality for each phytoplankton type. Models of this form are termed ‘zero-dimensional’ or 0D models as they do not include a spatial component and only vary through time. The model consists of a set of ordinary differential equations which describe the rates of change of each of the components of the model. The model was constructed and run using MATLAB R2010a.

Phytoplankton are represented by P with diatoms considered functional type 1 and dinoflagellates as type 2, both denoted by subscripts throughout the model. Both functional types are governed by the same equations. Phytoplankton ($P_{1,2}$) and nutrients (N) are modelled by two basic equations which detail changes in concentration of each term as a function of time:

$$\frac{dP_i}{dt} = Growth\ (P_i) - Loss\ (P_i) \qquad \text{where } i = 1,2 \quad (1)$$

$$\frac{dN}{dt} = -Growth\ (P_{1+2}) + x * [Loss\ (P_{1+2})] \qquad \text{where } x \in [0,1] \quad (2)$$

The two types of phytoplankton are governed by the same equations with different parameter values accounting for their physiological differences. The proportion of nitrogen returning to the system is governed by x, such that $x = 0$ describes a system where all nitrogen is exported through grazing or sinking and $x = 1$ describes a system where all nitrogen is immediately returned to the medium and is therefore available for uptake by phytoplankton. For this model x was set at 0.5. Each of the terms in the above equation can be examined. Phytoplankton concentration changes through the difference between growth and loss (Equation 1) which are in turn governed by nutrient uptake, growth, and mortality rates. Phytoplankton nitrogen uptake rates (v) approach an asymptote at high nitrogen conditions but slow down at low nitrogen conditions. The maximum uptake rate is determined by the organism specific growth rate (μ_i). The relationship is modelled with the Michaelis-Menten function (Equation 3) such that:

$$v_i = \mu_i * \frac{N}{K_{Ni} + N} \qquad \text{where } i = 1,2 \quad (3)$$

$$Growth(P_i) = v_i * P_i \qquad \text{where } i = 1,2 \quad (4)$$

The growth rate (μ_i) determines the maximum uptake rate and the half saturation constant (K_{Ni}) gives the nitrogen concentration for which the uptake rate is half the maximum. These are the two parameters which are altered to represent the different phytoplankton forms (Figure 3). Combined these represent the total growth of the population of phytoplankton at a given time. Growth rate and half saturation constant were based on the model by Litchman *et al.* (2006). Although the model of Litchman *et al.* (2006) is based on the North Sea, the parameters chosen are representative of

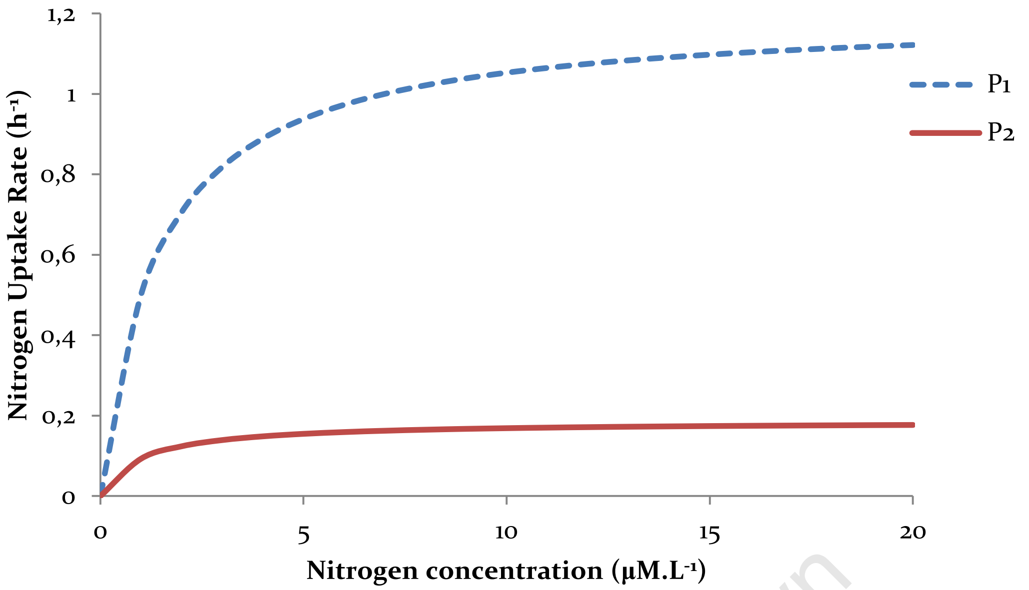


Figure 3. Michaelis-Menten curve governed by equation (3) showing uptake rates for diatoms (*P₁*, μ_1=1.2 h^{-1} K_{N1}=1.4 µM.L^{-1}) and dinoflagellates (*P₂*, μ_2=0.65 h^{-1} K_{N2}=3.0 µM.L^{-1}).

functional types and not specific species and are therefore adequate within the scope of this study. Parameter values are given in Table 1.

Phytoplankton mortality (*m*) is modelled as a quadratic function of the standing crop of phytoplankton and a proportion of the growth rate such that:

$$m_i = 0.1 * \mu_i \qquad \text{where } i = 1,2 \qquad (5)$$

$$Loss(P_i) = m_i {P_i}^2 \qquad \text{where } i = 1,2 \qquad (6)$$

At each time step in the model the concentrations of P_1, P_2, and N are updated and the new values are applied to the next time step. The model was run over the length of a bloom, approximately 14 days, with a time step of 0.01days..

Turbulence

If it is assumed that turbulence either decreases or increases the growth/uptake rate of a cell, then it can be implemented into a model in a few basic ways. According to Margalef's Mandala, diatoms are expected to be positively affected by turbulence while dinoflagellates are negatively

Table 1. Symbols, values and units of parameters and variables used in the model, Phytoplankton parameter values are based on ranges appropriate for dinoflagellates and diatoms (Litchman *et al.* 2006) and initial nitrogen concentration is based on the Benguela upwelling (Walker and Pitcher *et al.* 1991)

Symbol	Description	Value	Unit
Variables			
t	time	-	Days
N	Nitrogen concentration	-	μM.L^{-1}
P_1	Diatom concentration	-	μM. L^{-1}
P_2	Dinoflagellate concentration	-	μM. L^{-1}
T	Turbulence	-	-
Parameters			
μ_1	Diatom maximum nitrogen specific growth rate	1.2	Day^{-1}
μ_2	Dinoflagellate maximum nitrogen specific growth rate	0.65	Day^{-1}
K_{N1}	Diatom half saturation constant for nitrogen uptake	1.4	μM. L^{-1}
K_{N2}	Dinoflagellate half saturation constant for nitrogen uptake	3.0	μM. L^{-1}
P1	Initial concentration of diatoms	1.0	μM. L^{-1}
P2	Initial concentration of dinoflagellates	1.0	μM. L^{-1}
m_1	Diatom mortality rate	0.1	Day^{-1}
m_2	Dinoflagellate mortality rate	0.1	Day^{-1}
N_{in}	Initial Nitrogen concentration as a result of an upwelling event	15.0	μM. L^{-1}

affected. In a meta-analysis by Peters and Marrasé (2000) a general negative relationship between turbulence and phytoplankton growth rates was found; however it is noted that this result is caused by a strong bias towards dinoflagellates.

The effect of turbulence was added to the model by altering the growth rate of a type of plankton with respect to its expected response to turbulence. The growth rate of each plankton type was multiplied by a variable T, which is a unitless, time dependent variable varying between zero and one (Figure 4). Given that growth rate (μ) represents a species maximum growth rate, it is logical that the effect of turbulence/stratification is proportionally decreasing this value depending on the phytoplankton functional type. Therefore T has a value of one when turbulence is not negatively affecting an organism, i.e. for diatoms in turbulent environments (Figure 4) and dinoflagellates in

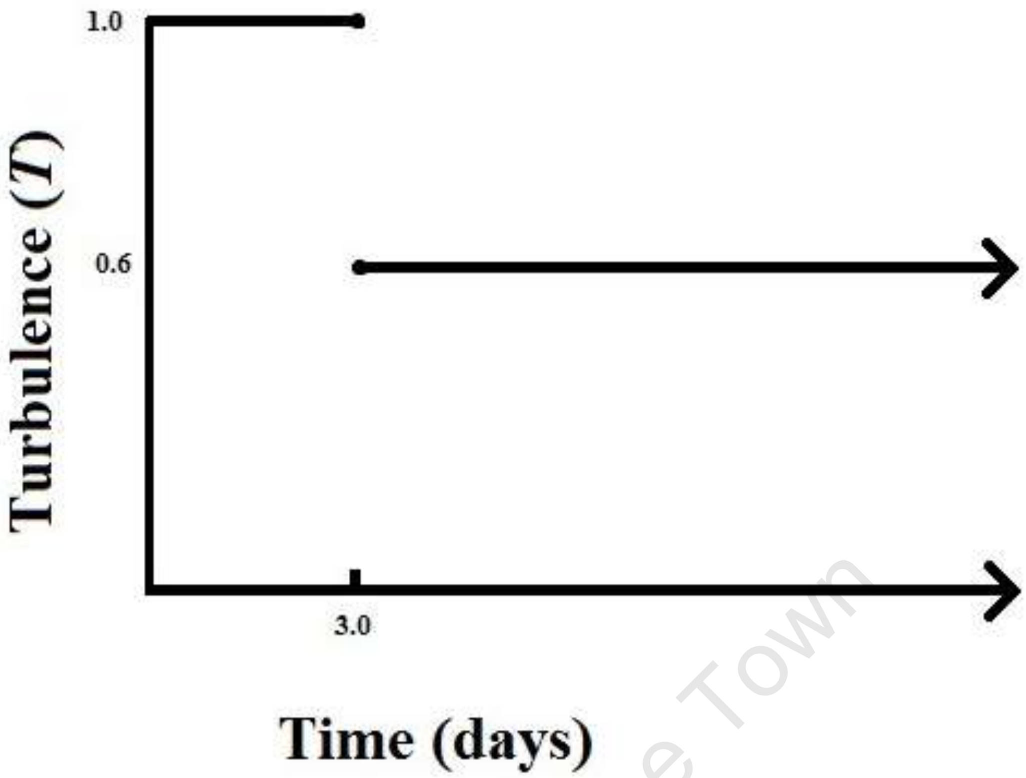


Figure 4. A schematic of the effect of turbulence on an organism reaching maximum growth rate from day 0-3, and reaching 60% growth rate thereafter.

turbulent conditions. Therefore growth rate either equalled μ or $T * \mu$ changing from one to the other after day three. This simulates a change in water column condition from turbulent to stratified at day three, although this timing is arbitrary it is not unrealistic for the Benguela system (Pitcher *et al.* 1992). The effect of turbulence was implemented in four separate permutations (Table 2). The value of T was set at 0.6 based on the finding of Peters *et al.* (2006) that diatom growth in still water is 0.58 times less than in water with some degree of turbulence; however since the exact effect of turbulence on growth rate of both types of plankton is uncertain this value is tentative, and was tested from 0.1-0.9.

Table 2. Growth rates of diatoms (P_1) and dinoflagellates (P_2) were systematically altered by the effect of turbulence. + indicates no effect of turbulence such that maximum growth rate (μ) can be achieved, - indicates a limited maximum growth rate ($T\mu$). Conditions were changed from 'turbulent' to 'stratified' on day 3 of the model.

		Turbulent	Stratified
a	P_1	+	+
	P_2	+	+
b	P_1	+	+
	P_2	-	+
c	P_1	+	-
	P_2	-	+
d	P_1	+	-
	P_2	+	+

Nutrients

The availability of nutrients is of equal importance to turbulence in Margalef's Mandala (1979). Specifically red tides are expected to occur in low turbulence, high nutrient conditions. The occurrence of red tides in the Benguela is also associated with dinoflagellate dependence on regenerated nitrogen (Hutchings *et al.* 1995). The nutrient aspect of the mandala was investigated by changing two key factors in the basic phytoplankton-turbulence model: by altering the concentration of the initial incoming nitrogen, N_{in}, from 10 - 35μM.L^{-1}, this was done in the model without T and with T in order to ascertain whether or not a high incoming nutrient concentration could cause a dinoflagellate succession; and by altering the nitrogen recycling efficiency such that x in equation (2) was increased in intervals of 0.25 from 0.25 to 0.75. Zero and one were excluded as they do not hold any real world significance, 0.5 was used as the standard in the tests on the efficacy of the T variable and of the incoming nitrogen concentration. In this way a system with variable efficiency can be simulated whereby higher values of x indicate a more efficient system possibly as a result of higher sinking rates or loss of nitrogen to higher predators.

The Mandala

The four quadrants of the model, explained in detail by Wyatt (2012), were investigated. This was done through modelling four situations: i) high turbulence-high nitrogen; ii) low turbulence-high nitrogen; iii) low turbulence-low nitrogen, and; iv) high turbulence-low nitrogen. These scenarios correspond to quadrants i-iv) in Figure 1. High and low incoming nutrients were set to $35\mu M.L^{-1}$ and $10\mu M.L^{-1}$ respectively. Low turbulence was represented by a shift to stratified waters after 1.5 days, and high turbulence conditions were represented by a shift after 4.5 days. This is based on the assumption that if turbulence is originally higher than usual, it will take longer to dissipate. In addition, T was applied to dinoflagellates in high turbulent conditions (scenario i and iv) to further simulate the effect on growth rate. The outcome of this experiment highlights the usefulness of this model in illustrating Margalef's Mandala.

RESULTS

Turbulence

The basic model of diatom-dinoflagellate-nutrient dynamics adequately described a diatom bloom, with diatom concentration exceeding dinoflagellate concentration for the entire model run when turbulence was not included (Figure 5a). The introduction of a term for turbulence had variable effects on the outcome of the model. Most notable, only one combination of disadvantaging organisms resulted in dinoflagellates outcompeting diatoms in stratified conditions (Figure 6).

Overall changing the value of T did not affect the overall patterns observed in the model, except for $T > 0.8$; heights of peaks, timing of maximum concentrations and shift from diatom to dinoflagellate dominance were affected.

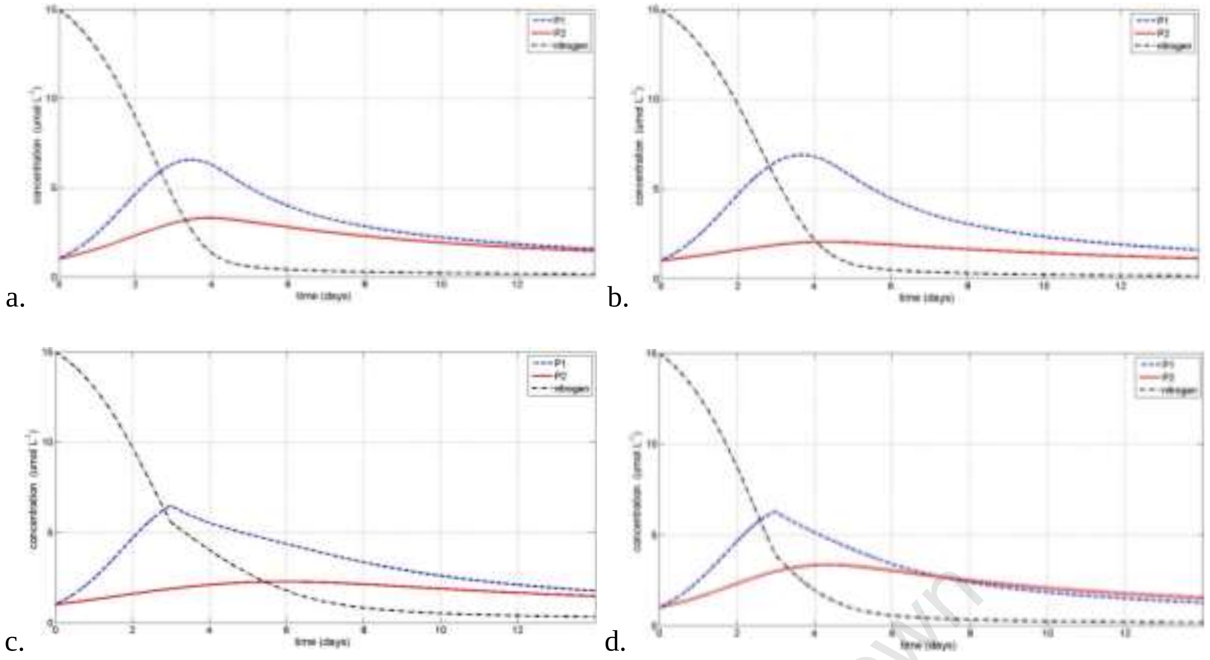


Figure 5. Four possible permutations to test the usefulness of disadvantaging (reducing μ by a proportion T=0.6) diatoms (P_1) and dinoflagellates (P_2) in stratified and turbulent water (respectively), a) no turbulence term, b) dinoflagellates disadvantaged by T for days < 3, c) dinoflagellates disadvantaged for days <3 and diatoms disadvantaged for days > 3, d) only diatoms disadvantaged for days >3.

Nutrients

When the effect of turbulence on growth rates was not included in the model diatoms dominated dinoflagellates regardless of incoming nitrogen concentrations (Figure 6).

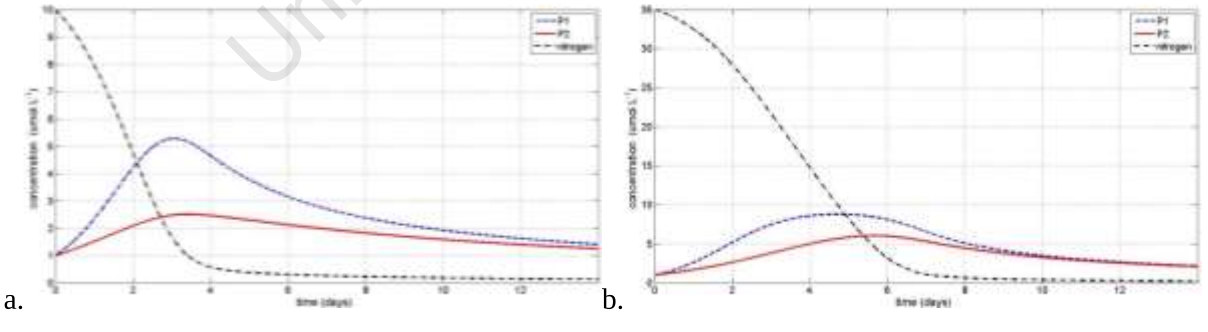
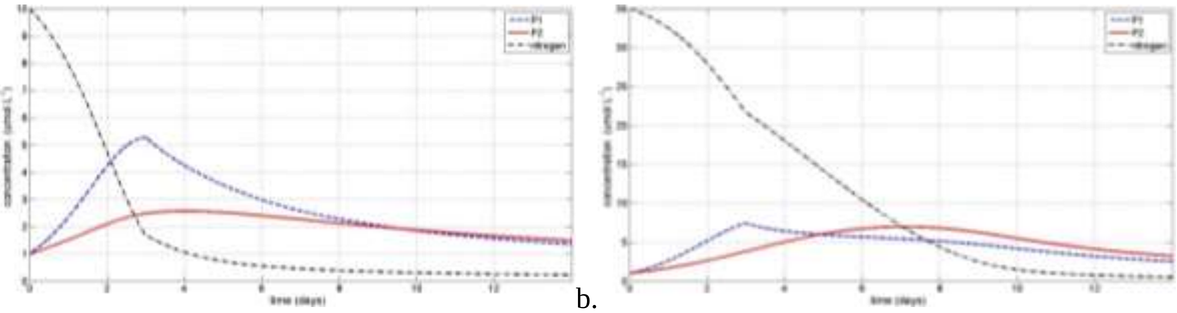


Figure 6. Modelled biomass of diatoms (P_1) and dinoflagellates (P_2) competing for nitrogen with model parameters as outlined in Table 1 and no effect of turbulence, a) N_{in}=10μM.L^{-1}; b) N_{in}=35μM.L^{1}.

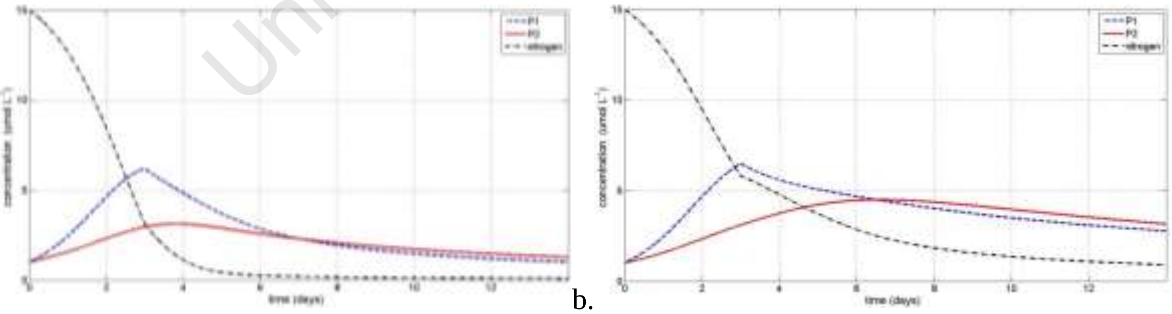


a. b.

Figure 7. Modelled biomass of diatoms (P_1) and dinoflagellates (P_2) competing for nitrogen with model parameters as outlined in Table 1 and turbulence acting on diatoms as in Table 2d and Figure 5d, a) N_{in}=10µM.L^{-1}; b) N_{in}=35µM.L^{1}.

An increased N_{in} led to increased overall phytoplankton concentration and an earlier succession of dinoflagellates when turbulence was included in the model (Figure 6) as in scenario d (Table 2). That is, with diatoms (P_1) disadvantaged by stratification after day 3 through a reduction in maximum growth rate (Figure5d).

In a system with low nutrient recycling, x=0.25, dinoflagellates succeeded diatoms after day 7. In a more efficient system, where 75% of nitrogen is returned to the nutrient pool (x=0.75), succession occurred after 6.5 days. Overall phytoplankton concentration is increased in a more efficient system. The standard chosen condition of x=0.5 results in succession after 7.3 days with plankton biomass intermediate to the situations of Figure 8.



a. b.

Figure 8. Simulated concentrations of diatoms (P_1) and dinoflagelattes (P_2) competing for nitrogen with parameters as outlined in Table 1, a) x =0.25 and b) x=0.75. This models variable nutrient recycling efficiency of the system.

The Mandala

The expected successions predicted by Margalef's Mandala were modelled by changing the length of the turbulent period and the implementation of the *T* variable (Figure 9). Dinoflagellate succession is seen in quadrants II (Figure 9b) and quadrant III (Figure 9c) and a diatom bloom is seen in quadrant I (Figure 9a).

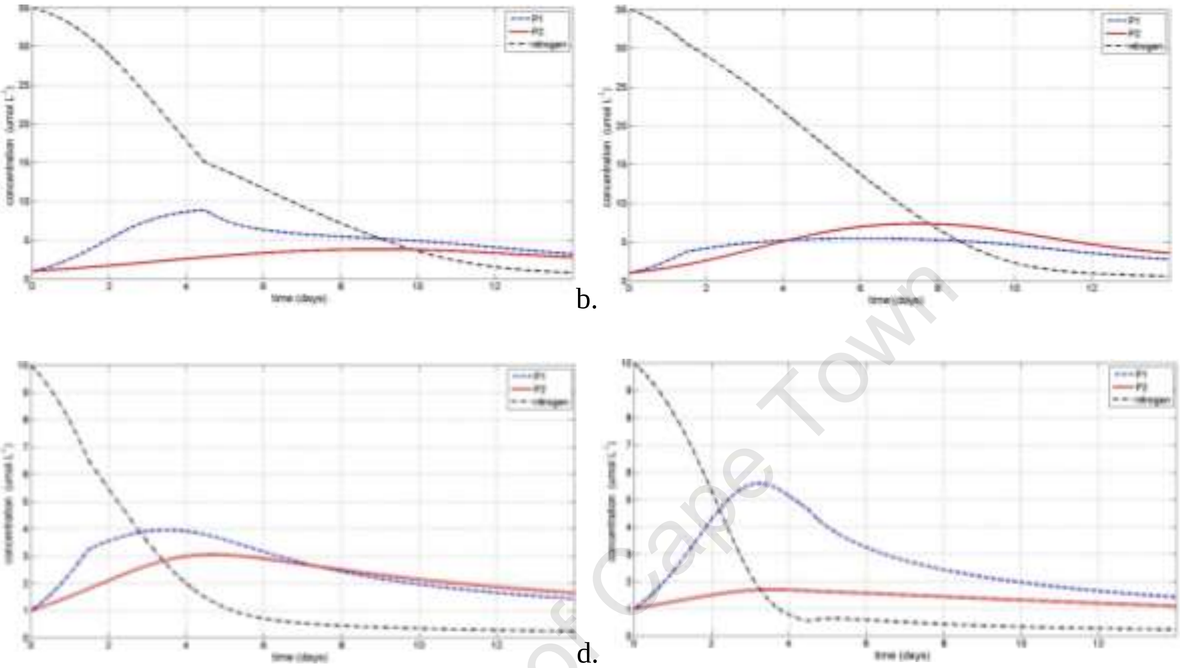


Figure 9. The four quadrants of Margalef's Mandala, a) quadrant I, high turbulence-high nitrogen; b) quadrant II, low turbulence-high nitrogen; c) quadrant III low turbulence-low nitrogen, and; d) quadrant IV, high turbulence-low nitrogen, parameters changed as in text.

DISCUSSION

A simple numerical model was created which accounted for two phytoplankton functional types and which modelled the formation of a diatom bloom as seen in the Southern Benguela upwelling system. The commonly seen trend of dinoflagellate blooms following diatom blooms was also successfully modelled through the introduction of a single term accounting for the effect of turbulence on the growth rate of both plankton types. The introduction of this term was only successful in one of the four possible applications (Figure 5d) where diatoms were negatively affected by the absence of turbulence after day three. In this model dinoflagellates were left to reach maximum growth rate throughout the modelled time and not directly disadvantaged by the turbulence of the upwelling event. The low growth rate and slow nutrient uptake rate of dinoflagellates, compared to diatoms, implies that succession was only possible in conditions where dinoflagellates are strongly favoured compared to a competing phytoplankton functional type. This lends to the idea that dinoflagellate blooms are strongly linked to periods of calm following upwelling events where stratified waters disadvantage the usually dominant diatoms (Smayda 1997).

Interestingly, the relative levels of dinoflagellates are over all lower than that of diatoms. This is ultimately a result of the lower growth rate attributed to them in the model. Type III waters describing the later part of the bloom are expected to have high phytoplankton concentrations (Barlow 1982). The values used to parameterise this model where all based on the ranges proposed by Litchman *et al.* (2006), and it appears that using these values a proliferation of dinoflagellates could not be modelled. Litchman *et al.* (2006) suggests low nitrogen half saturation constants (K_N) for diatoms and high constants for dinoflagellates. This is contrary to the positive allometric relationship suggested by Moloney and Field (1991). Although in general dinoflagellates are smaller cells, in the Southern Benguela, dinoflagellate blooms can be very high biomass, and it is during these high biomass events that red tides are seen to occur (Pitcher *et al.* 2005). It would be useful to perform more in depth sensitivity analysis of the parameters of the model, such as changing maximum growth rate for each group, in order to allow a higher maximum dinoflagellate biomass.

Given that the causes of shifts in phytoplankton community structure from common diatom dominance to the dominance of dinoflagellate species is poorly understood (Smayda and Reynolds 2001), this result is important. Turbulence and nutrient concentrations are the most commonly investigated and accepted drivers of this shift (Margalef 1978, Estrada and Berdalet 1997); however turbulence is not commonly included in numerical models of phytoplankton biomass. The model used in this investigation is overly simplistic ignoring many environmental variations such as additional nutrient limitations, light availability and temperature, which are all commonly added to the basic NPZ model (Franks 2002). Turbulence influences phytoplankton dynamics in various ways which are not easily translated into numerical models. Maximum growth and uptake rates of an organism are imposed by external conditions, they are variable and subject to the effects of irradiance, day length and temperature (Eppley *et al.* 1969). It is therefore likely that growth and uptake rates are similarly subject to the effect of turbulence. This has been shown to be the case for many diatom and dinoflagellate species (White 1976; Peters *et al.* 2006).

Altering the maximum growth rate of each functional type in response to turbulence led to a model of dinoflagellate succession; however the effect of turbulence on growth rate is variable due to the complexity of turbulence operating at various scales (Estrada and Berdalet 1997). Models typically attribute a maximum growth rate to a collection of organisms with similar traits (Litchman *et al.* 2006), this does not account for the multiple ways in which maximum growth rate may be unachievable, the presence or absence of turbulence is just one of these possible constraints. The modelling of a turbulence parameter for different systems could give specific insight into the influence of turbulence on the local community assemblage and patterns of succession.

Growth rate was chosen as the term affected by turbulence as it has received the most attention (Peters and Marrasé 2000), compared to uptake or mortality rates. Pasciak and Gavis (1975) and Savidge (1981) have both found an increase in uptake rate of diatom species associated with increased turbulence; however the relationship is complex and difficult to interpret and more experimental data is needed before these factors can be generalised (Estrada and Berdalet 1997). Given the nature of this model, the application of the turbulence term may be distributive, implying that altering the uptake rate or the maximum growth rate would have the same effect on the model. A similar case may be found in investigating the effects of altering the mortality rate as a response to turbulence. These are possible avenues of exploration in the search for the relationship between turbulence and phytoplankton succession and the formation of blooms.

Nutrient availability plays an important role in determining whether dinoflagellates are able to succeed diatoms. Diatoms are able to out-compete dinoflagellates at both low and high incoming nitrogen levels (Figure 6). In the scenario where turbulence is included (Figure 7), high N_{in} results in a more successful dinoflagellate bloom. High initial nitrogen concentrations, without a turbulence parameter, show the inability of dinoflagellates to outcompete diatoms without a change in turbulence. High nitrogen concentrations at the initialization of the model dictate higher nitrogen concentrations once diatoms are disadvantaged by stratified waters. These conditions allow for dinoflagellate succession. The efficiency of the system is also of importance, a more efficient system (Figure 8b) results in prolonged high nitrogen levels, improving dinoflagellates chances of growth once diatoms are disadvantaged. As important to calm conditions for the formation of HABs is the availability of regenerated nitrogen (ammonium and urea) (Pitcher *et al.* 2005). By allowing for higher rates of nutrient recycling this factor could be added to the model. This study did not alter the affinity for regenerated nitrate that dinoflagellates are believed to have, but altering uptake parameters or including various forms of nitrogen in the model pose interesting avenues of further work in developing a simple NPZ model of HABs.

The application of the model to the four quadrants of Margalef's Mandala indicates some success of the model. The need to change the inclusion of dinoflagellate disadvantage in turbulent conditions compared to the earlier case where this could not be included highlight a shortcoming in the model. The interplay between turbulence and nutrient concentration in the formation of blooms, both diatom and dinoflagellate, is clearly key in predicting succession. This is illustrated by the ease with which the 3 predictive quadrants could be produced by the model (Figure 9). The case of the forth quadrant is interesting as there is no natural equivalent (Wyatt 2012), while the model predicts a diatom bloom. This is not surprising as the high growth and uptake rate attributed to diatoms in the model increases their competitive ability in low nutrient conditions and the model did not disadvantage diatom maximum growth rates in this case as was done in earlier scenarios.

The Southern Benguela upwelling system is characterised by high turbulence associated with the high nutrients of the upwelling event (Pitcher *et al.* 1991). This system is of great economic importance and experiences frequent HABs (Pitcher *et al.* 2005). The close link of a model such as the one built in this study could therefore work towards understanding the factors contributing to HABs in the system. This level of applicability encourages the growth of this model beyond its current state with the possibility of answering the questions posed by the GEOHAB research project on HABs in upwelling systems (Pitcher *et al.* 2005). This model reveals some of the links turbulence and nutrient availability, and the pattern of succession from diatom to dinoflagellate dominated phytoplankton blooms in the Southern Benguela upwelling system.

This model could be improved by assigning a turbulence coefficient to each functional type. In this study *T* was given a value of one, where a factor of turbulence (or lack thereof in the case of diatoms in stratified water) was not reducing the growth rate, or a constant proportion. This assumes that each functional type is equally disadvantaged by the presence (in the case of dinoflagellates) or absence (in the case of diatoms) of turbulence. This improvement to the model can be easily made with the improvement of understanding of the direct effects of turbulence on species specific maximum growth rates.

In conclusion, the effect of turbulence on phytoplankton maximum growth rate is a promising method of modelling phytoplankton functional type succession and the development of Harmful Algal Blooms. The basic effects can be added to the system through a basic term for turbulence. The altering of parameters to accommodate for the effects hydrodynamics is obviously an important aspect of phytoplankton modelling. This can be expanded to close the gap between simple numerical phytoplankton models and coupled biophysical models. Lastly the model proposed by Margalef (1978) offers insight into the development of phytoplankton blooms, and the possibilities proposed can be accounted for in a simple numerical model. Both this model and Margalef's Mandala are proof that the complexity of events such as phytoplankton blooms can be investigated and understood through simplification of the appropriate interactions.

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