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The Diversity of Harmful Algal Bloom-Triggering Mechanisms and the Complexity of Bloom Initiation

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ABSTRACT

Mechanisms influencing initiation of harmful algal blooms (HABs) are diverse, and are not likely to be mutually exclusive. Rather, initiation of HABs is a result of interactions between processes, which result in biological, physical, and chemical conditions optimal for a bloom. Due to the complexity of some bloom initiation processes, bloom-preventative management may be possible. Results from a modeling exercise and a laboratory experiment indicated that a phytoplankton bloom could be circumvented through manipulation of the nutrient-loading mode, *i.e.*, pulsed vs. continuous loading. These findings, should they prove consistent in more robust field experiments, may provide insights for the development of new management approaches for some HABs. Optimal bloom conditions, however, vary between HAB species. Consequently, it is unlikely that a single management solution will exist. Preventative management efforts will require early warning of HAB initiation, perhaps even before the appearance of an HAB species. An indicator based on the dynamic nature of phytoplankton succession events and phytoplankton species diversity may prove useful for this purpose. Applying this index to an existing plankton data set showed that *Microcystis* blooms might have been predicted months before the start of the bloom.

Key Words: HAB demographics, pulsed flow, dynamic succession, species diversity

INTRODUCTION

The occurrence of harmful algal blooms (HABs) appears to be on the rise and linked to human activity (Hallegraeff 1993; Smayda 1990). While the immediate charge of the scientific community and resource managers is protection of human health, *e.g.*, development of early-warning technology and communication infrastructure, our culminating objective must be development of bloom-preventative management practices, *i.e.*, socioeconomically based landscape manipulations aimed

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at sustaining ecosystem form and function. Management schemes of this nature will require, in part, understanding of algal bloom-initiating mechanisms and their sensitivity to various abiotic and biotic processes. They will also require an indicator of ecosystem health, one that monitors ecosystem integrity well before the appearance of harmful bloom-forming species.

The purposes of this manuscript are three-fold. First, we summarize the diversity of perceived mechanisms that contribute to the initiation of harmful algal blooms. Second, we highlight the potential sensitivity of these processes with reference to HAB management. And third, we explore the utility of an early-warning indicator based on the rate and magnitude of phytoplankton succession events, and phytoplankton species diversity. Regarding our discussion of HAB-initiating mechanisms, our intent is not to review this subject. Rather our intent is to highlight the diversity of perceived mechanisms by providing case specific examples. Reviews on HABs have been presented elsewhere (Anderson and Garrison 1997; Paerl 1988; Shumway *et al.* 1990).

DIVERSITY OF BLOOM-INITIATING MECHANISMS

To better illustrate the diversity of bloom-initiating mechanisms, and to emphasize the utility of approaching this issue from a population demographics viewpoint, we categorize and discuss processes according to a generic differential equation that depicts population demographics of an HAB species, which is

$$\frac{d\phi_{HAB}}{dt} = \mu\phi_{HAB} - \gamma G_{Z,HT} - vP_{B,V,F,D} \pm AdvDiff \quad (1)$$

where μ is the specific growth rate of the HAB species, ϕ_{HAB} is the biomass of the HAB species, γ is the clearance rate on the HAB species as a function of feeding by zooplankton and other organisms of higher trophic level, $G_{Z,HT}$ is the biomass of zooplankton and higher trophic level organisms, v is the mortality rate on the HAB species resulting from encounter with pathogens, $P_{B,V,F,D}$ is the pathogen biomass, which may include some bacteria, viruses, fungi, and/or dinoflagellates, and $AdvDiff$ represents the transport of the HAB species via advection and diffusion.

HAB Specific Growth Rate, μ

The value of μ is a function, in part, of a phytoplankter's ability to uptake, store, and utilize nutrients. Models of varying detail have been developed to illustrate this process (Droop 1983; Roelke *et al.* 1999a; Zonneveld 1996). Not surprisingly, there is a myriad of biotic and abiotic factors that impact μ of HAB species, and their competitors. Most are directly related to the availability of growth-limiting nutrients, while other factors include allelochemical interactions and turbulence inhibition.

Elevated nutrient concentrations in many water bodies are a result of anthropogenic inputs. It is unclear whether this impacts the initiation of HABs. However, in some cases it may. Ancillary evidence from phytoplankton cultures regarding maximum specific growth rates (μ_{max}) and half saturation coefficients of nutrient uptake (K_s) indicate some HAB species are characteristic of high μ_{max} and K_s , and relatively

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low μ_{\max}/K_s (see Smayda 1997). According to resource-saturation models (Kilham and Kilham 1984), such species will gain a competitive advantage at high growth-limiting resource concentrations. Using this model, it seems likely that anthropogenic nutrient enrichment may favor some HAB species by differentially increasing μ , and potentially be responsible for bloom initiation.

Other processes that may result in elevated nutrient concentrations, and therefore enhance μ of HABs, include upwelling, wind-induced mixing, and eddy-induced vertical mixing. It was suggested that upwelling events provided infusion of growth-limiting nutrients that fuel *Gymnodinium breve* blooms off the west Florida shelf (Tester and Steidinger 1997), and cyanobacteria blooms in the Baltic Sea (Kononen and Nommann 1992). Wind-induced mixing of nutrients from deeper waters into the euphotic zone, and eddy-induced vertical mixing were believed to stimulate cyanobacteria blooms in the Baltic Sea (Kahru *et al.* 1981; Kononen *et al.* 1996).

Water column stratification is a function of many factors that include solar warming of surface waters, decreased wind stress, and rainfall and runoff events. Stratified water column conditions were shown to be advantageous to many HAB dinoflagellates, such as *Alexandrium catenella*, *Gymnodinium catenatum*, and *Dinophysis* sp. (Belgrano *et al.* 1999; Hallegraeff *et al.* 1995; Nishitani and Chew 1984), and cyanobacteria, such as *Nodularia* sp., *Aphanizomenon* sp., and *Anabaena circinalis* (Paerl 1988; Sellner 1997). The advantage is gained because phytoplankton species that are able to regulate their position in the water column are able to visit both nutrient-rich deeper water and irradiance-saturated shallower water. In addition, by moving vertically through the water column they are more likely to come into contact with nutrient-rich patches found in microlayers. The result of these processes is that motile phytoplankton will encounter more growth-limiting nutrients than their non-motile competitors, which will enhance μ (Smayda 1997).

In addition to simply encountering more nutrients, migration through the water column will allow motile phytoplankton to experience a temperature gradient, which may boost certain physiological characteristics important to competition, and therefore bloom initiation. For example, it was shown that for many species μ_{\max} is positively correlated with temperature, as is the case for the brown tide organism *Aureococcus anophagefferens* (Bricelj and Lonsdale 1997). Consequently, warmer surface waters may provide an environment where some HAB species are able to outgrow competitors. Affinity for nutrients is also temperature sensitive in that it is negatively correlated to temperature, *i.e.*, K_s decreases with decreasing temperature. This allows phytoplankton to uptake nutrients at lower concentrations. This was evident for the dinoflagellate *Gymnodinium sanguineum* that showed an ~6-fold decrease in its value of (see Smayda 1997). Therefore, access to cooler deeper waters for some HAB species may give them a selective advantage over competitors not as sensitive to temperature changes.

Increased turbulence that leads to cessation of stratification can have a negative impact on μ of some HAB species. To illustrate, growth of *Alexandrium minutum* was inhibited when turbulence exceeded a species-specific threshold (Thomas *et al.* 1997), presumably through break-up of dinoflagellate chains and inhibition of cell division. As stated above, factors leading to decreased turbulence, *i.e.*, below species-

specific thresholds for some HAB species, may initiate blooms. In this example, however, the mechanisms are different.

Continental shelf frontal systems are dynamic areas of mixing of varied degrees, which results in a highly variable temporal and spatial nutrient and light regime. Some HAB species are more versatile than their competitors, *i.e.*, they are able to adapt quickly to changing conditions of irradiance and nutrient concentration, thereby allowing them to maintain relatively higher μ . It was suggested that this might have contributed to the initiation of *G. breve* and *Gyrodinium cf. aureoleum* dinoflagellate blooms in these areas (Tester and Steidinger 1997).

Shifting growth-limiting nutrient ratios can alter phytoplankton community composition through the processes of resource competition and competitive exclusion (Sommer 1989; Tilman 1977). For example, in nutrient regimes where dissolved inorganic nitrogen (N) concentrations are low, and the nitrogen to phosphorus ratio (N:P) is low, it was said that species of cyanobacteria may form HABs (Kilham and Hecky 1988; Sellner 1997). Similarly, it was suggested that decreases in the availability of silica relative to N and P may result in community shifts away from diatoms and toward less desirable phytoplankton forms (Riegman *et al.* 1992). Finally, blooms of the brown tide organism *Aureococcus* sp. appeared to be controlled by the availability of iron (Gobler and Cosper 1996), and may have occurred due to increasing iron inputs relative to other growth-limiting nutrients from run off (Schneider 1994).

Some HAB species are able to utilize alternative sources of nutrients, which would give them a competitive advantage when dissolved inorganic nutrients are depleted, *i.e.*, of the HAB species is maintained, while μ of competitors decreases. For example, species of *Chrysochromulina* were shown to phagocytize bacteria and small flagellates when limited by inorganic nutrients (Jones *et al.* 1993; Nygaard and Tobiesen 1993), which may have enabled them to continue growth while competitors were senescent. Similarly, through osmotrophy some dinoflagellates were shown to take up dissolved organic nutrients in addition to dissolved inorganic nutrients (Iwasaki 1979).

Robust growth of competing phytoplankton may actually stimulate growth in some HAB species. For instance, it was suggested that a bloom of *Chrysochromulina polylepis* in Scandinavian waters may have been stimulated, in part, by preconditioning of an earlier *Skeletonema costatum* bloom that may have elevated the cobalt and vitamin B₁₂ concentrations (Graneli and Risinger 1995). Also, it was shown that μ of multiple red-tide forming dinoflagellates were enhanced when co-occurring *S. costatum* showed robust growth (Iwasaki 1979).

Catabolism of dissolved organic matter by bacteria may stimulate HABs by releasing growth-limiting micronutrients. A case in point, it was suggested that in Tasmanian waters allochthonous input of DOM followed by bacterial catabolism may have promoted μ of *G. catenatum* (Blackburn *et al.* 1989; Doblin *et al.* 1999). Similarly, it was determined that red tide blooms of *Chattonella* sp. in Japanese waters may have been controlled by the production and consumption relationship between the HAB and co-occurring bacteria (Nishijima and Hata 1989).

Through allelochemical-enhanced interspecific competition, or chemical warfare, some HAB species are able to gain a selective advantage by suppressing μ of competitors. These interactions were observed between *Prorocentrum concavum* and

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Gambierdiscus toxicus (Bomber 1990), and species of *Chattonella* and *A. catenella* (Iwasaki 1979).

HAB Biomass, ϕ_{HAB}

Initiation of some HABs may be through inoculation of cells, *i.e.*, increase in ϕ_{HAB} , into an area previously uninhabited by the invading species. Blooms of *G. catenatum* in Tasmanian waters, for example, were believed to have originated through discharge of ballast water (Hallegraeff *et al.* 1995). Elevated ϕ_{HAB} may also occur when motile HAB species are chemically stimulated to migrate to a certain locale. For example, the presence of healthy schooling fish and an unidentified excretion compound were suggested to stimulate *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates to swarm toward a target prey (Burkholder and Glasgow 1997).

Clearance Rate for the HAB Species, γ

Some HAB species are capable of producing grazing-inhibiting compounds that either deter grazers or are lethal to grazers (see Turner and Tester 1997). This ultimately results in decreased γ , which may then initiate a bloom. Example HABs where predator avoidance was observed in fish and/or zooplankton include *Gymnodinium splendens*, *G. aureolum*, and *Nodularia spumigena* (Fiedler 1982; Lenanton *et al.* 1985; Potts and Edwards 1987). HAB species whose blooms are known to result in fish mortality and/or a myriad of deleterious effects to zooplankton include *G. breve*, *Chattonella subsalsala*, and *Aureococcus* sp. (Buskey and Stockwell 1993; Dundas *et al.* 1989; Shumway *et al.* 1990).

Biomass of HAB Grazers, $G_{\text{Z,HT}}$

Reducing grazer performance, which will reduce $G_{\text{Z,HT}}$, is another mechanism by which some HABs may initiate. This can occur simply because of low nutritional value or resistance to digestion of some HAB species. For example, because of its low content of polyunsaturated fatty acids and vitamin C, *Phaeocystis* sp. were believed to be unsuitable food sources for copepods (Claustre *et al.* 1990). In addition, it was suggested that the gelatinous nature of *Phaeocystis* sp. may shield it from digestion once ingested (see Turner and Tester 1997). Similarly, either due to nutritional deficiencies or resistance to digestion, ingested cells of *Trichodesmium* sp. were believed to be of poor quality to copepods (Guo and Tester 1994).

Some HAB species may gain an advantage over competitors simply due to a decoupling of predator and prey populations. For example, when mortality rates on $G_{\text{Z,HT}}$ are high initiation of HABs may result because top-down control is relaxed. It was determined that this may have been the case for initiation of an *Aureococcus* sp. bloom, where mortality rates on protozoan grazers were high due to heavy grazing by larger zooplankton (Charon *et al.* 1989). HABs may also initiate as a result of small $G_{\text{Z,HT}}$ populations at the time conditions arise that favor a bloom, which may have been the case for the Texas brown tide. It was determined that once the bloom was established the brown tide simply outgrew its predators (see Turner and Tester 1997) and may have reached cell concentrations inhibiting to grazing processes.

Mortality Rate of the HAB Species, v

While pathogens play a role in termination of some HABs (Doucette *et al.* 1999), they may also play a role during initiation. For example, if v is high enough to counter μ , a bloom may never initiate, but when v is reduced an HAB may result. It was suggested that this process might have occurred during an incident involving *A. catenella*, where this HAB species could not bloom due to the presence of the parasitic dinoflagellate, *Amoebophyra ceratii* (Nishitani *et al.* 1985).

Biomass of HAB Pathogens, $P_{B,V,F,D}$

Just as nutritional mismatches between predator and prey, *i.e.*, zooplankton grazing on an HAB species, appears to be an important factor in initiation of some blooms, the nutrient content of a host relative to the demand of the pathogen may also be important. Although we were unable to find an example referring to an HAB species, previous work with the diatom *Asterionella formosa* and a fungus pathogen elucidated this concept (Donk 1989). This work showed that when a host is of poor food quality the performance and propagation of the pathogen was reduced. In the case for HAB species, it may be that the cell quality effects pathogens to the point where they cannot propagate at a rate greater than μ the of the HAB species. In turn, this may allow a bloom to occur.

Transport of the HAB Species, AdvDiff

Vertical mixing processes, categorized under AdvDiff, that are important for nutrient infusions to the euphotic zone are also important bloom initiation factors in regards to resuspension of sediments containing resting cysts of HAB species. Resuspension of cysts was suggested to play a major role in the initiation of some dinoflagellate blooms, including *Pyrodinium bahamense*, *Alexandrium* sp., *G. breve* (Anderson 1997; Babaran *et al.* 1998; Tester and Steidinger 1997).

The AdvDiff term is also important in that blooms in a particular area may be a result of transport of cells from another area, *i.e.*, local processes other than advection had nothing to do with the bloom initiation. This was believed to be the case for some blooms of *G. breve* off the western Florida shelf (Tester and Steidinger 1997), and blooms of *Dinophysis* sp. off the Swedish coast (Lindahl 1993). Once transported onshore the blooms may then magnify because of increased nutrient availability.

Similarly, blooms can be a function of mostly physical mechanisms only, *i.e.*, all the processes discussed above, except for the requirement that cells be motile, can be disregarded. For example, intense blooms of *Noctiluca scintillans* occurring off the coast of La Jolla, CA, which dissipated and reformed daily, were thought to be a function of an ageostrophic front (Franks 1997). Physical mechanisms associated with formation and dissipation of fronts and how they can result in phytoplankton blooms have been reviewed (Franks 1992).

POTENTIAL MANAGEMENT

As illustrated above, perceived HAB-initiating mechanisms are quite diverse and are not likely to be mutually exclusive. Rather, HAB initiation is a result of optimal

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biological, physical, and chemical conditions that are influenced by interacting phenomena that range from climatological shifts to anthropogenic activities. A case in point, initiation of the Texas brown tide, a bloom that has lasted seven years, is believed a result of multiple events that led to optimal conditions for bloom initiation (Buskey *et al.* 1997). In this case, it was determined that microzooplankton populations, the major grazer of the brown tide organism, were diminished in the area possibly as a result of increased salinity, which resulted from decreased fresh-water input because of societal demand. Larger zooplankton species that feed on competing phytoplankton, however, were not as adversely affected. This likely contributed to the competitive advantage gained by the brown tide. In addition, a series of cold fronts in the area resulted in widespread fish kills that upon their decay provided the brown tide nutrients necessary to bloom. In regards to N, the nutrient-limiting productivity in this system, ammonium likely became the dominant form. It was demonstrated that the brown tide is an efficient competitor for ammonium, and it likely gained a competitive advantage over other phytoplankton when ammonium was the dominant form of N. In this case, all of these events were necessary to create the optimal conditions necessary for HAB initiation.

From a management perspective, the complexity of HAB initiation may be encouraging. For instance, if initiation of an HAB is dependent on a series of events or a complex set of optimal conditions, it may be possible to circumvent a bloom by disrupting the sequence of events or altering the optimal conditions. In other words, it may be easier to find a weak link in a long chain. To illustrate this concept, we refer to a previous modeling study (Roelke 2000) where a focus was on some of the bloom-initiating factors discussed above, *i.e.*, nutritional value of prey, resource ratio competition, and hydraulic conditions. We also refer to work in progress that tests some of the model's predictions using laboratory experiments on natural plankton assemblages (Buyukates and Roelke 2000; Roelke and Buyukates 2000).

The model to which we refer was built to simulate interactions between three competing phytoplankton functional groups, a capstone predator, the microbial loop, multiple growth limiting nutrients, and light. No growth- or grazing-inhibiting characteristics were built into the model, yet phytoplankton blooms still occurred during some of the simulations (Figure 1). It was shown that the reasons for this were twofold. First, one of the phytoplankton groups, which was mostly parameterized based on the dinoflagellate *Prorocentrum minimum*, was characterized by having a very low critical cell-quota for N (represented in Figure 1 as $Q_{\min N}$), *i.e.*, it was a poor food source when it was in a starved condition (depicted in Figure 1 when $Q_N/Q_{\min N}$ approached a value of 1). Second, the ratio of loaded nutrients was at the optimum for this group, *i.e.*, as resources became limiting this group was able to out-compete the other phytoplankton groups (Roelke *et al.* 1999a). In some of the simulations it was impossible for the capstone predator to ingest the required number of prey cells that would have provided enough N to support growth in excess of losses, *e.g.*, hydraulic flushing, respiration, mortality, etc, because the prey $Q_N/Q_{\min N}$ was too low. Under such conditions the grazer was eliminated and a phytoplankton bloom ensued (Figure 1a). These conditions only arose when bottom-up control of the phytoplankton groups, *i.e.*, nutrient limitation (which lead to a starved condition and prey of poor food quality) occurred prior to any significant top-down effects, *i.e.*, grazing.

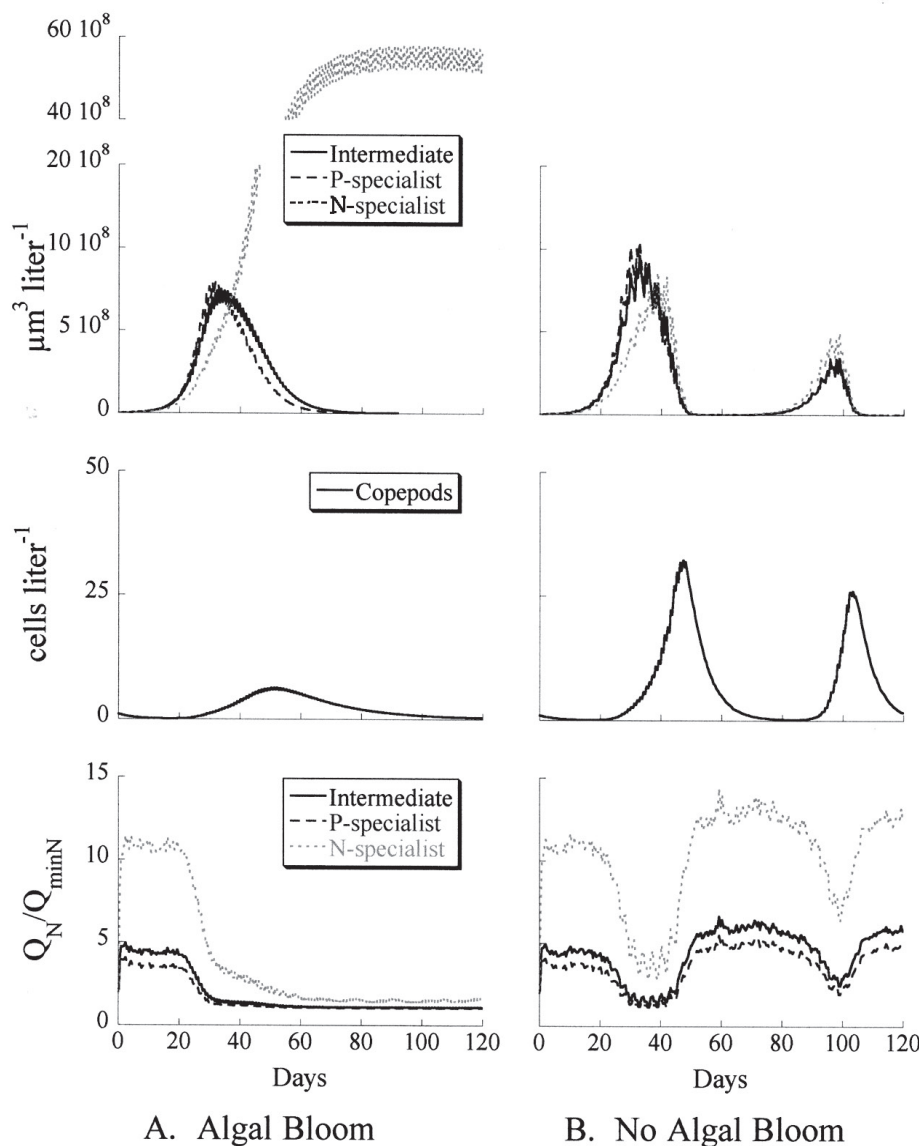


Figure 1.

Using a numerical simulation of a plankton model that depicted interactions between three competing phytoplankton functional groups, a capstone predator, the microbial loop, multiple growth limiting nutrients, and light (Roelke 2000), it was shown that the mode of nutrient delivery effected occurrence of algal blooms. In these simulations the degree of hydraulic-flushing and nutrient-loading was identical over the course of the simulations, but the mode of delivery differed. A phytoplankton bloom resulted when hydraulic-flushing and nutrient-loading were delivered in a continuous mode (A), but when delivered in pulses with a 3-day frequency a bloom did not result (B). The mechanism controlling whether a bloom would occur was the timing of the onset of bottom-up control, *i.e.*, nutrient limitation, which lead to phytoplankton cells of poor food quality (depicted when value of $Q_N/Q_{\min N}$ approached (1) relative to top-down control, *i.e.*, grazing. The continuous loading simulation led to onset of bottom-up control before top-down, and vise-versa for the pulsed simulation.

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There is much ancillary data supporting the concept of poor food quality as a bloom-initiating mechanism (see $G_{Z,HT}$ discussion above), but little direct evidence. In some laboratory experiments, however, this concept was demonstrated. In feeding experiments using starved cultures of *Scenedusmus acutus*, it was shown that the cladoceran *Daphnia galeata* failed to grow. When fed the same culture, but not in a starved condition, it was shown that the cladocerans could flourish (Sommer 1992). Similarly, in nutrient-loading experiments with natural plankton assemblages it was shown that phytoplankton could bloom, despite the initial presence of a diverse grazer community and no presence of any HAB species (Figure 2a). It was presumed that this bloom occurred because of the poor food quality of the prey and the demise of the predator populations (Buyukates and Roelke 2000; Roelke and Buyukates 2000), as suggested by the model simulations described above.

The model simulations reported in Roelke (2000) indicated that the conditions leading to the initiation of the theoretical bloom were sensitive to some factors that could be managed, *i.e.*, the magnitude, mode, and ratio of nutrient-loading. Here we only reiterate the impact of nutrient-loading mode. It was demonstrated that when nutrients were loaded in a pulsed fashion, instead of continuous, the timing of the onset of bottom-up control relative to top-down control was altered in such a way that when grazing pressure became significant none of the phytoplankton groups were in a starved condition. Consequently, grazer biomass accumulated and phytoplankton biomass was cropped, *i.e.*, no phytoplankton bloom occurred (Figure 1b). In part, this result came about because of the ability of the phytoplankton groups to uptake and store nutrients at a rate greater than their reproductive growth rate. This resulted in brief periods, which coincided with the nutrient pulses, where the nutritional value of the prey was elevated (Roelke *et al.* 1999a). The experimental work in progress lends support to this finding, where under conditions of pulsed nutrient-loading it was shown that greater secondary productivity was supported and a phytoplankton bloom did not occur (Figure 2b).

This work is still in progress and needs to be replicated with additional laboratory experiments, and demonstrated in the environment. However, this example illustrates the complexity of bloom initiation, and the potential sensitivity of the sequence of events and optimal conditions leading to bloom initiation. In other words, it may be possible to find and break weak links in a long chain. Of course this assumes that we have an understanding of all the chain's links. Unfortunately, few HAB-initiating mechanisms are understood as well as that of the Texas brown tide. What we do understand of HAB-initiating mechanisms reveals that the sequence of events or optimal conditions for bloom initiation varies widely between HAB species.

POTENTIAL MONITORING

Our perception of healthy, functioning environments are those that are structurally diverse and dynamic. That is, a natural temporal and spatial succession of species should be evident. In regards to phytoplankton, which species dominate a succession pattern will be a function of many factors. These include nutrient and light limitation, ratio of available nutrients, preferential grazing, species specific parasitism, and magnitude and frequency of disturbance (Donk 1989; Hambright

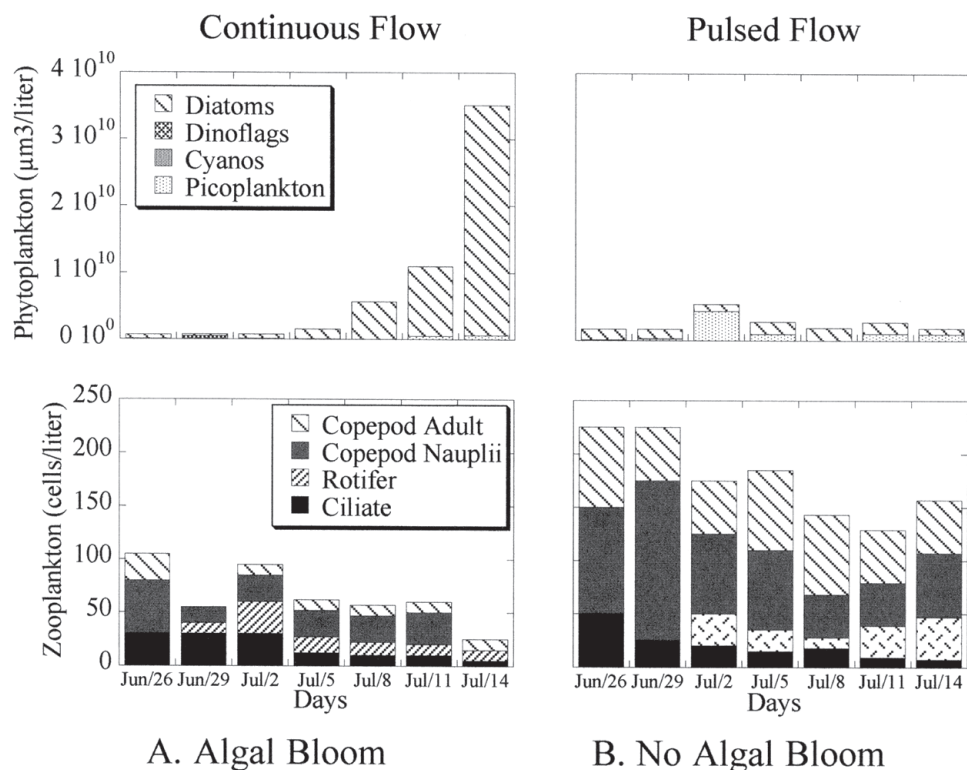


Figure 2. Using flow-through incubator experiments with a natural plankton assemblage it was shown that the mode of nutrient delivery effected accumulation of algal biomass (Buyukates and Roelke 2000; Roelke and Buyukates 2000). In these experiments the degree of flushing and nutrient-loading were identical over the course of the experiment, but the mode of delivery varied. Similar to the model results, a phytoplankton bloom resulted when hydraulic-flushing and nutrient-loading were delivered in a continuous mode (A), but when delivered in pulses with a 3-day frequency a bloom did not result (B).

and Zohary 2000; Roelke *et al.* 1997; Sommer 1989; Sterner 1989). The temporal and spatial variability of these processes influence phytoplankton species diversity. Theoretically, when process variability is low relative to the competitive exclusion rate, phytoplankton species diversity will decline. Similarly, when the process variability is high relative to the competitive exclusion rate, phytoplankton species diversity will decline. But when process variability is at some intermediate rate a greater number of species is supported (Hutchinson 1961; Connell 1978).

The mechanisms influencing succession patterns, and the synergistic interactions between these mechanisms, are difficult to predict. Consequently, the exact progression of species is difficult to predict. Regarding the occurrence of HABs, one thing is certain, the variability in the processes that maintain species diversity have broken down in some way such that phytoplankton species diversity during HAB events is often low. As stated previously, preventative management schemes will require an early-warning indicator, one that infers ecosystem stability well before the initiation

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of the HAB. From a modeling perspective, this will be difficult because the synergistic interactions between mechanisms impacting phytoplankton succession patterns are unclear.

Another approach, however, may be to monitor the dynamic nature of the succession events coupled to species diversity, while operating under the assumption that the more dynamic the succession events and greater the species diversity the more healthy the ecosystem. In this case, which species are dominant in the succession pattern is not important, as long as they are displaced by another species in a timely manner.

This concept was illustrated in a study that focused on the dynamic nature of phytoplankton succession events and species diversity prior to occurrence of noxious blooms of *Microcystis* sp. (Roelke and Buyukates, *In Review*) that occurred in Hartbeespoort Dam, South Africa (see Hambright and Zohary 2000 and Zohary *et al.* 1996). In this study it was demonstrated that after periods where either the dynamic nature of succession events (quantified by summing the absolute value of the 1^o derivative of the population curve for each phytoplankton species) or the species diversity (using the Shannon-Weaver index) was low a *Microcystis* sp. bloom ensued. But when both the dynamic nature of succession events and species diversity were high for periods spanning weeks a *Microcystis* sp. bloom did not follow (Figure 3). This suggests that an early-warning HAB indicator may be rooted in the dynamic nature of succession events coupled to species diversity. In the case of the Hartbeespoort Dam *Microcystis* sp. blooms, an indicator of this nature may have provided a three-month early notice of the HAB.

The Hartbeespoort Dam phytoplankton data set required much work to assemble and years to complete. Obviously, an early-warning indicator strategy based on population dynamics of individual species and species diversity, which can only be produced with confidence using microscopy, is not appropriate over relevant time scales for preventative management. It may be that other parameters can be measured that directly correlate to shifts in phytoplankton community structure that are sensitive enough to infer population dynamics and diversity. For example, using hyperspectral absorption data from culture work it was shown that multiple taxonomic groups could be distinguished using discriminant analysis (Johnsen *et al.* 1994; Millie *et al.* 1997; Roelke *et al.* 1999b). It was also concluded that the addition of taxon-specific hyperspectral scatter properties to the discriminant analysis may dramatically increase the utility of this statistical tool (Roelke *et al.* 1999b). It may be that shifts in the taxonomic groups delineated by the discriminant analysis, although they will not reflect actual species shifts, will directly correlate to the dynamic nature of succession events in the natural environment, and perhaps be useful as an early-warning indicator of ecosystem stability. Advances in other optical technologies, such as spectral fluorometry and submersible flow cytometry (Cullen *et al.* 1997; Sieracki *et al.* 1998), may further enhance our ability to estimate the dynamic nature of succession events, or perhaps through a combination of available technologies.

CONCLUSIONS

Bloom-initiating mechanisms are diverse, complex, and in many cases are not mutually exclusive. Consequently, a single preventative management solution is not

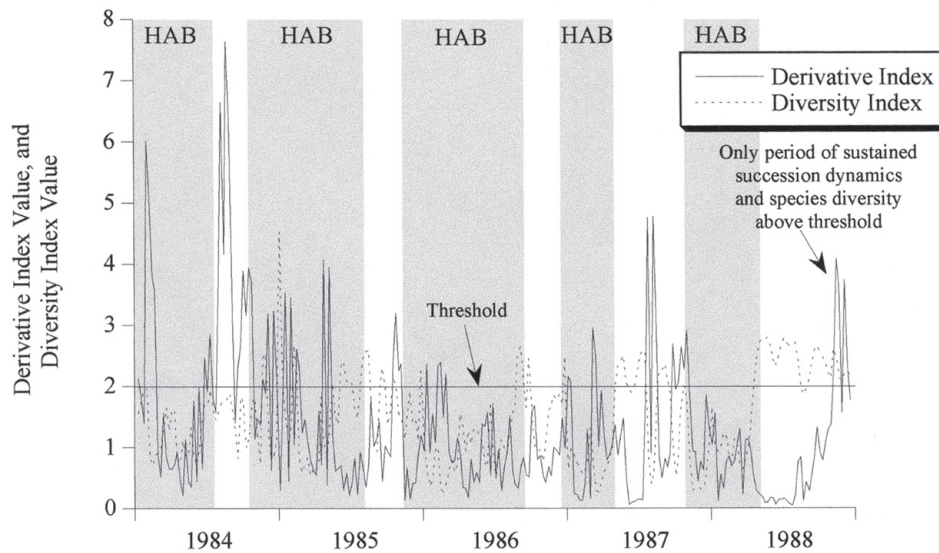


Figure 3. Using data from Hartbeespoort Dam, South Africa were recurrent blooms of *Microcystis* sp. eventually subsided (Hambright and Zohary 2000; Zohary *et al.* 1996) it was demonstrated that after periods were either the dynamic nature of succession events (quantified by summing the absolute value of the 1st derivative of the population curve for each phytoplankton species) or the species diversity (using the Shannon-Weaver index) was below a specific threshold a *Microcystis* sp. bloom ensued. But when both the dynamic nature of succession events and species diversity were above the threshold for periods spanning weeks a *Microcystis* sp. bloom did not follow (Roelke and Buyukates, *in review*).

likely. However, regional preventative management solutions may be impossible. The ecological complexity of bloom-initiating mechanisms of some HAB species may allow for the possibility of preventative management. Design of such strategies will require detailed understanding of processes underlying bloom initiation, which can only arise through a combination of detailed field sampling, laboratory experimentation, and numerical modeling. Should a preventative management scheme be feasible, it will most likely require an indicator of ecosystem health well before HAB development, or potentially even before the appearance of an HAB species. An indicator based on the dynamic nature of succession events and species diversity may be useful for this purpose. Because this approach emphasizes population dynamics of interacting species, and not simply presence of indicator species, high-resolution temporal data will be needed (perhaps on the scale of hours). New optical and particle sensors deployed *in situ* may be the best approach to collect such data.

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