26 The Complex Relationships Between Increases in Fertilization of the Earth, Coastal Eutrophication and Proliferation of Harmful Algal Blooms

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26.1 Introduction

The past five decades have witnessed a dramatic increase in the availability of nutrients on land, in the atmosphere, and in the oceans. This change has occurred largely due to the development of industrial fertilizers, changing practices in the raising of animals for consumption on land and in the sea, and increased consumption of fossil fuels (Vitousek 1997; Smil 2001). Over-enrichment of coastal waters by nutrients is considered a major pollution problem worldwide (Vitousek et al. 1997; Howarth et al. 2002) and one of the important factors contributing to global habitat change, including the geographic and temporal expansion of some harmful algal bloom (HAB) species (Smayda 1990; Anderson et al. 2002; Glibert et al. 2005a, 2005b). In this chapter, major trends impacting global nutrients are first reviewed, followed by a review of the concept of eutrophication and a synopsis of some of the evidence that HABs are increasing in frequency or extent in parallel with these trends. Lastly, these patterns are placed in context with other factors that must also be considered when understanding the relationship between eutrophication and HABs.

26.2 Global Trends in Population, Agricultural Fertilizer Usage and Implications for Export to Coastal Waters

The global population has expanded nearly five-fold in past half-century (Fig. 26.1A). It has been suggested that the "expansion from 1.6 billion people in 1900 to today's 6 billion…would not have been possible without the synthe-

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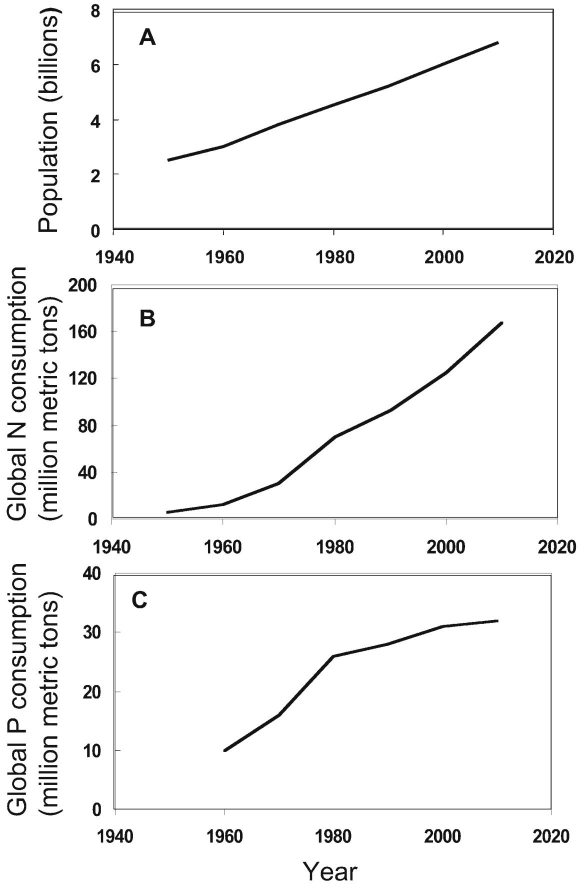

Fig. 26.1. A The change in world human population (in billions) from 1950 through 2000, projected to the year 2010. Data and projection are from www.census.gov/ipc/www/img/ worldpop.gif. **B** The change in global consumption of total synthetic nitrogen fertilizers (in million metric tons of N) for the same years as in panel A. **C** The change in global consumption of phosphate (in million metric tons of P) for the same years as in panel A. Data for panels B and C are from the Global Fertilizer Industry (International Fertilizer Industry 2005) and the projections through 2010 are based on an increase of 3 %

sis of ammonia" (Smil 2001). Industrial synthesis of ammonia permitted enormous expansion in agriculture, from improved yields per crop to improved protein diets of the global population (Smil 2001; Dalgaard et al. 2003). This process has also transformed the global nitrogen cycle and budget, however, with impacts ranging from atmospheric emissions to coastal pollution. Global use of nitrogen fertilizers has increased roughly 20-fold over the past five decades, while global use of phosphorus has increased only about 4-fold over the same period (Fig. 26.1B, C; International Fertilizer Industry 2005). In addition, the dominant form of synthetic nitrogen used worldwide has changed from inorganic nitrogen to organic nitrogen, primarily urea (Glibert et al. 2006). Urea is projected to represent nearly 70 % of global nitrogen fertilizer within the next decade (Glibert et al. 2006). Surface waters across the Earth are also sustaining impacts from anthropogenic nutrient enrichment from many other sources. Sewage (still untreated or poorly treated in many countries) has increased from the growing population. The development of concentrated animal feed operations (CAFOs), as well as large-scale aquaculture operations, have led to large amounts of organic feed and waste concentrated in small areas of the land, with high concentrations of nutrients and other pollutants added to adjacent rivers and estuaries (e.g., Mallin 2000). Atmospheric deposition of nitrogen has also grown in significance, from local emissions near large-animal operations (U.S. Environmental Protection Agency 1998) and from the production and consumption of fossil fuels (e.g., Driscoll et al. 2003).

Estimating nutrient export to the coastal zone thus remains a challenge because nutrient discharge is highly variable both globally and locally in time and space; nutrient forms and ratios vary with land use; and the composition of nutrient discharges is rapidly changing, reflecting changes in land use patterns and agricultural practices. Despite these challenges, models of both inorganic and organic nutrient export are now available (Seitzinger and Kroeze 1998; Seitzinger et al. 2002; Harrison et al. 2005a, 2005b). Such models show that nitrogen and phosphorus exports are greatest from European and Asian lands, followed by the United States. As explained below, not only the total load but also the nutrient form affects its fate in global nutrient transport and cycling, and its likelihood to stimulate HABs.

26.3 Nutrient Limitation versus Eutrophication: Basic Conceptual Framework

A long-standing paradigm in aquatic science is that primary production in freshwater systems typically is limited by phosphorus, whereas the primary limiting nutrient in marine systems is nitrogen (Hecky and Kilham 1988). Although many have questioned this paradigm as too simplistic, the fundamental principle remains: the nutrient in least availability relative to the needs of the organisms, that is, the nutrient that algae deplete first, will limit total production (e.g., Leibig's Law of the Minimum, reviewed in Wetzel 2001). Total algal production cannot increase infinitely, however; a maximum is attained as other factors begin to play a more important controlling role (Cloern 2001).

The concept of limiting nutrients in a eutrophic system actually is very complex. Ecosystem response to nutrient enrichment, or eutrophication, is a continual process rather than a static condition or a trophic state (Cloern 2001; Smayda 2005). There are several published formal definitions of eutrophication, all of which consider the changes accompanying nutrient enrichment as a continuum or a process. Nixon (1995), for example, defined eutrophication as an increase in the rate of organic carbon production in an ecosystem. Historically, the term was mostly applied to the natural aging of lakes, from deeper waters to a marsh (Wetzel 2001); more recently, the terms "accelerated" or "cultural" eutrophication have been used in recognition of major human influences. As relationships are explored between eutrophication and HAB species, it is important to recognize that different systems occur at different points along the eutrophication continuum.

26.4 Nutrient Loading, Nutrient Composition, and HABs

Nutrient enrichment of the globe has impacted the proliferation of harmful algal species in several major ways. Increases in total nutrient load can support higher HAB biomass, and alterations in nutrient form can lead to a nutrient regime favoring HAB growth relative to other algal species. Numerous direct relationships between nutrient load and HAB abundance have been established and recently reviewed (e.g., Cloern 2001; Anderson et al. 2002; Sellner et al. 2003; Glibert et al. 2005b); here, only a few examples can be highlighted. In Northern European waters, blooms of the mucus-forming HAB species *Phaeocystis globosa* have been shown to be directly related to the excess nitrate content of riverine and coastal waters, that is, the nitrate remaining after other species of algae deplete silicate (Fig. 26.2A; Lancelot 1995). In the USA, a strong positive relationship has been documented between increased nitrate loading from the Mississippi River to the Louisiana shelf and increased abundance of the toxigenic diatom *Pseudo-nitzschia pseudodelicatissima,* based on the geological record of the siliceous cell walls of

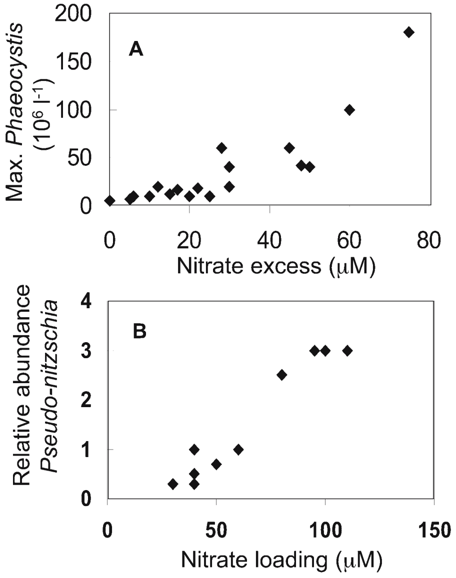

Fig. 26.2. Two examples of the relationship between nitrate and the occurrences of specific HAB outbreaks. **A** Maximum observed cells of the colony-forming prymnesiophyte, *Phaeocystis,* as a function of the excess nitrate (that remaining upon silicate depletion) in the Eastern Channel and Southern Bight of the North Sea for 1980–1990 (redrawn from Lancelot 1995). **B** Average abundance (%) of the diatom, *Pseudo-nitzschia*, in the sedimentary record as a function of the nitrate loading in the northern Gulf of Mexico (redrawn from Turner and Rabalais 1991; Parsons et al. 2002)

this species found in sediment cores (Fig. 26.2B; Parsons et al. 2002). In Puget Sound, Washington, USA, a striking correlation has been found between the growth in documented cases of paralytic shellfish toxins over four decades and the growth in the human population, based on USA census statistics, strongly indicative of nutrient loading and eutrophication as the causative agent of change (Trainer et al. 2003). Most notable are the blooms off the Chinese coast that have expanded in recent years in geographic extent (from km^2 to tens of km^2), in duration (days to months), species and harmful impacts (Fig. 26.3). These blooms parallel the increase in fertilizer use that has occurred during the past two decades (Fig. 26.3). The Baltic, Aegean, northern Adriatic, and the Black Sea have all experienced increases in HABs coincident with increases in nutrient loading (e.g., Larsson and Elmgren 1985; Bodenau 1993; Moncheva et al. 2001). On a shorter time scale, Beman et al. (2005) recently found a strong positive relationship between nitrogen-rich agricultural runoff to the Gulf of California and the development, 3–5 days later, of massive (~50–580 km^2) phytoplankton blooms. The broad relationship between nitrogen loading and HAB proliferation is also evident from the comparison of the global distribution of nitrogen export (based on the models of Seitzinger and Kroeze 1998) and the documented occurrences of several HABs (Fig. 26.4). Globally, harmful algal species that are responsible for paralytic shellfish poisoning (PSP), and the high biomass, toxigenic species *Proro-*

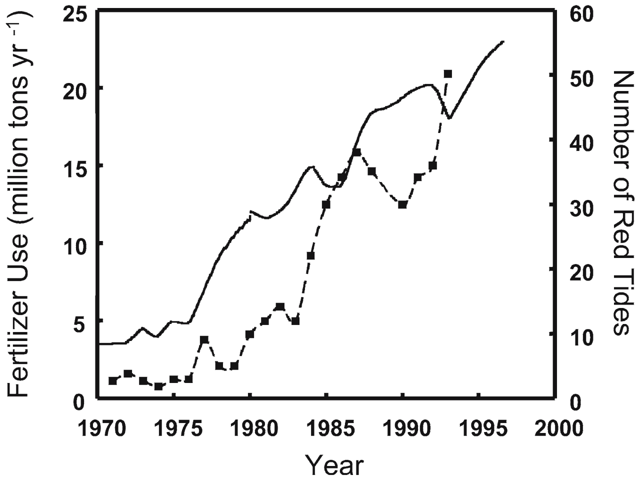

Fig. 26.3. Trends in nitrogen fertilizer use (*solid line*) and the number of red tides (*dashed line*) reported for Chinese coastal waters through the mid-1990s. Data were derived from Smil (2001) for fertilizer use and Zhang (1994) for red tide abundance (reproduced from Anderson et al. 2002 with permission of the Estuarine Research Federation). A review of species, the extent of the blooms and their impacts can be found at www.pices.int/publications/ scientific_reports/Report 23/HAB_china.pdf

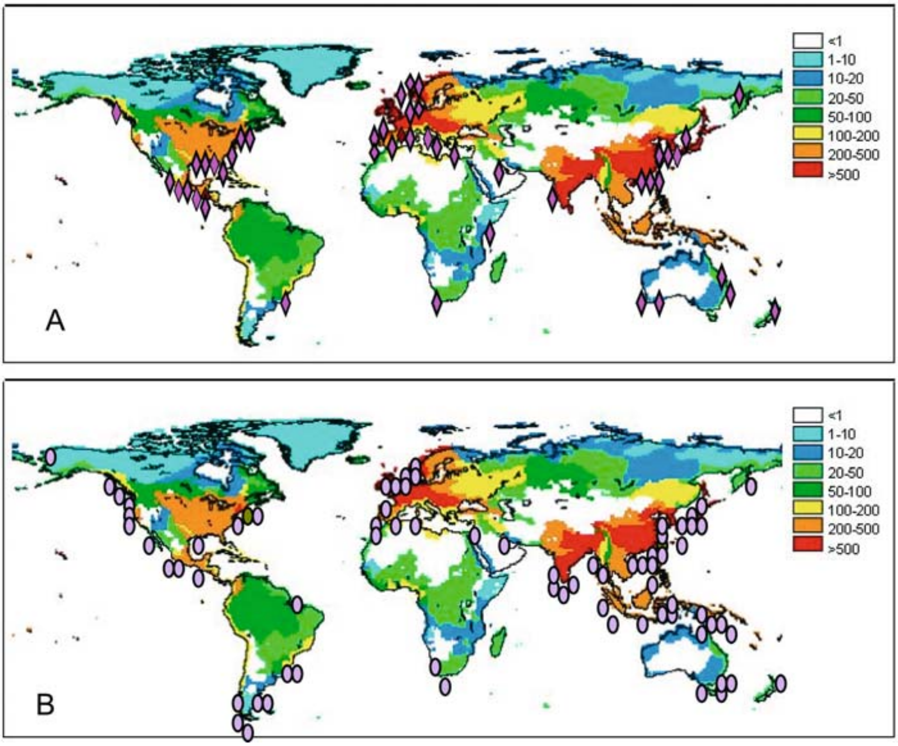

Fig. 26.4. Global distribution of recorded incidences of two major HABs types superimposed on a global map of modeled nitrogen export (base map from Seitzinger and Kroeze 1998; reproduced with permission of American Geophysical Union). Nitrogen export is calculated as kg N km^{-2} watershed $year^{-1}$. **A** Documented occurrences of *Prorocentrum minimum*, based on the review by Heil et al. (2005). **B** Documented occurrences of those HABs that produce paralytic shellfish poisoning (PSP, e.g., the dinoflagellates *Alexandrium tamarense, A. minutum, Gymnodinium catenatum* and *Pyrodinium bahamense* var. *compressum*), modified from the synthesis of GEOHAB (2001)

centrum minimum, are most common along the coasts of Asia, Europe, and North America where fertilizer use is high and consequently nitrogen export is also high (Heil et al. 2005).

Whereas total nitrogen loads are associated with some blooms, and total nitrogen loading exceeds phosphorus loading on a global basis, increased occurrences of other HABs have been associated with alterations in nutrient composition, especially decreases in the N:P ratio of the nutrient pool that reflect regional, disproportionate phosphorus loading relative to nitrogen. For example, in Tolo Harbor, Hong Kong, where phosphorus loading increased in parallel with increasing human population growth in the late 1980s, a distinct shift from diatoms to dinoflagellates was observed, coincident with a decrease in the ambient N:P ratio from roughly 20:1 to <10:1

(Hodgkiss and Ho 1997; Hodgkiss 2001). Along the eastern seaboard of the USA, outbreaks of the toxigenic dinoflagellate *Pfiesteria* spp. have been associated with low N:P ratios due to high phosphorus loading from CAFOs (Mallin 2000). Blooms of *Karenia brevis* on the western Florida shelf are found in waters with low N:P ratios due to phosphorus loading from local phosphate mining (Vargo et al. 2006).

The importance of organic nutrients in the nutrition of many HABs is also increasingly recognized, and some HABs have been related to organic nutrient load (see Glibert and Legrand, Chap. 13). For example, *Aureococcus anophagefferens* preferentially uses organic nitrogen over nitrate, and *Prorocentrum minimum*, *Lingulodinium polyedrum*, *Alexandrium catenella* and various other species are stimulated by organic nutrients (Glibert and Legrand, Chap. 13). Many harmful algal species prefer some forms of organic nutrients over inorganic forms, may have multiple acquisition mechanisms to obtain them, or may exhibit faster rates of growth on these nutrients (e.g., Berg et al. 1997; Berman and Chava 1999; Mulholland et al. 1999). Moreover, some species are obligate mixotrophs or heterotrophs, requiring organic forms of nutrients (Jones 1994).

Relationships between eutrophication and HABs extend beyond correlations between total nutrient load and changes in nutrient composition, however, as nutrients additionally can stimulate or enhance the impact of toxic or harmful species in more subtle ways. Nutrient availability or composition may also alter the toxin content of individual species without altering their total abundance, or may impact other members of the food web, such as bacteria and viruses, which in turn directly or indirectly impact the abundance or toxicity of harmful algal species (e.g., Carlsson et al. 1998; Anderson et al. 2002).

26.5 Factors Complicating the Relationship Between Eutrophication and HABs

Both eutrophication and the frequency and duration of many HABs have increased, but finding direct links between eutrophication and HABs has often been difficult because not all eutrophic waters support HABs, and not all HABs occur in waters rich in nutrients. One of the difficulties in linking nutrient loading to HABs is the multiplicity of factors contributing to HAB species responses to nutrient loading. The inability to universally apply a single criterion, such as total N concentration or N:P (or other nutrient) ratio, or organic:inorganic nutrient ratio, to determine whether eutrophication is stimulating HABs does not negate the utility of this approach. Rather, it underscores the interdependence of conducive environmental factors, physiological factors, and trophic interactions in the outcome of any species succession, as well as the importance of appropriately scaled temporal and spatial data (Glibert et al. 2005b). Thus, a given suite of nutrients may be insufficient to yield an outbreak of a harmful algal species. Nutrient availability must be matched with the preferences of the cells and their physiological condition, and with the physical and trophic structure of the water column at the time of nutrient delivery.

A classic example of differences in absolute nutrient requirements by specific species groups is that of diatoms, which, unlike most HAB species, require silica to construct their cell walls. If nutrient loading causes a proportional enrichment of nitrogen or phosphorus relative to hydrated silica, then a proportional shift away from a diatom-dominated community might be expected. Nitrogen-fixing cyanobacteria represent another example. Their ability to fix gaseous nitrogen can allow them to dominate under conditions in which dissolved inorganic or organic nitrogen is depleted but other nutrients, such as phosphorus and iron, are sufficiently available. Thus, high N:Si ratios (due to hydrated Si depletion) may favor flagellate or dinoflagellate abundance, while low N:P ratios may favor noxious cyanobacteria (Tilman 1977; Smayda 1990).

While some species have an absolute requirement for a particular nutrient, other species seem to have lost the ability to acquire specific nutrients. For example, the brown tide species, *Aureoumbra lagunensis*, apparently is incapable of assimilating nitrate (DeYoe and Suttle 1994). In such a case, nutrient ratios based solely on inorganic nutrients may not yield insights into the regulation of this species by nutrients.

A recent conceptual framework of the nutritional responses by HAB species included nine categories of dinoflagellates, each having distinctive morphological and habitat preferences, ranging from invasive species that dominate in habitats with enriched nutrient loading, to those that thrive in more oligotrophic, stratified systems (Smayda and Reynolds 2001). Large blooms of *P. minimum*, found in many regions affected by anthropogenic nutrient inputs (Heil et al. 2005), are an example of the former. In contrast, *Karenia brevis* and *K. mikimotoi* bloom in open coastal waters, aggregate in fronts, and are transported by coastal currents (Dahl and Tangen 1993; Walsh et al. 2001). As noted by Smayda (2005, p. 96), "It may be that as eutrophication progresses through its various stages, changes in life-form conditions occur which determine which life-form type of phytoplankter will predominate."

As a further, more fundamental complication, different strains within the same species often respond to nutrients differently. It is commonly assumed that the characteristics of one strain, maintained for years under highly artificial laboratory conditions, are representative of all strains of that species in the natural environment. This assumption overlooks the fact that for nearly all algal species studied, different strains within the same species commonly have shown marked differences in fundamental traits ranging from growth characteristics, toxicity, and bloom-forming behavior to responses to nutrients and other environmental conditions (Wood and Leatham 1992; Burkholder et al. 2001, 2005; Burkholder and Glibert 2006).

Nutritional history also affects the affinity of an algal cell for a particular form of nutrient, the immediate fate of that nutrient once taken up and, in the case of some harmful algal species, the degree of toxicity (e.g., Johansson and Granéli 1999; Skovgaard et al. 2003; Leong et al. 2004). For a nutrient-replete cell, the rate of incorporation of newly acquired nutrient may be slower than the rate of incorporation by a nutrient-deficient cell. Several decades of research on short-term physiological responses by various phytoplankton species have demonstrated that nitrogen-limited cells enhance nutrient uptake capabilities by orders of magnitude, relative to their rates of nutrient uptake when nitrogen-sufficient (e.g., McCarthy and Goldman 1979; Goldman and Glibert 1982). Thus, a nutrient pulse will be assimilated by species at different rates depending on whether they are nutrient-limited or nutrient-sufficient. Moreover, the same strain, as well as a group of strains with the same species, can show a different response to the same nutrient pulse at different phases of growth.

Physiological rate processes such as uptake or growth also vary in response to other environmental factors, such as temperature or salinity. Most physiological rates tend to increase with increasing temperature. This generalization appears to hold for the uptake of ammonium (e.g., Paasche and Kristiansen 1982), but not for uptake of all forms of nitrogen (Fan et al. 2003). During estuarine spring diatom blooms, for example, it has been shown that nitrate uptake is inversely related to temperature: uptake rates decrease with increasing temperature (Lomas and Glibert 1999). Differences in the temperature response of the enzyme responsible for nitrate uptake, nitrate reductase, in some diatoms compared to flagellates may help to explain such observations (Lomas and Glibert 2000). Nutrient pulses delivered at different times of year potentially can stimulate different species groups that are each adapted to specific temperature regimes. Meteorological conditions are also important, as the impact of nutrient delivery depends on seasonality and the extent to which nutrients may be delivered in a pulsed fashion, such as following rainfall, or in more continuous fashion, such as may occur via groundwater flow.

The relationship between nutrient availability/composition and HAB species is also constrained by the extent to which grazers assimilate select fractions of the plankton community (e.g., Neuer and Cowles 1995; Polis and Winemiller 1996). Thus, the nutrient pool may select for growth of a particular group of species, but if the rate of grazing exceeds the rate of growth of those species, such a relationship will not be observed. Some bloom species have predation avoidance mechanisms, such as spines or toxic compounds, that allow then to escape predation (Irigoien et al. 2005), which, in combination with nutrient availability, will aid bloom formation. Selective feeding by microzooplankton on certain species can alter the structure of a community that developed under a specific nutrient regime. Micro-predators can include some heterotrophic dinoflagellates that have been shown to graze [other] harmful algal species (e.g., Nakamura et al. 1995; Jeong et al. 2001). The close coupling of production and consumption by the microbial community, and the blurred distinction of autotrophic and heterotrophic nutrition of many flagellates, can make it difficult to differentiate the role of dissolved nutrients in bloom development from other mechanisms that structure populations.

26.6 Conclusions

For many HAB species, the effects of nutrient enrichment are complex. Nevertheless, fundamental physiological relationships have permitted some generalizations to be drawn about the role of nutrient quality and harmful algal species composition. Organic as well as inorganic nutrient forms are important in controlling HAB species responses to nutrient enrichment. Mixotrophy, via direct uptake of dissolved organic nutrients, cell surface oxidation, or phagotrophy, is common among flagellates, especially dinoflagellates (Glibert and Legrand, Chap. 13). Determination of the overall role of nutrient quantity and quality in affecting HAB species composition requires a fundamental understanding of physiological differences within and between species groups, their nutritional history, and intraspecific differences in response. While necessary, such information still can be insufficient to predict species outcomes in natural systems because physiological capabilities are also modulated by environmental conditions such as temperature, and by the community composition at the time of nutrient delivery. Thus, the same nutrient load – in quantity and quality – can have different impacts in different sites or at different times because of the ambient environmental conditions at the time of delivery. The ultimate success of a given species, and its response to nutrient enrichment, will depend on its ability to exploit both quantity and quality of available nutrients, the timing and intensity of the nutrient supply, and the interaction of other environmental factors and competitor or consumer species.

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