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Ocean Urea Fertilization for Carbon Credits Poses High Ecological Risks

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Abstract

The proposed plan for enrichment of the Sulu Sea, Philippines, a region of rich marine biodiversity, with thousands of tonnes of urea in order to stimulate algal blooms and sequester carbon is flawed for multiple reasons. Urea is preferentially used as a nitrogen source by some cyanobacteria and dinoflagellates, many of which are neutrally or positively buoyant. Biological pumps to the deep sea are classically leaky, and the inefficient burial of new biomass makes the estimation of a net loss of carbon from the atmosphere questionable at best. The potential for growth of toxic dinoflagellates is also high, as many grow well on urea and some even increase their toxicity when grown on urea. Many toxic dinoflagellates form cysts which can settle to the sediment and germinate in subsequent years, forming new blooms even without further fertilization. If large-scale blooms do occur, it is likely that they will contribute to hypoxia in the bottom waters upon decomposition. Lastly, urea production requires fossil fuel usage, further limiting the potential for net carbon sequestration. The environmental and economic impacts are potentially great and need to be rigorously assessed.

Keywords

Urea dumping; ocean fertilization; carbon credits; Sulu Sea; carbon sequestration; harmful algae; toxic dinoflagellates; cyanobacteria; hypoxia

Introduction

Large-scale ocean enrichment experiments have been conducted over the past two decades to understand the response of the oceans to limiting nutrients. Most of these experiments have involved iron additions to the equatorial North Pacific, the subarctic Pacific, and the Southern Ocean, which are regions known as high-nutrient, low-chlorophyll (HNLC) areas where there is apparent ample macro-nutrient availability (nitrogen, phosphorus), but limited micro-nutrients (iron), and thus limited phytoplankton accumulation (de Baar et al. 2005, Boyd et al. 2007, Buesseler et al. 2008). Application of such research has led some to suggest that with such ocean enrichment, carbon sequestration can be enhanced, and this may serve as one approach to reduce the build-up of greenhouse gases in the atmosphere.

Iron experiments, now totaling more than a dozen (de Baar et al. 2005, Boyd et al. 2007, Buesseler et al. 2008), have shown that phytoplankton blooms can be successfully

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manufactured, and this has caught the attention of the business community as a means to promote engineered solutions to climate change. The carbon-offsets market is rapidly expanding, and new enterprises are seeking methods to sequester atmospheric carbon as part of cap-and-trade programs. If phytoplankton blooms can lock away carbon through sinking to the deep sea, the market for these carbon offsets could be very large, particularly if an international quota system for carbon trading is agreed upon. However, large-scale manipulation of iron in regions of the ocean where this element is limiting is economically unfeasible. Thus, entrepreneurs are turning to regions where the limiting nutrient is nitrogen, not iron, with the hopes of enriching waters with this element.

A current plan, as announced by the Ocean Nourishment Corporation of Sydney, Australia, calls for the dispersment of 1000 tonnes of urea in the Sulu Sea, off the coast of the Philippines beginning in 2008 (Young 2007), although preliminary trials apparently have already begun (Aning 2007). Broader oceanic applications are also projected beyond the Sulu Sea in the future (<http://www.oceannourishment.com/technology.asp>). The goal is not only to remove carbon from the atmosphere by increasing algal biomass production and sequestration through sinking, but also to enhance primary production that leads to enhanced local fish production.

The effects of nutrient enrichment on an ecosystem must be considered from multiple perspectives, including physical, biological, and socioeconomic aspects (e.g. Nixon 1995, Howarth et al. 2000, Cloern 2001). Urea ($(\text{NH}_2)_2\text{CO}$) is a nitrogen fertilizer and feed additive, the global use of which has increased 100-fold in the past 4 decades (Glibert et al. 2006), and there is a large and growing body of literature on nitrogen cycling and urea metabolism by phytoplankton. These data permit us to propose several specific predictions about the Sulu Sea in particular and the fate of urea pumped into tropical or subtropical seas in general. Here we argue that this plan will likely not lead to enhanced fisheries or carbon sequestration. Instead, there is a real possibility that fisheries and the regional aquatic ecosystem could be significantly damaged for years to come, yielding environmental damage that could far outweigh the gains of carbon offsets.

The Sulu Sea

The Sulu Sea, a deep oceanic basin, is isolated from the surrounding ocean by a chain of islands, making it a region of restricted water exchange (Jones 2002). It is connected to the South China Sea in the south through the Balabac Strait, and in the north via the Palawan shelf and Mindoro Strait (Jones 2002, Campos and Villanoy 2007). These connections are believed to be pathways for water exchange and, more importantly, for plankton and larval exchange between adjacent basins, the so-called “marine corridors”. The region also supports high biodiversity and abundant marine corals (e.g. Nanola et al. 2004). Some of the richest fishing grounds of the Philippines are located in the Sulu Sea, as are the Tubbataha Reefs, a World Heritage Site (Aning 2007). It has been said that, “Tubbataha’s marine biodiversity is virtually unparalleled by any other in the world today” (Mission 1999). It is well established that nitrogen loading in coral reef areas can lead to community shifts towards algal overgrowth of corals and ecosystem disruption (Smith et al. 1981, Lapointe

1999; McCook et al. 2001a,b). This fact alone makes this region an inappropriate candidate for such experimentation.

Elemental stoichiometry : Limits to carbon biomass from nitrogen enrichment

Nitrogen fertilization stimulates the production of a higher phytoplankton biomass, but only to the extent that other nutrients are not also limiting. The chemical composition, by atoms, of a typical algal cell is 106 carbon: 16 nitrogen: 1 phosphorus: 0.0001 iron. Therefore, for each added unit of iron, about 1,000,000 units of carbon biomass can be produced, assuming all other elements are sufficiently available. However, for each unit of nitrogen that is added to a nitrogen-limited region, only ~7 units of carbon biomass can be produced; large amounts of nitrogen produce smaller amounts of carbon biomass than do large iron additions.

The plan by the Ocean Nourishment Corporation suggests that other elements, beyond carbon and nitrogen from urea, may be added in the addition “mix”, but in unspecified proportions. While global estimates of dissolved inorganic phosphorus for the basins of the South Pacific do suggest that natural phosphorus yield is moderately high (Harrison et al. 2005), the availability is far from that required to balance phytoplankton uptake of the additional urea in the proportion needed to sustain growth (e.g. Redfield et al. 1963). Notably, while an N:P ratio of 16 is an average, the N:P requirement of cyanobacteria is higher than the canonical 16 (Geider and LaRoche 2002). Thus, depending on the stoichiometry of concomitant additions of phosphorus and other micronutrients, the added urea may not yield the expected biomass or may only yield biomass of organisms with a high N:P ratio such as cyanobacteria and picoeukaryotes.

Urea fertilization likely to have eutrophication impacts

In addition to the specific regional concerns about the potential loss in biodiversity in the Sulu Sea, were urea fertilization to be undertaken at large scale there are other significant concerns which may apply to other tropical or subtropical regions.

While stoichiometry argues against efficient conversion of added urea to algal biomass, any increased algal biomass is of concern. The goal of the proposed plan is to enhance phytoplankton biomass to a concentration of 200 $\mu\text{g L}^{-1}$ of chlorophyll *a* (Young 2007). This is a concentration of biomass that is only observed in the most eutrophic waters, and a level that will reduce light penetration that is required to support sustained productivity in the euphotic zone (Raymont 1980). In fact, the US National Research Council (1993) has noted that chlorophyll *a* concentrations $>10 \mu\text{g L}^{-1}$ represents eutrophic waters, and the mean level of chlorophyll *a* in US coastal waters that are classified as eutrophic is only 15 $\mu\text{g L}^{-1}$. The Sulu Sea now has chlorophyll *a* concentrations that are generally $<0.2 \mu\text{g L}^{-1}$ (Jones 2002). Thus, the proposed enrichment, if successful as planned, would elevate chlorophyll *a* concentrations ~ 3 orders of magnitude.

Eutrophication causes a myriad of environmental effects, but two are of immediate concern: the potential for the development of hypoxic or anoxic zones, regions of reduced dissolved oxygen content, and the alteration of species composition leading to harmful algal blooms (Howarth et al. 2000, Diaz and Rosenberg 2001, Anderson et al. 2002, Anderson 2004, Glibert et al. 2005). High phytoplankton biomass in eutrophic waters is often not efficiently transferred to higher trophic levels by zooplankton, as some algae are not palatable to zooplankton, and algae have higher growth rates than do zooplankton. In the worse case, algae may sink to deeper waters, and cause hypoxia upon their decomposition. Hypoxia and anoxia have been associated with algal blooms in many aquatic environments and are responsible for fish kills in coastal waters throughout the world. Whether episodic or sustained, such “dead zones” are responsible for losses of millions of dollars of commercial fish annually (Joyce 2000, Mallin et al. 2006). The morphology and circulation of the Sulu Sea support an oxygen minimum zone (OMZ) starting at a depth of about 1000 m. This OMZ is maintained by restricted exchange with the South China Sea across the Mindoro Strait sill at 420 m depth. Water entering the Sulu Sea from the South China Sea is depleted in dissolved oxygen, with levels of about 100 $\mu\text{mol kg}^{-1}$. Dissolved oxygen in the Sulu Sea is about 50 $\mu\text{mol kg}^{-1}$ from about 1000 m to 5000 m (Gamo et al. 2007). This low dissolved oxygen level makes it susceptible to hypoxia and anoxia. Caution must also be exercised with any scheme that would increase the oxygen demand in these deep waters, as a declining temporal trend in dissolved oxygen has already been documented over the past decade at depths of 500–600 m (Gamo et al. 2007). Furthermore, anoxic zones may subsequently result in the release of the sequestered CO_2 as well as methane (a gas that enhances the greenhouse effect) and N_2 and N_2O from denitrification from any decaying biomass (Granéli and Granéli in press), thus counteracting the benefits of any initial carbon sequestration.

Urea fertilization may alter phytoplankton species composition and change carbon sequestration efficiency

The efficiency of the urea enrichment program is dependent on the efficiency of carbon burial to the deep sea, but burial efficiency will depend on the species composition of the stimulated blooms. Urea enrichment is likely to cause alterations in algal species composition and a loss of phytoplankton biodiversity. Based on our understanding of phytoplankton species dynamics, it is suggested that urea enrichment would preferentially lead to the enhanced production of cyanobacteria, picoeukaryotes, and dinoflagellates, rather than diatoms (e.g., Berg et al. 2001, Glibert et al. 2004, Solomon 2006, Heil et al. 2007, Glibert and Berg 2008). In subtropical regions, not only are rates of urea uptake higher in waters in which cyanobacteria are the dominant phytoplankton, but urea uptake is also positively correlated with the proportion of phytoplankton composed of cyanobacteria (as *Synechococcus* spp.) in the water column (Glibert et al. 2004). In contrast, the proportion of diatom biomass in the water is positively correlated with nitrate uptake and negatively correlated with urea uptake (Glibert et al., 2004, Heil et al. 2007). Urea is rapidly hydrolyzed to ammonium by the cellular enzyme urease, and the activity of the enzyme is positively correlated with temperature (e.g., Fan et al. 2003, Solomon 2006). Thus, the warm waters of the South Pacific are in the range of maximal enzyme activity. Furthermore, *Synechococcus*, *Prochlorococcus* sp. and related pelagic picoeukaryotes, such as *Aureococcus*

anophagefferens, have among the highest rates of urease activity per cell volume of any phytoplankton species measured, making them ideal competitors for urea (Fig. 1; Solomon 2006). *A. anophagefferens* forms harmful algal blooms in temperate, rather than tropical, coastal waters (e.g., Berg et al. 1997, Bricelj and Lonsdale 1997), but related species form harmful blooms in coastal lagoons along the Gulf of Mexico, indicating a potential threat of such “brown tides” in warmer coastal ecosystems (Buskey et al. 2001). Also common in tropical and subtropical regions are the cyanobacteria *Trichodesmium* spp., which fix nitrogen gas and contribute significantly to the biological nitrogen budget of the oceans (e.g. Capone et al. 1997, Breitbarth et al. 2007). *Trichodesmium* spp. have been found to not only grow faster on urea than on other fixed nitrogen sources, but when urea is available, preferentially use urea over nitrogen obtained from nitrogen fixation (Mulholland et al. 1999). Moreover, even if urea nitrogen is used by picoeukaryotes and dinoflagellates, they do not appear to use the urea carbon when uptake is measured using dually labeled urea (Fan and Glibert 2004, Mulholland et al. 2004).

Complicating the carbon sequestration plan is the fact that both *Synechococcus* and *Trichodesmium* are neutrally or positively buoyant and thus would not have a tendency to sink from the euphotic zone (Walsby 1991, Mulholland 2007). This contrasts with diatom blooms which tended to proliferate following iron enrichments in the open-ocean experiments in the Pacific and Southern Oceans (e.g. de Baar et al. 2005). Diatoms have a siliceous shell, while dinoflagellates and cyanobacteria do not, and this results in a strong tendency for diatoms to sink out of the surface waters. In fact, when *Trichodesmium* spp. bloom on a large scale, they can form extensive surface scums, some of which have been large enough to be visible from space (e.g., Dupouy 1992). Although visibility from space may be used to track the development of a phytoplankton bloom, surface slicks and scums do not sequester carbon to the deep ocean.

Of particular concern is any potential for an increase in abundance of toxin-producing dinoflagellates following urea enrichment. Many species of toxic marine algae bloom in response to anthropogenic nutrient loading (Burkholder et al. 1998). In many regions of the world where urea dominates the agricultural applications of nitrogen, increasing frequency and geographic extent of toxin-producing dinoflagellates have occurred. In fact, a global comparison of urea fertilizer use by watershed and the distribution of those dinoflagellates that are responsible for paralytic shellfish poisoning, one of the many syndromes caused by toxic dinoflagellates, shows apparent correspondence (Fig. 2; Glibert et al. 2006). Toxic dinoflagellates are responsible for fish kills as well as the accumulation of toxins in fish and shellfish, which in turn may cause serious human health impacts when the seafood is consumed (Landsberg 2002, Backer and McGillicuddy 2006).

A bloom of the toxic dinoflagellate species *Cochlodinium* spp. in 2005–2006, which extended ~ 500 km along the western side of Palawan, Philippines, apparently transported from Sabah, Malaysia, following the prevailing wind and current systems, caused massive fish kills in both countries (Azanza et al. 2008). In the Philippines, other known common toxic dinoflagellates are *Pyrodinium bahamense* and *Gymnodinium catenatum*, both of which cause paralytic shellfish poisoning (Bajarias et al. 2006). The Philippines have long

suffered from these toxic outbreaks, with >2000 intoxication events and 123 human deaths recorded from contaminated seafood consumption from 1983–2005 (Bajarias et al. 2006).

The relationships between urea and dinoflagellate proliferation are beginning to be understood. Dinoflagellates have higher urease activity on a per cell basis than other algal species (Fig. 1), further underscoring their likelihood to respond to urea additions. In the subtropical waters of Moreton Bay, Australia, the proportion that urea contributed to total nitrogen uptake rates was correlated with the percent of the phytoplankton assemblage that was composed of dinoflagellates (Glibert et al. 2006). Potentially toxic dinoflagellates *Lingulodinium polyedrum* and *Cochlodinium fulvescens* that form red-tide blooms off California (Kudela and Cochlan, 2000, Kudela et al., 2008) have been shown to utilize urea and its degradation product, ammonium, at rates far in excess of nitrate, and based on *in situ* light and nutrient conditions, these nitrogen forms could potentially provide the majority of the nitrogen needed to support such blooms. In Thau lagoon, southern France, urea pulses were followed by developments of the toxic dinoflagellate *Alexandrium catenella* (Collos et al. 2007).

Even if urea is not immediately used by toxic dinoflagellates, these organisms may proliferate over time. Dinoflagellate blooms have been found in association with *Trichodesmium* blooms, for example (Fig. 3), purportedly benefiting from the dissolved organic nutrients which are released by the cyanobacteria (Glibert and Bronk 1994, Karl et al. 1997, Glibert and O’Neil 1999, Lenos et al. 2001). Some dinoflagellates are also mixotrophic and graze on cyanobacteria, bacteria, or other microorganisms to sustain their nutrition (e.g., Jeong et al. 2005, Stoecker et al. 2006). Indirect pathways of nutrient assimilation and downstream effects must be considered as well as the direct pathways of urea assimilation.

Not only is the proliferation of toxic dinoflagellate species associated with higher urea loading, but so too is their cellular toxin content. In fact, the toxin content of urea-grown paralytic shellfish producing dinoflagellates is greater than that of nitrate-grown cells (Leong et al. 2004), as is the neurotoxin content of a dinoflagellate that is common in the Gulf of Mexico, *Karenia brevis* (Shimizu et al. 1993). Some cyanobacteria have also been shown to increase their toxicity levels in the presence of excess nitrogen (Stolte et al. 2002, Granéli and Flynn 2006).

Many of these common dinoflagellate species are known to produce viable cysts during their life cycle (e.g., Anderson et al. 1983, 2003). Cysts may initiate new blooms if conditions are suitable, or sustain populations throughout the year, germinating from bottom sediments. If cyst-forming species proliferate following fertilization, the numbers of cysts in the sediment will increase, thus increasing the probability that blooms of these toxic species will occur in subsequent years.

Urea fertilization may not benefit fisheries

In support of urea fertilization, it has been argued that, “For every tonne of reactive nitrogen added to the ocean in the form of urea, ...5.7 tonnes of phytoplankton will be produced,

ultimately leading to roughly an extra tonne of fish” (Young 2007). While trophic transfers to fish are known to be inefficient, and to decrease as primary production increases (e.g. Ryther 1969), the inefficiencies are particularly large when cyanobacteria and dinoflagellates dominate the phytoplankton assemblage (Karl et al. 1997). Many cyanobacteria and dinoflagellates are typically considered to be poor quality food for zooplankton grazers that support enhanced fish production. Rather, the phytoplankton that are likely to be produced from urea fertilization, cyanobacteria and dinoflagellates, will more likely lead to an enhanced “microbial loop” in which carbon and nutrients cycle among the members of the microbial community and are not efficiently transferred up the food chain (Azam et al. 1983). Furthermore, some of the phytoplankton produced may be responsible for decreased fish production from potential increased hypoxia and direct impacts on fish, or through gill clogging (Burkholder 1998, Landsberg 2002).

Urea in natural waters is metabolized to ammonium through urease enzymes of both cyanobacteria and bacteria (e.g. Mobley and Hausinger 1989, Collier et al. 1999, Palinska et al. 2000). Ammonium is another form of nitrogen that is preferentially used by dinoflagellates, in contrast to diatoms which have been shown to preferentially use nitrate under certain environmental conditions (e.g., Lomas and Glibert 1999). Although it is impossible to estimate what concentrations of ammonium may result in the water column from the planned urea injection, direct toxicity to fish by ammonium/ammonia is also possible. At seawater pH, approximately 5% of total ammonia is unionized (NH_3), while 95% is in the ionized form (NH_4^+ ; Millero 2006). Toxicity of NH_3 to fish increases not only with concentration, but also as oxygen content decreases, and with younger fish (i.e. juveniles compared to adults), although highly variable by species and other factors (reviewed by Randall and Tsui 2002). Even if it is only 5% of the total ammonia pool, NH_3 could reach toxic levels if concentrations are high enough. The Philippines has expansive aquaculture cages for fish production, and these cultured fish are especially vulnerable to low oxygen and NH_3 toxicity as they cannot escape from their immediate environment. The economic loss of fish aquaculture could be substantial. Ammonium can also be volatilized to the atmosphere, and carried from the site of original application, and redeposited with precipitation (Timperley et al. 1985), leading to potential effects far from the manipulated site of interest.

Urea fertilization not likely to sequester carbon to the deep ocean

None of the major ocean fertilization experiments involving iron enrichment was able to confirm a significant enhancement of carbon transport to the deeper ocean (e.g. de Barr et al. 2005, Lutz et al. 2007, Buesseler et al. 2008). Carbon production and transport following iron enrichment were found to be dependent on light, temperature, depth of the mixed layer, and grazing (de Baar et al. 2005). While massive sedimentation following some blooms has been documented, for example following a *Phaeocystis* sp. bloom in the Antarctic (e.g. DiTullio et al. 2000), clear seasonal and biogeographical differences exist in the vertical flux and in the efficiency of the biological pump (Lutz et al. 2007). Less carbon is transmitted to the deep during warm summers when the community is dominated by species such as cyanobacteria and dinoflagellates. In fact, the UN Intergovernmental Panel on Climate Change (IPCC; <http://www.ipcc.ch/>) has examined the ocean fertilization issue and

determined that it should not be pursued because there is very little documented increase in actual long-term sequestration of CO₂ in the deep waters or sediments.

Ocean fertilization programs require well designed verification and monitoring

The need to establish global agreements on carbon offsets that are based on sound science is underscored by this poorly conceived urea fertilization program. It is not sufficient to verify that a bloom develops, for example, using satellite imagery as a measure of the sequestration of carbon, which is the proposed method of choice of the commercial enterprise. Such information does not provide a quantification of the export out of the surface waters, and does not enable quantification of the potential for growth of harmful species. The costs of verification of sinking flux and of species compositional changes, particularly harmful species enumeration and monitoring must be included in the economic plan of urea fertilization.

Carbon offsets may be overestimated

The Ocean Nourishment Corporation has claimed that in the long run, beyond Sulu Sea trials, “One Ocean Nourishment plant will remove approximately 5–8 million tonnes of CO₂ from the atmosphere for each year of operation, equivalent to offsetting annual emissions from a typical 1200MW coal-fired power station or the short-term sequestration from one million hectares of new growth forest” (<http://www.oceannourishment.com/technology.asp>). However, urea production is itself a high-energy consuming process. Urea is produced from ammonia and CO₂ using energy from natural gas; the ammonium carbamate that is formed is subsequently dehydrated at high temperature to form urea and water (European Fertilizer Manufacturer Association). The production of ammonia through the Haber Bosch process (Smil 2001) uses about 3.4% of global natural gas consumption in support of the worldwide demand for nitrogenous fertilizer. The use of fossil fuel in this process releases CO₂ which had long been buried. Consequently, it is apparent that the CO₂ consumed by the phytoplankton in any manufactured bloom does not represent the net CO₂ flux from urea synthesis through consumption. Moreover, the breakdown of urea from biological processing in seawater results in the release of CO₂ (e.g., Leftley and Syrett 1973, Bekheet and Syrett 1977, Ge et al. 1990), further limiting the potential for carbon to be sequestered in biomass that sinks.

While the amount of urea to be used in the Sulu Sea is a small fraction (<1 %) of the global urea budget, it is worth considering what it would require to use urea fertilization to reduce the annual anthropogenic production of atmospheric carbon by just 1% globally, or 20% of the reduction required by the Kyoto Protocol (<http://ec.europa.eu/environment/climat/Kyoto.htm>). On a global scale, fossil fuel burning yields roughly 8×10^{15} g C yr⁻¹; this is similar to global ‘new’ oceanic production (*sensu* Dugdale and Goering 1967). Thus, in order to use oceanic production to sequester 1% of this carbon, it would require 8×10^{13} g C yr⁻¹ of additional oceanic carbon production. Conservatively, this would need $1-2 \times 10^{13}$ g N yr⁻¹, assuming high efficiency of conversion of nitrogen to carbon biomass and high efficiency of storage of new carbon biomass in the deep ocean, which, for the arguments put

forth above, is not realistic. This amount of nitrogen would be roughly equivalent to 10% of all the nitrogen fertilizer used in agricultural applications globally at the present time. In addition to the environmental problems this would likely cause, the economics of such a strategy would also be prohibitive, requiring a 10% increase in natural gas usage, in turn putting inflationary pressures on food and fuel costs worldwide.

Conclusions

In sum, the proposed plan for urea fertilization in the oceans to enhance carbon sequestration and fish production is a plan that will fail. The economics, efficacy and safety of large scale iron fertilization in order to enhance carbon sequestration have been questioned and repeatedly debated (e.g. Buesseler et al. 2008). The concerns for nitrogen enhancement in the form of urea thus appear to be even greater. Urea enrichment is not likely to produce the desired phytoplankton assemblage needed to support enhanced food chains. It also likely will not produce a phytoplankton assemblage that will sink and sequester carbon. Instead, urea enrichment of the oceans will more than likely lead to increased production of harmful algae. Once such harmful algae become established, they can continue to proliferate for years to come as nutrients are recycled and regenerated. We urge caution in use of any ocean fertilization program, iron or urea, for carbon offsets. Sequestration must be verified, biological and biogeochemical impacts on the ecosystem need to be monitored, and economic models need to be developed that account for any direct and indirect ecological impacts. The environmental and economic costs of urea enrichment are potentially great and need to be rigorously assessed.

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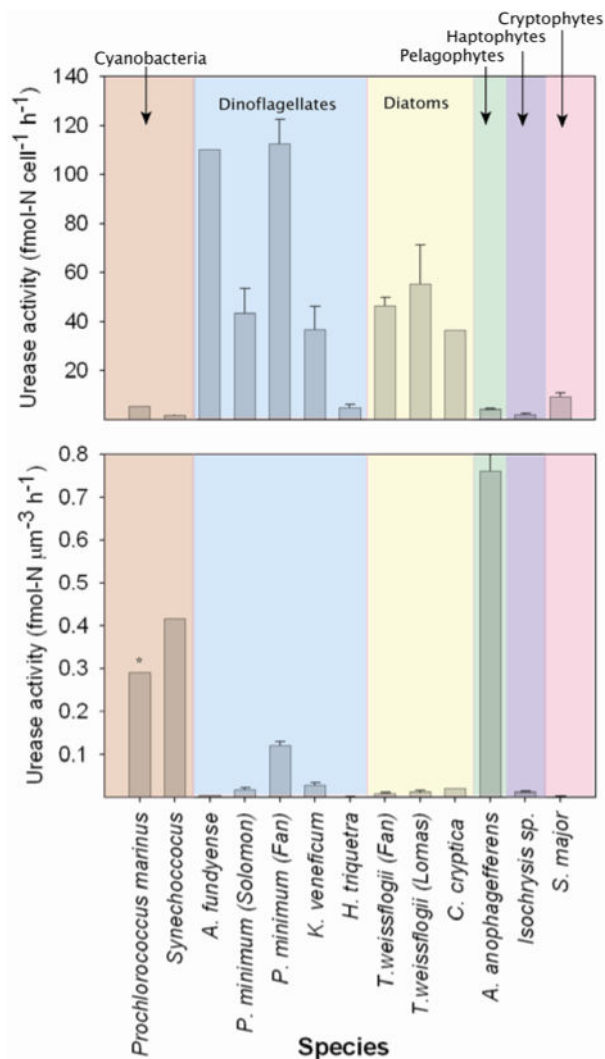


Figure 1.

The rate of urease activity, normalized per cell (upper panel) and to cell volume (lower panel), for phytoplankton species grown in culture. Species include cyanobacteria *Prochlorococcus marinus* (Palinska et al. 2000), *Synechococcus* spp. (Collier et al. 1999); dinoflagellates *Alexandrium fundyense* (Dyhrman and Anderson 2003), *Prorocentrum minimum* (Fan et al. 2003, Solomon 2006), *Karlodinium veneficum* (Solomon 2006), *Heterocapsa triquetra* (Solomon 2006); diatoms *Thalassiosira weissflogii* (Fan et al. 2003, Lomas 2004), *Cyclotella cryptica* (Oliveira and Antia 1986); pelagophyte *Aureococcus anophagefferens* (Fan et al. 2003); haptophyte *Isochrysis* sp. (Solomon 2006); and cryptophyte *Storeolata major* (Solomon 2006). Where two entries are given for the same species on the figure, the source author is given in parentheses. The asterisk by the value for *P. marinus* in the lower panel indicates that it has been divided by 10 to display on the graph. From Solomon (2006).

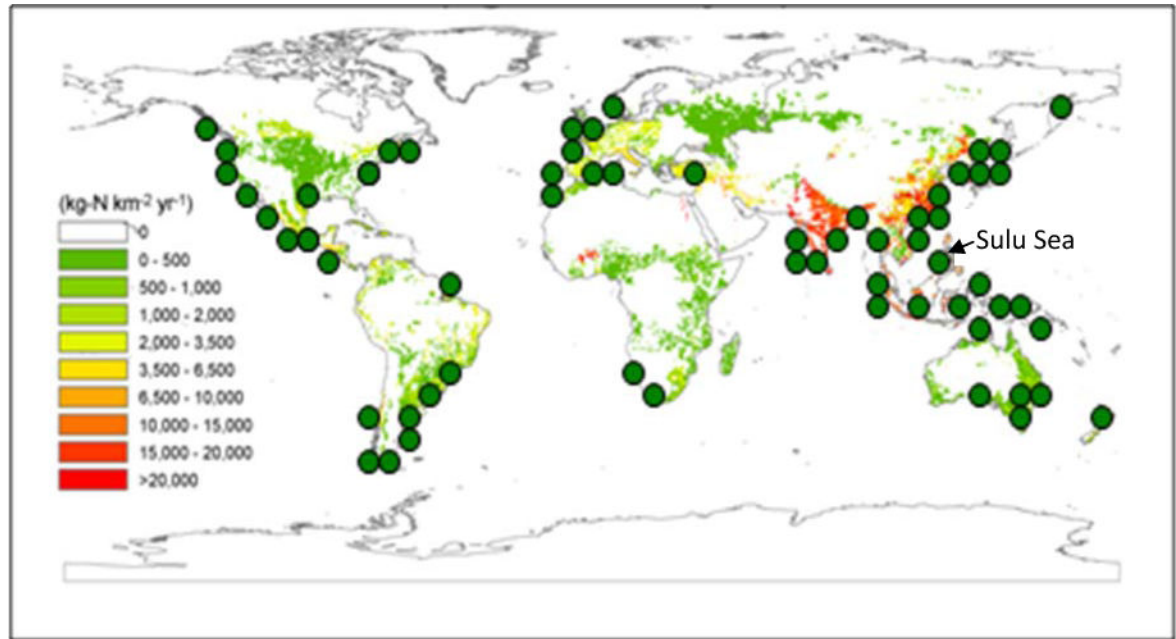


Figure 2. Global distribution of urea application by watershed (base map) and the global distribution of the documented occurrences of paralytic shellfish poisoning. From Glibert and Harrison (unpublished).

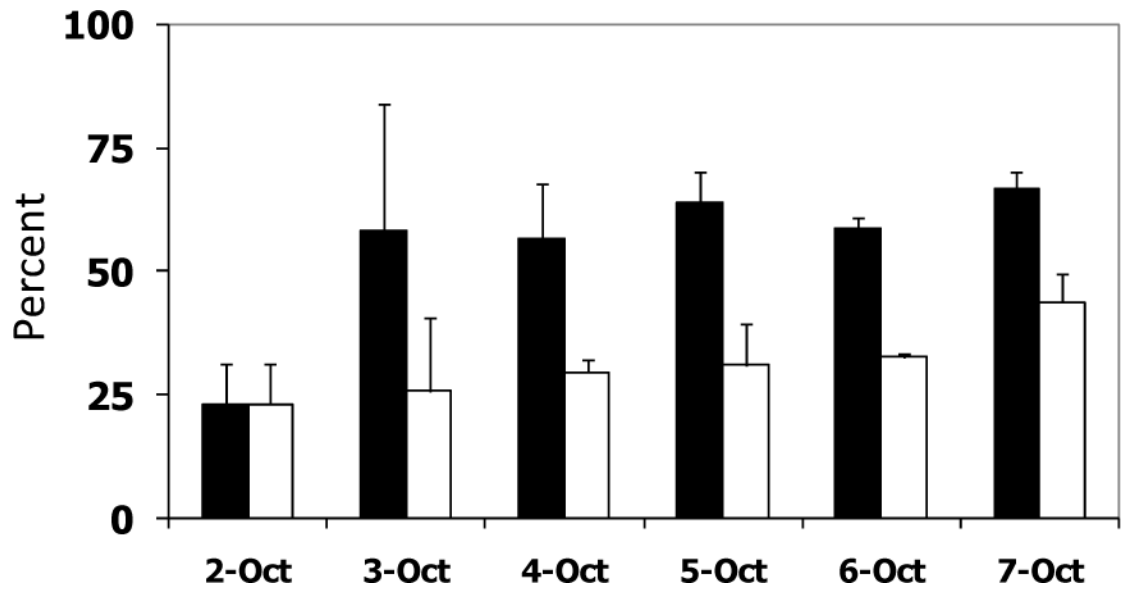


Figure 3. Percent of dinoflagellates in a phytoplankton assemblage inside a *Trichodesmium* bloom (black bars) compared to the percent of dinoflagellates in an adjacent parcel of water outside the bloom (white bars). This time series was for a *Trichodesmium* bloom off of Heron Island, Australia, 1996. The dinoflagellates were dominated by *Dinophysis*. From O'Neil, Glibert, Heil (unpublished).