

# THE ROLE OF EPISODIC ATMOSPHERIC NUTRIENT INPUTS IN THE CHEMICAL AND BIOLOGICAL DYNAMICS OF OCEANIC ECOSYSTEMS

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**A**TMOSPHERIC INPUTS of iron and nitrogen have been hypothesized to play an important role in the chemical and biological dynamics of open-ocean ecosystems (Menzel and Spaeth, 1962; Duce, 1986). This hypothesis has stimulated considerable discussion and controversy (see Martin, 1991, this issue; Miller et al., 1991, this issue; Morel et al., 1991, this issue). Much of this discussion has focused on the relative importance of atmospheric nutrient input rates over large time and space scales, the physiology and chemistry of iron nutrition, the elemental composition of phytoplankton (e.g., Fe/C), and the interpretation of assays for iron limitation of phytoplankton growth at a particular time and place. An interdisciplinary analysis has led to the realization that biological responses of oceanic ecosystems are likely to be dependent not only on biological requirements and the large-scale variability in annual-average atmospheric inputs but also on the temporal and spatial variability of these inputs, on the chemical and biological processes controlling the fate of those inputs, and on the biological, chemical, and physical interactions controlling the dynamics of open-ocean ecosystems receiving those inputs. The results of this interdisciplinary analysis are summarized below.

## Atmospheric Inputs as a Source of New Nutrients

How important is the atmosphere as a source of nutrients? The answer to this question depends on the large-scale variation in annual inputs, the magnitude of that input relative to other sources of nutrients, and the short-term temporal and spatial variability in inputs.

## Large-Scale Distribution of Atmospheric Inputs

Global estimates of the annual input for atmospherically derived mineral matter to the ocean in  $10^\circ \times 10^\circ$  (latitude  $\times$  longitude) areas have been made from measurements of mineral dust in air and rain and from consideration of the wet and dry removal mechanisms for the dust (Duce *et al.*, 1991). Numerous measurements from island sites and ships now enable estimation of the geographic and temporal variability of the atmospheric concentrations and fluxes of mineral matter to the ocean. The atmospheric input of iron to the world ocean (Fig. 1) is derived from these mineral dust measurements. Atmospheric iron input varies spatially by over four orders of magnitude (Fig. 1). The highest inputs occur in the western North Pacific, the Indian, and the Equatorial Atlantic Oceans, with lesser deposition in the regions around Australia and North and South America. The lowest inputs of atmospheric iron occur in the south central Pacific and Southern Ocean.

The importance of the above spatial differences in atmospheric inputs is dependent on the degree that nutrients limit biological production and the magnitude of alternate sources. In general, biological production in surface waters of the ocean is limited by light and the supply of nutrients, including nitrogen and phosphorus (Dugdale, 1967; Eppley, 1981), and possibly metals such as iron (Martin and Fitzwater, 1988; Sunda *et al.*, 1991). For oceanic systems at considerable distance from land or shallow benthic regeneration sites, there are three possible sources of these critical elements (in addition to nitrogen fixation). First, regeneration by zooplankton and bacteria supplies a significant fraction of the nutrients required to maintain primary production in the euphotic zone. Some of these nutrients, however, are removed from the euphotic zone with the gravitational flux of biogenic particles. In order to sustain primary production there must be a supply of "new" nutrients to replace those lost by

Atmospheric iron input varies spatially by over four orders of magnitude.

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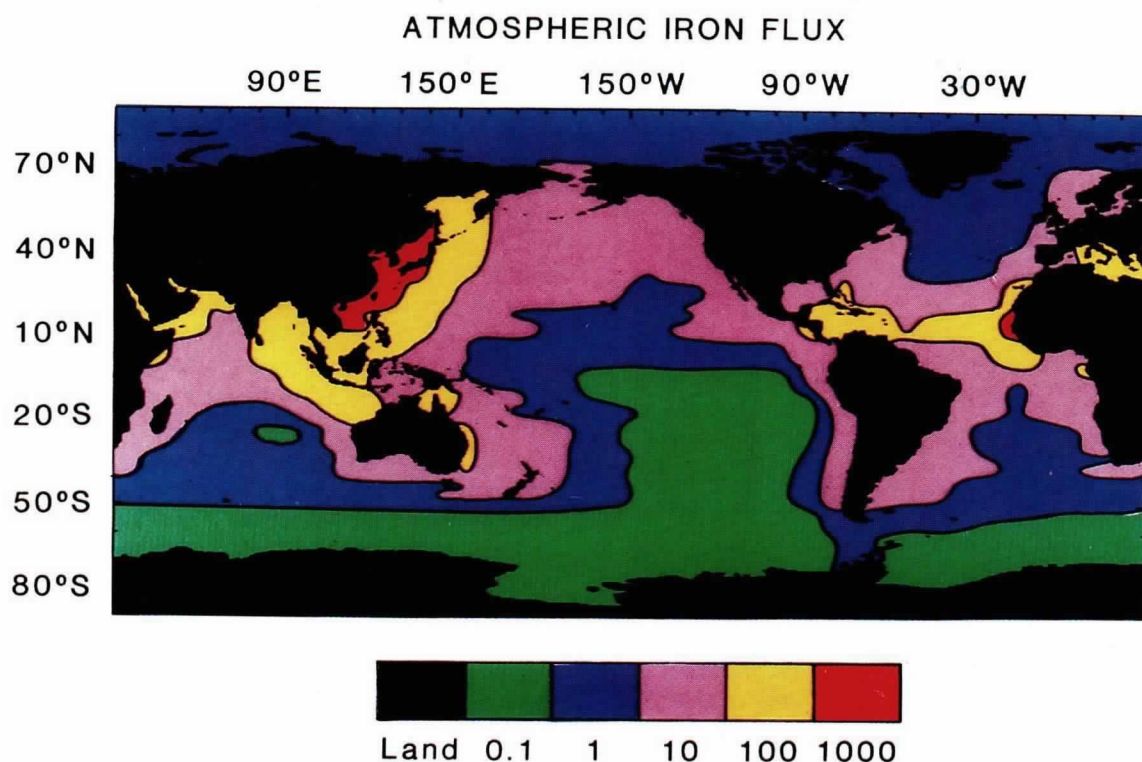


Fig. 1: Regional atmospheric-deposition flux of total iron to the ocean calculated from the atmospheric deposition of mineral matter given in Duce et al. (1991). This calculation assumes that 3.5% of the mineral dust is iron [the average concentrations reported by Taylor and McLennan (1985)].

the particle flux (Dugdale and Goering, 1967). Second, vertical mixing and upwelling processes in the pycnocline can provide an upward flux of new nutrients to the euphotic zone. Finally, atmospheric deposition provides another source of new nutrients (Menzel and Spaeth, 1962; Duce, 1986).

The role of atmospheric inputs as an annual source of new nitrogen, phosphorus, and iron to the euphotic zone has been recently evaluated for the Sargasso Sea and North Pacific Gyre (Duce, 1986). Sources of new nutrients considered were deep waters transported up into the euphotic zone by diffusive and advective processes, atmospheric inputs, and, in the case of nitrogen, in situ fixation by marine organisms. The results for iron and nitrogen, modified by more recent data on dissolved iron concentrations in surface seawater, are shown in Table 1. Despite the uncertainty in these calculations (see Table 1 legend), the atmosphere is clearly the dominant source of new iron in the North Pacific Gyre and Sargasso Sea. The atmosphere is a potentially significant, but not a dominant, source of new nitrogen on yearly time scales in these areas. In contrast, the atmosphere is not a significant source of phosphorus for either region (Duce, 1986). These results indicate that annual variation in atmospheric inputs should have dramatically different impacts on production processes in these regions depending on whether iron, nitrogen, or phosphorus is most limiting.

The average percentages given in Table 1 may

underestimate the importance of atmospheric supply of nitrogen on smaller temporal and spatial scales. The calculations used to obtain the estimates in Table 1 assume that the euphotic zone

Table 1  
Relative strengths of alternative sources for new nitrogen and iron to surface waters of the Sargasso Sea and the North Pacific Gyre\*

Element	Source	Flux, $\text{mmol m}^{-2} \text{yr}^{-1}$	
		Sargasso Sea	North Pacific Gyre
Nitrogen	Vertical advection	0-15	4-8
	Eddy diffusion	8-87	22-266
	Nitrogen fixation	0.2-1.8	0.1-0.7
	Atmospheric deposition	9-20	3-20
	Total	17-114	29-285
	Atmospheric deposition/total	9-71%	1-28%
Iron	Vertical advection	0-0.002	0.0002-0.0004
	Eddy diffusion	0.0007-0.015	0.0004-0.0024
	Atmospheric deposition**	0.07-0.3	0.03-0.6
	Total	0.07-0.32	0.03-0.6
	Atmospheric deposition/total	96-99%	91-99%

\* Adapted from Duce (1986). For iron, the analyses of Duce (1986) were modified with data from Martin and Gordon (1988) and by assuming a dissolved-iron concentration of  $0.1 \text{ nmol kg}^{-1}$  in the Sargasso Sea and North Pacific Gyre. The range of uncertainty in these calculations is indicated by the two values listed (as in Duce, 1986). Recently, hypothesized errors in generally accepted estimates of vertical advection/mixing (Holloway and Muller, 1989) could create several orders of magnitude in additional uncertainty.

\*\* Atmospheric-iron deposition listed here is for the dissolved fraction that is conservatively estimated to be  $\sim 10\%$  of the total (dissolved plus particulate) atmospheric-iron wet deposition.



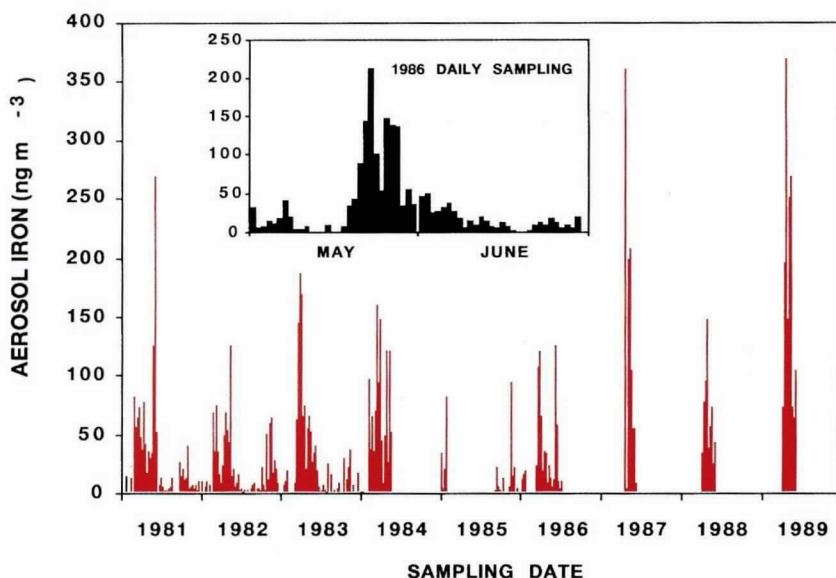


Fig. 2: Variability of atmospheric iron in dust at Midway Island in the North Pacific gyre. Iron concentrations were estimated by multiplying measured aluminum concentrations by the iron to aluminum ratio found in dust. The aluminum data are from Uematsu *et al.* (1985) and Arimoto (personal communication). These data were usually collected at weekly intervals, thus allowing calculation of weekly average aluminum concentrations per cubic meter of air. During May–June 1986, data were collected each day, thus allowing an estimate of variability on a daily time scale (insert). Weekly sampling was nearly continuous from 1981 to the spring of 1984; after that, data were collected during periods of maximum dust levels.

The primary source of atmospheric iron is mineral dust generated in arid desert, semi-desert, and loess regions . . .

is continuously well mixed, and thus all inputs are equally available to all parts of the system. In reality, the euphotic zone in most subtropical oceanic gyres (where nitrogen is usually limiting) is composed of a thin surface layer that mixes on diel frequencies and a deeper layer that is mixed only episodically (Jenkins and Goldman, 1985). In such regions much of the nutrient input from below the pycnocline will be consumed in the deep euphotic layer (Jenkins and Goldman, 1985) and most of the atmospheric input will be consumed in the thin surface layer. This will make the surface-layer euphotic zone far more dependent on atmospheric inputs. Even if the low estimates in Table 1 are the most accurate (as argued by Knap *et al.*, 1986), atmospheric inputs may still be a significant or even dominant source of new nitrogen on smaller temporal and spatial scales.

#### Variability in Atmospheric Input Events

The magnitude and frequency of atmospheric input events depend on the temporal and spatial characteristics of the processes controlling dust injection into the atmosphere, long-range dust transport over the ocean, and deposition of dust into the ocean. The primary source of atmospheric iron is mineral dust generated in arid desert, semi-desert, and loess regions of central and eastern Asia, Africa, Australia, India, and the Arabian peninsula. For example, in eastern Asia local

weather events, such as frontal passages or strong thunderstorms, generate large dust clouds that are carried into the upper levels of the troposphere where the dust is transported out over the North Pacific by strong westerly winds. The dust settles gradually into the lower atmosphere as it moves over the ocean, where some 80% is removed by rain (Uematsu *et al.*, 1985) and the remainder by dry deposition.

Most dust storms in Asia occur in the spring just after the winter snows have melted and when little or no vegetation is present. Fallout from such spring dust events can be observed at island sites in the central Pacific 5–10 days after an event in China. The spring maximum in the dust transport can be seen clearly over a several-year period at Midway Island in the central North Pacific (Fig. 2). Over much of the North Pacific most of the mineral dust (and thus iron) input to the ocean typically takes place during 3–5 events in the spring, each of which lasts 1–3 days. Actual inputs to any given location in the ocean may be even more variable than predicted by the large-scale gradients (Fig. 1) or atmospheric dust levels (Fig. 2). This is because wet deposition requires the co-occurrence of rainfall and of dust or fixed nitrogen in the atmosphere. Because rainfall events vary from small intense storms of a few square kilometers to large frontal systems that stretch for thousands of kilometers, inputs vary on the same spatial scales. Thus, atmospheric inputs are both episodic and spatially patchy.

Phytoplankton responses to input events depend not only on the size of the event but also on the pre-event nutrient concentration, the extent of vertical mixing during the input event, the chemical fate of the added nutrients, and any induced changes in bioavailability of other limiting or toxic elements. In an effort to evaluate the importance of event size and of physical mixing, we have used data sets from the Pacific and Atlantic to calculate expected changes in sea-water concentrations of iron and nitrogen following several types of atmospheric events. In the upper half of Table 2, we have used the time-series data in Fig. 2 to estimate the change in the iron concentration in surface sea water near Midway Island after low-dust, high-dust, and average storm input events during periods of shallow and deep physical mixing. In the lower half of Table 2, we have used the direct daily measurements of iron and nitrogen deposition to calculate expected concentrations of each of these elements in the Sargasso Sea near Bermuda after a similar range of events and mixing conditions. Both sets of calculations indicate that detectable changes will be dominated by a few relatively infrequent large input events that occur during periods of weak to moderate mixing. This conclusion is strengthened by the remarkable similarity of the range for estimated increases in surface nitrogen concentrations at Bermuda (Table 2) as compared with increases measured by

**Table 2**  
Wet deposition and consequential alteration of surface-ocean concentrations in the North Pacific Gyre near Midway Island  
and in the Sargasso Sea near Bermuda

	"Average" Storm Event	"Low-Dust" Storm Event	"High-Dust" Storm Event
Estimated atmospheric wet deposition fluxes at Midway*			
Atmospheric iron ( $\mu\text{g m}^{-3}$ )	0.029	0.0035	0.175
Iron in rain ( $\mu\text{g Fe cm}^{-3}$ )	0.025	0.0029	0.150
Total iron wet deposition flux ( $\mu\text{mol Fe m}^{-2} \text{ d}^{-1}$ )	0.58	1.3	65
Estimated increases in seawater concentrations at Midway* (nmol Fe $\text{kg}^{-1}$ )			
Rainwater mixed to 1 meter			
Dissolved iron	0.06	0.13	6.5
Rainwater mixed to 100 meters			
Dissolved iron	0.0006	0.001	0.065
Measured atmospheric wet deposition fluxes at Bermuda** ( $\mu\text{mol m}^{-2} \text{ event}^{-1}$ )			
Inorganic nitrogen	77	7	860
Total iron	1.7	0.2	4.4
Estimated increases in seawater concentration at Bermuda** (nmol $\text{kg}^{-1}$ )			
Rainwater mixed to 1 meter			
Inorganic nitrogen	77	7	860
Dissolved iron	0.17	0.02	0.44
Rainwater mixed to 100 meters			
Inorganic nitrogen	0.77	0.07	8.60
Dissolved iron	0.0017	0.0002	0.004

\* All estimates were made using the equations described by Duce (1986) and assuming atmospheric dust contains 3.5% Fe, a rain scavenging ratio of 1000 (Arimoto et al., 1985), and that a conservative 10% of the atmospheric iron in rainwater is readily dissolved in seawater (Duce, 1986). "Average" Storm Event estimates are based on the co-occurrence of average annual atmospheric-dust concentrations and average annual daily rainfall at Midway in 1981 (Uematsu et al., 1985). "Low-Dust" Storm Event estimates are based on the co-occurrence of a 2.5-cm rainfall with average nonpeak dust concentrations observed at Midway. "High-Dust" Storm Event estimates are based on co-occurrence of a 2.5-cm rainfall with high dust levels observed in the spring at Midway. The higher expected iron concentrations in the "Low-Dust" case than in the "Average" case is a direct reflection of the higher rainfall assumed in the "Low-Dust" case (2.5 versus 0.13 cm).

\*\* Data for nitrogen from Bermuda rainwater analysis of  $\text{NO}_3^-$  plus  $\text{NH}_4^+$  in samples collected from September 1982 to May 1984 (Knap et al., 1986); data for iron from rainwater samples collected from November 1981 to October 1982 (Jickells et al., 1984). Iron fluxes agree well with measurements of Lim and Jickells (1990).

Menzel and Spaeth (1962) in the same area after storms. These large atmospheric input events can cause several order-of-magnitude increases in both iron and nitrogen concentrations. As a result, in situ biological responses to atmospheric inputs may reflect changes in the bioavailability of iron and/or nitrogen.

### Chemical and Biological Fate of Atmospheric Inputs

What is the fate of the nutrients in the atmospheric material once it enters the ocean? The answer to this question is simple for nitrogen because most of the input is in the form of nitrate or ammonium that can be readily used by phytoplankton. This question is more difficult to answer for iron present in mineral particles because only truly dissolved forms of iron appear to be taken up and used by phytoplankton (Wells et al., 1983; Rich and Morel, 1990; Morel et al., 1991, this issue). It is also made difficult by critical gaps in our understanding of the underlying chemistry.

#### Aerosol Dissolution

The surface-layer retention and potential availability of iron from atmospheric particles is partly controlled by the rate of aerosol dissolution in sea water. The magnitude of this dissolution has been estimated conservatively at 10% for mineral iron (Moore et al., 1984; Duce, 1986), but as much as 40–60% of the atmospheric iron

can apparently dissolve in a few minutes when the total iron concentration in sea water is very low (i.e., less than a few nmol  $\text{kg}^{-1}$ ) (Zhuang et al., 1990). These higher estimates were obtained by transferring samples of mineral aerosols collected over the mid-North Pacific Ocean into stirred aliquots of aged filtered open-ocean seawater, then determining changes in the concentration of iron in the filtrate that passed through 0.45- $\mu\text{m}$  pore size filters. Some caution must be exercised in assuming that all this iron is bioavailable, because the iron present in the filtrate may include dissolved iron plus submicrometer colloidal iron oxides. This rapid conversion to dissolved and colloidal iron is extremely important, because it indicates that a major portion of the aerosol iron may be retained in the euphotic zone rather than settling into deeper waters.

Zhuang et al. (1990) hypothesized that the rapid dissolution of a significant fraction of the aerosol iron depends on chemical alteration of the mineral particles during atmospheric transport from their source regions. Andreae (1986) found that individual aerosol particles over the ocean are often a mixture of mineral, sea salt, and acidic sulfate aerosols. It is likely that these mixed aerosols form as a result of coalescence within clouds, with subsequent evaporation of the cloud droplets. The result is acidic hygroscopic aerosol particles in which partial dissolution occurs during atmo-

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spheric transport (Winchester and Wang, 1990). Significant concentrations of Fe(II), formed by photoreduction of Fe(III), have been observed in atmospheric samples in urban areas (Behra and Sigg, 1990) and over the remote North Pacific (Zhuang, 1991). Thus, aerosols can be rich in labile forms of Fe(III) and/or Fe(II) when the aerosol particles enter the ocean (Duce and Tindale, 1991).

#### *Fate of Atmospheric Iron in Surface Waters*

Once the atmospheric iron enters surface seawater, the chemical form of the dissolved iron may be altered, thus changing its solubility, retention in the euphotic zone, and bioavailability. The chemical speciation of iron in seawater is an important unresolved question in marine chemistry. Some of the most important forms and processes

are summarized in the conceptual model shown in Fig. 3. Iron can exist in seawater in two oxidation states [Fe(II) and Fe(III)], as various dissolved chemical species [e.g.,  $\text{Fe}^{+3}$ ,  $\text{Fe}(\text{OH})^{+2}$ ,  $\text{Fe}(\text{OH})_2^+$ ,  $\text{Fe}(\text{OH})_3^0$ ,  $\text{Fe}^{+2}$ ,  $\text{FeOH}^+$ ,  $\text{Fe}(\text{OH})_2^0$ ,  $\text{FeCl}^+$ ,  $\text{FeSO}_4^0$ , and  $\text{FeCO}_3^0$ ], in multiple colloidal forms with different reactivities, and in a variety of particulate forms ranging from inorganic iron colloids to iron in or adsorbed onto bacteria, plankton, detritus, and mineral particles. In oxygenated seawater at pH near 8, the thermodynamically stable oxidation state of iron is Fe(III) (Kester, 1986). Aerosol Fe(II) inputs should be oxidized rapidly (within a few minutes) to Fe(III), a form that has extremely low solubility in seawater ( $K_{sp} = 10^{-38}$ ) and precipitates as amorphous colloidal hydrous oxides (Byrne and Kester, 1976). Hydrous iron oxides have surface-active properties that allow the adsorption of organic substances and other trace-metal ions from solution. Hydrous iron oxides may coagulate or they may be adsorbed or incorporated into larger particles, resulting in size distributions that range from colloidal particles that will pass through a  $0.4\text{-}\mu\text{m}$  filter up to sizes that can settle from the system. These chemical processes tend to limit the concentrations of dissolved iron in oceanic waters to  $<1\text{ nmol kg}^{-1}$ .

Although bioavailable iron may represent a small fraction of the total iron in seawater, a variety of microbial and chemical processes may result in exchange between bioavailable and non-bioavailable forms (Fig. 3). Some possible mechanisms for increased dissolved iron availability in seawater include the following: 1) photochemical production of dissolved Fe(II) (Hong and Kester, 1986; O'Sullivan *et al.*, 1991); 2) the reductive photodissolution of colloidal iron oxides followed by immediate oxidation and reprecipitation of more soluble, faster dissolving, amorphous iron oxides on the colloidal surface (Waite and Morel, 1984; Morel *et al.*, 1991, this issue); 3) thermal dissolution of colloidal iron oxides (Wells *et al.*, 1983); 4) microbial reduction (Jones *et al.*, 1982) or remineralization of iron oxides; and 5) complexation by dissolved organic ligands (Kester, 1986).

Atmospheric inputs of iron can be expected to interact with the chemical pathways discussed above (solubilization, redox cycling, colloid formation) in several ways that depend significantly on the size of the input and its initial dilution by physical processes. From a chemical perspective, small inputs under all mixing conditions and intermediate inputs during strong mixing periods will produce in situ changes in dissolved iron that are analytically difficult to detect (Table 2). In contrast, large inputs during physically quiescent periods will not only be detectable but may result in precipitation of colloidal Fe(III). Such a process would put an upper limit on the potential increases in bioavailable iron and may coprecipitate

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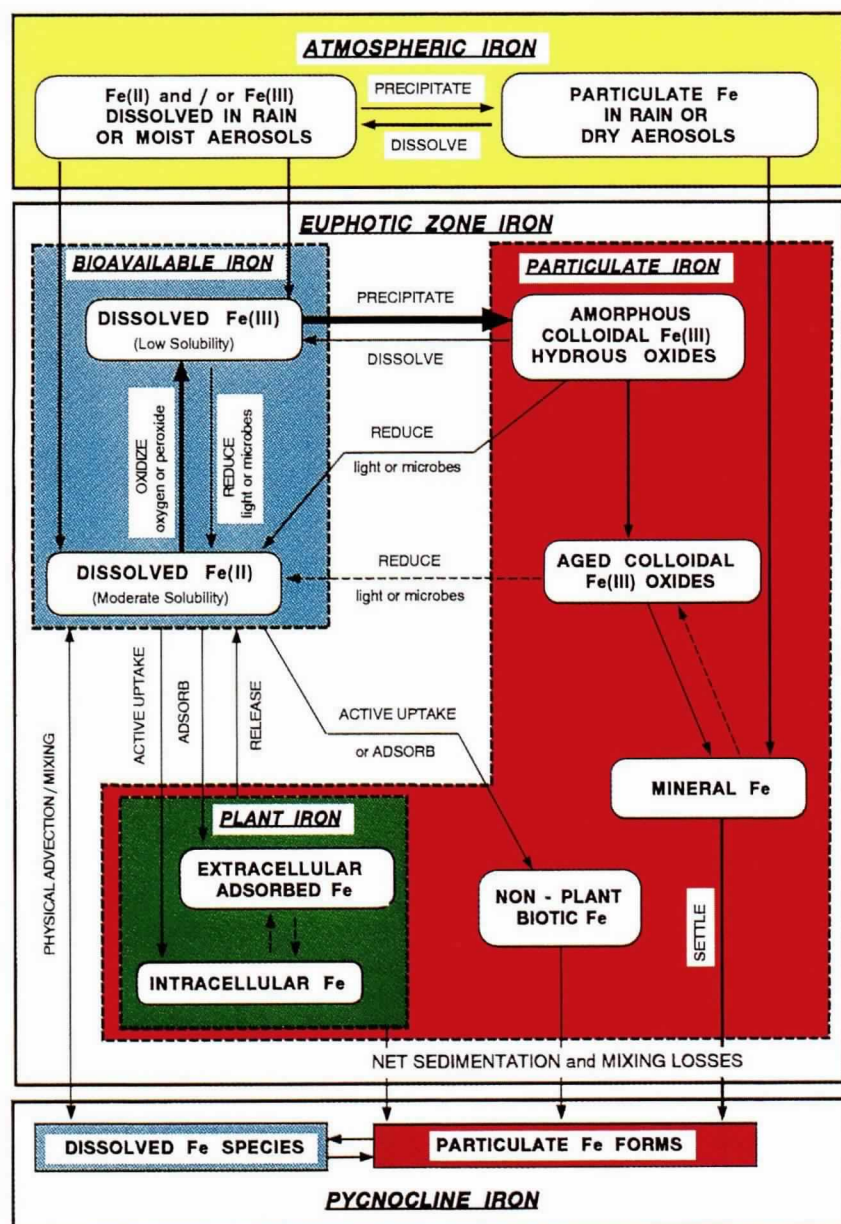


Fig. 3: Potential reservoirs, pathways, and processes controlling iron in the surface ocean.



other trace metals from the system. Thus, the bioavailability of other trace metals may depend not only on their own input rates and redox chemistry but also on that of iron. Another important effect of these chemical processes will be to increase the duration but reduce the size of the immediate increase in bioavailable iron. The magnitude of these buffering effects is poorly known but almost certainly important.

The chemical and biological processes controlling iron remineralization may influence strongly bioavailability and the temporal scales of biological responses. The concentration of bioavailable iron is also influenced by the rate and extent that iron taken up by organisms is recycled when those organisms are eaten or die. Such recycling has long been recognized to play a dominant role in controlling primary production in nitrogen limited oligotrophic gyres of the ocean (Eppley *et al.*, 1976). As a result of both iron redox chemistry and recycling, it seems likely that a significant fraction of the aerosol iron entering the dissolved pool during an input event will be re-partitioned into nonbioavailable forms that are slowly rereleased after the event. This release will tend to lengthen the time scale of any biological response and to provide a source of iron to support primary-production processes during periods between events.

### Ecosystem Responses to Episodic Nutrient Inputs

What will be the effect of an input event on phytoplankton and zooplankton productivity, biomass, and composition? It is tempting to suggest that the answer would be an increase in plankton production and biomass (assuming the event increased the bioavailability of a limiting nutrient). However, there is growing evidence that the biomass response also depends on the importance of grazing and predation by higher trophic levels, the temporal and spatial extent of the input event, and the magnitude of physical mixing and shearing processes during and after the event. Each of these factors will be considered in sequence below.

### Regulation by Resources and Higher Trophic Levels

The three major types of phytoplankton response are summarized in Fig. 4. If iron or nitrogen were not limiting the growth of any phytoplankton species in a given system, no changes should be observed in primary production, biomass, species composition, or sedimentation rates (left column, Fig. 4). This, of course, assumes that the input event is not associated with changes in other factors that control plankton dynamics. However, if iron or nitrogen does limit phytoplankton growth rates, two very different responses might occur, depending on the importance of grazing processes in controlling phytoplankton biomass and species composition. If

grazing by micro- and macrozooplankton is not important, then addition of the limiting nutrient should increase primary production and phytoplankton biomass (center column, Fig. 4). Increased vertical sedimentation fluxes to deep waters might occur as the added nutrient is depleted, but the magnitude and timing of such changes would depend on the species of phytoplankton that bloom. Recent experiments indicate differences in the degree of nutrient limitation between phytoplankton species may be large enough to induce shifts in composition (Martin and Gordon,

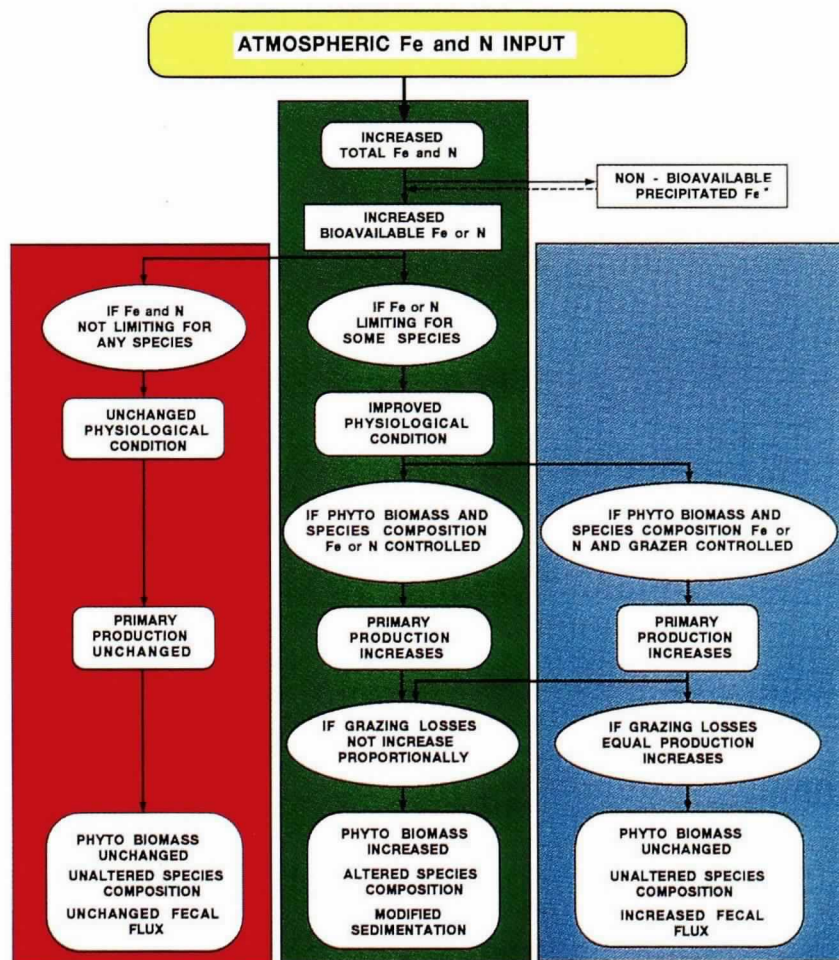


Fig. 4: Control diagram of potential phytoplankton responses to an atmospheric-nutrient input event to the surface ocean. These diagrams contain three elements: (1) an initial perturbation at the top of the diagram (atmospheric iron or nitrogen input for phytoplankton or food resource changes for zooplankton); (2) a series of sequential "if statements" to define critical alternatives (contained in ellipses in the figures); and (3) primary organism or system responses. These primary responses are divided further into those that can be measured directly in the field (rectangles with rounded corners) and those that are difficult or impossible to measure accurately in the ocean (rectangles with square corners). We assume in this figure that bioavailability of ambient trace metals (other than iron) is such that atmospheric inputs will not elicit a toxic biological response. If phytoplankton growth is suppressed by ambient toxic trace metals, then removal of these metals by co-precipitation with iron may lead to biological responses similar to those of an iron-limited population. \*The term "non-bioavailable" is particularly relevant to iron (Fig. 3), but may also apply to low levels of organic nitrogen found in atmospheric inputs (Knap *et al.*, 1986).



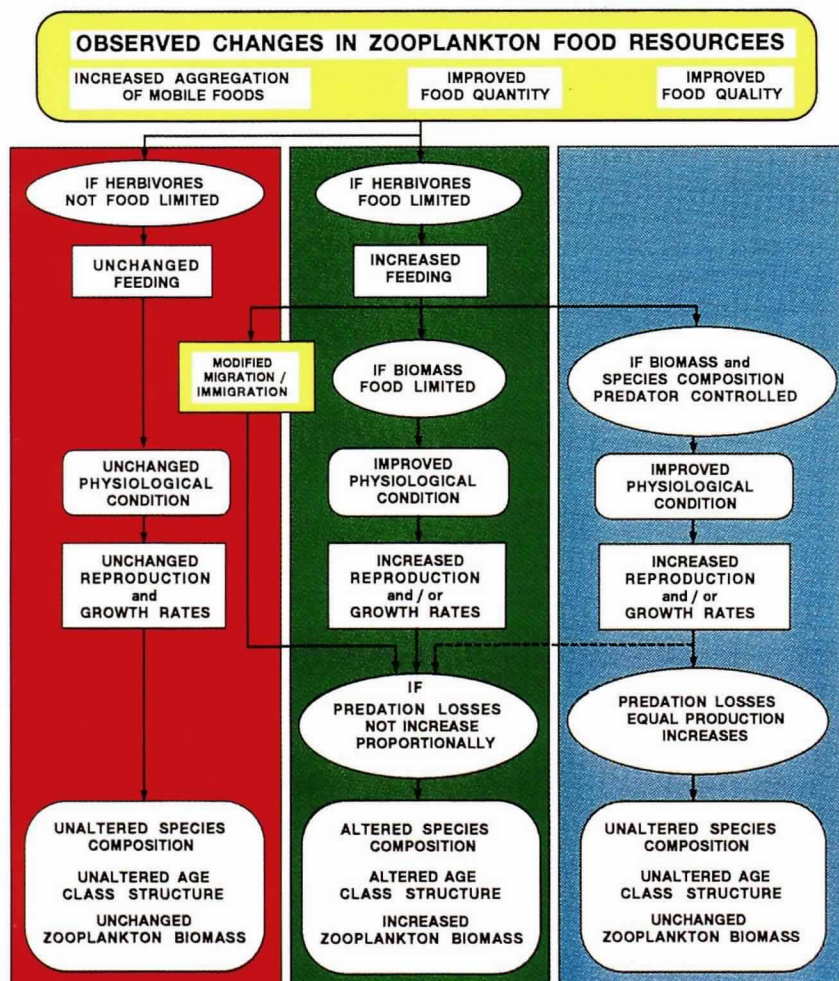


Fig. 5. Control diagram of potential zooplankton responses to changes in food resources caused by an atmospheric-nutrient input event to the surface ocean in a region where either iron or nitrogen are limiting. Control diagram elements are as defined in Figure 4 caption. The term zooplankton refers to both micro- and macrozooplankton although specific pathways may vary in importance for these two groups.

Episodic atmospheric inputs provide an important alternative source of new nutrients to stimulate ... patchiness.

1988; Morel *et al.*, 1991, this issue). However, if grazing processes are sufficient to balance exactly increases in the growth rates of all phytoplankton species (as argued by Miller *et al.*, 1991 this issue), no changes would be observed in phytoplankton abundance or composition, despite increases in growth rates and physiological condition of individual species (right column, Fig. 4). Toggweiler (1990) has used a similar biological model to suggest that a combination of grazing and high nutrient inputs from upwelling may explain the excess nutrients in the equatorial Pacific. Although a strong case can be made for such a grazing-dominated response in the subarctic Pacific (Miller *et al.*, 1991, this issue), the phytoplankton blooms that frequently follow nutrient input events in temperate and subtropical waters indicate that there are many cases where increases in grazing losses are insufficient to balance growth increases for all species (Donaghay, 1988). As a result, grazer control and iron limitation must be viewed as viable alternative explanations for excess

nutrients in the tropical Pacific until experiments are conducted to test both hypotheses rigorously.

The magnitude of the zooplankton response will depend on the extent and nature of the changes in phytoplankton, the degree to which zooplankton are food limited, the rate at which zooplankton can respond to changing resources, and the degree to which zooplankton biomass and species composition are regulated by predation from higher trophic levels (Fig. 5). If the zooplankton are not food limited, then zooplankton feeding, physiological condition, growth rates, and reproduction should remain unchanged and should result in unaltered species composition, age-class structure, and biomass (left column, Fig. 5). However, if zooplankton are limited by the quantity, quality, or spatial distribution of food, then changes in these parameters induced by atmospheric inputs should alter feeding, improve physiological condition, and increase reproduction and/or growth rates. The extent to which these changes are reflected by changes in species composition, age-class structure, and biomass will depend on the temporal scale of the phytoplankton response, the rate zooplankton can respond to changes in food (Donaghay, 1988), and the importance of predation in controlling these variables (center versus right column, Fig. 5). As with phytoplankton, higher trophic level effects may totally or partially mask the effects of improved food.

#### Patch Induction and Biological-Physical Interactions

Spatial aggregations or patches of phytoplankton and zooplankton have long been recognized as a major characteristic of oceanic ecosystems (Hardy and Gunther, 1935; Haury *et al.*, 1978). One explanation for these patches is that they reflect a response of phytoplankton growth rate and biomass to spatial and temporal heterogeneity of new nutrient inputs from below the pycnocline into surface waters. For example, phytoplankton patches can be interpreted to represent the product of recent episodic inputs, whereas zooplankton patches can be interpreted as older events that have stimulated phytoplankton, and then in situ zooplankton productivity. Episodic atmospheric inputs provide an important alternative source of new nutrients to stimulate such patchiness.

The temporal and spatial scale of the input event can be expected to influence strongly both the magnitude and mechanisms of zooplankton patch induction. Increases in zooplankton biomass from in situ growth should occur first in the rapidly growing microzooplankton, then in the slower growing macrozooplankton. Zooplankton patches also can be formed by immigration (Fig. 5). Interactions of vertical migration and vertical current shear in the ocean have been hypothesized as an important mechanism for the formation and dispersal of zooplankton patches (Hardy and

Gunther, 1935; Haury *et al.*, 1978; Steele, 1978). Immigration could be an important process if vertically migrating macrozooplankton respond to a phytoplankton patch by not migrating down to levels where currents can carry them away from the patch. Such immigration should be particularly important for increases of relatively slow growing macrozooplankton in submesoscale inputs. Blooms in such patches should be too brief for multiple generations of macrozooplankton, yet small enough to allow aggregation of zooplankton from larger areas.

The temporal and spatial scale of input-induced patches can depend on the physical regime during and after the input event. Vigorous mixing of the surface layer during the input event will increase initial dispersal of the iron and nitrogen both horizontally and vertically. This increased dispersal will reduce the magnitude of any biological response but increase its aerial extent. The intensity of surface-layer mixing and current shear after an input event will control the rate at which the resulting chemical and biological patch remains intact and spreads horizontally. As long as mixing is isotropic, the patch will remain coherent and spread horizontally at a decreasing rate with increasing size as defined by the ocean diffusion diagrams of Okubo (1971). As a result, larger patches will tend to persist longer, thus allowing more time for biotic responses to lead to detectable biomass differences (Haury *et al.*, 1978). However, if mixing is anisotropic (i.e., associated with strong vertical or horizontal shear), even large patches will tend to fragment into filaments and smaller patches (Okubo, 1971; Garrett, 1983). Work with patches of conservative tracers has shown that although coherent patches can persist for >10 days in isotropically mixed systems (Watson *et al.*, 1991), shear-induced filamenting in anisotropic systems can make patch tracking and in situ detection of chemical and biological effects extremely difficult (Garrett, 1983; Watson *et al.*, 1987). These results indicate that persistence of the nutrient patch and therefore, the temporal and spatial extent of biotic responses will depend on the match of the time scales for biological and chemical responses to the time scales of physical processes controlling the coherence of the patch.

### Future Directions

Atmospheric inputs of iron and nitrogen occur on a diversity of flux, time, and space scales. This diversity of scales leads to a diversity of potential chemical and biological responses to individual input events. Our preliminary analysis suggests that this range of responses extends from undetectable changes in chemical concentrations (and presumably biological responses) to relatively rare large events with easily detectable chemical signatures. The temporal persistence of such signatures depends on the chemical and biological fate of the nutrients from the atmosphere and on the

magnitude of physical dispersion. Similarly, the in situ biological response depends not only on the magnitude of the input event and the degree of limitation of primary production by the nutrient but also on the degree to which higher trophic levels limit the expression of changes in physiological condition as changes in biomass and composition. Regrettably, our understanding of these control mechanisms is extremely limited in many of the oceanic systems potentially affected by atmospheric inputs (for an exception, see Miller *et al.*, 1991, this issue). Hence, future interdisciplinary studies designed to test hypothesized effects of atmospheric inputs in these systems represent both a challenge and an opportunity to expand our understanding of the interactions of physical, chemical, and biological processes controlling open-ocean ecosystems.

An important component of such future studies will be efforts to examine directly episodic atmospheric-nutrient input events, either by following small (1–20 km) natural patches created by atmospheric input events or by creating such patches by artificial addition of the appropriate nutrients. A critical challenge of both approaches will be to identify control areas and separate the patchiness induced by the input event from the inherently patchy character of the oceanic environment. One promising approach to this problem is to use natural (Donaghay *et al.*, 1987) or artificial (Watson *et al.*, 1991) conservative tracers of the input event to follow the patch in time and space. Such tracer techniques also are essential to separating in situ biological and chemical responses from the effects of physical mixing and shearing. The success of such efforts will depend heavily on selecting sites where the combination of strong nutrient limitation and reduced physical dispersion/shearing maximize the magnitude and persistence of chemical and biological responses to the input event. The success of such experiments also will depend critically on measuring chemical and biological factors and processes (see Figs. 3–5) that provide unambiguous tests of the alternative hypotheses.

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**A**tmospheric inputs of iron and nitrogen occur on a diversity of flux, time, and space scales.



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