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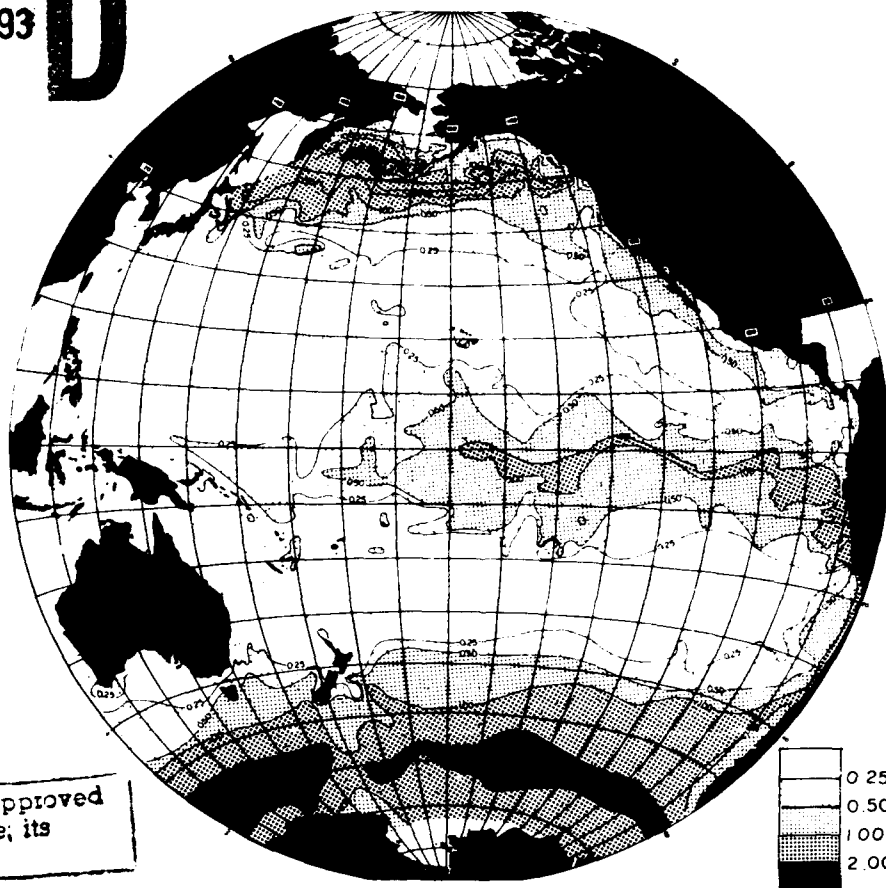
REPORT

AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY SYMPOSIUM

WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

February 22-24, 1991  
San Marcos, California

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Distribution of inorganic phosphate-phosphorus ( $\mu\text{g-at/l}$ ) at the surface of the Pacific Ocean (Reid, J.L., 1962).

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AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY

SYMPOSIUM REPORT:

# WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

February 22-24, 1991  
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The figure on the front cover first appeared in Reid, J.L., 1962. On the circulation, the phosphate-phosphorus content, and the zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr.* 7(3): 287-306.

## ACKNOWLEDGEMENTS

The symposium on "What Controls Phytoplankton Production in Nutrient-Rich Areas of the Open Sea?" was organized by the American Society of Limnology and Oceanography, through a Program Steering Committee composed of **Sallie W. Chisholm** (Co-Chair), Massachusetts Institute of Technology; **John J. Cullen** (Co-Chair), Bigelow Laboratory for Ocean Sciences; **Karl Banse**, University of Washington; **Bruce W. Frost**, University of Washington; **John H. Martin**, Moss Landing Marine Laboratory; **Diane M. McKnight**, United States Geological Survey; **Trevor Platt** (ex officio), Bedford Institute of Oceanography; and **C. Susan Weiler** (ex officio), Whitman College.

The consensus statement was developed by **Sallie W. Chisholm**, Massachusetts Institute of Technology; **John J. Cullen**, Bigelow Laboratory for Ocean Sciences; **Richard T. Barber**, Duke University; **Ann E. Gargett**, Institute of Ocean Sciences, Sidney; **John T. Lehman**, University of Michigan; **James J. McCarthy**, Harvard University; **James J. Morgan**, California Institute of Technology; **Barbara B. Prézelin**, University of California, Santa Barbara; **William G. Sunda**, U.S. Office of Naval Research; and **T. David Waite**, Australian Nuclear Science & Technology Organization.

This report was compiled by C. Susan Weiler, June 25, 1991.

The symposium and resulting publications would not have been possible without the early expression of interest and encouragement provided by Henry A. Walker of the U.S. Environmental Protection Agency's Environmental Research Laboratory in Narragansett, Rhode Island.

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## INTRODUCTION

The oceans play a critical role in regulating the global carbon cycle. Deep-ocean waters are roughly 200% supersaturated with CO<sub>2</sub> compared to surface waters, which are in contact with the atmosphere. This difference is due to the flux of photosynthetically derived organic material from surface to deep waters and its subsequent remineralization, i.e. the "biological pump". The pump is a complex phytoplankton-based ecosystem. It is driven by sunlight, and fueled by the supply of inorganic nutrients derived primarily from the deep ocean. In areas of the oceans where inorganic N and P are effectively exhausted by phytoplankton in surface waters during the growing season, the pump functions at maximal efficiency: The transport of carbon to depth is limited by the flux of N and P into the surface waters. In the Southern Ocean, near the equator, and in the subarctic Pacific, however, relatively high concentrations of nitrate and phosphate are found in the surface waters throughout the year, and phytoplankton biomass and net production are much lower than would be expected based on the availability of major nutrients. Thus in these areas of the oceans the biological pump appears to be operating at less than maximal efficiency. Consequently, these regions are receiving increased attention, not only as they relate to global biogeochemical cycles, but also as potential sites for anthropogenic enhancement of CO<sub>2</sub> flux into the ocean.

The paradoxical nature of ocean regions containing high nutrients and low phytoplankton populations has intrigued biological oceanographers for many years. Hypotheses to explain the paradox include the regulation of productivity by light, temperature, zooplankton grazing, and trace metal limitation and/or toxicity. To date, none of the hypotheses, or combinations thereof, has emerged as a widely accepted explanation for why the nitrogen and phosphorus are not depleted in these regions of the oceans. Recently, new evidence has emerged which supports the hypothesis that iron limitation regulates primary production in these areas. This has stimulated discussions of the feasibility of fertilizing parts the Southern Ocean with iron, and thus sequestering additional atmospheric CO<sub>2</sub> in the deep oceans, where it would remain over the next few centuries. The economic, social, and ethical concerns surrounding such a proposition, along with the outstanding scientific issues, call for rigorous discussion and debate on the regulation of productivity in these regions.

To this end, The American Society of Limnology and Oceanography (ASLO) held a Special Symposium on the topic at the Lake San Marcos Resort and Conference Center on Feb. 22- 24th, 1991. A total of 145 individuals attended the full symposium, and another six were present for one day. Participants included leading authorities, from the U.S. and abroad, on physical, chemical, and biological oceanography, plant physiology, microbiology, and trace metal chemistry. Representatives from government agencies and industry were also present.

## ***SYMPOSIUM SCOPE***

The three-day symposium addressed the general question of the role of the "biological pump" in the global carbon cycle, and the regulation of the pump in areas of the oceans where N and P are in excess, i.e. the subarctic and equatorial Pacific, and the Southern Ocean. A physical, chemical, and biological characterization of these areas of the oceans was presented, along with existing uncertainties in the global carbon budget and the role of the biota in models of this budget. Changes in the global CO<sub>2</sub> cycle over geological time scales, and hypothesized causes for the changes, were analyzed to provide a perspective and foundation for discussion.

The evidence in support of the various hypotheses for the regulation of productivity in the N- and P-rich oceans was presented and discussed. Particular attention was given to the "iron hypothesis" because of the unique set of concerns surrounding it, but alternate hypotheses and interpretations were also addressed at length.

Much of the last day of the symposium was devoted to discussing the feasibility and advisability of fertilizing large regions of the Southern Ocean with iron with the hope of mitigating the increase of atmospheric CO<sub>2</sub> and associated climate change. It was assumed, for the sake of discussion, that iron fertilization would allow the phytoplankton to completely utilize the excess N and P in these regions. Model analyses which estimate the amount of carbon that could, in theory, be drawn out of the atmosphere as a result of fertilization were presented and discussed. The discussion explored the potential effects on the food web, the influence on other areas of the oceans and atmosphere, and the time scale of change. Our confidence in our ability to predict consequences of such intervention from our current understanding of the ecology of aquatic ecosystems was discussed, and recommendations for the future were formulated.

The following statement, which was drafted by a subset of symposium participants charged with the task, reflects the general outcome of the meeting.

## ***CONSENSUS STATEMENT***

### **Introduction**

There is mounting concern over recent increases in concentrations of "greenhouse" gases in the Earth's atmosphere, and their potential consequences on global climate. Slowing the rate of increase of these gases will be difficult. Because of the multiple sources and complex fates of these compounds, a single significant solution to this problem is unlikely. Alternative technologies, such as the development and use of non-fossil fuel energy sources in developing and developed countries alike, should be pursued vigorously along with stringent conservation measures. Unfortunately, however, the time required to implement new technology, once developed, will be decades. Projections based upon current gas emissions, and trends in population growth and economic development, leave no doubt that all possible means of reducing the concentrations of greenhouse gases in the Earth's atmosphere must be given immediate and serious consideration. These include more efficient uses of

available energy, and enlightened management and stewardship of the natural sources and sinks for these compounds.

### **Potential Impact of Iron Fertilization**

The oceans play a critical role in the global carbon cycle, and it has been suggested that regions of the ocean with an excess supply of nitrogen and phosphorus, such as the Southern Ocean, could be fertilized with iron to sequester atmospheric CO<sub>2</sub>. Model calculations presently suggest that if iron fertilization of nutrient-rich seas succeeded in stimulating complete assimilation of nutrients, and was continued for the next 100 years, the buildup of CO<sub>2</sub> in the atmosphere (assuming the "business as usual" emissions scenario) could be reduced by 17 to 25%. We must consider, however, that the current generation of models may not have quantitative ability; they do not include a variety of important processes such as light limitation and zooplankton grazing, which could limit nutrient uptake long before nutrients are completely depleted.

Moreover, little if anything is known about the potential adverse effects such fertilization would have on marine ecosystem structure and function. For example, recent experiments have shown that iron enrichments to plankton communities enclosed in bottles can cause dramatic changes in phytoplankton species composition. If these types of changes were triggered on a larger scale, they would propagate through the food web causing major changes at the higher trophic levels. In addition, model simulations reveal the potential for other large-scale consequences of fertilization. The fertility of other regions of the world's oceans could be diminished if nutrients presently being supplied have been redistributed. The stimulation of production would also accelerate the nitrogen cycle, possibly increasing nitrous oxide release into the atmosphere. Moreover, large regions of the deep ocean could become anoxic as a result of increased productivity in the Southern Ocean. Deep-ocean anoxia would stimulate the production of methane which, like nitrous oxide, is a much more powerful greenhouse gas than CO<sub>2</sub>.

### **Evidence for Iron Limitation of Nutrient-Rich Seas**

Thus, based upon our current understanding of the regulation of productivity in nutrient-rich seas, we believe that massive iron fertilization of the Southern Ocean to mitigate greenhouse warming is unwarranted; the potential gains are small relative to unknown, perhaps large, risks. Nevertheless, a majority of the scientists assembled by ASLO to discuss this issue are convinced that sufficient evidence exists in support of the hypothesis that iron plays an important role in regulating the productivity and trophic structure of planktonic communities to warrant increased efforts to explore this hypothesis.

The evidence is as follows:

- ◆ All of the high-nutrient low chlorophyll areas of the oceans are regions with low eolian inputs of iron.
- ◆ Data from the Vostok ice cores reveal that during glacial times, when atmospheric CO<sub>2</sub> concentrations were lower than at present, the iron-rich atmospheric dust loads were 50 times higher than

during past and present interglacial periods, which suggests that this "natural" fertilization with iron might have resulted in increased phytoplankton production and consequent reduction in atmospheric CO<sub>2</sub>.

- ◆ Addition of small amounts of iron to plankton communities enclosed in bottles stimulates the net rate of particulate chlorophyll, carbon, and nitrogen production and in addition, changes the phytoplankton community composition. We note, however, that the magnitude of biomass increase might not be achieved in the presence of the large grazers, which are *de facto* excluded from such bottle experiments.
- ◆ Iron additions have been shown to cause a shift in the nitrogen utilization patterns of the phytoplankton from ammonium to nitrate, presumably because iron is required for nitrate reduction.
- ◆ Marine algal species exhibit wide differences in their growth requirements for iron, which closely match the differences in iron levels in the waters from which the species were isolated. This suggests that iron availability is an important agent of natural selection in the oceans.

Although the collected evidence is compelling, it has not yet been demonstrated that iron enrichment stimulates the specific growth rate (as opposed to final yield) of phytoplankton species in bottle experiments. Moreover, we have no way of predicting, at present, whether iron enrichment in the presence of the entire food web would result in increased net community production (i.e. carbon that would ultimately be sequestered in the deep ocean). The first of these questions can be addressed through bottle experiments, because the answer is independent of grazing pressure. The second, however, could only be addressed through an unenclosed enrichment experiment in the ocean.

### **Recommendations for Future Research**

Because iron is required in trace amounts by phytoplankton (C:Fe ratios in cultures range from 30,000 to 500,000) it is theoretically possible to carry out moderate-scale enrichment experiments with this element in areas of the oceans where it is hypothesized to limit plankton production. The power of this type of experimental manipulation of natural systems has been amply demonstrated by limnologists in their studies of the conditions that control productivity and food web dynamics in lakes.

Nutrient-rich seas that have very low *in situ* iron concentrations and very low rates of atmospheric iron input provide the perfect natural setting for such an experiment. The challenge, though, is not simply to demonstrate that iron limitation of phytoplankton production in these regions could be artificially alleviated, but to determine the implications of such increased productivity for carbon sequestration in the deep ocean. As described above, without a full study of the effect on planktonic food web dynamics, there is no assurance that an increase in productivity would result in a greater storage of carbon in the ocean.

It is important, therefore, that we examine this hypothesis in depth, and consider designing a modestly scaled iron-enrichment experiment in a high-nutrient region of the open sea. The scale of

the experiment must be both large enough to analyze planktonic food web dynamics, but small enough to avoid any long-term environmental impact. Such an experiment would not only yield insights into the role of iron in regulating productivity in these areas, but would also shed light on unresolved issues regarding the roles of light, macronutrients, and grazing pressure on regulating phytoplankton production in these and other marine ecosystems.

It was the view of the assembled group that several research directions should be pursued before implementation of an open-ocean iron-enrichment experiment would be justified. These include:

- ◆ Bottle experiments in which the specific growth rates of individual species of phytoplankton are measured in response to iron additions.
- ◆ Studies of iron-speciation chemistry in seawater, along with the chemical and photochemical processes that control that chemistry.
- ◆ Determination of the factors and mechanisms that regulate the acquisition of iron by marine plankton, including the possible role of siderophores in microbial iron uptake.
- ◆ Studies of the comparative physiology and biochemistry of iron utilization in phytoplankton isolated from coastal, oligotrophic, and nutrient-rich oceanic ecosystems.
- ◆ Development of physiological and biochemical indicators to diagnose the nutrient status of algal populations and communities *in situ*.
- ◆ Determination of the relative importance of eolian and *in situ* (e.g. upwelling) sources of iron to the euphotic zone in different oceanic regions, and examination of the relationship between iron supply and macronutrient utilization in the world's oceans.
- ◆ Studies of nutrient-rich oceanic regions that receive periodic eolian inputs of iron, or areas upstream and downstream of iron sources from sediments, to determine the response of planktonic communities to natural iron additions.
- ◆ Development of simulation models with more realistic biological components such as light limitation and food web dynamics.

Given recent projections, it is apparent that the buildup of greenhouse gases will continue well into the next century. The studies listed above will facilitate better predictions of the potential consequences of ocean manipulation. More importantly, they will fill critical gaps in our understanding of the role of the oceans in the global carbon cycle.

**RESOLUTION**  
***Ocean Fertilization and Atmospheric Carbon Dioxide***

The following resolution was drafted by the symposium participants on Feb. 24, 1991, and adopted by the American Society of Limnology and Oceanography on June 9, 1991:

Recent research suggests that primary production in some nutrient-rich areas of the open sea may be limited by iron deficiency. This suggestion has stimulated discussion concerning the feasibility of fertilizing the Southern Ocean with iron as a means of reducing carbon dioxide concentrations in the atmosphere.

WHEREAS major manipulations of the Southern Ocean by iron fertilization is a scientifically uncertain mitigation measure to reduce rising carbon dioxide levels in the atmosphere; and

WHEREAS even if fully implemented and successful, this measure would likely at best postpone the impending climate change by a few years if not combined with significant reduction in carbon dioxide emissions;

THEREFORE BE IT RESOLVED that the American Society of Limnology and Oceanography *urges all governments to regard the role of iron in marine productivity as an area for further research and not to consider iron fertilization as a policy option that significantly changes the need to reduce emissions of carbon dioxide.*

## **SYMPOSIUM AGENDA**

### ***“What Controls Phytoplankton Production in Nutrient-Rich Areas of the Open Sea?”***

Feb. 22-24, 1991, Lake San Marcos Conference Center  
San Marcos, California

**STEERING COMMITTEE:** Sallie W. Chisholm and John J. Cullen, Co-Chairs; Karl Banse, Bruce Frost, John Martin, Diane McKnight, Claire Schelske, Trevor Platt (ex officio), and Susan Weiler (ex officio)

#### **DAY 1, FRI, FEB. 22**

##### **Opening Statements**

08:30 - 09:00

##### **Processes and Hypotheses**

09:00 - 12:00, Sallie W. Chisholm, Chair

Ann Gargett: Physical Processes and the Maintenance of Nutrient-Rich Euphotic Zones.

Alan R. Longhurst: Role of the Marine Biosphere in the Global Carbon Cycle.

John Cullen: Hypotheses to Explain High-Nutrient, Low-Chlorophyll Conditions.

John Lehman: Bottom-Up vs Top-Down Control of Aquatic Food Webs: Lessons From Limnology.

##### **Regulation of Phytoplankton Production**

13:30 - 17:00, Theodore J. Smayda, Chair

Francois M. M. Morel: Micronutrient Utilization by Phytoplankton.

Paul Falkowski: Physiological Limitations and their Diagnosis.

John A. Raven: Inorganic Carbon Acquisition Mechanisms in Marine Phytoplankton and their Implications for the Use of Other Resources.

Bruce W. Frost: High Phytoplankton Production, High Nutrient Concentration and Low Phytoplankton Stock Implies Grazing Control.

Lawrence R. Pomeroy: Food Web Structure and Function: Potential Feedbacks to Phytoplankton.

##### **Posters**

17:30 - 19:15

#### **DAY 2, SAT, FEB. 23**

##### **Regional Descriptions**

08:30 - 10:00, James A. Yoder, Chair

Arnold L. Gordon: Antarctic Surface Water Renewal [cancelled].

Cornelius Sullivan: Antarctic Production, Patterns from CZCS Images [substituted for Gordon].

Charles B. Miller and Thomas M. Powell: If Nutrient-Rich Systems are Iron Limited, They are Adapted to it: the Subarctic Pacific Case.

Richard T. Barber: Regulation of Phytoplankton Production in the Nutrient-Rich Equatorial Pacific.

**DAY 2, SAT. FEB. 23, continued**

**Iron**

10:20 - 12:00, William G. Sunda, Chair

John H. Martin: The Case for Iron Limitation.

Robert A. Duce: The Atmospheric Transport of Iron and its Deposition in the Ocean.

Anita G. J. Buma: The Role of Iron and Manganese in Various Antarctic Plankton Communities.

**Other Perspectives**

13:30 - 15:00, David M. Karl, Chair

Karl Banse: Rates of Phytoplankton Growth.

Gregory Mitchell: Light Limitation in the Southern Ocean.

Kenneth Bruland: Potential Interactions Between Bioactive Trace Metals and Plankton.

**Panel Discussion: Evaluating the Evidence on Smaller Scales**

15:15 - 17:15, Patricia A. Wheeler, Chair

Contributing Panelists:

Alison Butler

Richard C. Dugdale

George A. Jackson

Neil M. Price

John Rueter

Dorothy G. Swift

**Posters**

18:00 - 21:00

**DAY 3, SUN. FEB. 24**

**Fertilizing Nutrient-Rich Seas: Considerations and Consequences**

08:30 - 10:00, James J. McCarthy, Chair

Jorge L. Sarmiento: Model Estimates of Potential Enhancement of Oceanic CO<sub>2</sub> Uptake by Iron Fertilization of the Southern Ocean.

Tsung-Hung Peng and W. Broecker: Uptake of CO<sub>2</sub> by an Iron-Fertilized Region of the Southern Ocean.

Wolfgang H. Berger: Antarctic Productivity, a Geologic Perspective.

**Panel Discussion: Larger-Scale Processes**

10:20 - 12:00, Thomas M. Powell, Chair

Contributing Panelists:

Osmund Holm-Hansen

Michael Pilson

Thomas M. Powell

Walker O. Smith

**Open Forum: A Search for Consensus  
(or Majority and Minority Opinions)**

13:30 - 15:00, James J. Morgan, Chair

Present state of our understanding

Critical uncertainties

Experimental Design

Course of Action, including consideration of a pilot experiment

## POSTER PRESENTATIONS

- Abbott, Mark:** CZCS Observations of Phytoplankton Pigment in the Southern Ocean.
- Ahmed, S.I., F. Azam and D.C. Smith:** The Role of the Microbial Foodweb in Iron Regulation of the Carbon Pump.
- Baum, Eric:** A Model for the Upper Ocean Mixed Layer Environment.
- Brand, Larry:** How Much Iron do Oceanic Phytoplankton Need?
- Butler, Alison:** Iron Acquisition by Marine Bacteria: Novel Siderophores.
- Chavez, Fransisco:** Equatorial Pacific Microbial Food Webs in Relation to Iron.
- Coale, Kenneth H:** Effects of Iron, Manganese, Copper, and Zinc Enrichments on Productivity and Biomass in the Subarctic Pacific.
- De Baar, Hein:** Distribution of Dissolved Cadmium, Copper and Iron in the Weddell and Scotia Seas.
- Fiedler, Paul & N. Philbrick:** Upwelling and Productivity Along Zonal Divergences in the Eastern Tropical Pacific.
- Fish, William:** Use of Ferredoxin as an Indicator of Iron Stress in Phytoplankton.
- Gottlieb, Peter and R. Gorecki:** An Ecosystem Model of Phytoplankton Limitation.
- Guildford, Stephanie J:** The Application of Phytoplankton Nutrient Status Indicators in Freshwater and Marine Environments.
- Hudson, Robert:** Complexation Kinetics, Diffusion and Phytoplankton Iron Uptake Mechanisms.
- Hall, Julie:** Perennially Low Biomass in a Nutrient-Rich Coastal Upwelling System.
- Iverson, Richard L:** The Relation Between Phytoplankton Carbon Production and Nitrogen New Production in Marine Environments.
- Jackson, George A:** Control of Phytoplankton Biomass During Blooms by Coagulation Processes.
- Keller, Maureen D:** DMS Production and Marine Phytoplankton: The Importance of Species Composition and Implications for a Changing Ocean System.
- Kirchman, David L:** Control of Bacterial Growth in the Subarctic Pacific, Station Papa.
- Michaels, Anthony:** Community Structure, Particle Export and Iron: Biological assumptions and Geochemical Implications.
- Miller, William L:** Studies of the Photochemical Cycling of Iron and its Role in Phytoplankton Growth.
- Neale, Patrick:** Does Vertical Mixing Enhance Diatom Growth Rates in Optically Deep Surface Layers?: Evidence from Long Time-Series in the English Lakes.
- Orr, James:** Oxygen Depletion as a Result of Iron Fertilization in a 3-D Ocean Model.
- O'Sullivan, Daniel W., A.K. Hanson and D.R. Kester:** The Distribution and Redox Chemistry of Fe(II) in Equatorial Pacific Surface Seawater.
- Richardson, Laurie L:** Phytoplankton Mediation of Manganese Cycling.
- Rueter, John:** Iron Content and Biochemical Efficiencies for Organisms Crucial to the Nitrogen Cycle.
- Sherr, Evelyn B:** Evaluation of Protistan Herbivory Using Fluorescently Labeled Algae.
- Sulzberger, Barbara:** Case Study on the Photoredox Cycling of Iron in Aquatic Systems.
- Sullivan, Cornelius W:** Chlorophyll a Standing Crops and Primary Productivity Rates in Antarctic Sea Ice.
- Sunda, William G:** Mutual Feedback Interactions Between Dissolved Zinc and Iron and Growth of Marine Phytoplankton.
- Swift, Dorothy, W.G. Sunda & S.A. Huntsman:** Oceanic Phytoplankton Need Less Iron.
- Thomas, William H:** Anomalous Nutrient-Chlorophyll Interrelationships in the Eastern Tropical Pacific Ocean.
- Tindale, Neil & J. Yoder:** Effect of Atmospheric Iron Addition on Shipboard Enrichment Experiments.
- Unsworth, Nancy & J. Rueter:** Iron Limitation Effects and Nitrogen Metabolism of *Synechococcus*.
- Vernet, Maria:** Phytoplankton Growth Rates During an Antarctic Spring Bloom.
- Watson, Andrew:** Proposal for a Small Scale In-Situ Fertilization Experiment.
- Wells, Mark:** What Fraction of Total Iron in Seawater is Available to Phytoplankton?
- Wilkerson, F. and R. Dugdale:** New Production in the Southern Ocean: Iron limited, Grazed or Cold-Adapted?
- Yang, Sung R., R.M. Kudela and R.C. Dugdale:** Control of New Production in the Pacific Equatorial Upwelling System: Experiments and Measurements with <sup>15</sup>N and Fe.

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