2 2004 WORKSHOP SUMMARY

2.1 What have we learned from the enrichment experiments?

Fate of carbon

SEEDS-I

- There was no significant increase in export flux (13%), and the major part (75%) of the fixed carbon stayed in the surface;
- A significant portion of the organic carbon production was observed as dissolved organic carbon (DOC);
- Good agreement was found in DOC/Chl-*a* production ratio between SEEDS and SERIES;
- Transparent exopolymer particle (TEP) concentrations were low compared to phytoplankton standing stocks, presumably because TEP production by the dominant oceanic diatoms is low.

SERIES

- Eddies were an important influence on patch behaviour; drifter tracks tended to slip eastward relative to patch centres by wind stress;
- Intercalibration and sampling coverage between ships was good;
- Bloom evolution was captured in detail;
- Bloom decline – 80% of the particulate organic carbon (POC), fixed following iron enrichment, was no longer in the mixed layer by Day 25;
- Budgets could account for up to 70% of this POC (but using indirect methods) and 80% in N;
- Nanophytoplankton caused high particulate carbon on Days 7–10 of the bloom;
- What occurred after Day 20 to bring salt, NO_3, $Si[OH]_4$ and dissolved inorganic carbon (DIC) into the base of the patch? Is the simultaneous crash of the bloom a coincidence?
- What is the source of the high $CaCO_3$ fluxes to sediment traps?
- Between 50 and 125 m, biogenic silica dissolution was faster than organic matter decay. Can we believe this? Historical sediment trap and nutrient data suggest *ye*s.
- Had bloom export terminated?
- An increase in DOC was not clear during the stationary and decline phases.

Ecosystem responses

SEEDS-I

- There were increases in Chl-*a* concentrations (× 26) and rate of primary production (× 13);
- A floristic shift to large cells (centric diatoms) was observed;
- Coastal diatoms responded quickly to the iron enrichment and built up a large biomass. So the presence of these coastal species as resting spores or cells are important factors for determining the time and magnitude of bloom evolution;
- Physiological stress by iron- and light-limitation was suggested after the development of the bloom;
- Enhancement of nitrate uptake rate (× 20) and marked consumption of macronutrients occurred;
- A large drawdown of pCO_2 was observed;
- Increase in bacterial abundance was × 2;
- Active heterotrophic dinoflagellates grazing on diatoms was observed after the development of the bloom;
- Gut-pigment contents of dominant copepods increased (× 4–18) but the absolute value was small;
- Picophytoplankton showed low growth rate before iron fertilization. Their growth rate was increased by iron fertilization. Quick responses in growth rate of picoeukariotes were observed on Day 2;
- Nanoheterotrophs showed a few days' delay to the increase in picoplankton growth, and grazing balanced picoplankton growth at the end of the experiment;
- Increase in grazing pressure on phytoplankton chain-forming *Chaetoceros debilis* by *Gyrodinium* sp. and *G. spilale* was observed during Days 9–13;
- Heterotrophic dinoflagellates (HDF) were the key grazers in SEEDS-I;
- Are larger HDF species abundant in the Western Subarctic Gyre compared with the eastern equatorial Pacific and the Southern Ocean?

- The contribution of HDF to the loss of diatoms in the surface mixed layer was significant during Days 9–13.

SERIES

- During phase II (Days 10–19) of the bloom, microplankton were dominant, comprising more than 80% of total Chl-*a*;
- There was a dynamic mixed layer ranging from less than 10 m to more than 40 m throughout the bloom, resulting in patch dilution;
- Dissolved iron concentrations were reduced to ambient levels by Day 12; F_v/F_m values suggest that phytoplankton were Fe stressed by Day 14;
- *Chaetoceros* spp. ceased increasing in abundance by Day 15, possibly due to iron stress;
- *Pseudo-nitzschi*a spp. maintained similar growth rates throughout the bloom, until SiO_3 concentrations were depleted;
- Although pennate diatoms dominated the bloom numerically with respect to carbon, both pennate and centric diatoms contributed equal proportions to algal biomass;
- The bloom peaked physiologically on ~July 21 (Day 12); this was the beginning of diatom iron stress;
- Primary production peaked on July 24 (Day 15); this was the beginning of diatom silicon stress;
- Chlorophyll peaked on July 27 (Day 18); after that, was the whole community beginning to suffer from iron limitation?
- Cells less than 20 μm increased from July 10 to 16 after which a major decline in coccolithophorids and other prymnesiophytes was observed;
- Susceptibility to photo-oxidation induced by the second iron addition(?)
- Microzooplankton: rapid response (abundance of flagellates and dinoflagellates increased from July 13);
- Grazing on diatoms might not be effectively carried out by abundant small copepods;
- *Eucalanus bungii* and *Neocalanus cristatus* were more effective diatom consumers but were in lower numbers;
- SERIES was not well matched with the spring period of maximum diatom grazing (*N. plumchrus*).

Iron biogeochemistry

SEEDS-I

- Increased dissolved iron was mainly in colloidal fraction;
- The dissolved iron concentration decreased rapidly, and loss rate gradually decreased;
- The half-life of initial dissolved iron was longer than that during IronEx and SOIREE;
- The disappearance of dissolved iron resulted from colloidal aggregation and/or iron biological uptake (less)
- Particulate iron remained at high levels;
- Bioavailability of the remaining iron (mainly particulate) was low;
- The character of organic ligands changed rapidly upon iron enrichment

SERIES

- Only 35% of the added iron was in a dissolved state after 8 h;
- The half-life of total iron was determined to be 6 days for an integrated water column of 0–40 m but 3 days for the 10 m depth concentration;
- If we also consider horizontal spreading, only half the total iron was still in the patch after 10 days;
- Colloidal iron % of total iron appeared to be decreasing while particulate iron increased;
- After 11 days there was still a considerable amount of iron left in the patch (~30%);
- Ligands seemed to track the dissolved iron concentration and seemed to disappear rapidly together with the dissolved iron concentration;
- Dissolved iron was near background level on July 22 (Day 13).

Trace-gas production, air–sea interaction

SEEDS-I

- There was no significant increase in dimethyl sulfide (DMS).

SERIES

- The iron enrichment created a bloom of DMSP-rich nanophytoplankton which crashed after July 20 (Day 11);

- Concentrations of particulate dimethyl-sulfoniopropionate (DMSPp) doubled during the nanophytoplankton (*Emiliana huxleyi*) bloom;
- The addition of iron created an overall DMS deficit of 7% in the mixed layer;
- The iron-induced increase in DMSPp had no clear effect on DMS concentrations, indicating that processes (*e.g.*, grazing) are more important than pool size;
- DMS concentrations were lower inside the patch during the peak of the diatom bloom;
- The iron-induced deficit in DMS concentrations during the peak of the diatom bloom resulted from a decrease in biological DMS net production.

Model studies

- A rapid response of microzooplankton grazing on small phytoplankton occurred;
- NH_4 buildup occurs after the bloom and stays in the subsurface layer up to early winter.

Similarity and differences between the eastern and western subarctic Pacific

Both SEEDS-I and SERIES have demonstrated increased productivity and biomass of phytoplankton as a response to the iron enrichment. Bloom evolution and decline were captured in detail during SERIES. However, there are differences in the physical and chemical environments, the plankton ecosystem and dominant species, and the zonal iron gradient between the Western Subarctic Gyre (WSG) and the Alaskan Gyre (AG). From SEEDS-I and SERIES, the following similarities and differences in biogeochemical and ecosystem responses to the iron addition were pointed out:

Similarities

- A diatom bloom occurred accompanied by a floristic shift to large cells;
- Vertically-integrated Chl-*a* and primary production increased;
- Heterotrophic dinoflagellates grazed on diatoms after the development of the bloom, which led to significant loss of diatoms in the mixed layer;
- Copepods were not the primary grazers; SERIES was not well matched with the spring period of maximum diatom (*Neocalanus plumchrus*) grazing;
- DOC increased during the growth phase of bloom, was constant through the stationary phase, and decreased during the bloom decline; DOC production was about 10% of primary production;
- Increased dissolved iron was mainly in colloidal fraction;
- Dissolved iron concentration decreased rapidly by colloidal aggregation and biological uptake (less), and loss rate gradually decreased;
- Particulate iron concentrations remained high; bioavailability of the remaining iron (mainly particulate) was low;
- The majority of macronutrients were consumed;
- An increase in Si/NO_3 drawdown ratio was observed after an occurrence of physiological stress, such as iron and light limitations.

Differences

- A larger and faster response (in terms of biomass) was observed in the WSG;
- Initial diatom populations were largely neritic for the WSG and pelagic for the AG; neritic species responded quickly to the iron enrichment and built up a large biomass, suggesting that the presence of coastal species as resting spores or cells is important in determining the magnitude of bloom evolution;
- The bloom was characterized by two ecological phases in SERIES. Phase I consisted of nanophytoplankton (prymnesiophytes) and occurred before Day 10 of the experiment; phase II was mainly diatoms and began after Day 10;
- Sediment traps collected large $CaCO_3$ fluxes after phase I, and high biogenic silica and POC fluxes after phase II during SERIES, but not in SEEDS-I. SEEDS-I occupation may have been too short to observe an export event;
- more than 50% of the mixed-layer POC deficit was attributed to bacterial re-mineralization and mesozooplankton grazing in the AG; NH_4 in surface waters increased throughout the bloom;
- Characteristics of organic ligands changed rapidly upon iron enrichment in the WSG; ligand concentrations tracked dissolved iron concentrations in the AG, rapidly disappearing together with the dissolved iron concentration;
- The iron enrichment created a bloom of

DMSP-rich nanophytoplankton (*Emiliania huxleyi*) which crashed after Day 11 in SERIES, but no significant increase in DMS/DMSP was observed in the WSG;

- The iron-induced increase in DMSPp had no clear effect on DMS concentrations in the AG;
- The iron-induced deficit in DMS concentrations during the peak of the diatom bloom resulted from a decrease in biological DMS net production in the AG.

Southern Ocean Iron Experiment

The Southern Ocean Iron Experiment (SOFeX) was performed in 2002 to investigate the effects of iron enrichment in regions with high and low concentrations of silicic acid. From the results of SOFeX, the following questions were identified to be resolved in future experiments.

- What are Fe:C:Si:N:P uptake and re-generation stoichiometries? How are these stoichiometries related to phytoplankton community structure? How do they change under macronutrient limitation (Si)? What are the spatial scales over which these elements are regenerated?
- What is the steady-state condition? Is this a relevant question?
- What is the periodicity and magnitude of natural iron enrichment, both seasonally and inter-annually, and on glacial–interglacial time scales?
- What is the effect of iron enrichment on the geochemistry (low O_2 and de-nitrification) and ecology (nitrification) below and within the iron patch?
- Do ecosystems respond in a natural manner to artificial iron enrichments? Effects on all biogeochemical parameters were well outside the contemporary climatological mean. What are the similarities and differences between natural and artificial iron supply?
- How important is NH_4 inhibition on NO_3 uptake and nutrient dynamics?

We need to rethink the effects of iron enrichment in low silicate and high nitrate environments, Si-limitation limited diatom growth in the North. We must address this issue as it bears directly on the significance for iron forcing of glacial–interglacial transitions and unintended consequences.

2.2 What are the outstanding questions?

SEEDS-II is the second meso-scale iron enrichment experiment in WSG designed to investigate the longer-term effects of iron enrichment on the plankton ecosystem, carbon export and trace gas production. SEEDS-II will involve about 50 researchers from universities and government institutions in Japan, the United States and Canada. The iron-enriched patch will be monitored by two ships, the R/V *Hakuho Maru* (Japan) and the R/V *Kilo Moana* (U.S.A.), for 34 days from July 21 to August 23, 2004. Through the integration and synthesis of the findings from SEEDS-I, SERIES and SOFeX, the workshop participants identified the following key themes and key scientific questions for the SEEDS-II experiment.

Fate of carbon

- What portions of organic carbon fixed by coastal centric diatoms in the WSG will be exported from the surface mixed layer, and what portions will be regenerated?
- To what extent would heterotrophic dinoflagellates (*Gyrodinium*) respire iron-induced carbon fixation?
- What is the turnover time, size spectrum, gross production rate, and gross decomposition rate of produced DOC?
- What are community respiration rates?
- Are C:N:P:Si regeneration ratios in surface and subsurface layers crucial to our understanding of iron-induced ecological response and nutrient dynamics?
- Is biological patchiness in species and export within the patch significant?
- How does physical dilution from outside affect the patch chemistry and biology? What is the effect of dilution on budget calculations?
- What is the difference between single and multiple iron additions? What is the difference in iron availability?
- To understand the fate of carbon during the iron fertilization-induced diatom bloom, studies on grazing rate, assimilation rate, and "mini pellets" sinking rates, are essential.

Ecosystem responses

- Why did SEEDS-I and SERIES have opposite trends in dominant diatom composition?
- What is the role of cell lysis on changes in available nutrients, sources of DMSP, bacterial community structure and iron chemistry?
- What roles will sinking and grazing play in the decline of the bloom?
- What is the long-term effect of iron availability on the ecosystem? How is the response to further iron addition affected?
- The ecological response to iron enrichment is largely determined by the seed population. What will the species variability and ecosystem differences be between iron-induced blooms in the same location?
- How predictable will the species response be to iron addition?
- Why does iron addition to bottles result in N limitation, but the large-scale iron additions show Si depletion?

Seasonal timing

- If natural events occur, should we try to emulate those that occur at other times of the year?
- What is the importance of the presence of endemic zooplankton at the time of iron enrichment?

Iron biogeochemistry

- What controls iron retention and loss after iron release?
- What is the main source of ligand production? How does it respond to iron enrichment?
- What is the role of iron ligands in iron bioavailability and recycling?
- What is the role of Fe(II) and redox-photochemical cycling in the phytoplankton bloom?
- What is the uptake of iron by different biota?
- What is the difference between single and multiple iron additions, and their effect on availability of iron?

- How different is the natural iron supply from the supply during the iron enrichment experiment? Labile particulate iron was significantly higher in the surface mixed layer in the WSG, but dissolved iron was at the same level as in the eastern region.
- Is bioavailability of iron (not total iron input) most important for ecosystem response?
- What form of iron best indicates bioavailability?
- What are the changes in iron bioavailability during phytoplankton bloom?
- Is there a significant iron supply by horizontal advection and winter vertical mixing in the western region? Supplied dissolved iron may be rapidly transformed to suspended particles during the phytoplankton bloom, and reduce bioavailability.
- To construct an iron budget, more detail is needed from vertical iron flux–sediment trap data, both horizontally and vertically, for a better understanding of the various forms of iron.
- Is there atmospheric deposition in these two different regions?
- How much iron do we need to add to get "the" ecosystem response?
- How different are export and recycling in "nature" versus bottle? Si versus N depletion?

Trace-gas production

- What is the fate of DMSP? Is it consumed by bacteria? Does it sink?
- What are the roles of physiological stress, Fe availability, light and macronutrients on DMSP cycling?
- What is the extent of emissions to the atmosphere?
- We need a consistent location (maybe tagged with SF_6) outstation for more reliable or consistent outsampling.

2.3 Recommendations for SEEDS-II

- It was recommended to lengthen the experiment if possible; the decline will depend on patch physical dynamics, bloom dynamics, *etc*.
- An additional suite of measurements is required to study bloom evolution, including fast repetition rate fluorometry (FRRF), flavodoxin, sinking rates, TEPS, and supplement these with ^{15}N and ^{32}Si uptake rates;
- Additional methods are required to determine the role of the microbial community and zooplankton in the fate of POC and O_2 profiles of the upper ocean, community respiration, labelled particle decomposition experiments;
- Additional experiments are required for measuring export flux, such as trap calibration with thorium, large-volume pump thorium samples, more fluorometers for the upper trap moorings;
- Estimates of silica dissolution, bacterial production and respiration (Bacterial C demand), and bacterial iron-stress should occur;
- Measurements of micro and mesozooplankton grazing on bacteria, phytoplankton, zooplankton and detritus are desirable;
- Biological patchiness in species and export within the patch should be considered;
- Response by changes in physiology of phytoplankton cells should be distinguished from that by changes in dominant species;
- Physical dilution from outside affects the patch chemistry and biology. The correction of dilution effects on budget calculations is essential;
- Intercalibration and data coverage between ships should be as robust as for SERIES.