Throughout $ is generic null/not given/not available placeholder

Project Name: Subarctic-Pacific Iron Experiment for Ecosystem Dynamics Study I

Acronym: SEEDS 2001

Synonym: $

Program: Subarctic-Pacific Iron Experiment for Ecosystem Dynamics Study

Project url: http://www.seeds-exp.jp/en/index.html   (English)
                 http://www.seeds-exp.jp/index.html   (Japanese)

Related Program: SOLAS-Japan (Surface Ocean Lower Atmosphere Study).
                     http://solas.jp/index.html

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Start date:
28 June 2001

End date:
6 August 2001

Logo url:
$

Geolocation:
Western subarctic gyre in the North Pacific at 48.5°N, 165°E.

Description:

Tsuda , A et al.(2003). A Mesoscale Iron Enrichment in the Western Subarctic Pacific Induces a Large Centric Diatom Bloom. *Science*, 300 (5621), 958 – 961. doi: 10.1126/science.1082000.

We have performed an in situ test of the iron limitation hypothesis in the subarctic North Pacific Ocean. A single enrichment of dissolved iron caused a large increase in

phytoplankton standing stock and decreases in macronutrients and dissolved carbon dioxide. The dominant phytoplankton species shifted after the iron addition from pennate diatoms to a centric diatom, *Chaetoceros debilis*, that showed a very high growth rate, 2.6 doublings per day. We conclude that the bioavailability of iron regulates the magnitude of the phytoplankton biomass and the key phytoplankton species that determine the biogeochemical sensitivity to iron supply of high-nitrate, low-chlorophyll waters.

Publications:

Most publications appeared in a special issue of *Progress in Oceanography*, 64, (2-4)

Publication abstracts are given at the end of this file.

Harrison, P. J. (2005): Editorial. *Progress In Oceanography* 64(2-4), 91-93.

Takeda, S. & Tsuda, A. (2005): An in situ iron-enrichment experiment in the western subarctic Pacific (SEEDS): Introduction and summary. *Progress In Oceanography* 64(2-4), 95-109.

Tsumune, D., Nishioka, J., Shimamoto, A., Takeda, S. & Tsuda, A. (2005): Physical behavior of the SEEDS iron-fertilized patch by sulphur hexafluoride tracer release. *Progress In Oceanography* 64(2-4), 111-127.

Kinugasa, M., Ishita, T., Sohrin, Y., Okamura, K., Takeda, S., Nishioka, J. & Tsuda, A. (2005): Dynamics of trace metals during the subarctic Pacific iron experiment for ecosystem dynamics study (SEEDS2001). *Progress In Oceanography* 64(2-4), 129-147.

Noiri, Y., Kudo, I., Kiyosawa, H., Nishioka, J. & Tsuda, A. (2005): Influence of iron and temperature on growth, nutrient utilization ratios and phytoplankton species composition in the western subarctic Pacific Ocean during the SEEDS experiment. *Progress In Oceanography* 64(2-4), 149-166.

Suzuki, K., Hinuma, A., Saito, H., Kiyosawa, H., Liu, H., Saino, T. & Tsuda, A. (2005): Responses of phytoplankton and heterotrophic bacteria in the northwest subarctic Pacific to in situ iron fertilization as estimated by HPLC pigment analysis and flow cytometry. *Progress In Oceanography* 64(2-4), 167-187.

Tsuda, A., et al. (2005a): Responses of diatoms to iron-enrichment (SEEDS) in the western subarctic Pacific, temporal and spatial comparisons. *Progress In Oceanography* 64(2-4), 189-205.

Kudo, I., Noiri, Y., Imai, K., Nojiri, Y., Nishioka, J. & Tsuda, A. (2005): Primary productivity and nitrogenous nutrient assimilation dynamics during the

Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study. *Progress In Oceanography* 64(2-4), 207-221.

Saito, H., Suzuki, K., Hinuma, A., Ota, T., Fukami, K., Kiyosawa, H., Saino, T. & Tsuda, A. (2005): Responses of microzooplankton to in situ iron fertilization in the western subarctic Pacific (SEEDS). *Progress In Oceanography* 64(2-4), 223-236.

Tsuda, A., Saito, H., Nishioka, J. & Ono, T. (2005b): Mesozooplankton responses to iron-fertilization in the western subarctic Pacific (SEEDS2001). *Progress In Oceanography* 64(2-4), 237-251.

Ramaiah, N., et al. (2005): Effect of iron enrichment on the dynamics of transparent exopolymer particles in the western subarctic Pacific. *Progress In Oceanography* 64(2-4), 253-261.

Aono, T., Yamada, M., Kudo, I., Imai, K., Nojiri, Y. & Tsuda, A. (2005a): Export fluxes of particulate organic carbon estimated from 234Th/238U disequilibrium during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS 2001). *Progress In Oceanography* 64(2-4), 263-282.

Yoshie, N., Fujii, M. & Yamanaka, Y. (2005): Ecosystem changes after the SEEDS iron fertilization in the western North Pacific simulated by a one-dimensional ecosystem model. *Progress In Oceanography* 64(2-4), 283-306.

Fujii, M., Yoshie, N., Yamanaka, Y. & Chai, F. (2005): Simulated biogeochemical responses to iron enrichments in three high nutrient, low chlorophyll (HNLC) regions. *Progress In Oceanography* 64(2-4), 307-324.

Aono, T., Yamada, M., Kudo, I., Imai, K., Nojiri, Y. & Tsuda, A. (2005b): Export fluxes of particulate organic carbon estimated from Th-234/U-238 disequilibrium during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS 2001). *Progress in Oceanography* 64(2-4), 263-282.

Saito, H., Ota, T., Suzuki, K., Nishioka, J. & Tsuda, A. (2006): Role of heterotrophic dinoflagellate Gyrodinium sp in the fate of an iron induced diatom bloom. *Geophys. Res. Lett.* 33(9), L09602

Metadata:

There are 27 Microsoft Excel 2003 files (xls format) that describe metadata and include some processed data.

Data was collected at a total of 13 stations and from 3 moored sediment traps.

Stations were occupied IN patch for days 0, 2, 4, 7, 9, 11 and 13.
Stations were occupied OUT patch for days 2, 4, 7, 9, 11, 13.
It is not explicitly stated but it appears that at all stations two CTD sampling rosette casts were made: clean and rms. The clean rosette appears to have typically sampled the mixed layer (<50 m) e.g. 5, 10,

20, 30, 50 m. The rms rosette appears to have typically sampled the euphotic zone (<200m) e.g. 10, 20, 30, 40, 50, 80, 100, 150, 200 m.

Sediment traps were deployed at
>
> CENTRE: 20 m
> IN: 40, 60, 100, 200 m
> OUT: 20, 40, 60 and 100 m
>
> Traps were recovered several times. Deployment times (days):
> CENTRE: 3.95, 2.83, 2.02, 1.98, 1.93, 2.05
> IN: 3.99, 2.84, 2.03, 2.00, 1.95, 2.01
> OUT: 5.17, 3.97, 3.42

Data exist for the following parameters:
- Biosilica
- Chlorophyll
- Dissolved Inorganic Carbon
- Total alkalinity
- FRRF
- DOC
- Pigments
- Iron
- Mesozooplankton
- Microzooplankton
- N uptake
- Nutrients
- PAR
- Euphotic zone depth
- Phosphorus (total dissolved, PO4)
- POC
- PON
- Primary production (mass carbon per area per time)
- Salinity
- Dissolved oxygen
- Sediment traps
  - mass flux
  - metal flux (Al, Ca, Fe, Mg, Mn, P, Sr, Ti, Zn)
  - Si flux
  - d13C
- TEP
- dissolved trace metals (Fe, Co, Ni, Cu, Zn, Cd)
- Underway fCO2 and SF6 for patch mapping
- Underway Fe, chl a, and nutrients (NO3, NO2, Si, PO4, NH4).

There are 27 Microsoft Excel 2003 files (xls format) that describe metadata and include some processed data.

File list.xls
This file gives English-Japanese versions of file names listed below.

```
CTD                    □□□
2minLog                □□□
BioSi                  □□□□
Buoy position          □□□
Chlorophyll            □□□□
Diatom                 □□□□
DIC Alk                □□□□
DOC                    □□□□
FRRF                   □□□□
HPLC-pigment           □□□□
Iron                   □□□
Mesozaooplankton       □□□
Microzooplankton       □□□□
N-uptake               □□□
Nutrient               □□□□
PAR                    □□□□
Phosphorus             □□□
POCN                   □□□□
Primary
production             □□□□
PRR                    □□□□
Salinity DO            □□□□
Sinking
particles              □□□□
TEP                    □□□□
Trace metal            □□□□
Underway data          □□□
```

Station List.xls
This file gives time and location (lat long) of all sampling stations.
> There are associated CTD files in .hdr and .asc format. File names are D*-X where * is the day since iron infusion and X is either I (IN patch) or O (OUT patch). For days 9 (IN) and 13 IN and OUT) a second cast was made at each station (e.g D13-I2). Files are in SEABIRD format but can also be read with a text editor.

Buoy position.xls
Three buoys were set out: OBN4 (reference), OBN5 (centre), OBN6 (trap-IN). Sediment traps were deployed from the buoys. This file gives buoy location (lat long) in 10 minute increments.

BioSi.xls
This file gives biosilica for all stations IN and OUT at 5, 10, 20, 30, 50 m.

Chlorophyll.xls
This file gives size fractionated chlorophyll for all stations IN and OUT.
Duplicate samples from clean and rms rosettes.
Clean samples taken at 5, 10, 20, 30, 50, 70 m and all filtered gff only.
Rms samples taken at 5, 10, 20, 30, 40, 50, 60, 70, 80, 100, 150, 200 m and all filtered
gff. Days 0, 2, 4, 7, 9, 11, 13 also filtered to give 0.2-2 um, 2-10um and >10um.
Extraction: N,N-dimethylformamide
Measurement: Turner Designs fluorometer A-110.

Diatoms.xls
This file gives diatom cell abundance IN patch ONLY at 2-5 m by species. Total cell
abundance alos given and dinoflagellate abundance estimated as (total – diatoms).

DIC Alk.xls
This file gives Dissolved Inorganic Carbon for all stations IN and OUT at 5, 10, 20,
30, 40, 50, 60, 70, 80, 100, 150 and 200 m. Total alkalinity for days 9, 11 and 13 only.

DOC.xls
This file gives Dissolved Organic Carbon for all stations IN and OUT at 5, 10, 20, 30,
50, 70 and 100 m. Also gives calculated integrated between each sample.

FRRF.xls
This file gives FRRF Fv/Fm for all stations IN and OUT at 5, 10, 20, 30, 50 m.

HPLC-Pigement.xls
This file gives pigments for all stations IN and OUT at 5, 10, 20, 30, 50 m. Depth (m).
Peridinin, 19'-But, Fucox, 19'-Hex, Prasinox, Violax, Diadino, Allox, Chl b, Chl a,
and Chllide a.

Iron.xls
This file gives underway dissolved iron (<0.22 um) for days 1, 3, 5, 6, 8, 10, 10 (i.e.
NOT the on station days) sampled at 1.5-3 m from a clean towed fish.
This file gives discrete dissolved (<0.22 um) and total (unfiltered) iron for all stations
IN and OUT at 5, 10, 20, 30, 50, 70 m.
Analysis after Obata 8-hydroxyquinoline chemiluminesence.
This file also has greater depth of details about sample collection and treatment than
most of the other files.

Mesozooplankton.xls
This file gives abundance of zooplankters for most stations IN and OUT (all except
day 13). Samples were collected with 100 um mesh net between 0-20, 20-50, 50-100

and 100-200 m. Results are given as individuals per m2 by species 9and copepodite stage).
This file gives wet weight copepods and non-copepods collected.

Microzooplankton.xls
This file gives abundance (individuals / L), biomass and size (length + width) of Ologotrichs, Tintinnids, Gyrodinium, Nauplii for all stations IN and OUT and 5 and 10 m. (Confirmation of details asked for from PI)$

N-uptake.xls
This file gives (NO3+NO2), NH4 and *chla a* measurements, for all IN stations and day 4, 9, 13 OUT stations at 5 and 15 m.

Nutrients.xls
This file gives nutrients and related information (Temperature, CTD Salinity, Dissolved Oxygen, Chl.a, NO3, NO2, Si, PO4, NH4, and Fe) for all stations IN and OUT or patch.
Duplicate samples from clean and rms rosettes.
Clean at 5, 10, 20, 30, 50, 70 m.
rms (NO Fe data) at 5, 10, 20, 30, 50, 70, 100, 150, 200 m.

PAR.xls
This file gives PAR averaged every 10 minutes for the duration of the experiment. Daily fluxes are calculated.

PRR data for DAT SET.xls
This file gives PAR coefficient of attenuation and uses this to calculate euphotic zone depth for each day.

Phosphorous.xls
This file gives total dissolved phosphorous, PO4, dissolved organic phosphorous (by difference) and particulate phosphorus for all stations IN at 5, 10, 20, 30, 50, 70, 100, 150, 200m.
This file gives and dissolved phosphorous, PO4, dissolved organic phosphorous (by difference) but NOT particulate phosphorus for stations OUT at 5, 10, 20, 30, 50, 70, 100, 150, 200m.

POCN.xls
This file gives Particulate Organic Carbon and Particulate Organic Nitrogen for all stations IN and OUT at 5, 10, 20, 30, 40, 50, 70, 80, 100 m. Ratio C/N is calculated.

PrimaryProduction.xls

This file gives primary production (as comparison between POC, chla a and 3 light plus 1 dark culture) for all stations IN patch and stations OUT patch on days 4, 9 and 13. Depth of sampling varied.

Salinity-DO.xls
This file gives the salinity and dissolved oxygen for rosette samples for all stations IN and OUT patch.
Duplicate samples from clean and rms rosettes.
Clean (salinity ONLY) at 5, 10, 20, 30, 50, 70 m.
rms at 5, 10, 20, 30, 50, 70, 100, 150, 200 m. (some gaps for DO)

Sinking Particles.xls
This file describes the design and deployment of sediment traps.
Traps were suspended from each of the buoys:
CENTRE: 20 m
IN: 40, 60, 100, 200 m
OUT: 20, 40, 60 and 100 m

Traps were recovered several times. Deployment times (days):
CENTRE: 3.95, 2.83, 2.02, 1.98, 1.93, 2.05
IN: 3.99, 2.84, 2.03, 2.00, 1.95, 2.01
OUT: 5.17, 3.97, 3.42

This file gives:
      mass flux (average of 4 cups) for each depth and each deployment.
      POC and PON (used to calculate C and N flux).
      Metals (by ICP-AES)
            Al, Ca, Fe, Mg, Mn, P, Sr, Ti, and Zn on dry material
            Ba, Cr, Cu also measured but subject to analytical problems.
            Na, K, S used to check seasalt mass balance.
      Si also measured (but on different filter to metals).
      d13C

TEP.xls
This file gives Transparent ExoPoloymer results for all IN stations at 5, 10, 20, 30, 50, 70 m and OUT patch stations on days 4, 9, 13 at 5, 10, 20, 30, 50, 70 m.

TEP??SEEDS.xls
This file is poorly described. Clarification has been sought $

Trace metal.xls
This file gives dissolved (filter size not specified; clarification sought) trace metal (Fe, Co, Ni, Cu, Zn, Cd) for all stations IN and OUT at 5, 10, 20, 30, 50, 70 m.

Underway.xls
This file gives underway measurements made on days 3, 6, 8, 10, and 12.

fCO2 and SF6 were sampled from the ships pumping system (6 m depth) at 1 and 6 minute intervals, respectively.

dissolved Fe (<0.22 um), chl a, and nutrients (NO3, NO2, Si, PO4, NH4) were sampled from a towed clean fish (depth not given) at 5-10 minute intervals.

Underway data.xls
This file is identical to underway.xls content but lacks the cell fill and highlighting that is present in underway.xls. The meaning of the highlighting is unclear (e.g. does NOT designate IN and OUT).

Platform Name: R/V Kaiyo-maru

platform type: vessel

deployment: KY0103
Pre-infusion observations = Leg 1: 28 Jun 2001 (Tokyo) to 10 Jul 2001 (Kushiro)
Patch enrichment = Leg 2:13 Jul 2001 (Kushiro)--06 Aug 2001 (Tokyo)

PUBLICATION ABSTRACTS

Harrison, P. J. (2005): Editorial. *Progress In Oceanography* 64(2-4), 91-93.

Takeda, S. & Tsuda, A. (2005): An in situ iron-enrichment experiment in the western subarctic Pacific (SEEDS): Introduction and summary. *Progress In Oceanography* 64(2-4), 95-109.

To test the iron hypothesis in the subarctic Pacific Ocean, an in situ iron-enrichment experiment (SEEDS) was performed in the western subarctic gyre in July-August 2001. About 350 kg of iron (as acidic iron sulfate) and 0.48 mol of the inert chemical tracer sulfur hexafluoride were introduced into a 10-m deep surface mixed layer over an 80 km2 area. This single iron infusion raised dissolved iron levels to ~2.9 nM initially. Dissolved iron concentrations rapidly decreased after the infusion, but levels remained close to 0.15 nM even at the end of the 14-day experimental period. During SEEDS there were iron-mediated increases in chlorophyll a concentrations (up to 20 [mu]g l-1), primary production rates, biomass and photosynthetic energy conversion efficiency relative to waters outside the iron-enriched patch. The rapid and very high accumulation of phytoplankton biomass in response to the iron addition appeared to be partly attributable to shallow mixed-layer depth and moderate water

temperature in the western subarctic Pacific. However, the main reason was a floristic shift to fast-growing centric diatom Chaetoceros debilis, unlike the previous iron-enrichment experiments in the equatorial Pacific and the Southern Ocean, in both of which iron stimulated the growth of pennate diatoms. The iron-mediated blooming of diatoms resulted in a marked consumption of macronutrients and drawdown of pCO2. Biological and physiological measurements indicate that phytoplankton growth in the patch became both light- and iron-limited, making phytoplankton biomass relatively constant after day 9. The increase in microzooplankton grazing rate after day 9 also influenced the net growth rate of phytoplankton. There was no significant increase in the export flux of carbon to depth during the 14-day occupation of the experimental site. The export flux between day 4 and day 13 was estimated to be only 13% of the integrated primary production in the iron-enriched patch. The major part of the carbon fixed by the diatom bloom remained in the surface mixed layer as biogenic particulate matter. Our findings support the hypothesis that iron limits phytoplankton growth and biomass in a [`]bottom up' manner in this area, but the fate of algal carbon remains unknown. To test the iron hypothesis in the subarctic Pacific Ocean, an in situ iron-enrichment experiment (SEEDS) was performed in the western subarctic gyre in July-August 2001. About 350 kg of iron (as acidic iron sulfate) and 0.48 mol of the inert chemical tracer sulfur hexafluoride were introduced into a 10-m deep surface mixed layer over an 80 km2 area. This single iron infusion raised dissolved iron levels to ~2.9 nM initially. Dissolved iron concentrations rapidly decreased after the infusion, but levels remained close to 0.15 nM even at the end of the 14-day experimental period. During SEEDS there were iron-mediated increases in chlorophyll a concentrations (up to 20 [mu]g l-1), primary production rates, biomass and photosynthetic energy conversion efficiency relative to waters outside the iron-enriched patch. The rapid and very high accumulation of phytoplankton biomass in response to the iron addition appeared to be partly attributable to shallow mixed-layer depth and moderate water temperature in the western subarctic Pacific. However, the main reason was a floristic shift to fast-growing centric diatom Chaetoceros debilis, unlike the previous iron-enrichment experiments in the equatorial Pacific and the Southern Ocean, in both of which iron stimulated the growth of pennate diatoms. The iron-mediated blooming of diatoms resulted in a marked consumption of macronutrients and drawdown of pCO2. Biological and physiological measurements indicate that phytoplankton growth in the patch became both light- and iron-limited, making phytoplankton biomass relatively constant after day 9. The increase in microzooplankton grazing rate after day 9 also influenced the net growth rate of phytoplankton. There was no significant increase in the export flux of carbon to depth during the 14-day occupation of the experimental site. The export flux between day 4 and day 13 was estimated to be only 13% of the integrated primary production in the iron-enriched patch. The major part of the carbon fixed by the diatom bloom remained in the surface mixed layer as biogenic particulate matter. Our findings support the hypothesis that iron limits phytoplankton growth and biomass in a 'bottom up' manner in this area, but the fate of algal carbon remains unknown.

Tsumune, D., Nishioka, J., Shimamoto, A., Takeda, S. & Tsuda, A. (2005): Physical behavior of the SEEDS iron-fertilized patch by sulphur hexafluoride tracer release. *Progress In Oceanography* **64(2-4), 111-127.**

The first iron (Fe) - fertilization experiment in the western North Pacific was carried out using SF6 to trace the Fe-fertilized water mass. A solution in 10,800 liters of seawater of 350 kg of Fe and 0.48 M of SF6 tracer was released into the mixed layer over a 8 × 10 km area. On the first underway transects through the patch after the Fe release, we observed a significant increase of dissolved Fe (ave. 2.89 nM). The fertilized patch was traced for 14 days by on-board SF6 analysis. A Lagrangian frame of reference was maintained by the use of a drogued GPS buoy released at the center of the patch. The patch moved westward at a rate of 6.8 km d-1. Mixed layer depth increased from 8.5 to 15 m during the experiment. Horizontal diffusivity was determined by the change of SF6 concentration in the patch. The horizontal diffusivity increased during the experiment. We evaluate here the fate of Fe in a Fe-fertilized patch using the dilution rate determined from sulphur hexafluoride (SF6) concentration. Dissolved Fe concentrations subsequently decreased rapidly to ~0.15 nM on Day 13. However, the dissolved Fe half-life of ~43 h was relatively longer than in previous Fe-enrichment studies, and we observed a larger increase of the centric diatom standing stock and corresponding drawdown of macro-nutrients and carbon dioxide than in the previous studies. The most important reason for the larger response was the phytoplankton species in the western North Pacific. In addition, the smaller diffusivity and shallower mixed layer were effective to sustain the higher dissolved Fe concentration compared to previous experiments. This might be one reason for the larger response of diatoms in SEEDS. The first iron (Fe) - fertilization experiment in the western North Pacific was carried out using SF6 to trace the Fe-fertilized water mass. A solution in 10,800 liters of seawater of 350 kg of Fe and 0.48 M of SF6 tracer was released into the mixed layer over a 8 × 10 km area. On the first underway transects through the patch after the Fe release, we observed a significant increase of dissolved Fe (ave. 2.89 nM). The fertilized patch was traced for 14 days by on-board SF6 analysis. A Lagrangian frame of reference was maintained by the use of a drogued GPS buoy released at the center of the patch. The patch moved westward at a rate of 6.8 km d-1. Mixed layer depth increased from 8.5 to 15 m during the experiment. Horizontal diffusivity was determined by the change of SF6 concentration in the patch. The horizontal diffusivity increased during the experiment. We evaluate here the fate of Fe in a Fe-fertilized patch using the dilution rate determined from sulphur hexafluoride (SF6) concentration. Dissolved Fe concentrations subsequently decreased rapidly to ~0.15 nM on Day 13. However, the dissolved Fe half-life of ~43 h was relatively longer than in previous Fe-enrichment studies, and we observed a larger increase of the centric diatom standing stock and corresponding drawdown of macro-nutrients and carbon dioxide than in the previous studies. The most important reason for the larger response was the phytoplankton species in the western North Pacific. In addition, the smaller diffusivity and shallower mixed layer were effective to sustain the higher dissolved Fe concentration compared to previous experiments. This might be one reason for the larger response of diatoms in SEEDS.

Kinugasa, M., Ishita, T., Sohrin, Y., Okamura, K., Takeda, S., Nishioka, J. & Tsuda, A. (2005): Dynamics of trace metals during the subarctic Pacific iron experiment for ecosystem dynamics study (SEEDS2001). *Progress In Oceanography* 64(2-4), 129-147.

During the first iron-enrichment experiment in the northwest subarctic Pacific (SEEDS2001), the dynamics of dissolved and acid dissolvable trace metals were studied. Seawater samples were collected from the upper water column (5-70 m) of In- and Out-patch stations. Immediately after the collection, an aliquot of seawater for dissolved species was filtered through an 0.2 [mu]m filter and acidified to pH 2.2. An aliquot for acid dissolvable species was acidified without filtration and stored for 3 years at an ambient temperature. Before the Fe enrichment, the dissolved Fe concentration in the surface mixed layer was <0.13 nM (the detection limit) and the acid dissolvable Fe concentration was 4.7 nM. The difference was a particulate fraction. Since the photochemical quantum efficiency of algal photosystem II was low, Fe in this fraction was not easily available to phytoplankton. After the Fe enrichment, acid dissolvable Fe in the patch decreased from 9.6 nM on day 2 to 4.6 nM on day 13, which was still ~3 nM higher than that at the Out-patch station. Dissolved Fe was 1.4 nM on day 2 and decreased exponentially to <0.13 nM on day 11. The concentration ratio of the acid dissolvable fraction to the dissolved fraction for the other trace metals was lower than that for Fe. The acid dissolvable concentrations for Mn, Co, Ni, Cu, Zn and Cd did not show significant change during the observation. The dissolved concentrations for Co, Ni, Cu, Zn and Cd in the surface layer on day 2 were 0.039, 5.0, 1.7, 2.2 and 0.27 nM, respectively. They decreased exponentially to 0.013, 4.3, 1.2, 0.87 and 0.21 nM on day 13, respectively. The mole ratio of the concentration difference between days 2 and 13 was similar to the elemental ratio reported for phytoplankton. These are the first data showing that mesoscale iron fertilization alters the dynamics of dissolved Co, Ni, Cu and Zn.

Noiri, Y., Kudo, I., Kiyosawa, H., Nishioka, J. & Tsuda, A. (2005): Influence of iron and temperature on growth, nutrient utilization ratios and phytoplankton species composition in the western subarctic Pacific Ocean during the SEEDS experiment. *Progress In Oceanography* 64(2-4), 149-166.

On-board bottle incubation experiments were carried out by adding different amounts of iron as part of the SEEDS (Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study) experiment to elucidate the phytoplankton community response to various iron concentrations. A temperature gradient from 5 to 18 °C was also applied to the incubation experiment because temperature also affects growth rate and metabolic functions such as enzyme reactions. Chlorophyll-a increased with increasing iron concentration, while the increase in chlorophyll-a in the control bottles (no iron addition) was nominal. Size-fractionated chlorophyll-a indicated that micro-phytoplankton (>10 [mu]m) became dominant in the iron-enriched bottles below 13 °C, which was consistent with the results from in situ observations in the simultaneous mesoscale iron-enrichment experiment and similar experiments for the other high nitrate and low chlorophyll (HNLC) waters. Macronutrients (silicate, nitrate and phosphate) were consumed in the bottles below 13 °C. The consumption ratio of silicate to nitrate was around 1:1 for iron-enriched bottles, but this ratio was slightly higher for control bottles, indicating a physiological stress due to low iron concentration on the diatoms. In contrast, nanophytoplankton (<10 [mu]m) were dominant in the iron-enriched bottles at 18 °C. There was no silicate utilization, but nitrate and phosphate were consumed in these bottles. Bacillariophyceae were dominant in the bottles below 13 °C, but Prymnesiophyceae became dominant at 18 °C. This is the first report demonstrating that temperature influences phytoplankton composition after iron addition in HNLC waters. The Chlorophyll-a specific increase rate for micro-plankton (>10 [mu]m) doubled from 5 to 8 °C and was the highest between 8 and 13 °C at the same iron concentration. The surface mixed layer temperature was 8 °C at the beginning of iron fertilization, but it had been 5 °C just 2 weeks before the experiment. This dramatic increase in growth rate with temperature is hypothesized to be the reason for SEEDS 2001 biomass changes being the highest reported response to a mesoscale Fe-enrichment experiment in HNLC waters. On-board bottle incubation experiments were carried out by adding different amounts of iron as part of the SEEDS (Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study) experiment to elucidate the phytoplankton community response to various iron concentrations. A temperature gradient from 5 to 18 °C was also applied to the incubation experiment because temperature also affects growth rate and metabolic functions such as enzyme reactions. Chlorophyll-a increased with increasing iron concentration, while the increase in chlorophyll-a in the control bottles (no iron addition) was nominal. Size-fractionated chlorophyll-a indicated that micro-phytoplankton (>10 [mu]m) became dominant in the iron-enriched bottles below 13 °C, which was consistent with the results from in situ observations in the simultaneous mesoscale iron-enrichment experiment and similar experiments for the other high nitrate and low chlorophyll (HNLC) waters. Macronutrients (silicate, nitrate and phosphate) were consumed in the bottles below 13 °C. The consumption ratio of silicate to nitrate was around 1:1 for iron-enriched bottles, but this ratio was slightly higher for control bottles, indicating a physiological stress due to low iron concentration on the diatoms. In contrast, nanophytoplankton (<10 [mu]m) were dominant in the iron-enriched bottles at 18 °C. There was no silicate utilization, but

nitrate and phosphate were consumed in these bottles. Bacillariophyceae were dominant in the bottles below 13 °C, but Prymnesiophyceae became dominant at 18 °C. This is the first report demonstrating that temperature influences phytoplankton composition after iron addition in HNLC waters. The Chlorophyll-a specific increase rate for micro-plankton (>10 [mu]m) doubled from 5 to 8 °C and was the highest between 8 and 13 °C at the same iron concentration. The surface mixed layer temperature was 8 °C at the beginning of iron fertilization, but it had been 5 °C just 2 weeks before the experiment. This dramatic increase in growth rate with temperature is hypothesized to be the reason for SEEDS 2001 biomass changes being the highest reported response to a mesoscale Fe-enrichment experiment in HNLC waters.

Suzuki, K., Hinuma, A., Saito, H., Kiyosawa, H., Liu, H., Saino, T. & Tsuda, A. (2005): Responses of phytoplankton and heterotrophic bacteria in the northwest subarctic Pacific to in situ iron fertilization as estimated by HPLC pigment analysis and flow cytometry. *Progress In Oceanography* **64(2-4), 167-187.**

To verify the hypothesis that the growth of phytoplankton in the Western Subarctic Gyre (WSG), which is located in the northwest subarctic Pacific, is suppressed by low iron (Fe) availability, an in situ Fe fertilization experiment was carried out in the summer of 2001. Changes over time in the abundance and community structure of phytoplankton were examined inside and outside an Fe patch using phytoplankton pigment markers analyzed by high-performance liquid chromatography (HPLC) and flow cytometry (FCM). In addition, the abundance of heterotrophic bacteria was also investigated by FCM. The chlorophyll a concentration was initially ca. 0.9 [mu]g l-1 in the surface mixed layer where diatoms and chlorophyll b-containing green algae (prasinophytes and chlorophytes) were predominant in the chlorophyll biomass. After the iron enrichment, the chlorophyll a concentration increased up to 9.1 [mu]g l-1 in the upper 10 m inside the Fe patch on Day 13. At the same time, the concentration of fucoxanthin (a diatom marker) increased 45-fold in the Fe patch, and diatoms accounted for a maximum 69% of the chlorophyll biomass. This result was consistent with a microscopic observation showing that the diatom Chaetoceros debilis had bloomed inside the Fe patch. However, chlorophyllide a concentrations also increased in the Fe patch with time, and reached a maximum of 2.2 [mu]g l-1 at 5 m depth on Day 13, suggesting that a marked abundance of senescent algal cells existed at the end of the experiment. The concentration of peridinin (a dinoflagellate marker) also reached a maximum 24-fold, and dinoflagellates had contributed significantly (>15%) to the chlorophyll biomass inside the Fe patch by the end of the experiment. Concentrations of 19'-hexanoyloxyfucoxanthin (a prymnesiophyte marker), 19'-butanoyloxyfucoxanthin (a pelagophyte marker), and alloxanthin (a cryptophyte marker) were only incremented a few-fold increment inside the Fe patch. On the contrary, chlorophyll b concentration reduced to almost half of the initial level in the upper 10 m water column inside the Fe patch at the end of the experiment. A decrease with time in the abundance of eukaryotic ultraphytoplankton (<ca. 5 [mu]m in size), in which chlorophyll b-containing green algae were possibly included was also observed by FCM. Overall, our results indicate that Fe supply can dramatically alter the abundance and community structure of phytoplankton in the WSG. On the other hand, cell density of heterotrophic bacteria inside the Fe patch was maximum at only

ca. 1.5-fold higher than that outside the Fe patch. This indicates that heterotrophic bacteria abundance was little respondent to the Fe enrichment. To verify the hypothesis that the growth of phytoplankton in the Western Subarctic Gyre (WSG), which is located in the northwest subarctic Pacific, is suppressed by low iron (Fe) availability, an in situ Fe fertilization experiment was carried out in the summer of 2001. Changes over time in the abundance and community structure of phytoplankton were examined inside and outside an Fe patch using phytoplankton pigment markers analyzed by high-performance liquid chromatography (HPLC) and flow cytometry (FCM). In addition, the abundance of heterotrophic bacteria was also investigated by FCM. The chlorophyll a concentration was initially ca. 0.9 [mu]g l-1 in the surface mixed layer where diatoms and chlorophyll b-containing green algae (prasinophytes and chlorophytes) were predominant in the chlorophyll biomass. After the iron enrichment, the chlorophyll a concentration increased up to 9.1 [mu]g l-1 in the upper 10 m inside the Fe patch on Day 13. At the same time, the concentration of fucoxanthin (a diatom marker) increased 45-fold in the Fe patch, and diatoms accounted for a maximum 69% of the chlorophyll biomass. This result was consistent with a microscopic observation showing that the diatom Chaetoceros debilis had bloomed inside the Fe patch. However, chlorophyllide a concentrations also increased in the Fe patch with time, and reached a maximum of 2.2 [mu]g l-1 at 5 m depth on Day 13, suggesting that a marked abundance of senescent algal cells existed at the end of the experiment. The concentration of peridinin (a dinoflagellate marker) also reached a maximum 24-fold, and dinoflagellates had contributed significantly (>15%) to the chlorophyll biomass inside the Fe patch by the end of the experiment. Concentrations of 19'-hexanoyloxyfucoxanthin (a prymnesiophyte marker), 19'-butanoyloxyfucoxanthin (a pelagophyte marker), and alloxanthin (a cryptophyte marker) were only incremented a few-fold increment inside the Fe patch. On the contrary, chlorophyll b concentration reduced to almost half of the initial level in the upper 10 m water column inside the Fe patch at the end of the experiment. A decrease with time in the abundance of eukaryotic ultraphytoplankton (<ca. 5 [mu]m in size), in which chlorophyll b-containing green algae were possibly included was also observed by FCM. Overall, our results indicate that Fe supply can dramatically alter the abundance and community structure of phytoplankton in the WSG. On the other hand, cell density of heterotrophic bacteria inside the Fe patch was maximum at only ca. 1.5-fold higher than that outside the Fe patch. This indicates that heterotrophic bacteria abundance was little respondent to the Fe enrichment.

Tsuda, A., et al. (2005a): Responses of diatoms to iron-enrichment (SEEDS) in the western subarctic Pacific, temporal and spatial comparisons. *Progress In Oceanography* **64(2-4), 189-205.**

Phytoplankton species composition was analyzed inside and outside of the iron-enriched patch during the SEEDS experiment. Before the iron-enrichment, the phytoplankton community consisted of similar proportions of pico-, nano- and micro-sized phytoplankton, and the micro-phytoplankton was dominated by the pennate diatom Pseudo-nitzschia turgidula. Although all the diatoms, except the nano-sized Fragilariopsis sp., increased during the two weeks of the observation period, the flora in the patch dramatically changed with the increase of phytoplankton biomass to a centric diatom-dominated community. Neritic diatoms, especially Chaetoceros

debilis, showed higher growth rates than other diatoms, without any delay in the initiation of growth after the enrichment, and accounted for 90% of the micro-phytoplankton after day 9. In contrast, the oceanic diatoms showed distinct delays in the initiation of growth. We conclude that the responses of the diatoms to the manipulation of iron concentration were different by species, and the fast and intensive response of the phytoplankton to iron-enrichment resulted from the presence of a small amount of neritic diatoms at the study site. The important factors that determine the dominant species in the bloom are the potential growth rates under an iron-replete condition and the growth lag. Abundant species in the patch are widely distributed in the North Pacific and their relative contributions in the Oyashio area and at Stn KNOT are high from spring to summer. However, a characteristic difference of species composition between the SEEDS bloom and natural blooms was the lack of Thalassiosira and Coscinodiscus species in the patch, which usually account for a major part of the phytoplankton community under blooming conditions in the western North Pacific. Phytoplankton species composition was analyzed inside and outside of the iron-enriched patch during the SEEDS experiment. Before the iron-enrichment, the phytoplankton community consisted of similar proportions of pico-, nano- and micro-sized phytoplankton, and the micro-phytoplankton was dominated by the pennate diatom Pseudo-nitzschia turgidula. Although all the diatoms, except the nano-sized Fragilariopsis sp., increased during the two weeks of the observation period, the flora in the patch dramatically changed with the increase of phytoplankton biomass to a centric diatom-dominated community. Neritic diatoms, especially Chaetoceros debilis, showed higher growth rates than other diatoms, without any delay in the initiation of growth after the enrichment, and accounted for 90% of the micro-phytoplankton after day 9. In contrast, the oceanic diatoms showed distinct delays in the initiation of growth. We conclude that the responses of the diatoms to the manipulation of iron concentration were different by species, and the fast and intensive response of the phytoplankton to iron-enrichment resulted from the presence of a small amount of neritic diatoms at the study site. The important factors that determine the dominant species in the bloom are the potential growth rates under an iron-replete condition and the growth lag. Abundant species in the patch are widely distributed in the North Pacific and their relative contributions in the Oyashio area and at Stn KNOT are high from spring to summer. However, a characteristic difference of species composition between the SEEDS bloom and natural blooms was the lack of Thalassiosira and Coscinodiscus species in the patch, which usually account for a major part of the phytoplankton community under blooming conditions in the western North Pacific.

Kudo, I., Noiri, Y., Imai, K., Nojiri, Y., Nishioka, J. & Tsuda, A. (2005): Primary productivity and nitrogenous nutrient assimilation dynamics during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study. *Progress In Oceanography* 64(2-4), 207-221.

Primary productivity and uptake rates of nitrate and ammonium were measured during an iron enrichment-experiment in the western subarctic Pacific Ocean using stable 13C and 15N isotope methods with simulated, on-board, for 24-h incubations. Nitrate, phosphate and silicate before the iron enrichment in the surface mixed layer (0-10 m) were abundant at 17, 1.5 and 34 [mu]M, respectively. Primary productivity

in the upper 20 m ranged from 10 to 30 mg C m-3 d-1 on Day 0 (the day of iron fertilization) and did not change outside the iron patch during 13 days of the observation. Primary productivity in the iron patch increased more than 10-fold after Day 7 and the maximum of 310 mg C m-3 d-1 was observed on Day 9. The elevated primary productivity continued until Day 13 (end of the observation). The integrated primary productivity in the photic zone was about 2 g C m-2 d-1 after Day 7. During 13 days of the observation, 16.5 g C m-2 was fixed in the patch, while C fixation was 4.5 g C m-2 outside. Absolute nitrate uptake at 5 m depth was 0.2 [mu]M d-1 on Day 0, almost same as the ammonium uptake rate. Nitrate uptake sharply increased 20 times after Day 7. The maximum rate of 4.2 [mu]M d-1 was observed on Day 9. Total nitrate uptake at 5 m between Days 4 and 9 was 10.8 [mu]M, which was comparable to the net decrease of nitrate at 8.5 [mu]M at this depth. Uptake rate of ammonium was 0.2 [mu]M d-1 on Day 0 and had not changed by Day 13. The f-ratio (a ratio of nitrate uptake to total nitrogen (nitrate and ammonium) uptake) was 0.4-0.6 before Day 4, but increased to 0.95 on Day 7 and remained high until Day 13. These results suggest that the nitrate assimilation pathway was induced by the iron enrichment to meet the high nitrogen demand from rapid growth of the dominant diatom Chaetoceros dedilis. Relative uptake rate among nutrients was estimated from their apparent concentration change at 5 m in the patch. Nitrate and phosphate decreased at a molar ratio of 15.5, close to Redfield's stoichiometry. Silicate to nitrate uptake ratio, however, changed sharply on Day 9 from 1.6 to 3.0, indicating physiological stress on growing diatoms. Photosynthetically active radiation (PAR) at 5 m decreased from 400 to <100 [mu]mol m-2 s-1 after Day 8 due to the high biomass of phytoplankton within the patch. Dissolved iron concentration also decreased to less than 0.3 nM after Day 9. This concentration was below the half saturation level for iron (Ks) obtained from on-board iron-addition incubations. These results suggest that low light and low iron concentration caused the physiological stress on diatoms after Day 8. Primary productivity and uptake rates of nitrate and ammonium were measured during an iron enrichment-experiment in the western subarctic Pacific Ocean using stable 13C and 15N isotope methods with simulated, on-board, for 24-h incubations. Nitrate, phosphate and silicate before the iron enrichment in the surface mixed layer (0-10 m) were abundant at 17, 1.5 and 34 [mu]M, respectively. Primary productivity in the upper 20 m ranged from 10 to 30 mg C m-3 d-1 on Day 0 (the day of iron fertilization) and did not change outside the iron patch during 13 days of the observation. Primary productivity in the iron patch increased more than 10-fold after Day 7 and the maximum of 310 mg C m-3 d-1 was observed on Day 9. The elevated primary productivity continued until Day 13 (end of the observation). The integrated primary productivity in the photic zone was about 2 g C m-2 d-1 after Day 7. During 13 days of the observation, 16.5 g C m-2 was fixed in the patch, while C fixation was 4.5 g C m-2 outside. Absolute nitrate uptake at 5 m depth was 0.2 [mu]M d-1 on Day 0, almost same as the ammonium uptake rate. Nitrate uptake sharply increased 20 times after Day 7. The maximum rate of 4.2 [mu]M d-1 was observed on Day 9. Total nitrate uptake at 5 m between Days 4 and 9 was 10.8 [mu]M, which was comparable to the net decrease of nitrate at 8.5 [mu]M at this depth. Uptake rate of ammonium was 0.2 [mu]M d-1 on Day 0 and had not changed by Day 13. The f-ratio (a ratio of nitrate uptake to total nitrogen (nitrate and ammonium) uptake) was 0.4-0.6 before Day 4, but increased to 0.95 on Day 7 and remained high until Day 13. These results suggest that the nitrate assimilation pathway was induced by the iron enrichment to meet the high nitrogen demand from rapid growth of the dominant diatom Chaetoceros dedilis. Relative uptake rate among nutrients was estimated from their

apparent concentration change at 5 m in the patch. Nitrate and phosphate decreased at a molar ratio of 15.5, close to Redfield's stoichiometry. Silicate to nitrate uptake ratio, however, changed sharply on Day 9 from 1.6 to 3.0, indicating physiological stress on growing diatoms. Photosynthetically active radiation (PAR) at 5 m decreased from 400 to <100 [mu]mol m-2 s-1 after Day 8 due to the high biomass of phytoplankton within the patch. Dissolved iron concentration also decreased to less than 0.3 nM after Day 9. This concentration was below the half saturation level for iron (Ks) obtained from on-board iron-addition incubations. These results suggest that low light and low iron concentration caused the physiological stress on diatoms after Day 8.

Saito, H., Suzuki, K., Hinuma, A., Ota, T., Fukami, K., Kiyosawa, H., Saino, T. & Tsuda, A. (2005): Responses of microzooplankton to in situ iron fertilization in the western subarctic Pacific (SEEDS). *Progress In Oceanography* **64(2-4), 223-236.**

Microzooplankton grazing plays an important role in maintaining the phytoplankton biomass low in HNLC waters where iron depletion limits the phytoplankton growth. When the iron limitation is relieved by natural iron supply or manipulation, phytoplankton biomass increases with a floristic shift because responses of phytoplankton and its grazer to such a perturbation are variable by species. During the first in situ iron fertilization (IF) experiment in the western subarctic Pacific (SEEDS), microzooplankton responses to changes in phytoplankton community structure and biomass were examined. Gross growth rate (GGR) of eukaryotic ultraphytoplankton (EUKU, < ca. 5 [mu]m in size) increased 2 days after the IF (D2) and that of the cyanobacteria Synechococcus spp. (SYN) peaked on D4 and then decreased gradually with time until D13, the end of the experiment. Net growth rate (NGR: GGR - grazing rate) increased after the IF however, the GGRs and the grazing rates on EUKU and SYN balanced well at the end of the experiment as well as observed prior to the IF. Total chlorophyll a concentration increased after D4 and increased to >16 mg m-3 after D9. Although primary productivity was >1.6 g C m-2 d-1 in the surface mixed layer and GGRs of total phytoplankton were >0.8 d-1 during D9 and D13, the total chlorophyll a concentration was more or less steady after D9. This phytoplankton bloom in response to the IF was dominated by a centric diatom Chaetoceros debilis and most of the other diatom species and nano-phytoplankton increased their biomass. Grazing rates on total phytoplankton decreased with the increase in chlorophyll a concentration after the IF from 0.3 d-1 initially to <0.2 d-1 on D9, and then rapidly increased to 0.70 d-1 on D11. Aloricate ciliates were the most dominant microzooplankton (>10 [mu]m) both in abundance and biomass prior to the IF and gradually decreased with the developing diatom bloom. Heterotrophic dinoflagellates, dominated by Gyrodinium spp., increased rapidly after D11. Both the abundance and biomass of heterotrophic dinoflagellates on D13 were 5 times those prior to the IF, and they were the most dominant micrograzer at the end of the experiment. This indicates that grazing by dinoflagellates prevented further development of the diatom bloom after D9, together with limitations of light and iron bioavailability. The present study showed that micrograzers responded to the floristic shift induced by the IF with a time lag and their grazing was an important controlling factor not only on the pico- and nano-phytoplankton but also on the microphytoplankton including chain-forming diatoms. It also showed that heterotrophic dinoflagellate grazing has an important role

in the food-web dynamics and biogeochemical cycle after natural or manipulated perturbations in the HNLC western subarctic Pacific. Microzooplankton grazing plays an important role in maintaining the phytoplankton biomass low in HNLC waters where iron depletion limits the phytoplankton growth. When the iron limitation is relieved by natural iron supply or manipulation, phytoplankton biomass increases with a floristic shift because responses of phytoplankton and its grazer to such a perturbation are variable by species. During the first in situ iron fertilization (IF) experiment in the western subarctic Pacific (SEEDS), microzooplankton responses to changes in phytoplankton community structure and biomass were examined. Gross growth rate (GGR) of eukaryotic ultraphytoplankton (EUKU, < ca. 5 [mu]m in size) increased 2 days after the IF (D2) and that of the cyanobacteria Synechococcus spp. (SYN) peaked on D4 and then decreased gradually with time until D13, the end of the experiment. Net growth rate (NGR: GGR - grazing rate) increased after the IF however, the GGRs and the grazing rates on EUKU and SYN balanced well at the end of the experiment as well as observed prior to the IF. Total chlorophyll a concentration increased after D4 and increased to >16 mg m-3 after D9. Although primary productivity was >1.6 g C m-2 d-1 in the surface mixed layer and GGRs of total phytoplankton were >0.8 d-1 during D9 and D13, the total chlorophyll a concentration was more or less steady after D9. This phytoplankton bloom in response to the IF was dominated by a centric diatom Chaetoceros debilis and most of the other diatom species and nano-phytoplankton increased their biomass. Grazing rates on total phytoplankton decreased with the increase in chlorophyll a concentration after the IF from 0.3 d-1 initially to <0.2 d-1 on D9, and then rapidly increased to 0.70 d-1 on D11. Aloricate ciliates were the most dominant microzooplankton (>10 [mu]m) both in abundance and biomass prior to the IF and gradually decreased with the developing diatom bloom. Heterotrophic dinoflagellates, dominated by Gyrodinium spp., increased rapidly after D11. Both the abundance and biomass of heterotrophic dinoflagellates on D13 were 5 times those prior to the IF, and they were the most dominant micrograzer at the end of the experiment. This indicates that grazing by dinoflagellates prevented further development of the diatom bloom after D9, together with limitations of light and iron bioavailability. The present study showed that micrograzers responded to the floristic shift induced by the IF with a time lag and their grazing was an important controlling factor not only on the pico- and nano-phytoplankton but also on the microphytoplankton including chain-forming diatoms. It also showed that heterotrophic dinoflagellate grazing has an important role in the food-web dynamics and biogeochemical cycle after natural or manipulated perturbations in the HNLC western subarctic Pacific.

Tsuda, A., Saito, H., Nishioka, J. & Ono, T. (2005b): Mesozooplankton responses to iron-fertilization in the western subarctic Pacific (SEEDS2001). *Progress In Oceanography* 64(2-4), 237-251.

A mesoscale iron-fertilization experiment was carried out in the western subarctic Pacific during summer 2001. The iron-patch was traced for 14 days after the fertilization, and the abundance and behavior of mesozooplankton were compared with those outside of the patch. The phytoplankton biomass in the patch rapidly increased to over 15 times the initial level by the later half of the observation period,

and was composed of large-sized (>10 mm), centric diatoms. Dominant zooplankton species in the upper 200-m depth were large copepods: Neocalanus plumchrus, Neocalanus cristatus, Eucalanus bungii and Metridia pacifica. Mesozoplankton biomass as well as species composition did not change significantly in the patch over the observation period. Furthermore, no changes of vertical distribution or diel vertical migration were observed for any species or stages of mesozooplankton throughout the observation period. However, the abundance of the first copepodite stages of N. plumchrus and E. bungii increased several fold in the patch after the diatom bloom formation compared to the densities outside the patch. The increases of both species are considered to be due to lowered mortality during the egg and nauplius stages. Spawning of N. plumchrus takes place at depth using lipid storage, while spawning of E. bungii takes place in the surface layer supported by grazing. These facts suggest that the relative importance of nauplii in the diets of the large copepods was decreased in the patch by the diatom bloom. Gut-pigment contents of dominant copepods in the patch increased 4-18 times, and the maximum values were observed during the bloom peak. However, the grazing impact on phytoplankton was low throughout the experiment, especially during the bloom period (<6% of the primary production). A mesoscale iron-fertilization experiment was carried out in the western subarctic Pacific during summer 2001. The iron-patch was traced for 14 days after the fertilization, and the abundance and behavior of mesozooplankton were compared with those outside of the patch. The phytoplankton biomass in the patch rapidly increased to over 15 times the initial level by the later half of the observation period, and was composed of large-sized (>10 mm), centric diatoms. Dominant zooplankton species in the upper 200-m depth were large copepods: Neocalanus plumchrus, Neocalanus cristatus, Eucalanus bungii and Metridia pacifica. Mesozoplankton biomass as well as species composition did not change significantly in the patch over the observation period. Furthermore, no changes of vertical distribution or diel vertical migration were observed for any species or stages of mesozooplankton throughout the observation period. However, the abundance of the first copepodite stages of N. plumchrus and E. bungii increased several fold in the patch after the diatom bloom formation compared to the densities outside the patch. The increases of both species are considered to be due to lowered mortality during the egg and nauplius stages. Spawning of N. plumchrus takes place at depth using lipid storage, while spawning of E. bungii takes place in the surface layer supported by grazing. These facts suggest that the relative importance of nauplii in the diets of the large copepods was decreased in the patch by the diatom bloom. Gut-pigment contents of dominant copepods in the patch increased 4-18 times, and the maximum values were observed during the bloom peak. However, the grazing impact on phytoplankton was low throughout the experiment, especially during the bloom period (<6% of the primary production).

Ramaiah, N., et al. (2005): Effect of iron enrichment on the dynamics of transparent exopolymer particles in the western subarctic Pacific. *Progress In Oceanography* 64(2-4), 253-261.

Dynamics of transparent exopolymer particles (TEP) was studied during the first in situ iron-enrichment experiment conducted in the western subarctic Pacific in July-August 2001, with the goal of evaluating the contribution of TEP to vertical flux as a

result of increased primary production following iron enrichment in open ocean ecosystems. Subsequent to the enhancement of phytoplankton production, we observed increase in TEP concentration in the surface layer and sedimentation of organic matter beneath it. Vertical profiles of TEP, chlorophyll a (Chl a) and particulate organic carbon (POC) were obtained from six depths between 5 and 70 m, from a station each located inside and outside the enriched patch. TEP and total mass flux were estimated from the floating sediment traps deployed at 200 m depth. Chl a and TEP concentrations outside the patch varied from 0.2 to 1.9 [mu]g L-1 and 40-60 [mu]g XG equiv. L-1, respectively. Inside the patch, Chl a increased drastically from day 7 reaching the peak of 19.2 [mu]g L-1 on day 13, which coincided with the TEP peak of 189 [mu]g XG equiv. L-1. TEP flux in the sediment trap increased from 41 to 88 mg XG equiv. m-2 d-1, with 8-14% contribution of TEP to total mass flux. This forms the basic data set on ambient concentrations of TEP in the western subarctic Pacific, and evaluation of the effect of iron enrichment on TEP. Dynamics of transparent exopolymer particles (TEP) was studied during the first in situ iron-enrichment experiment conducted in the western subarctic Pacific in July-August 2001, with the goal of evaluating the contribution of TEP to vertical flux as a result of increased primary production following iron enrichment in open ocean ecosystems. Subsequent to the enhancement of phytoplankton production, we observed increase in TEP concentration in the surface layer and sedimentation of organic matter beneath it. Vertical profiles of TEP, chlorophyll a (Chl a) and particulate organic carbon (POC) were obtained from six depths between 5 and 70 m, from a station each located inside and outside the enriched patch. TEP and total mass flux were estimated from the floating sediment traps deployed at 200 m depth. Chl a and TEP concentrations outside the patch varied from 0.2 to 1.9 [mu]g L-1 and 40-60 [mu]g XG equiv. L-1, respectively. Inside the patch, Chl a increased drastically from day 7 reaching the peak of 19.2 [mu]g L-1 on day 13, which coincided with the TEP peak of 189 [mu]g XG equiv. L-1. TEP flux in the sediment trap increased from 41 to 88 mg XG equiv. m-2 d-1, with 8-14% contribution of TEP to total mass flux. This forms the basic data set on ambient concentrations of TEP in the western subarctic Pacific, and evaluation of the effect of iron enrichment on TEP.

Aono, T., Yamada, M., Kudo, I., Imai, K., Nojiri, Y. & Tsuda, A. (2005a): Export fluxes of particulate organic carbon estimated from 234Th/238U disequilibrium during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS 2001). *Progress In Oceanography* **64(2-4), 263-282.**

The Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) was carried out in the western subarctic gyre of the North Pacific to verify the iron-limitation hypothesis. Activities of dissolved 234Th in the upper 200 m of the water column and of particulate 234Th collected in a drifting sediment trap were measured during SEEDS 2001. Dissolved 234Th activities decreased and suspended particulate 234Th increased in the upper 20 m of the water column with the formation of an iron-induced phytoplankton bloom. The calculated residence times of the dissolved and particulate 234Th in the upper 20 m of the water column ranged from 2 to 13 d and 13 to 29 d, respectively. The ratios of particulate organic carbon (POC)/234Thp ([mu]mol dpm-1) in the settling particles at 200 m depth varied between 1.94 and

4.02, and these levels were 10% those for the suspended particles. No large increase of the POC export flux was observed for the drifting sediment trap deployments during the observation period. In addition, the POC export fluxes derived from 234Th with a non-steady-state model varied from 10.1 to 38.3 mmol m-2 d-1. The ratio of the estimated POC export flux to primary production, ThE, was nearly constant (0.23-0.24) from July 20 to 27 (D2 and D9 after iron-enrichment) and decreased to 0.18 on July 31 (D13 after iron-enrichment). Regardless of whether the POC export fluxes increased, there was no change in ThE. The increase of the POC export fluxes estimated from 234Th was much smaller than the increase of primary production. Thus, no large POC export fluxes are concluded to have occurred from the iron-enrichment patch, though the removal flux of 234Th in settling particles increased with particulate biogenic silica fluxes as the phytoplankton bloom progressed. The Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) was carried out in the western subarctic gyre of the North Pacific to verify the iron-limitation hypothesis. Activities of dissolved 234Th in the upper 200 m of the water column and of particulate 234Th collected in a drifting sediment trap were measured during SEEDS 2001. Dissolved 234Th activities decreased and suspended particulate 234Th increased in the upper 20 m of the water column with the formation of an iron-induced phytoplankton bloom. The calculated residence times of the dissolved and particulate 234Th in the upper 20 m of the water column ranged from 2 to 13 d and 13 to 29 d, respectively. The ratios of particulate organic carbon (POC)/234Thp ([mu]mol dpm-1) in the settling particles at 200 m depth varied between 1.94 and 4.02, and these levels were 10% those for the suspended particles. No large increase of the POC export flux was observed for the drifting sediment trap deployments during the observation period. In addition, the POC export fluxes derived from 234Th with a non-steady-state model varied from 10.1 to 38.3 mmol m-2 d-1. The ratio of the estimated POC export flux to primary production, ThE, was nearly constant (0.23-0.24) from July 20 to 27 (D2 and D9 after iron-enrichment) and decreased to 0.18 on July 31 (D13 after iron-enrichment). Regardless of whether the POC export fluxes increased, there was no change in ThE. The increase of the POC export fluxes estimated from 234Th was much smaller than the increase of primary production. Thus, no large POC export fluxes are concluded to have occurred from the iron-enrichment patch, though the removal flux of 234Th in settling particles increased with particulate biogenic silica fluxes as the phytoplankton bloom progressed.

Yoshie, N., Fujii, M. & Yamanaka, Y. (2005): Ecosystem changes after the SEEDS iron fertilization in the western North Pacific simulated by a one-dimensional ecosystem model. *Progress In Oceanography* 64(2-4), 283-306.

We have developed a one-dimensional ecosystem model considering explicitly two groups of diatoms: centric and pennate. The model was applied to the iron-enrichment experiment, SEEDS (Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study) in the western North Pacific (48.5°N, 165°E). We assumed that the pennate diatoms are not stressed by the iron limitation, but that the centric diatoms are significantly stressed and their photosynthetic rate is high when released from iron limitation. The iron-enrichment experiment was conducted by changing the physiological parameters for diatoms (the initial slope of the photosynthetic rate and the potential maximum photosynthetic rate). The model successfully reproduced the

time-series of CO2 fugacity and the vertical distributions of chlorophyll-a and nutrients observed in SEEDS. The simulated results in the two-group model, especially the starting time of the diatom bloom, are better than those in the one-group model. We find that it is the transition of dominance, from pennate to centric diatoms, rather than a physiological response of each group that causes the lag between iron-enrichment and the diatom bloom. In the simulations, the added iron's effect on the ecosystem continues for about 40 days. The model results suggest that the export flux during the observation period is only about 20% of the total export flux generated by iron-enrichment. For SEEDS, our simulated uptake of atmospheric CO2 and the export of particulate organic carbon at 100 m depth are 0.57 and 1.29 mol C m-2, respectively, which are converted to 1720 and 3880 tC by assuming the patch's area to be 250 km2, and to 4.90 and 11.1 tC kg-1 Fe with the addition of 350 kg of iron. We have developed a one-dimensional ecosystem model considering explicitly two groups of diatoms: centric and pennate. The model was applied to the iron-enrichment experiment, SEEDS (Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study) in the western North Pacific (48.5°N, 165°E). We assumed that the pennate diatoms are not stressed by the iron limitation, but that the centric diatoms are significantly stressed and their photosynthetic rate is high when released from iron limitation. The iron-enrichment experiment was conducted by changing the physiological parameters for diatoms (the initial slope of the photosynthetic rate and the potential maximum photosynthetic rate). The model successfully reproduced the time-series of CO2 fugacity and the vertical distributions of chlorophyll-a and nutrients observed in SEEDS. The simulated results in the two-group model, especially the starting time of the diatom bloom, are better than those in the one-group model. We find that it is the transition of dominance, from pennate to centric diatoms, rather than a physiological response of each group that causes the lag between iron-enrichment and the diatom bloom. In the simulations, the added iron's effect on the ecosystem continues for about 40 days. The model results suggest that the export flux during the observation period is only about 20% of the total export flux generated by iron-enrichment. For SEEDS, our simulated uptake of atmospheric CO2 and the export of particulate organic carbon at 100 m depth are 0.57 and 1.29 mol C m-2, respectively, which are converted to 1720 and 3880 tC by assuming the patch's area to be 250 km2, and to 4.90 and 11.1 tC kg-1 Fe with the addition of 350 kg of iron.

Fujii, M., Yoshie, N., Yamanaka, Y. & Chai, F. (2005): Simulated biogeochemical responses to iron enrichments in three high nutrient, low chlorophyll (HNLC) regions. *Progress In Oceanography* 64(2-4), 307-324.

To fill temporal gaps in iron-enrichment experimental data and gain further understanding of marine ecosystem responses to iron enrichments, we apply a fifteen-compartment ecosystem model to three iron-enrichment sites, namely SEEDS (the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study; 48.5°N, 165°E) in the western North Pacific, SOIREE (the Southern Ocean Iron RElease Experiment; 61°S, 140°E) in the Southern Ocean, and IronExII (the second mesoscale iron enrichment experiment; 3.5°S, 104°W) in the Equatorial Pacific. The ecological effects of iron in the model are represented by changing two photosynthetic parameters during the iron-enrichment period. The model results successfully reproduce the observed biogeochemical responses inside and outside the iron patch at

each site, such as rapid increases in plankton biomass and biological productivity, and decreases in surface nutrients and pCO2, inside the patch. However, the modeled timing and magnitude of changes differ among the sites because of differences in both physical environments and plankton species. After the iron enrichment, the diatom productivity is strongly controlled by light at SOIREE and by silicate at IronExII and SEEDS. Light limitation due to self-shading by the phytoplankton is significant during the bloom at all sites. Sensitivity analysis of the model results to duration of the iron enrichment reveals that long-term multiple infusions over more than a week would not be effective at SEEDS because of strong silicate limitation on diatom growth. Sensitivity of the model to water temperature shows that export production is higher at lower temperatures, because of slower recycling of particulate organic carbon. Therefore, the e-ratio (the ratio of export production to primary production) is inversely correlated with temperature, and the relationship can be described with a linear function. Through this study, we conclude that ecosystem modeling is a powerful tool to help design future iron-enrichment experiments and observational plans. To fill temporal gaps in iron-enrichment experimental data and gain further understanding of marine ecosystem responses to iron enrichments, we apply a fifteen-compartment ecosystem model to three iron-enrichment sites, namely SEEDS (the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study; 48.5°N, 165°E) in the western North Pacific, SOIREE (the Southern Ocean Iron RElease Experiment; 61°S, 140°E) in the Southern Ocean, and IronExII (the second mesoscale iron enrichment experiment; 3.5°S, 104°W) in the Equatorial Pacific. The ecological effects of iron in the model are represented by changing two photosynthetic parameters during the iron-enrichment period. The model results successfully reproduce the observed biogeochemical responses inside and outside the iron patch at each site, such as rapid increases in plankton biomass and biological productivity, and decreases in surface nutrients and pCO2, inside the patch. However, the modeled timing and magnitude of changes differ among the sites because of differences in both physical environments and plankton species. After the iron enrichment, the diatom productivity is strongly controlled by light at SOIREE and by silicate at IronExII and SEEDS. Light limitation due to self-shading by the phytoplankton is significant during the bloom at all sites. Sensitivity analysis of the model results to duration of the iron enrichment reveals that long-term multiple infusions over more than a week would not be effective at SEEDS because of strong silicate limitation on diatom growth. Sensitivity of the model to water temperature shows that export production is higher at lower temperatures, because of slower recycling of particulate organic carbon. Therefore, the e-ratio (the ratio of export production to primary production) is inversely correlated with temperature, and the relationship can be described with a linear function. Through this study, we conclude that ecosystem modeling is a powerful tool to help design future iron-enrichment experiments and observational plans.

Aono, T., Yamada, M., Kudo, I., Imai, K., Nojiri, Y. & Tsuda, A. (2005b): Export fluxes of particulate organic carbon estimated from Th-234/U-238 disequilibrium during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS 2001). *Progress in Oceanography* **64(2-4), 263-282.**

The Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) was carried out in the western subarctic gyre of the North Pacific to verify the iron-limitation hypothesis. Activities of dissolved Th-234 in the upper 200 m of the water column and of particulate Th-234 collected in a drifting sediment trap were measured during SEEDS 2001. Dissolved Th-234 activities decreased and suspended particulate Th-234 increased in the upper 20 m of the water column with the formation of an iron-induced phytoplankton bloom. The calculated residence times of the dissolved and particulate Th-234 in the upper 20 m of the water column ranged from 2 to 13 d and 13 to 29 d, respectively. The ratios of particulate organic carbon (POC)/Th-234(p) (μ mol dpm(-1)) in the settling particles at 200 m depth varied between 1.94 and 4.02, and these levels were 10% those for the suspended particles. No large increase of the POC export flux was observed for the drifting sediment trap deployments during the observation period. In addition, the POC export fluxes derived from Th-234 with a non-steady-state model varied from 10.1 to 38.3 mmol m(-2) d(-1). The ratio of the estimated POC export flux to primary production, Th-E, was nearly constant (0.23-0.24) from July 20 to 27 (D2 and D9 after iron-enrichment) and decreased to 0.18 on July 31 (D13 after iron-enrichment). Regardless of whether the POC export fluxes increased, there was no change in Th-E. The increase of the POC export fluxes estimated from Th-234 was much smaller than the increase of primary production. Thus, no large POC export fluxes are concluded to have occurred from the iron-enrichment patch, though the removal flux of Th-234 in settling particles increased with particulate biogenic silica fluxes as the phytoplankton bloom progressed. All rights reserved. The Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) was carried out in the western subarctic gyre of the North Pacific to verify the iron-limitation hypothesis. Activities of dissolved Th-234 in the upper 200 m of the water column and of particulate Th-234 collected in a drifting sediment trap were measured during SEEDS 2001. Dissolved Th-234 activities decreased and suspended particulate Th-234 increased in the upper 20 m of the water column with the formation of an iron-induced phytoplankton bloom. The calculated residence times of the dissolved and particulate Th-234 in the upper 20 m of the water column ranged from 2 to 13 d and 13 to 29 d, respectively. The ratios of particulate organic carbon (POC)/Th-234(p) (μ mol dpm(-1)) in the settling particles at 200 m depth varied between 1.94 and 4.02, and these levels were 10% those for the suspended particles. No large increase of the POC export flux was observed for the drifting sediment trap deployments during the observation period. In addition, the POC export fluxes derived from Th-234 with a non-steady-state model varied from 10.1 to 38.3 mmol m(-2) d(-1). The ratio of the estimated POC export flux to primary production, Th-E, was nearly constant (0.23-0.24) from July 20 to 27 (D2 and D9 after iron-enrichment) and decreased to 0.18 on July 31 (D13 after iron-enrichment). Regardless of whether the POC export fluxes increased, there was no change in Th-E. The increase of the POC export fluxes estimated from Th-234 was much smaller than the increase of primary production. Thus, no large POC export fluxes are concluded to have occurred from the iron-enrichment patch, though the removal flux of Th-234 in settling particles increased with particulate biogenic silica fluxes as the phytoplankton bloom progressed. All rights reserved.

Saito, H., Ota, T., Suzuki, K., Nishioka, J. & Tsuda, A. (2006): Role of heterotrophic dinoflagellate Gyrodinium sp in the fate of an iron induced diatom bloom. *Geophys. Res. Lett.* **33(9), L09602**

Iron enrichment to high-nutrient low-chlorophyll (HNLC) regions is being considered as a possible way of atmospheric CO2 sequestration to the deep sea. Mesoscale iron-enrichment to the HNLC subarctic Pacific induced a massive diatom bloom and led to a large decrease in pCO(2). In response to the diatom bloom, the heterotrophic dinoflagellate Gyrodinium sp. increased and phagotrophically fed on the diatoms up to 12 times their length. Mathematical simulations show the carbon fixed by diatoms is mostly respired by Gyrodinium sp. in the sea surface. The emergence of initially rare species and their key biogeochemical roles were unexpected due to our limited understanding of food-web components. This indicates that the prediction of ecosystem responses to natural or anthropogenic perturbation remains a challenging issue. Effective carbon sequestration as a geoengineering technique may not be accomplished by purposeful iron-enrichment, at least in the western subarctic Pacific where rapid-growth diatom grazers stand by. Iron enrichment to high-nutrient low-chlorophyll (HNLC) regions is being considered as a possible way of atmospheric CO2 sequestration to the deep sea. Mesoscale iron-enrichment to the HNLC subarctic Pacific induced a massive diatom bloom and led to a large decrease in pCO(2). In response to the diatom bloom, the heterotrophic dinoflagellate Gyrodinium sp. increased and phagotrophically fed on the diatoms up to 12 times their length. Mathematical simulations show the carbon fixed by diatoms is mostly respired by Gyrodinium sp. in the sea surface. The emergence of initially rare species and their key biogeochemical roles were unexpected due to our limited understanding of food-web components. This indicates that the prediction of ecosystem responses to natural or anthropogenic perturbation remains a challenging issue. Effective carbon sequestration as a geoengineering technique may not be accomplished by purposeful iron-enrichment, at least in the western subarctic Pacific where rapid-growth diatom grazers stand by.