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Evidence for the Grazing Hypothesis: Grazing Reduces Phytoplankton Responses of the HNLC Ecosystem to Iron Enrichment in the Western Subarctic Pacific (SEEDS II)

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A mesoscale iron-enrichment study (SEEDS II) was carried out in the western subarctic Pacific in the summer of 2004. The iron patch was traced for 26 days, which included observations of the development and the decline of the bloom by mapping with sulfur hexafluoride. The experiment was conducted at almost the same location and the same season as SEEDS (previous iron-enrichment experiment). However, the results were very different between SEEDS and SEEDS II. A high accumulation of phytoplankton biomass (~18 mg chl m^{-3}) was characteristic of SEEDS. In contrast, in SEEDS II, the surface chlorophyll-*a* accumulation was lower, 0.8 to 2.48 mg m^{-3}, with no prominent

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diatom bloom. Photosynthetic competence in terms of F_v/F_m for the total phytoplankton community in the surface waters increased after the iron enrichments and returned to the ambient level by day 20. These results suggest that the photosynthetic physiology of the phytoplankton assemblage was improved by the iron enrichments and returned to an iron-stressed condition during the declining phase of the bloom. Pico-phytoplankton (<2 μm) became dominant in the chlorophyll-*a* size distribution after the bloom. We observed a nitrate drawdown of 3.8 μM in the patch (day 21), but there was no difference in silicic acid concentration between inside and outside the patch. Mesozooplankton (copepod) biomass was three to five times higher during the bloom-development phase in SEEDS II than in SEEDS. The copepod biomass increased exponentially. The grazing rate estimation indicates that the copepod grazing prevented the formation of an extensive diatom bloom, which was observed in SEEDS, and led to the change to a pico-phytoplankton dominated community towards the end of the experiment.

1. Introduction

The waters of the subarctic Pacific are characterized by high nitrate and low chlorophyll-*a* concentration (HNLC) throughout the year (Banse and English, 1999). The main cause of HNLC in the subarctic Pacific was originally considered to be the seasonal occurrence of ontogenetic vertical migrating copepods (*Neocalanus* spp. and *Eucalanus bungii*) before the onset of phytoplankton growth (Parsons and Lalli, 1988). However, Martin and Fitztwater (1988) suggested iron deficiency as an alternative cause of HNLC in the subarctic Pacific as well as the Southern Ocean and the eastern equatorial Pacific. Subsequently, the grazing pressure by the ontogenetic vertical migrators has come to be considered as a relatively minor factor regulating phytoplankton dynamics in the subarctic Pacific (Dagg, 1993a; Tsuda and Sugisaki, 1994). After an intensive debate on the iron-limitation hypothesis (e.g. Banse, 1990; Martin *et al*., 1990), mesoscale iron-enrichment studies have confirmed the iron hypothesis in three regions with HNLC waters (Coale *et al*., 1996, 2004; Boyd *et al*., 2000, 2004; Tsuda *et al*., 2003).

SEEDS (Subarctic iron Enrichment for Ecosystem Dynamics Study) was the first meso-scale iron enrichment study in the subarctic Pacific to test the iron-limitation hypothesis (Takeda and Tsuda, 2005). A single enrichment of dissolved iron caused a large increase in the phytoplankton standing stock and decreases of macronutrients and CO_2 fugacity in surface waters. The dominant phytoplankton species shifted after the iron-enrichment from open-ocean species to neritic diatoms (Tsuda *et al*., 2005a). The primary production in the iron patch increased more than ten-fold and the chlorophyll-*a* concentration increased from 0.8 to 20 mg m^{-3} (Kudo *et al*., 2005). SEEDS was characterized by the highest chlorophyll-*a* concentration and the largest drawdown of macronutrients and dissolved carbon dioxide among the mesoscale iron enrichment experiments (de Baar *et al*., 2005). de Baar *et al*. (2005) suggested that the surface mixed layer depth play an important role in determining the magnitude of biological responses in the iron-enrichment experiments, and Yoshie *et al*. (2005) suggested that the presence of the rapidly growing neritic diatoms is important in reproducing the results of the modeling experiment.

The export flux in SEEDS from the surface mixed layer between day 4 and 13 was 11% of the integrated primary production, while 78% of the organic carbon remained in the surface mixed layer as particulate organic carbon (Tsuda *et al*., 2003), which suggests that the 13-day observation period was not sufficient to examine the fate of carbon accumulated in the iron-induced bloom. Tsuda *et al*. (2003) suggested that a substantial diatom sinking event occurred after the observation period, judging from the similarities in bloom intensity and species composition between iron-induced bloom and spring bloom in the coastal areas of the North Pacific. However, Saito *et al*. (2006a) suggested the possibility that the accumulated diatom cells in the surface mixed layer might be grazed down by heterotrophic dinoflagellates and most of the POC (particulate organic carbon) would be respired in the mixed layer within a week after our observation. A large percentage of decomposition of the accumulated organic matter by micro-organisms in an iron-enrichment experiment was also observed in the eastern subarctic Pacific (SERIES, Boyd *et al*., 2004).

We carried out a second iron-enrichment experiment in the western subarctic Pacific (SEEDS II) to examine the decline and fate of the iron-induced phytoplankton bloom in summer 2004. However, the phytoplankton responses in SEED II were quite different from those of SEEDS. Here we present the outline of the experimental results and discuss the causes of the differences.

2. Materials and Methods

The experiment was performed by two research vessels: R.V. Hakuho Maru (HK) and R.V. Kiro Moana (KM). In a preliminary survey of the area, the iron-enrichment and the observations for the first two weeks were carried out by HK until day 14 and the observation period was continued by KM until day 22. HK then took over the observation from day 23 to 26, leaving the site and returning to the area on day 31; unfortunately, we failed to find the iron-enriched patch. The observation periods were therefore 26 days for the iron-enriched patch and 32 days outside the patch from the first iron-enrichment.

The preliminary survey confirmed that an area around the site had high nitrate (>18 μM), high silicic acid (>31 μM) and low chlorophyll (<1 mg m^{-3}) concentrations prior to the iron enrichment, although the area was relatively heterogeneous compared to SEEDS (Tsuda *et al*., 2003). We then chose a location 93 km SE of the SEEDS site (Fig. 1), because we observed a relatively broad area of HNLC water there. Dissolved iron concentrations in the ambient surface seawater were extremely low (<0.02 nM), suggesting that phytoplankton growth in this area was limited by iron bioavailability.

A GPS-navigated buoy attached to a drogue centered at 10 m depth was launched at 48°N, 166°E on the day before the iron addition (Fig. 1). The first iron addition was carried out from 0:50 GMT on 20 July to 0:00 GMT on 21 July (GMT). Day 1 was defined as 21 July (GMT). The ship started to inject iron and sulfur hexafluoride (SF_6) as an inert tracer of the water mass, executing an 8 km × 8 km grid pattern centered on the buoy with an interval of 400 m. The ship was navigated with a lagrangian coordination system (Tsumune *et al*., 2005), and buoy position was transmitted to the ship every 10 min to update the navigation frame of reference to account for surface water advection. The amount of iron added to the patch was 332 kg Fe as $FeSO_4$. During the iron fertilization, 4000 L of saturated SF_6 solution was also simultaneously injected. The saturated SF_6 solution was made onboard using the method previously detailed in Tsumune *et al*. (2005). Note that the saturated SF_6 concentration in seawater is about 0.2 mM (Ledwell and Watson, 1991). A second iron addition was performed on day 6 without SF_6 tracer, when an additional 159 kg of iron was added to the patch, which was traced using the SF_6 signal.

The observation consisted of a mapping survey and in- and out-patch hydrocasts. The mapping survey consist of underway sampling to determine the position and shape of the patch using the ship's pumping system, which had an intake at 6 m below the surface for measurements of pCO_2 and SF_6 (Upstill-Goddard *et al*., 1990; Law *et al*., 1998). The SF_6 signal was mainly used for the mapping survey from the beginning to day 12 and pCO_2 signals were used thereafter because the SF_6 concentration

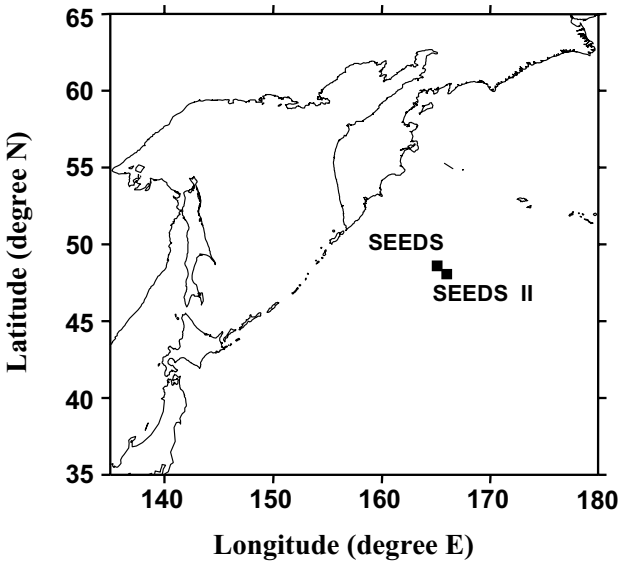

Fig. 1. Location of the iron enrichment experiments, SEEDS II and SEEDS.

dropped to a very low value during this period. Sampling intervals during the underway sampling of chlorophyll-*a*, pCO_2 and SF_6 were, 5–10, 1 and 6 min, respectively with a ship speed of ca. 29.6 km h^{-1} for HK and 18.5 for KM. The in- and out-patch survey consisted of vertically stratified water sampling with a CTD-Carousel multi-sampling system and ultraclean sampling using Kevlar wire and acid-cleaned Niskin-X bottles, near the center of the patch and outside the patch. The hydrocast stations in and outside the patch were determined by the horizontal survey of SF_6 and pCO_2 concentrations.

The pCO_2 was continuously determined by a system with a bubbling equilibrator with an open air flow and a non-dispersive infrared analyzer (Nojiri *et al*., 1999). The SF_6 concentration was determined by a twin sparge-cryogenic trap system coupled to an electron-capture detector gas chromatograph (Upstill-Goddard *et al*., 1990). The iron concentration was measured by filtering the seawater samples through 0.22 μm Durapore filters (Millipak 100, Millipore Corp.) connected to the Niskin-X spigot under gravity pressure, and collected in acid-cleaned, 125-ml LDPE bottles (Nalgene Co., Ltd). Dissolved iron concentrations in the seawater samples were determined with a flow analytical system using chelating resin preconcentration and chemiluminescence detection (Obata *et al*., 1993, 1997). The maximum photochemical quantum efficiencies of the algal photosystem II (F_v/F_m, where F_v is the difference between the maximum (F_m) and minimum (F_0) chlorophyll fluorescence yield), were measured by collecting the water in amber plastic bottles and acclimation in the dark for 30 min, followed by analysis with a fast repetition rate fluorometer (Chelsea Tech-

nologies Group, FAST tracka I) according to the method of Suzuki *et al*. (2002). For the chlorophyll-*a* concentration, 115 ml of seawater was filtered with a glass-fiber filter (GF/F), and the pigments on the filter were extracted with 6 ml of *N*,*N*-dimethylformamide (DMF) for over 24 h (Suzuki and Ishimaru, 1990), after which chlorophyll-*a* concentration was measured with a Turner Designs fluorometer using a non-acidification protocol (Welschmeyer, 1994). We also measured the size-fractionated chlorophyll-*a* concentration by sequential filtration of 500 ml seawater with Nuclepore filters (10, 2, and 0.2 μm pore size).

Knauer-type sediment traps were attached to a drifting system at a depth of 40 m inside and outside the patch, retrieved at 3 day intervals in the patch, and 4 to 7 day intervals outside the patch to collect sinking particles. The trap consisted of 8 plastic cylinders filled with hyper-saline seawater with sodium azide (10 mmol l^{-1}). Part of the samples were filtered with a pre-combusted glass-fiber filter (GF/F) after removing the swimmers using a mesh (1 mm mesh opening) and stored in a freezer (–20°C). The filters were placed in acid fumes to remove the inorganic carbon content and organic carbon and nitrogen contents were measured with an elemental analyzer (CE Instruments, EA1110).

A VMPS net (opening-closing multi-layer net: 50 × 50 cm mouth opening, 0.33 mm mesh opening, Terazaki and Tomatsu, 1997) was towed from 200-m depth to the surface on HK, and a NORPAC net (45 cm mouth diameter, 0.33 mm mesh opening) from 20-m depth on KM to estimate the standing stock of mesozooplankton in the iron patch. The sampling layers of the VMPS net were divided into 0–20, 20–50, 50–100, 100–200 m. The samples were immediately preserved with 10% buffered formalin seawater. In a laboratory, all individuals except for small copepods (mainly *Oithona* spp.) were sorted for measurements of wet weight. Carbon biomass was estimated using the wet weight and a conversion factor of 0.08 (Peters and Downing, 1984).

3. Results and Discussion

3.1 Patch characteristics

The iron patch was successfully followed from day 1 to 26, by tracking the SF_6 and pCO_2 signals. The initial conditions in the patch were similar to those of SEEDS, except for the surface mixed layer depth and iron concentration (Table 1). The initial dissolved iron concentration was lower in SEEDS II than in SEEDS because the bottom of the surface mixed layer was deeper in SEEDS II (Fig. 2). However, the initial iron concentration was similar to SERIES, the iron-enrichment experiment in the eastern subarctic Pacific which was conducted at a similar surface mixed layer depth (Wong *et al*., 2006), and the dissolved iron concentrations were almost same among three experiments after day 10. Moreover, dissolved iron half-life values did not differ significantly among the experiments (Nishioka, pers. com.). The iron patch moved southwestward at around 7.6 km d^{-1} from day 1 to day 4 along the contour of sea surface height in the clockwise eddy, and moved southeastward at around 14 km d^{-1} from day 4 to day 5 due to a strong wind. After the strong wind the patch moved southward across the contour of sea surface height at around 5 km d^{-1} up to day 9 and moved along the sea surface height in the anti-clockwise eddy at a lower speed. The patch size increased from 64 to 1000 km^2 on day 15 and then the detectable patch size decreased to 830 km^2 on day 22. The iron concentration in the patch decreased to the ambient level on day 16–17, even though the second iron addition was made on day 6 (Fig. 2).

Table 1. Comparison of initial conditions between SEEDS and SEEDS II. Values are averages in the surface mixed layer on day 2. Values in parentheses are dissolved iron concentrations just after enrichment.

	SEEDS	SEEDS II
Enrichment date	18 July 2001	20 July 2004
Enriched area (km^2)	80	64
Location	48.5°N, 165°E	48°N, 166°E
Temperature (°C)	8.38 + 0.13	8.10 + 0.07
Surface mixed layer		
Depth (m)	8.5	28
Chl.-*a* (mg m^{-3})	0.92 + 0.31	0.80 + 0.14
Nitrate (μM)	17.86 + 0.16	18.42 + 0.11
Silicate (μM)	30.3 + 1.03	36.1 + 0.05
Dissolved iron (nM)	1.50 (2.89*)	0.17 + 0.06 (1.38**)

*Averaged value in the surface mixed layer.
**Value at 5-m depth.

3.2 Chl biomass and phytoplankton assemblage

Surface chlorophyll-*a* concentration in the patch increased from day 4, peaking between day 11 and 13 (Fig. 3). After day 13, chlorophyll-*a* concentration gradually decreased, returning to the initial level on day 20. The layer in which the chlorophyll-*a* level increased was the same as the surface mixed layer. We did not observe significant changes in the chlorophyll-*a* concentration outside the patch until day 18, when it decreased from 1 to 0.2 mg m^{-3} in the surface mixed layer. These results suggest that the 26 days of the observation period covered the development and decline phases of the bloom induced by the iron enrichment. However, the maximum chlorophyll-*a* concentrations were much lower than those of

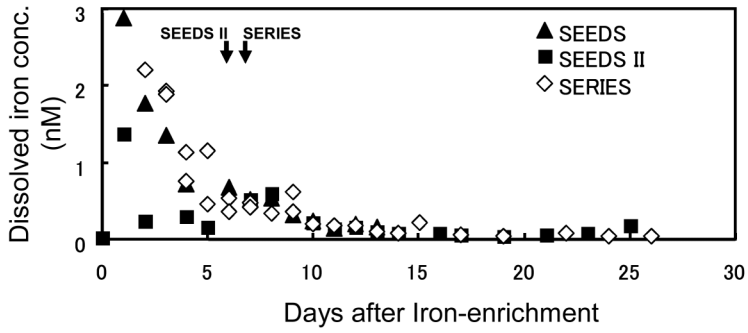

Fig. 2. Temporal changes in dissolved iron concentration in the patch at the surface mixed layer in SEEDS (solid triangles), SEEDS II (solid squares) and SERIES (open squares). SEEDS and SEEDS II data are values at 5 m (Tsuda *et al*., 2003), and SERIES data are values at 10 m (Wong *et al*., 2006). Arrows indicate the day of 2nd iron-enrichments in each experiment.

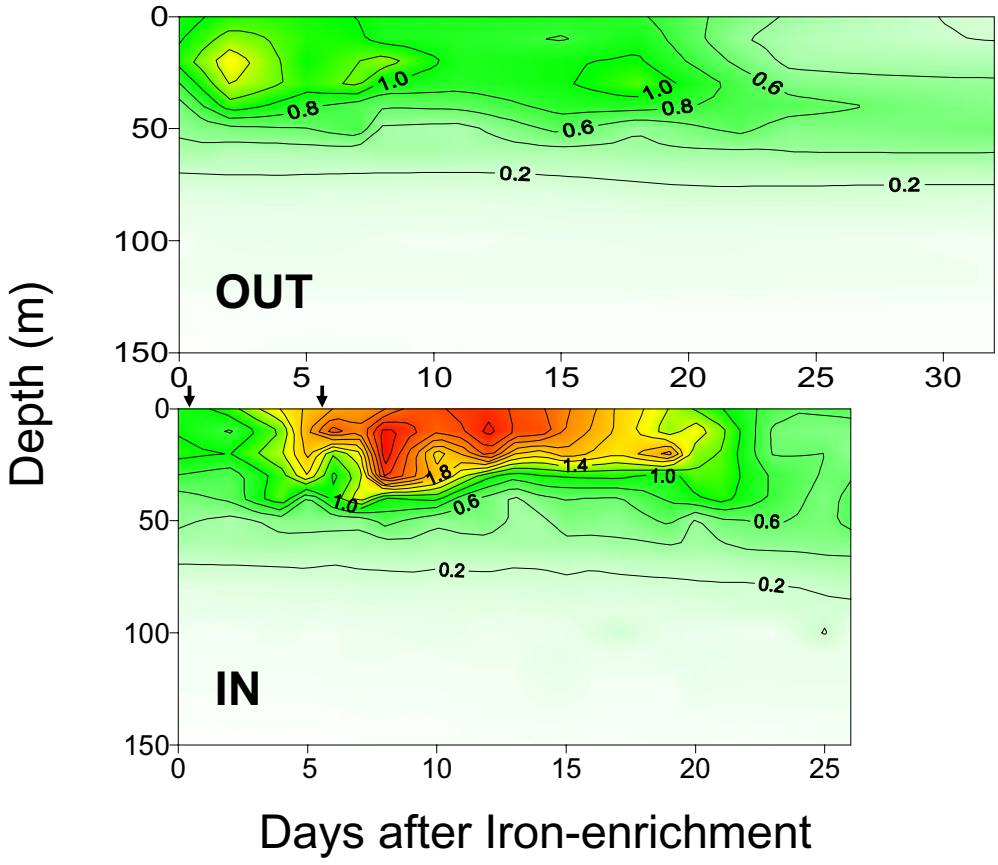

Fig. 3. Temporal changes in chlorophyll-*a* concentrations (mg m^{-3}) in the upper 150-m inside and outside the iron patch in SEEDS II. Arrows indicate the day of 1st and 2nd iron-enrichment.

SEEDS (Fig. 4). The initial concentration was almost identical to that of SEEDS until at least day 5, but the chlorophyll-*a* concentration in SEEDS increased exponentially after day 4 to over 15 mg m^{-3}. The maximum chlorophyll-*a* concentration (3.0 mg m^{-3}) in SEEDS II was observed on day 12 at the surface and the average concentration between day 11 and 13 in the upper 20 m water column was 2.48 ± 0.35 mg m^{-3}. Therefore, the

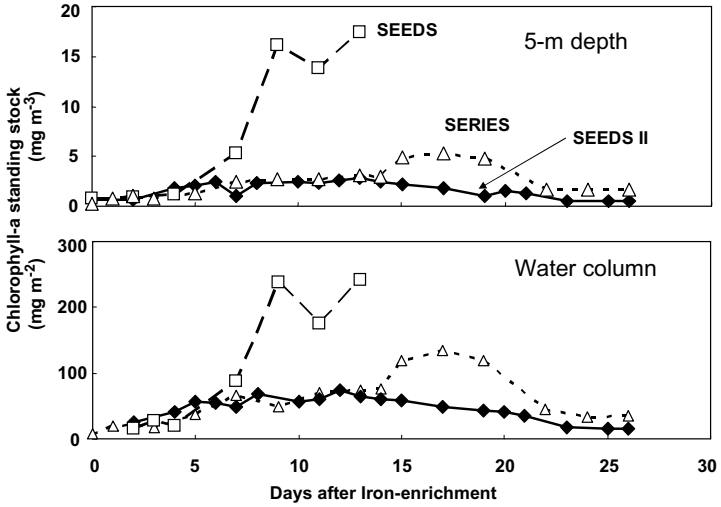

Fig. 4. Temporal changes in chlorophyll-*a* concentration in the patch at 5-m depth (upper) and the water column integrated values (lower) in SEEDS (open squares and broken line), SEEDS II (solid squares and solid line) and SERIES (open triangles).

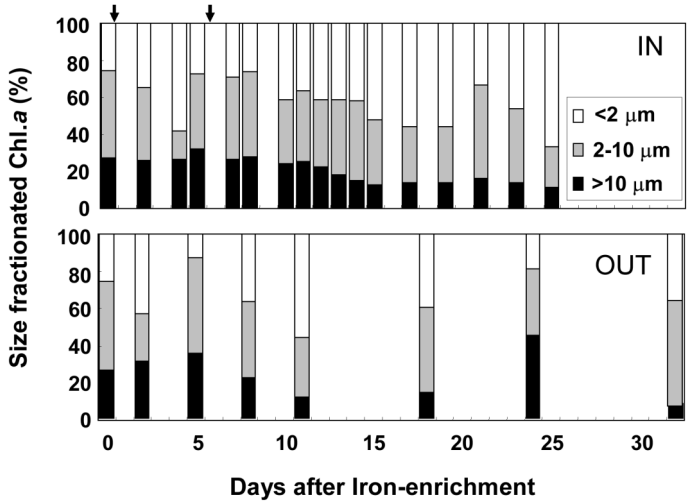

Fig. 5. Temporal changes in the relative composition of size-fractionated chlorophyll-*a* concentration inside (upper) and outside (lower) the patch in SEEDS II. Arrows indicate the day of 1st and 2nd iron-enrichment.

increase in chlorophyll-*a* concentration in SEEDS II was about 85% lower than that of SEEDS. The chlorophyll-*a* concentration in SERIES also showed an almost identical variation with SEEDS II until day 14, then it increased to around 5 mg m^{-3} due to a bloom of micro-sized diatoms (Marchetti *et al*., 2006a).

Micro, nano and pico-sized chlorophyll-*a* accounted for 27, 43 and 30% of the total chlorophyll-*a* concentration before the increase of phytoplankton (between days 0 and 2). This ratio did not change during the development of the bloom (day 2 to 8), then the contribution of pico-phytoplankton increased and that of micro-phytoplankton gradually decreased (Fig. 5). On the final observation day (day 26), pico-phytoplankton accounted for 67% of the total chlorophyll-*a*. In contrast to SEEDS II, 95% of the total chlorophyll-*a* was accounted for by micro-sized phytoplankton on the day of the peak chlorophyll-*a* concentration in SEEDS (Tsuda *et al*., 2003), which is a similar trend to other iron-enrichment experiments in HNLC oceans (e.g. Boyd *et al*., 2000, 2004). Outside the patch, the size distributions of chlorophyll-*a* were rather variable compared to those in the patch, probably due to local heterogeneity (Fig. 5).

The photosynthesis competence (F_v/F_m) closely fol-

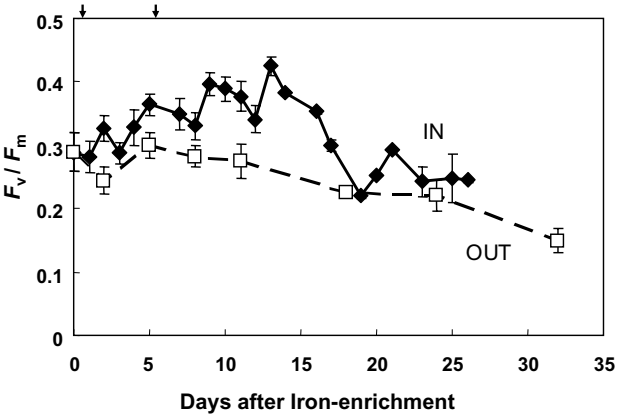

Fig. 6. Temporal changes in photosynthetic competence (F_v/F_m) at 5-m depth inside (solid squares and solid line) and outside (open squares and broken line) the patch in SEEDS II. Vertical bars indicate ±1 SD. Arrows indicate the day of 1st and 2nd iron-enrichment.

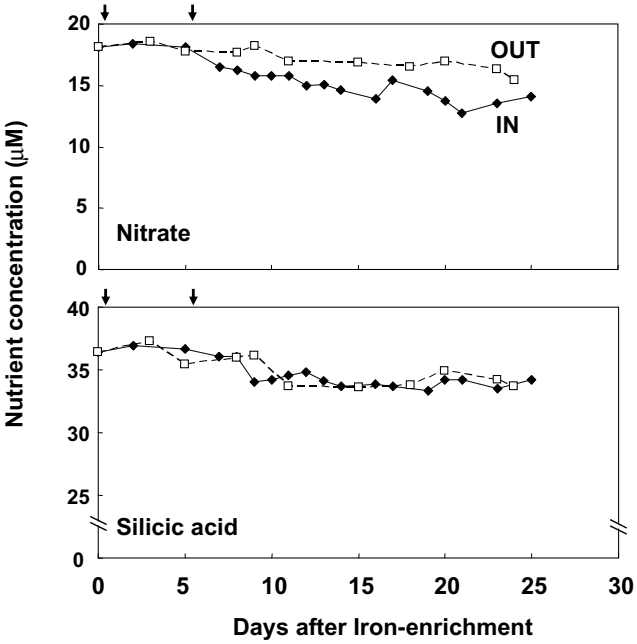

Fig. 7. Temporal changes in nitrate (upper) and silicic acid (lower) concentrations at 5-m depth inside (solid squares and solid line) and outside (open squares and broken line) the patch in SEEDS II. Arrows indicate the day of 1st and 2nd iron-enrichment.

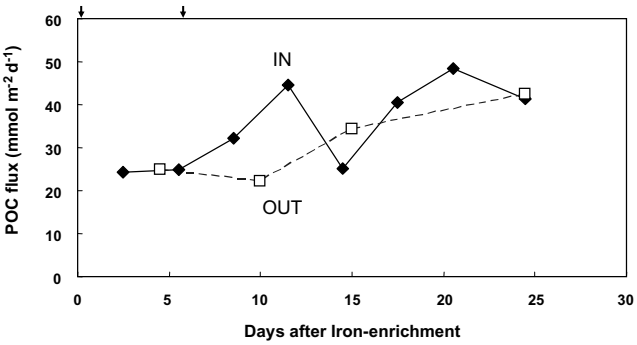

Fig. 8. Temporal changes in particulate organic carbon (POC) flux at 40-m depth inside (solid squares and solid line) and outside (open squares and broken line) the patch in SEEDS II. The *x*-axis is plotted as the median day of sampling period. Arrows indicate the day of 1st and 2nd iron-enrichment.

lowed the chlorophyll-*a* variation (Fig. 6). The initial value was 0.29 and the ratio increased to around 0.4 between days 9 and 14 and returned to approximately the initial level on day 17. The F_v/F_m decreased further to 0.24 as the bloom entered the decline phase. Outside the patch, F_v/F_m levels were relatively stable until day 11, whereafter they gradually decreased to 0.15. The observed initial and the maximum values of F_v/F_m were identical to those of SEEDS and SERIES (Tsuda *et al.*, 2003; Boyd *et al.*, 2005). These variations in F_v/F_m suggest that phytoplankton growth was initially stressed by iron, improved after the iron enrichments, and returned to an iron-stressed condition during the declining phase. The euphotic layer integrated primary production gradually increased by up to three times (day 12) the initial value in the patch, but it was smaller than that in SEEDS (five times) (Kudo, pers. com.).

3.3 Nutrients

Nitrate concentration in the patch decreased at a significantly higher rate than that outside the patch (Fig. 7). The concentrations were relatively stable during the first 5 days, decreased to 12.7 μM on day 21, and increased somewhat to the end of the observation period, which might be caused by the dilution of the patch water with its surrounding waters. The maximum difference in nitrate concentrations at 5-m depth inside and outside the patch was 3.80 μM on day 21 (outside concentration on day 21 was estimated from the linear regression between days 5 and 23). Silicic acid concentration also decreased from day 5 to day 10, becoming relatively stable thereafter both inside and outside the patch (Fig. 7). No significant difference in the silicic acid concentrations was observed inside and outside the patch. These nutrient variations are also in contrast to those of SEEDS and SERIES. SEEDS was characterized by a large drawdown of macronutrients (Tsuda *et al.*, 2003; de Baar *et al.*, 2005) and the maximum differences in nitrate and silicic acid concentrations inside and outside the patch were 13.4 and 24.8 μM on day 13, respectively. Moreover, silicic acid

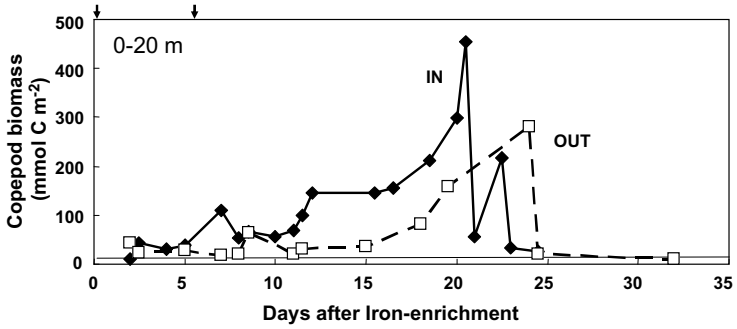

Fig. 9. Temporal changes in the copepod biomass in the 0–20-m water column inside (solid squares and solid line) and outside (open squares and broken line) the patch in SEEDS II. Horizontal line indicates averaged copepod biomass (0–20 m) in SEEDS (Tsuda *et al*., 2005b). Arrows indicate the day of 1st and 2nd iron-enrichment.

Table 2. Comparison of meso-zooplankton biomass at the beginning of the experiments for other mesoscale iron-enrichment experiments.

Experiment	Location	Initial carbon biomass (mg C m^{-3})	Category	Sampling layer (m)	Ref.
IronEx II	EP	3.4–4.1	Zooplankton	0–55	1)
SOIREE	SO	22.8	Copepods	0–65	2)
SEEDS	NP	6.8 ± 11.1	Copepods	0–20	3)
SERIES	NP	7.3 ± 1.3	Copepods	0–30	4)
SEEDS II	NP	18.9 ± 8.0	Copepods	0–20	this study

EP: Equatorial Pacific, SO: Southern Ocean, NP: North Pacific.
1) Rollwagen Bollens and Landry (2000), 2) Zeldis (2001), 3) Tsuda *et al*. (2005b), 4) Sastri and Dower (2006).

depletion together with the large drawdown of nitrate was observed during the diatom bloom period in SERIES (Marchetti *et al*., 2006b; Saito *et al*., 2006b). These results suggest that diatoms were major contributors to the nutrient drawdown and accumulation of chlorophyll-*a* in SEEDS and SERIES, but non-diatom phytoplankton were the major fraction of the phytoplankton that increased in SEEDS II. According to algal pigment signatures, phytoflagellates such as Cryptophytes, Prasinophytes, Chlorophytes, and Prymnesiophytes predominated in the phytoplankton community during SEEDS II (Suzuki, pers. com.).

POC flux at 40-m depth, just below the surface mixed layer, was around 24 mmol $m^{-2}d^{-1}$ in the patch before the bloom, and a relatively high flux of over 40 mmol C $m^{-2}d^{-1}$ was observed during the decline phase of the bloom (Fig. 8). A similar trend of POC flux was observed outside the patch, although the flux was somewhat lower than that inside the patch during the bloom period. The integrated flux of organic matter between day 1 and 25 was 60.8% of the nitrate + nitrite drawdown of the 0–30-m water column in the estimation of nitrogen budget (Saito, pers. com.).

3.4 Copepod biomass

The copepod biomass in the 0–20 m water column increased with time until day 20 inside and day 24 outside the patch, after which the biomass suddenly decreased (Fig. 9). These decreases were caused by the downward migration of the ontogenetic vertical migrating copepod, *Neocalanus plumchrus*. *N. plumchrus* comprised about 60% of the total copepod abundance both inside and outside the patch and accounted for the major part of the copepod biomass throughout the observation period (Tsuda, unpubl. results). At the beginning of the experiment, the *N. plumchrus* population was dominated by second and third copepodite stages (C2 and C3) and the copepodite stage composition progressed with time, so that finally 66–68% of the populations both inside and outside the patch were composed of C5 individuals. During the first five days, the biomass difference inside and outside the patch was not significant (average in the patch: 18.9 ± 8.0 gC m^{-3}, Fig. 9 and Table 2), but the biomass inside the patch was higher than the biomass outside from day 5 until the descent of the copepods. A very high biomass, over 200 mmol C m^{-2}, was observed around day 20, just before the downward migration, and the increase

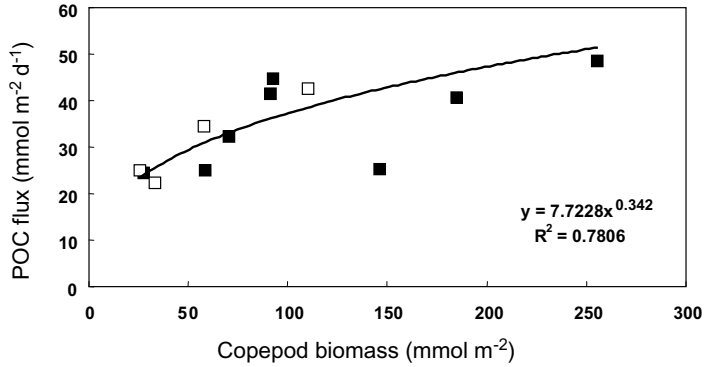

Fig. 10. Relationship between the copepod carbon biomass and POC flux at 40-m depth inside (solid squares) and outside (open squares) the patch in SEEDS II. Solid line denotes the fitted curve. Copepod biomass was the average value of each sediment trap sampling period.

in the biomass in the patch was well described by an exponential growth curve, $y = 0.22e^{0.145x}$ ($r^2 = 0.83$). The exponential growth curve and the development through the copepodite stages of *N. plumchrus* suggest that the observed increases in the copepod biomass are mainly explained by the growth of the copepod during this period. When we compare the initial biomass of copepods with the other iron-enrichment experiments, the copepod biomass in this experiment was the highest among the North Pacific experiments (SEEDS and SERIES) and comparable to SOIREE in the Southern Ocean experiment (Table 2).

3.5 Comparison of SEEDS with SEEDS II

SEEDS and SEEDS II were carried out at almost the same location and season (Table 1), and the initial nutrient and chlorophyll-*a* concentrations as well as the algal size distribution were quite similar between SEEDS and SEEDS II. Although the dissolved iron concentration was lower and the surface mixed layer depth was deeper in SEEDS II than in SEEDS, these conditions were similar to those of SERIES. The increase in photosynthesis competence (F_v/F_m) as observed in SEEDS and SERIES confirmed that the photosynthetic physiological status of the phytoplankton assemblage improved after the iron enrichments (Fig. 6). In both SEEDS and SERIES, a 15 to 20 fold increase in chlorophyll-*a* was observed and these increases in phytoplankton biomass were mainly caused by an increase in diatom species. In contrast, in SEEDS II, chlorophyll-*a* concentration only increased from 0.8 to 2.48 mg m^{-3} (3.1 times) and the size distribution did not change during the development of the bloom.

The two most plausible causes of the different response by the phytoplankton assemblages between SEEDS and SEEDS II are mesozooplankton grazing and the absence of rapidly growing neritic diatom species in SEEDS II. The importance of neritic diatoms was suggested in a numerical modeling study to reproduce the observed rapid, intense increase of phytoplankton biomass in SEEDS (Yoshie *et al*., 2005). Microscopic examination suggests that neritic diatom species such as *Chaetoceros debilis* were not observed in the initial condition of SEEDS II, but we observed an increase in oceanic diatoms such as *Pseudo-nitzschia* spp. and *Neodenticula seminae* (Kiyosawa, pers. com.) during the development of the bloom. In SERIES, the bloom was mainly composed of oceanic diatoms such as *Pseudo-nitzschia* spp., *N. seminae* and *Chaetoceros convolutus* (Marchetti *et al*., 2006a), which were also the common diatom species in SEEDS II. We thus might have expected a diatom bloom of the same magnitude to SERIES in SEEDS II. Therefore, we consider that the absence of neritic diatoms had some effect on the responses in SEEDS II, especially the magnitude and timing of the bloom, but this was not sufficient to explain the differences between SERIES and SEEDS II.

The initial copepod biomass in SEEDS II was about three times higher than that of SEEDS. When we compare the biomass during the first 13 days (total duration of SEEDS), the copepod biomass in SEEDS II was 5 times higher than that of SEEDS, and copepod biomass increased to 33 and 20 times of the average copepod biomass in SEEDS just before the copepod downward migration, inside and outside the patch, respectively. Primary production at the start of the experiment was estimated as 43.9 mmol C $m^{-2}d^{-1}$ (Kudo, unpubl. results), and the copepod grazing rate during the same period was estimated as 14.9 mmol C $m^{-2}d^{-1}$, assuming a homogeneous distribution in the surface mixed layer and a daily ratio of 0.31 (Tsuda *et al*., 2005b). The copepod community grazing rate was 35% of the primary production, but *Neocalanus* spp. and *Eucalanus bungii*, both major com-

ponents of the copepod community, are considered mainly to graze on micro-sized organisms (Kobari *et al*., 2003) and micro-phytoplankton accounted for 27% of the total chlorophyll-*a* concentration (Fig. 5). Thus, the primary production of micro-phytoplankton and copepod grazing rate should be comparable and the copepod grazing most likely prevented the large scale development of the diatom bloom. In SERIES, the initial copepod biomass was similar to that of SEEDS II (Table 2) and chlorophyll-*a* concentration was almost identical to SEEDS II and SERIES until day 14 (Fig. 4). A diatom bloom then formed around day 14 to day 19 in SERIES (Saito *et al*., 2006b; Marchetti *et al*., 2006a). During this period, the copepod biomass was much higher in SEEDS II than SERIES, in which the highest copepod biomass in the surface mixed layer was 56 mmol C m^{-2} (Tsuda *et al*., 2006). In addition, the copepod species compositions were different between SEEDS II and SERIES, *Eucalanus bungii* being the most dominant species in SERIES (Sastri and Dower, 2006; Tsuda *et al*., 2006), which was generally distributed below the surface mixed layer and regarded as a sinking particle feeder (Mackas *et al*., 1993; Dagg, 1993b). In SERIES, *E. bungii* migrated up to the surface mixed layer during the diatom bloom, but they were considered to be present below the surface mixed layer before the bloom (Tsuda *et al*., 2006).

During the decline phase of the bloom (day 13 to 24), the primary production returned to the initial level and the estimated copepod grazing rate (>50 mmol C $m^{-2}d^{-1}$) apparently exceeded the primary production. The dominance of pico-phytoplankton during the decline phase of the bloom might be caused by the release of top-down control of micro-sized heterotrophic organisms, which are suggested to be major food sources for *Neocalanus* copepods after the diatom bloom season in the Oyashio region (Kobari *et al*., 2003).

The POC flux was relatively high inside the patch compare to outside (Fig. 8). It seems that the higher biomass or production of primary producers inside the patch caused the higher export flux of POC. However, if we plot the POC flux as a function of the average copepod biomass in each sampling period, the relationship between copepod biomass and POC flux was well fitted by an exponential curve with no difference inside and outside the patch (Fig. 10). These observations suggest that the POC flux was a function of the copepod biomass, and the iron-enhanced growth of phytoplankton had a minor effect on the export flux in SEEDS II.

The reason why the abundance of *N. plumchrus* was much higher in SEEDS II than SEEDS is unknown. However, Tadokoro *et al*. (2005) reported a decadal oscillation of *N. plumchrus* abundance in the western North Pacific with a factor of 13.7. Boyd *et al*. (1999) suggested that a five times higher biomass of mesozooplankton than the in-situ mesozooplankton was needed to consume the iron-stimulated growth of diatoms. These observations suggest that copepods could possibly graze down the iron-enhanced diatom growth even in the range of natural fluctuations observed in SEEDS II. Martin's iron hypothesis (Martin and Fitzwater, 1988) appeared to be a more convincing explanation of the dynamics of HNLC waters than the grazing hypothesis. More recently, "the ecumenical iron hypothesis" has become generally accepted which suggests that iron controls the growth of large phytoplankton while microzooplankton grazing controls the smaller phytoplankton which have a lower iron requirement and are less vulnerable to mesozooplankton grazing (e.g. Cullen, 1995; Landry *et al*., 1997). However, the results of SEEDS II suggest that copepod grazing is more crucial than we envisaged for shaping HNLC conditions in the subarctic North Pacific and the response of phytoplankton to any natural iron inputs.

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References

Banse, K. (1990): Does iron really limit phytoplankton production in the offshore subarctic Pacific? *Limnol. Oceanogr*., **35**, 772–775.

Banse, K. and D. C. English (1999): Comparing phytoplankton seasonality in the eastern and western subarctic Pacific and the western Bering Sea. *Prog. Oceanogr*., **43**, 235–288.

Boyd, P. W., R. H. Goldblatt and P. J. Harrison (1999): Mesozooplankton grazing manipulations during in vitro iron enrichment studies in the NE subarctic Pacific. *Deep-Sea Res. Part II*, **46**, 2645–2668.

Boyd, P. W., A. J. Watson, C. S. Law, E. R. Abraham, T. Trull, R. Murdoch, D. C. E. Bakker, A. R. Bowie, K. O. Buesseler, H. Chang, M. Charette, P. Croot, K. Downing, R. Frew, M. Gall, M. Hadfield, J. Hall, M. Harvey, G. Jameson, J. LaRoche, M. Liddicoat, R. Ling, M. T. Maldonado, R. M. McKay, S. Nodder, S. Pickmere, R. Pridmore, S. Rintoul, K. Safi, P. Sutton, R. Trezepek, K. Tanneberger, S. Turner, A. Waite and J. Zeldis (2000): A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature*, **407**, 695–702.

Boyd, P. W., C. S. Law, Y. Nojiri, C. S. Wong, Y. Nojiri, A. Tsuda, M. Levasseur, S. Takeda, R. Rivkin, P. J. Harrison,

R. Strzepek, J. Gower, R. M. McKay, E. Abraham, M. Arychuk, J. Barwell-Clarke, W. Crawford, D. Crawford, M. Hale, K. Harada, K. Johnson, H. Kiyosawa, I. Kudo, A. Marchetti, W2. Miller, J. Needoba, J. Nishioka, H. Ogawa, J. Page, M. Robert, H. Saito, A. Sastri, N. Sherry, T. Soutar, N. Sutherland, Y. Taira, F. Whitney, S.-K. E. Wong and T. Yoshimura (2004): The decline and fate of an iron-induced subarctic phytoplankton bloom. *Nature*, **428**, 549–553.

Boyd, P. W., R. Strzepek, S. Takeda, G. Jackson, R. M. McKay, C. Law, H. Kiyosawa, H. Saito, N. Sherry, K. Johnson, J. Gower and N. Ramaiah (2005): The evolution and termination of an iron-induced mesoscale bloom in the northeast subarctic Pacific. *Limnol. Oceanogr.*, **50**, 1872–1886.

Coale, K. H., K. S. Johnson, S. E. Fitzwater, R. M. Gordon, S. Tanner, F. P. Chavez, L. Ferioli, C. Sakamoto, P. Rogers, F. Millero, P. Steinberg, P. Nightingale, D. Cooper, W. P. Cochlan, M. R. Landry, J. Constantinou, G. Rollwagen, A. Trasvina and R. Kudela (1996): A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature*, **383**, 495–501.

Coale, K. H., K. S. Johnson, F. P. Chavez, K. O. Buesseler, R. T. Barber, M. A. Brzezinski, W. P. Cochlan, F. J. Millero, P. G. Falkowski, J. E. Bauer, R. H. Wanninkhof, R. M. Kudela, M. A. Altabet, B. E. Hales, T. Takahashi, M. R. Landry, R. R. Bidigare, X. Wang, Z. Chase, P. G. Strutton, G. E. Friederich, M. Y. Gorbunov, V. P. Lance, A. K. Hilting, M. R. Hiscock, M. Demarest, W. T. Hiscock, K. F. Sullivan, S. J. Tanner, R. M. Gordon, C. N. Hunter, V. A. Elrod, S. E. Fitzwater, J. L. Jones, S. Tozzi, M. Koblizek, A. E. Roberts, J. Herndon, J. Brewster, N. Ladizinsky, G. Smith, D. Cooper, D. Timothy, S. L. Brown, K. E. Selph, C. C. Sheridan, B. S. Twining and Z. I. Johnson (2004): Southern Ocean iron enrichment experiment: Carbon cycling in high- and low-Si waters. *Science*, **304**, 408–414.

Cullen, J. J. (1995): Status of the iron hypothesis after the open-ocean enrichment experiment. *Limnol. Oceanogr.*, **40**, 1336–1343.

Dagg, M. J. (1993a): Grazing by the copepod community does not control phytoplankton production in the subarctic Pacific Ocean. *Prog. Oceanogr.*, **32**, 163–183.

Dagg, M. J. (1993b): Sinking particles as a possible source of nutrition for the calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. *Deep-Sea Res.*, **40**, 1431–1445.

de Baar, H., P. W. Boyd, K. Coale, M. R. Landry, A. Tsuda, P. Assmy, D. C. E. Bakker, Y. Bozec, R. T. Barber, M. A. Brzezinski, K. O. Buesseler, M. Boyé, P. L. Croot, F. Gervais, M. Y. Gorbunov, P. J. Harrison, W. T. Hiscock, P. Laan, C. Lancelot, C. S. Law, M. Levasseur, A. Marchetti, F. J. Milero, J. Nishioka, Y. Nojiri, T. van Oijen, U. Riebesell, M. J. A. Rijkenberg, H. Saito, S. Takeda, K. R. Timmermans, M. J. W. Veldhuis, A. M. Waite and C. S. Wong (2005): Synthesis of iron fertilization experiments: From the iron age in the age of enlightenment. *J. Geophys. Res.*, **110**, C09S16, doi:10.1029/2004JC002601.

Kobari, T., A. Shinada and A. Tsuda (2003): Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr.*, **57**, 279–298.

Kudo, I., Y. Noiri, K. Imai, Y. Nojiri and A. Tsuda (2005): Primary production and nitrogenous nutrients assimilation dynamics during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS). *Prog. Oceanogr.*, **64**, 207–221.

Landry, M. R., R. Barber, R. Bidigare, F. Chai, K. Coale, H. Dam, M. Lewis, S. Lindley, J. McCarthy, M. Roman, D. Stoecker, P. Verity and J. White (1997): Iron and grazing constraints on primary production in the central equatorial Pacific: an EqPac synthesis. *Limnol. Oceanogr.*, **42**, 405–418.

Law, C. S., A. J. Watson, M. I. Liddicoat and T. Stanton (1998): Sulphur hexafluoride as a tracer of biogeochemical and physical processes in an open-ocean iron fertilization experiment. *Deep-Sea Res. II*, **45**, 977–994.

Ledwell, J. R. and A. J. Watson (1991): The Santa Monica Basin tracer experiment: a study of diapycnal and isopycnal mixing. *J. Geophys. Res.*, **96**, 8695–8718.

Mackas, D. L., H. Sefton, C. B. Miller and A. Raich (1993): Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. *Prog. Oceanogr.*, **32**, 259–294.

Marchetti, A., N. D. Sherry, H. Kiyosawa, A. Tsuda and P. J. Harrison (2006a): Phytoplankton processes during a mesoscale iron enrichment in the NE subarctic Pacific: Part I—Biomass and assemblage. *Deep-Sea Res. II*, **53**, 2095–2113.

Marchetti, A., P. Juneau, F. Whitney and P. J. Harrison (2006b): Phytoplankton processes during a mesoscale iron enrichment in the NE subarctic Pacific: Part II—Nutrient utilization. *Deep-Sea Res. II*, **53**, 2114–2130.

Martin, J. H. and S. E. Fitzwater (1988): Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature*, **331**, 341–343.

Martin, J. H., W. W. Broenkow, S. E. Fitzwater and R. M. Gordon (1990): Yes, it does: A reply to comment by Banse. *Limnol. Oceanogr.*, **35**, 775–777.

Nojiri, Y., Y. Fujinuma, J. Zeng and C. S. Wong (1999): Monitoring of pCO_2 with complete seasonal coverage utilizing a cargo ship M/S Skaugran between Japan and Canada. *Proc. 2nd Int. Symp. CO_2 Ocean*, **CGER-I037-'99**, 17–23.

Obata, H., H. Karatani and E. Nakayama (1993): Automated determination of iron in seawater by chelating resin concentration and chemiluminescence detection. *Anal. Chem.*, **65**, 1524–1528.

Obata, H., H. Karatani, M. Matsui and E. Nakayama (1997): Fundamental studies for chemical speciation of iron in seawater with an improved analytical method. *Mar. Chem.*, **56**, 97–106.

Parsons, T. R. and C. R. Lalli (1988): Comparative oceanic ecology of plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr. Mar. Biol. A. Rev.*, **26**, 317–359.

Peters, R. H. and J. A. Downing (1984): Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.*, **29**, 763–784.

Rollwagen Bollens, G. C. and M. R. Landry (2000): Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). II. Mesozooplankton abundance, biomass, depth distribution and grazing. *Mar. Ecol. Prog. Ser.*, **201**, 43–56.

Saito, H., T. Ota, K. Suzuki, J. Nishioka and A. Tsuda (2006a): Role of heterotrophic dinoflagellate *Gyrodinium* sp. in the fate of an iron-enrichment induced diatom bloom. *Geophys. Res. Lett.*, **33**, L09602, 10.1029/2005GL025366.

Saito, H., A. Tsuda, Y. Nojiri, J. Nishioka, S. Takeda, H. Kiyosawa, I. Kudo, Y. Noiri, T. Ono, Y. Taira, K. Suzuki, T. Yoshimura and P. W. Boyd (2006b): Nutrient and phytoplankton dynamics during the stationary and declining phases of a phytoplankton bloom induced by iron-enrichment in the eastern subarctic Pacific. *Deep-Sea Res. II*, **53**, 2168–2181.

Sastri, A. R. and J. F. Dower (2006): Mesozooplankton community response to a phytoplankton bloom in the subarctic NE Pacific. *Deep-Sea Res. II*, **53**, 2268–2280.

Suzuki, K., H. Liu, T. Saino, H. Obata, M. Takano, K. Okamura, Y. Sohrin and Y. Fujishima (2002). East-west gradients in the photosynthetic potential of phytoplankton and iron concentration in the subarctic Pacific during early summer. *Limnol. Oceanogr.*, **47**, 1581–1594.

Suzuki, R. and T. Ishimaru (1990): An improved method for the determination of phytoplankton chlorophyll using N,N-dimethylformamide. *J. Oceanogr. Soc. Japan*, **46**, 190–194.

Tadokoro, K., S. Chiba, T. Ono, T. Midorikawa and T. Saino (2005): Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. *Fish. Oceanogr.*, **14**, 210–222.

Takeda, S. and A. Tsuda (2005): An in situ iron-enrichment experiment in the western subarctic Pacific (SEEDS): Introduction and summary. *Prog. Oceanogr.*, **64**, 95–109.

Terazaki, M. and C. Tomatsu (1997): A vertical multiple opening and closing plankton sampler. *J. Adv. Mar. Sci. Tech. Soc.*, **3**, 127–132.

Tsuda, A. and H. Sugisaki (1994): In-situ grazing rate of the copepod population in the western subarctic North Pacific during spring. *Mar. Biol.*, **120**, 203–210.

Tsuda, A., S. Takeda, H. Saito, J. Nishioka, Y. Nojiri, I. Kudo, H. Kiyosawa, A. Shiomoto, K. Imai, T. Ono, A. Shimamoto, D. Tsumune, T. Yoshimura, T. Aono, A. Hinuma, M. Kinugasa, K. Suzuki, Y. Sohrin, Y. Noiri, H. Tani, Y. Deguchi, N. Tsurushima, H. Ogawa, K. Fukami, K. Kuma and T. Saino (2003): A mesoscale iron enrichment in the western subarctic Pacific induces large centric diatom bloom. *Science*, **300**, 958–961.

Tsuda, A., H. Kiyosawa, A. Kuwata, M. Mochizuki, N. Shiga, H. Saito, S. Chiba, K. Imai, J. Nishioka and T. Ono (2005a): Responses of diatoms to iron-enrichment (SEEDS) in the western subarctic Pacific, temporal and spatial comparisons. *Prog. Oceanogr.*, **64**, 189–205.

Tsuda, A., H. Saito, J. Nishioka and T. Ono (2005b): Mesozooplankton responses to iron-fertilization in the western subarctic Pacific (SEEDS2001). *Prog. Oceanogr.*, **64**, 237–251.

Tsuda, A., H. Saito, J. Nishioka, T. Ono, Y. Noiri and I. Kudo (2006): Mesozooplankton response to iron enrichment during the diatom bloom and bloom decline in SERIES (NE Pacific). *Deep-Sea Res. II*, **53**, 2281–2296.

Tsumune, D., J. Nishioka, A. Shimamoto, S. Takeda and A. Tsuda (2005): Physical behavior of the iron fertilized patch by SF_6 tracer release experiment. *Prog. Oceanogr.*, **64**, 111–127.

Upstill-Goddard, R. C., A. J. Watson, P. S. Liss and M. I. Liddicoat (1990): Gas transfer velocities in lakes measured with SF_6. *Tellus*, **42B**, 364–377.

Welschmeyer, N. A. (1994): Fluorometric analysis of chlorophyll-*a* in the presence of chlorophyll-*b* and phaeopigments. *Limnol. Oceanogr.*, **39**, 1985–1992.

Wong, C. S., W. K. Johnson, N. Sutherland, J. Nishioka, D. A. Timothy, M. Robert and S. Takeda (2006): Iron speciation and dynamics during SERIES, a mesoscale iron enrichment experiment in the NE Pacific. *Deep-Sea Res. II*, **53**, 2075–2094.

Yoshie, N., M. Fujii and Y. Yamanaka (2005): Ecosystem changes after the SEEDS iron fertilization in the western North Pacific simulated by a one-dimensional ecosystem model. *Prog. Oceanogr.*, **64**, 283–306.

Zeldis, J. (2001): Mesozooplankton community composition, feeding, and export production during SOIREE. *Deep-Sea Res. II*, **48**, 2615–2634.