

Are mesoscale perturbation experiments in polar waters prone to physical artefacts? Evidence from algal aggregation modelling studies

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Received 11 October 2001; revised XX Month 2001; accepted 18 February 2002; published 13 June 2002.

[1] The longevity (>50d) of the phytoplankton bloom following mesoscale iron-enrichment of Southern Ocean waters (SOIREE) exceeded that for naturally occurring polar blooms (15–20d). During SOIREE, SF₆-labelled waters increased 20-fold, and the greatest algal loss term was lateral advection. To test whether such advective losses could delay the onset of mass sedimentation, an algal aggregation model was employed. It successfully simulated temporal trends in mass sedimentation during the tropical IronEx II bloom, yet suggested no such event during SOIREE. However, when an iron-enrichment of 100 km length-scale (i.e. tenfold greater than for SOIREE) was mimicked, a marked increase in algal aggregate size occurred after 15d, indicative of increased export. Thus, careful interpretation of experimental results—especially for the fate of algal carbon—is essential, particularly for polar studies where the ratio of net algal growth to advective losses is low, if they are to be extrapolated to open-ocean waters. **INDEX TERMS:** 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4855 Oceanography: Biological and Chemical: Plankton; 4842 Oceanography: Biological and Chemical: Modeling

1. Introduction

[2] In the last decade the ability to label and track a mesoscale parcel of open-ocean water using the tracer SF₆ [Watson *et al.*, 1991] has enabled oceanographers to conduct holistic mesoscale [>50 km²] experiments which overcome the artefacts associated with bottle incubations [Banse, 1991]. To date, such perturbation experiments have been used successfully to investigate the effect of iron-enrichment on the resident cells of HNLC (High Nitrate Low Chlorophyll) waters in the Equatorial Pacific [Martin *et al.*, 1994; Coale *et al.*, 1996] and polar Southern Ocean [Boyd *et al.*, 2000; Smetacek, 2001]. Indeed, new international programmes—such as SOLAS (Surface Ocean Lower Atmosphere Study)—have advocated the widespread adoption of this experimental design to test a number of hypotheses in a controlled manner in the natural environment [SOLAS, 2000].

[3] Several mesoscale perturbation experiments have now been conducted [Coale *et al.*, 1996; Boyd *et al.*, 2000] and enable comparisons to be made between observed biogeochemical trends due to iron-enrichment [Boyd, in press]. Moreover, such studies provide the opportunity to assess the physical evolution of a discrete patch of SF₆-labelled waters and its interactions with the surrounding waters, as reported for the 13 day SOIREE [Abraham *et al.*, 2000]. Many of the trends reported for the IronEx II and

SOIREE studies, such as changes in phytoplankton community structure from small to large cells [Landry *et al.*, 2000a; Gall *et al.*, 2001a], were similar in the two experiments, but the fates of these iron-mediated blooms were not. In IronEx II, phytoplankton biomass peaked after 6–7 days and returned to ambient HNLC levels after 15/16 days [Coale *et al.*, 1996], whereas in SOIREE the bloom was observed—via SeaWiFS—>50 days after its onset [Abraham *et al.*, 2000]. The fate of the iron-elevated algal stocks during IronEx II was thought to be controlled by both grazing [Landry *et al.*, 2000b] and downward particulate export [Bidigare *et al.*, 1999].

[4] For the open waters of the Southern Ocean, remotely-sensed data from SeaWiFS have provided information on the magnitude of algal blooms but have been able to offer only relatively low resolution information on the timescales for bloom development [Moore *et al.*, 1999]. The most detailed description of the evolution of an open-ocean bloom is from an array of ten bio-optical moorings near the Polar Front (PF) [Abbott *et al.*, 2000] which yielded timescales of bloom evolution (15–20d) and decline (15–20d). This timescale for evolution is similar to that reported for the SOIREE bloom [Boyd *et al.*, 2000], but no decline was observed for SOIREE. Abbott *et al.* [2000] suggest that the PF bloom decline was due to grazing pressure and/or silicic acid limitation of the resident phytoplankton. Moreover, Honjo *et al.* [2001] recorded a marked increase in the downward export of biogenic silica at a deep-moored trap site [1 km subsurface] in the vicinity of the mooring array some 20 days after the PF bloom [Abbott *et al.*, 2000], indicating that a large fraction of the bloom was rapidly exported.

[5] A putative “chemostat” effect was put forward by Boyd *et al.* [2000] as an explanation for the longevity of the SOIREE bloom. They suggested that entrainment of the surrounding HNLC waters, and subsequent dilution of bloom stocks in the labelled patch [Abraham *et al.*, 2000; Boyd and Law, 2001] may have artefactually extended the bloom duration. Specifically, by delaying the onset of algal aggregation required to initiate a massive and relatively rapid sedimentation event as observed in blooms in the field [Riebesell, 1991] and in the lab [Allredge and Jackson, 1995]. In this study, the delay in export of the iron-elevated phytoplankton biomass due to the exchange between the surrounding waters and the SF₆ labelled “patch”, and the resulting dilution of patch algal cells was explored using a phytoplankton aggregation model [Jackson and Lochmann, 1992] in conjunction with field data (Table 1A).

2. Methods

[6] Evidence for the exceptional longevity of the SOIREE bloom, relative to other polar open-ocean blooms [Abbott *et al.*, 2000] is based on SeaWiFS images of high chlorophyll in the vicinity of the SOIREE site, and reports that the largest algal loss term from the bloom was due to lateral advection (0.1 d⁻¹ – i.e. 75% of net algal growth rate) [Abraham *et al.*, 2000]. In tandem, these suggest that despite the loss of up to 40% of algal production daily, and the increase in areal extent of the SF₆ labelled waters from 50 to >1100 km², chlorophyll levels (from SeaWiFS) were >2 mg m⁻³ on day 55 [Abraham *et al.*, 2000].

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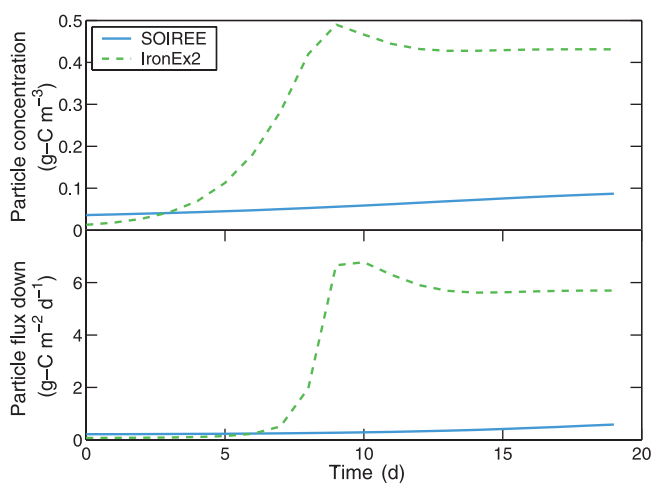
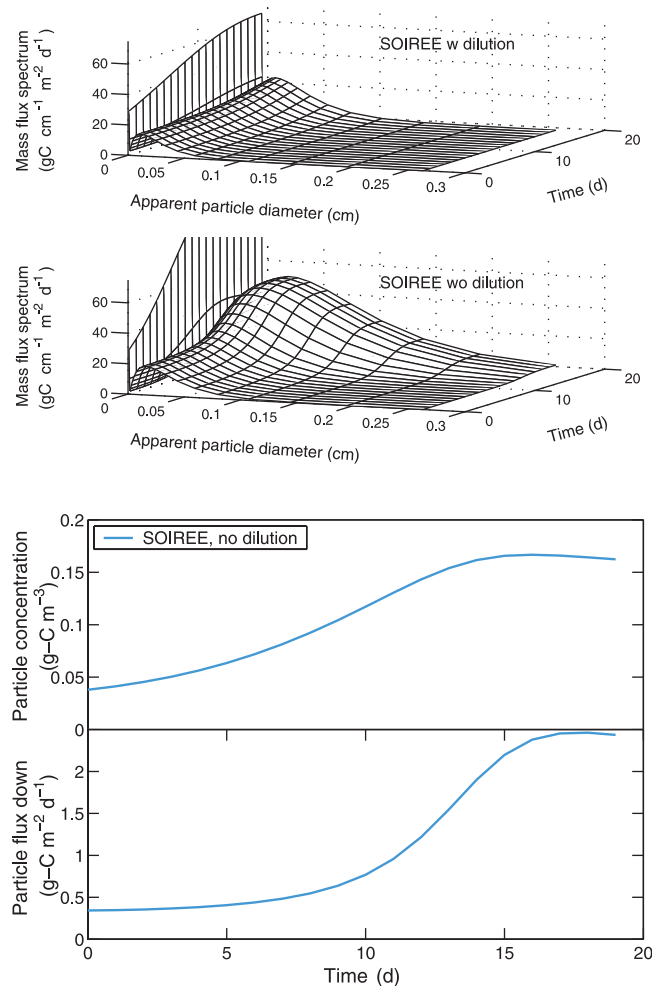
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Table 1A. The Input Data from SOIREE and IronEx II Used in Conjunction with the *Jackson and Lochmann* [1992] Model

Parameter	SOIREE	IronExII
Mixed layer depth (m)	65 ^a	25 ^{b,1}
Specific accumulation rate (d ⁻¹)	0.15 ^c (0.25) ^{c,d}	0.6 ^e
Equiv. Spher. Diameter (μm)	20.8 ^f	9 ^e
Stickiness ^j	1	1
Fluid density (g cm ⁻³) ^j	1.0275	1.0275
Particle density (g cm ⁻³)	1.0969 ^g	1.0998 ^h
Fractal dimension ^k	2.33	2.33
Average shear (s ⁻¹)	0.1 ^d	0.1 ⁱ
C to volume (g-C cm ⁻³)	0.067 ^{e,f}	0.0785 ^e
Initial particle conc. (# cm ⁻³)	35 ^f	150 ^e

^a Denotes *Boyd et al.* [2000].^b *Coale et al.* [1996].^c *Gall et al.* [2001b].^d *Abraham et al.* [2000].^e *Landry et al.* [2000a, 2000b].^f H. Chang, unpublished data.^g Calculated to give a settling velocity of 1.37 m d⁻¹.^h *Jackson* [1990].ⁱ From meteorological data, *Nightingale et al.* [2000].^j Assumed.^k *Jackson et al.* [1997].¹ Denotes variations in mixed layer depth were reported during this study.

[7] The model of *Jackson and Lochmann* [1992] was modified by imposing a constant specific algal growth rate for each iron enrichment experiment (Table 1A), using a fractal coagulation kernel to describe the particle collision rates [*Jackson*, 2001], and a fractal dimension of 2.33 to describe the relationship between aggregate mass and diameter [*Jackson et al.*, 1997]. It was used to investigate the relationship between lateral losses of phytoplankton cells from the labelled “patch” and the timing of the onset of algal aggregation. This model can be used to simulate aggregation within an algal monoculture. This single species model was selected, as opposed to a multiple phytoplankton species model [*Jackson*, 2001], because of the limited datasets available from IronEx II and SOIREE studies, and since only one algal species/group dominated in both experiments: 25 μm long pennate diatoms in IronEx II [*Landry et al.*, 2000a], and larger heavily-silicified *Fragilariopsis kerguelensis* [*Boyd et al.*, 2000]. During SOIREE

**Figure 1.** Twenty day simulations of (a) particle concentration and (b) downward particle flux for the IronEx II and SOIREE iron-mediated phytoplankton blooms. For IronEx II, input data for the model [*Jackson and Lochmann*, 1992] are presented in Table 1A. Note, in each case the upper bound in aggregation is predicted; no data were available from either study on algal stickiness, and a value of 1 was assumed.**Figure 2.** (a) Simulations of the evolution of the mass flux spectrum ($\text{g C cm}^{-1} \text{m}^{-2} \text{d}^{-1}$) and apparent particle diameter (cm) over 20 days for the SOIREE bloom (with observed dilution rate, upper panel), and in the lower panel for a simulation mimicking the SOIREE bloom if based on a larger length-scale of iron enrichment (i.e. 100 km, and no dilution). In the latter case it was assumed that all properties observed during SOIREE would remain the same, but that due to the longer length scale the net algal growth would be 0.25 d^{-1} (i.e. 0.15 d^{-1} (as reported during SOIREE) plus 0.1 d^{-1} (the lateral loss term estimated for SOIREE)). Mass flux spectrum is the mass of carbon/unit particle diameter/area/time. It is calculated as $m(d) \cdot n(d) \cdot v(d)$, where $m(d)$ is the mass for a particle of diameter d , $n(d)$ is the particle number spectrum, and $v(d)$ is the particle settling rate. (b) Simulation of the particle concentration (upper panel) and the downward particle flux (lower panel), expressed as for Figure 1, for the SOIREE simulation without dilution (Figure 2a, lower panel).

other diatom species and haptophytes increased in abundance after iron enrichment [*Gall et al.*, 2001a] but were not modelled because they are thought to have a relatively minor influence on aggregation in this study as a result of their low abundances [diatoms] or small sizes [haptophytes].

[8] The output of the model was expressed as both particle concentration and downward particle flux. The former refers to the concentration of both single cells and algal aggregates. Parameters for the model were estimated using observations from IronEx II and SOIREE (Table 1A) for physical shear, surface mixed layer depth, algal geometry, and cellular abundance. Because data on algal stickiness were unavailable, the high value of 1 was arbitra-

Table 1B. A Summary of Available Data on Ambient Water Temperatures, Net Algal Growth Rates, and Estimated Algal Loss Rates Due to Lateral Advection for Iron Perturbation Experiments in Tropical and Polar Waters

Perturbation Study	Region	Water temp (C)	Net Algal growth (d ⁻¹)	Lateral loss term (d ⁻¹)	Algal Growth: Lateral advection
IronEx I ^a	Equatorial Pacific	24.6	1.00	n.a.	n.a.
IronEx II ^{b,c,d}	Equatorial Pacific	25.2	0.60	0.1 ^h	6.0
SOIREE ^{e,f}	Polar S. Ocean	2.2	0.15	0.1	1.5
EISENEX ^g	Polar S. Ocean	ca. 2	n.a.	n.a.	n.a.

It is proposed that the ratio of net algal growth:lateral advection is a key determinant of the extent of the influence of underlying ocean physics on the outcome of such experiments.

^aDenotes [Martin et al., 1994]. ^bCoale et al. [1996]. ^cLandry et al. [2000b]. ^dNightingale et al. [2000]. ^eBoyd et al. [2000]. ^fAbraham et al. [2000]. ^gSmetacek [2001].

^hDenotes derived from data presented in Coale et al. [1996] on the temporal evolution of SF₆-labelled waters. During EISENEX, although only preliminary information is presently available, the fate of the iron-mediated bloom was reported to be unknown (i.e. no marked increase in downward particulate export) after 22 days of the enrichment [Smetacek, 2001].

rily assigned. The relationship between stickiness and algal physiology can be species-specific [Kiorboe et al., 1990]. It is, therefore, likely that the timing and rates of aggregation are upper estimates for the effect of coagulation. In addition, the conversion from model units (particle volume) to measured units (g-C) requires the application of generic conversion constants [Strathmann, 1967].

[9] Two sets of runs are presented here. Firstly, a standard set of runs for IronEx II and SOIREE that provide the best guess for the experimental conditions were made and compared with observed trends in the timing of increases in downward particle flux during each field study. Secondly, the SOIREE standard run was compared with a modified SOIREE simulation in which a higher net algal growth rate was applied. A net growth rate of 0.25 d⁻¹ was assigned in the latter case in order to mimic a larger length-scale iron enrichment event of ca. 100 km as observed naturally in the ocean [Boyd et al., 1998; Abbott et al., 2001; Boyd and Law, 2001]. In the large-scale enrichment it was assumed the dilution of the blooming cells via lateral advection would be negligible, the magnitude of algal loss terms reduced, and thus the net growth rate would be correspondingly higher. The addition of the lateral loss term [0.1 d⁻¹, Abraham et al., 2000] to the reported net growth rate of (0.15 d⁻¹) for SOIREE [Gall et al., 2001b] yielded a net growth rate of 0.25 d⁻¹.

3. Results and Discussion

[10] The standard runs for the IronEx II and SOIREE simulations are presented in Figure 1. In the former there was a marked increase in particle concentration after 4–5 days, and a subsequent increase in the downward particle flux from <0.1 to >6 g C m⁻² d⁻¹ between days 8 and 10. Particle concentration and downward flux remained relatively high for the remainder of the 20 d simulation; the model was not developed to consider processes such as grazing pressure. In contrast, during the SOIREE simulation the particle concentration increased slowly, as did the downward particle flux (0.3 g C m⁻² d⁻¹ by day 20). During IronEx II, algal carbon increased from 0.02 to 0.12 g C m⁻³ in 6/7 days, and decreased to HNLC levels after 15 d [Landry et al., 2000a]. The downward particle flux from the base of the mixed layer was estimated using Thorium/Uranium [Th/U] disequilibria during IronEx II, [Bidigare et al., 1999]. The downward particle flux was around 0.12 g C m⁻² d⁻¹ from days 1–5, then increased fivefold by day 11 ± 3d (the last Th/U measurement made). During SOIREE, algal carbon increased from 0.03 to 0.1 g C m⁻³ [Boyd et al., 2000] over 13 d. Over this period, Nodder and Waite [2001] and Charette and Buesseler [2000] recorded no significant increase in downward particle flux (0.15 g C m⁻² d⁻¹) relative to the surrounding HNLC waters. In addition, the simple coagulation model did reproduce the size dependence of settling particles reported by Waite and Nodder [2001] and Jackson et al. [in prep].

[11] Despite the need for assumptions regarding algal stickiness in the model, in IronEx II the predicted timing of marked increases in both particle concentrations and downward particle flux (mediated by algal aggregation) closely matched that observed. Similarly, the relatively slow increase in particle concentrations observed in SOIREE, and the small changes in downward particle flux from days 0–13 of SOIREE were relatively closely matched in the simulation.

[12] The magnitude of the predicted changes in particle concentration and downward flux matched observations less well than for the timing of events. Particle concentrations from the simulation were around fourfold greater than those observed during IronEx II. In part, this may result from the need to choose conversion constants for the model in the absence of measurements. In addition, comparing algal carbon estimates obtained from rosette bottle samples with a model simulation that computes the stocks of both single cells and algal aggregates is problematic [Gardner et al., 1993]. Furthermore, there was no pronounced decline in particle concentrations after the predicted peak because the present model does not include the effects of grazing pressure or algal nutrient limitation (both reported during IronEx II [Landry et al., 2000a, 2000b]). The predicted particle concentrations for SOIREE were close to those observed [0.1 g C m⁻³ by day 13, Gall et al., 2001a]. For the simulated downward particle fluxes, similar trends of overestimation of the IronEx II observations, and comparable fluxes for SOIREE were evident.

[13] A comparison of how the mass flux spectrum changed during a 20 day run for the SOIREE standard and modified run is presented in Figure 2a. Although increases in both particle properties are evident in the standard run, as observed by Waite and Nodder [2001], these increases are clearly insufficient to initiate mass sedimentation, and subsequently increase downward particle flux. No significant increase in this flux was reported during SOIREE [Charette and Buesseler, 2000; Nodder and Waite]. In contrast, there are marked increases for the modified run in both particle diameter and volume from day 10/11 until the end of the simulation, indicative of the onset of aggregation, the precursor of mass sedimentation. Such changes in particle properties result in a doubling of particle concentration relative to the standard run and a greater than fourfold increase in downward particle flux after day 12, relative to the standard run. Indeed, this timing in the model simulation (Figure 2b) is similar to trends recorded by Abbott et al. [2000]. They noted a peak in chlorophyll levels (>1 mg m⁻³) after 15 days, and that this maximum was maintained for 2–3 d prior to a decline in stocks, which may have been due to grazing, nutrient limitation [Abbott et al., 2000], and downward export [Honjo et al., 2001].

[14] During IronEx II and SOIREE chlorophyll attained levels of > 1.5 mg m⁻³ [Boyd, in press], yet a pronounced export event was observed only during IronEx II. Clearly, understanding the factors controlling export, and the timing and magnitude of mass sedimentation is of central importance in interpreting the results of

such experiments, but as yet this second tenet of Martin's [1990] iron hypothesis has yet to be fully tested in polar waters [Nodder et al., 2001; Smetacek, 2001]. Charette and Buesseler [2000] suggested that the impact of colder temperatures on the biota—in polar regions—may have delayed the onset of such an export event, and Maldonado et al. [2001] report that the magnitude of algal growth rates after 12 days of the SOIREE bloom were probably limited by the cells' ability to utilise organically-bound iron at less than maximal rates. From the present study it is apparent that lateral advective losses, by delaying the onset of algal aggregation, probably resulted in a bloom of exceptional longevity, the fate of which under other circumstances (Figure 2) probably would have been mass sedimentation over a relatively short timescale [$<20d$, Honjo et al., 2001]. Furthermore, it is suggested that the reason why elevated export was observed in IronEx II but not in SOIREE is due to the ratio of net algal growth to advective loss: a ratio of at least 6 in IronEx II indicates a bloom that was less influenced by the exchange of waters between the "patch" and the surrounding HNLC waters [Table 1B].

4. Conclusions

[15] The outcome of mesoscale perturbation experiments conducted in polar waters may be less representative of naturally-occurring iron-enrichment events in the present day or geological past as they appear to be prone to the effects of physical artefacts. If such an experimental approach is to be used widely in the future care must be taken to assess the extent of such artefacts and how they influence the results of mesoscale perturbation studies.

[16] **Acknowledgments.** P.W.B was supported by the New Zealand PGSF via the Ocean Ecosystems programme. G.A.J. had financial support from the NSF JGOFS/ Synthesis and Modeling Program, OCE 97260771 and OCE 9986765. A.M.W. acknowledges support from the University of Western Australia. We are grateful to H.Chang (NIWA) for the provision of unpublished data on the geometry of phytoplankton during SOIREE bloom. We thank two anonymous reviewers for their helpful comments which improved this manuscript.

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