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Iron-mediated changes in phytoplankton photosynthetic competence during SOIREE

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Abstract

Active fluorescence (fast repetition rate fluorometry, FRRF) was used to follow the photosynthetic response of the phytoplankton community during the 13-day Southern Ocean Iron RElease Experiment (SOIREE). This in situ iron enrichment was conducted in the polar waters of the Australasian–Pacific sector of the Southern Ocean in February 1999. Iron fertilisation of these high nitrate low chlorophyll (HNLC) waters resulted in an increase in the photosynthetic competence (F_v/F_m) of the resident cells from around 0.20 to greater than 0.60 (i.e. close to the theoretical maximum) by 10/11 days after the first enrichment. Although a significant iron-mediated response in F_v/F_m was detected as early as 24 h after the initial fertilisation, the increase in F_v/F_m to double ambient levels took 6 days. This response was five-fold slower than observed in iron enrichments (in situ and in vitro) in the HNLC waters of the subarctic and equatorial Pacific. Although little is known about the relationship between water temperature and F_v/F_m, it is likely that low water temperatures — and possibly the deep mixed layer — were responsible for this slow response time. During SOIREE, the photosynthetic competence of the resident phytoplankton in iron-enriched waters increased at dissolved iron levels above 0.2 nM, suggesting that iron limitation was alleviated at this concentration. Increases in F_v/F_m of cells within four algal size classes suggested that all taxa displayed a photosynthetic response to iron enrichment. Other physiological proxies of algal iron stress (such as flavodoxin levels in diatoms) exhibited different temporal trends to iron-enrichment than F_v/F_m during the time-course of SOIREE. The relationship between F_v/F_m, algal growth rate and such proxies in Southern Ocean waters is discussed.

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1. Introduction

In the last decade, the use of fluorescence induction techniques in biological oceanography has resulted in significant advances in our understanding of phytoplankton photosynthesis in the ocean (Falkowski and Kolber, 1995). Pump and probe fluorometry (PPF) and fast repetition rate fluorometry (FRRF) have been used as survey tools to assess the physiological status of phytoplankton assemblages in close to real-time (Kolber and Falkowski, 1993). These approaches provide evidence of iron limitation during in situ mesoscale iron enrichments (Kolber et al., 1994; Behrenfeld et al., 1996), particularly when interpreted in conjunction with concurrent chemical oceanographic datasets. Basin-scale surveys using fluorescence induction techniques have demonstrated that, for phytoplankton cells, the photosynthetic competence of Photosystem II (F_v/F_m) is sub-optimal over much of the annual cycle due to limiting macro-nutrient (temperate Atlantic Ocean, Olaizola et al., 1996; Geider et al., 1993a) or micronutrient levels (Southern Ocean, Strutton et al., 1997; Boyd et al., 1999). During surveys of iron-poor oligotrophic regions of the South Pacific, Behrenfeld and Kolber (1999) observed night-time depression of F_v/F_m, relative to day-time values. They interpreted this depression as a manifestation of iron limitation on the fluoresence signature of state transitions (see Allen, 1992) in the dominant prokaryotic picophytoplankton in these waters, and suggested this physiological mechanism could be used as a non-destructive assay for iron limitation.

The FRRF technique has also been recently used in the Southern Ocean, both in polar (Strutton et al., 1997, 2000; Olson et al., 2000) and sub-polar (Boyd et al., 1999) waters. Strutton et al. (1997, 2001) obtained a series of underway (1997) and CTD (2000) FRRF transects close to the marginal ice zone off E. Antarctica (i.e. south of the SOIREE site) and reported that the resident algal community exhibited sub-optimal levels of F_v/F_m during late summer 1996. Olson et al. (2000) conducted deckboard iron enrichments (using both FRRF and pump-probe flow-cytometry/micro-fluorometry) in the Ross Sea in late summer 1997, and at stations along the AESOPS 170°W meridian (south of the Polar Front) in late summer 1998. During deckboard experiments, they observed that the phytoplankton community in the Ross Sea responded to iron enrichment by increasing F_v/F_m. However, this was not always the case for deckboard incubations at stations along the 170°W meridian transect. Boyd et al. (1999) obtained vertical profiles of F_v/F_m using FRRF in subantarctic waters south of New Zealand and observed that the populations in these waters were iron-stressed (low F_v/F_m), and that the resident diatoms exhibited high levels of flavodoxin. Active fluorescence is therefore a useful diagnostic probe of algal iron limitation in both the sub-polar and polar waters of the Southern Ocean.

During SOIREE, active fluorescence (FRRF) was used to examine the magnitude and timing of the photosynthetic response to iron enrichment during the 13-day site occupation. For further details of the main findings of SOIREE, see Boyd et al. (2000).

2. Methods

SOIREE was initiated on 9 February 1999 at 61°S 140°E. Iron (ferrous sulphate in acidified seawater) was added with the conservative tracer sulphur hexafluoride (SF_6) on day 0 (February 9)

over a 50-km^2 area. Due to rapid decreases in iron concentrations in the SF_6 labelled waters (henceforth referred to as the patch), further iron infusions were required on days 3, 5 and 7, but no further additions of SF_6 were needed (for more details see Boyd et al., 2000). By day 13 the areal extent of patch was $> 200\,km^2$.

The biophysical parameters of the phytoplankton within the iron-fertilised SOIREE patch and in the surrounding waters were assessed using three approaches: underway sampling, vertical profiling, and analysis of discrete samples. Two Chelsea Instruments Fastracka's (based on the FRRF design outlined in Kolber and Falkowski, 1993; Kolber et al., 1998) were used. One instrument (denoted as FRRF#1) was dedicated to underway sampling of surface waters throughout the voyage, while the other (FRRF#2) was deployed for all vertical profiling, and discrete sampling in benchtop mode. A comparison of the F_v/F_m data sets obtained using FRRF#1 and #2 was favourable (Fig. 1).

Surface water was sampled underway from the vessel's non-toxic supply (PVC pipes, intake at 5 m depth). Seawater from the main supply (2 min residence time from hull intake to supply outflow, see Bakker et al., 2001) was diverted, then run through 100 m of acid-washed silicone rubber tubing housed within an insulated light-tight container. The seawater flow was then directed upwards through a plastic (perspex) debubbler tube into a perspex dark chamber in which the FRRF (#1) optical head was mounted pointing downwards. The flow of the incoming seawater was adjusted to give > 5 min of darkness (i.e. dark adaptation) between the hull intake and the FRRF dark chamber. For each FRRF sampling period, 13 iterations were run and averaged (100

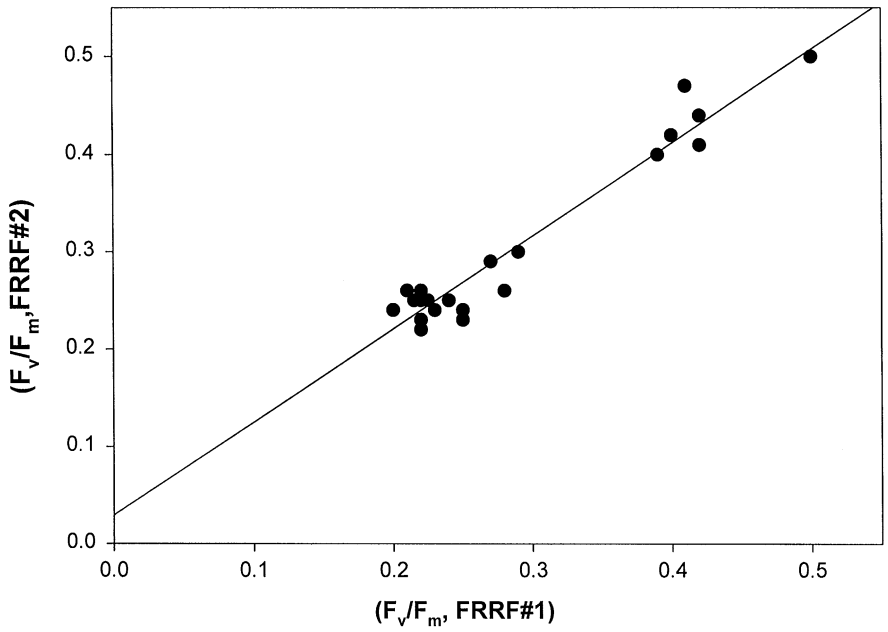

Fig. 1. Cross-comparison of concurrently obtained F_v/F_m data derived from FRRF#1 (underway, 5 m) and #2 (CTD data, 5 m) prior to and during SOIREE. All data (CTD, underway) were obtained during periods of low incident irradiance and/or dark-adapted. The range of values was 0.22–0.50 ($n = 22$, $r^2 = 0.94$, $y = 0.96x + 0.03$).

saturation flashes (1 μs duration, 4 μs interval) and 20 relaxation flashes (1 μs duration, 20 μs interval)), with a 10 s interval between iterations providing a measurement of photosynthetic properties every 2.5 min (i.e. longer than the residence time of seawater in the vessel's non-toxic system, which minimised smearing of the FRRF signal). The instrument calibration protocols and software routines (to curve-fit the data) were supplied by Chelsea Instruments and were similar to those of Kolber and Falkowski (1993).

The debubbler and dark chamber were rinsed with 1% HCL (v/v) every 2 days to remove any particles or mesozooplankton. F_v/F_m was calculated from the raw FRRF data and was logged directly onto the vessel's data acquisition system (DAS), and thus can be directly related to other logged datasets (such as ship position, dissolved iron, and SF_6 levels). Unfortunately, due to the DAS configuration, the raw data were not saved and so only F_v/F_m data are available from the underway sampling at 5 m depth. Limited data on other biophysical variables, such as σ (the cross-sectional area of photosystem II), were obtained using the FRRF in conjunction with a tow-body, and from CTD vertical profiles.

On one occasion (20 February 1999, day 11 of SOIREE) FRRF#2 was deployed in a tow-body (Chelsea Instruments Aqua-shuttle) and towed level (30 m depth). During this deployment, FRRF#2 was programmed with the same flashlet sequence as FRRF#1. This allowed algal biophysical parameters to be mapped concurrently at 5 m (underway intake) and 30 m (tow-body), providing some depth resolution for the underway surveys. Vertical profiles (0–150 m) of biophysical parameters were obtained by mounting FRRF#2 and Chelsea Instruments calibrated irradiance (PAR) and pressure sensors onto the CTD-rosette frame. During vertical profiling FRRF#2 was programmed to have 2 iterations each of 100 saturation flashes (1 μs duration, 4 μs interval) and 20 relaxation flashes (1 μs duration, 20 μs interval), with a 0.1-s interval between iterations providing a measurement of photosynthetic properties every 2 s. The winch speed was 30 m min^{-1}, and thus the FRRF interrogated the phytoplankton community every 1 m (for alternating light and dark chamber measurements), providing a sampling interval of 2 m. No water bottle sampling was carried out during these dedicated FRRF profiles. The vertical profiles presented are from the upcasts only. Temperature, salinity and chlorophyll *a* fluorescence data were collected concurrently using a Seabird plus 9/11 CTD. On several occasions when time did not permit a dedicated vertical FRRF profile, discrete water samples were taken from each of 6 depths on casts sampled for planktonic stocks and rate processes (such as primary production). Each sample was dark-adapted in clean 1 l opaque polypropylene bottles for 15 min (plus a period of dark-adaptation within the Niskin bottle prior to sub-sampling). The bottles were stored in an insulated light-tight container during this period. Replicate samples (30 ml) were analysed using the FRRF#2 dark chamber in bench-top mode. Some additional samples (size-fractionated, > 20, < 20, < 5 and < 2 μm) were also analysed (FRRF#2) in this way. All samples (< 2 μm excepted; filtered under gentle vacuum (30 mm Hg)) were prepared by gravity filtration under conditions to minimise thermal shock (see Boyd et al., 1998).

Underway FRRF data were obtained prior to the onset of SOIREE during the pre-release hydrographic survey upstream of the SOIREE site (i.e. 139°E; see Boyd et al., 2000), and during the nightly SF_6 mapping of the patch (a 6–10 h period between 0600 and 1700 h UTC). At the experimental site, dusk and dawn were around 1100 and 1900 h UTC, respectively, so the majority of underway sampling took place during darkness. There were few opportunities for CTD sampling just after the initial fertilisation of the patch due to the need for a comprehensive initial survey of

the iron-fertilised waters. Although underway data were obtained immediately after the first iron infusion, this initial survey was followed by an 18 h period of high winds and large seas when the ship was hove to and the CTD/FRRF package was unable to be deployed.

3. Results

3.1. SOIREE—background

SOIREE took place between the Polar Front (PF) and the southern branch of the Antarctic Circumpolar Current (ACC) (Boyd et al., 2000; Trull et al., 2001), at a site which had a mixed-layer depth of 65 m. Sampling prior to the experiment indicated that the F_v/F_m of the resident algal population was consistently around 0.20 or less along a 100 km S to N section to the west (i.e. upstream) of the SOIREE site. Chlorophyll *a* levels increased during the experiment by more than six-fold (Fig. 2a), mainly due to iron-elevated diatom growth rates (see Gall et al., 2001a). There were decreases in macronutrient levels (Frew et al., 2001) and a marked drawdown in pCO_2 (Bakker et al., 2001; Watson et al., 2000). The temporal trends in F_v/F_m of the phytoplankton community within and outside the patch — at 5 and 30 m depths — are presented (Fig. 2b) to provide a summary of the changes in phytoplankton photosynthetic competence during SOIREE.

3.2. Water column structure

The top of the seasonal thermocline remained at around 65 m throughout the experiment, with some cast-to-cast variation caused by internal waves (Fig. 3). The water above this was initially well mixed, but a stratified surface layer began to develop in the upper 20 m on day 4. The surface stratification persisted until day 10 when a wind-event caused a secondary surface mixed-layer to form to a depth of 40–50 m. Subsequent warming of the surface meant that by the end of the experiment the upper water column had a three layer structure (with layers at 0–20 m, 20–50 m and 50–70 m).

3.3. Underway sampling — surface waters

The F_v/F_m of the resident cells in HNLC waters surrounding the patch remained at the levels observed prior to the onset of SOIREE throughout the 13 d experiment (Fig. 2b). Within 24 h of iron infusion #1 there were small but significant increases in F_v/F_m in the iron-fertilised waters relative to those outside. After 2 days there was a slight decrease in F_v/F_m followed by a subsequent increase after iron infusion #2 to close to double ambient levels. This trend was repeated with a slight decrease in F_v/F_m, followed by an increase after infusion #3. F_v/F_m again decreased between iron infusions #3 and #4, but there was no immediate increase after infusion #4. F_v/F_m dropped markedly on day 10, in response to the mixing of the surface layer (see Fig. 3), but then increased to close to 0.5 by the end of the site occupation on day 13. The magnitude of the increases in F_v/F_m was greater at 30 m depth and showed less variability (Fig. 2b; see below).

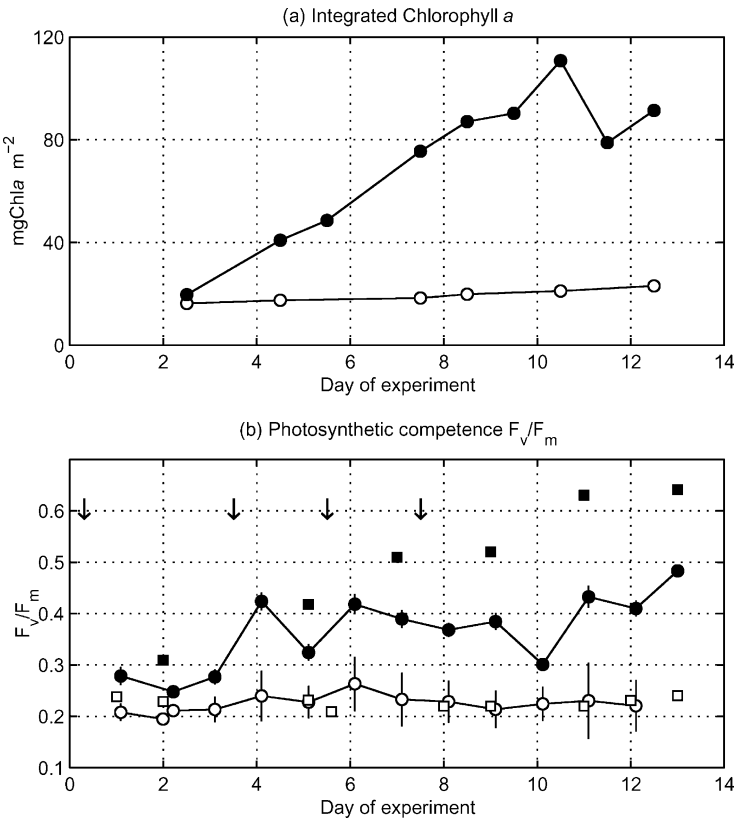

Fig. 2. Summary of SOIREE results: (a) water column-integrated (0–65 m, 6 depths) chlorophyll *a*, from inside (filled symbols) and outside (open symbols) the patch; (b) F_v/F_m at 5 m (underway, circles) and 30 m (CTD, mean of 10 samples, squares), from inside (solid symbols) and outside (open symbols) the patch. The underway data were obtained by first selecting measurements that were made during the hours of darkness (between 1100 and 1800 UTC). The in-patch data show the mean ($\pm$ standard deviation) of the measurements made when the SF_6 concentration was above 50% of its peak value during the night period. The out-patch data are the mean ($\pm$ standard deviation) of measurements made when the SF_6 data was less than 10 fM. Because there were some elevated values of F_v/F_m in waters with SF_6 concentrations less than this value (see Fig. 5) the standard deviations of the out patch data are high. The four arrows show the timing of the iron infusions (days 0, 3, 5, and 7).

These trends in F_v/F_m in surface waters were observed throughout the areal extent of the patch (as denoted by elevated SF_6 levels, see Fig. 4), with the low spatial variability in F_v/F_m being seen in the small standard deviations shown in Fig. 2b. There was a close correspondence between the areal extent and the location of the patch boundaries (defined by SF_6) and surface waters with elevated F_v/F_m see Fig. 4. Underway transects of F_v/F_m along the length of the patch on day 9 (18 February) are compared with those of other variables in Fig. 5. In contrast to the data for SF_6 and dissolved iron, which are peaked in the middle of the transect, F_v/F_m has a plateau, or 'top-hat', distribution with uniformly high values (up to two-fold higher than levels in outside waters) over a 30 km length scale. Scatterplots of F_v/F_m versus dissolved iron, derived from the underway data, provide evidence of a threshold response of F_v/F_m to dissolved iron concentration with an increase

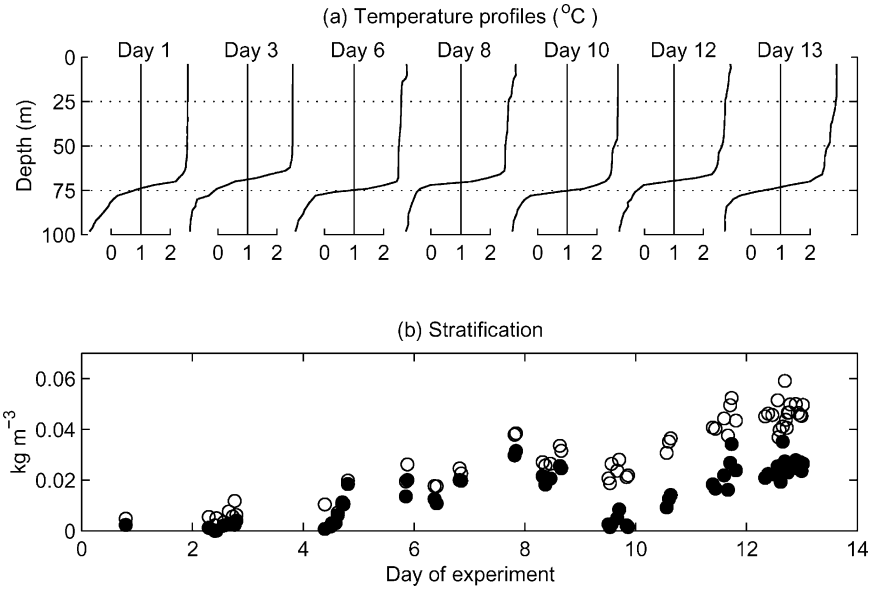

Fig. 3. Changes in the water column structure during SOIREE. (a) Vertical temperature profiles from selected CTD casts. (b) Changes in the stratification over the course of the experiment, shown as the density difference between 10 and 40 m depth (filled symbols) and between 10 and 56 m depth (open symbols). Data from all CTD casts have been plotted.

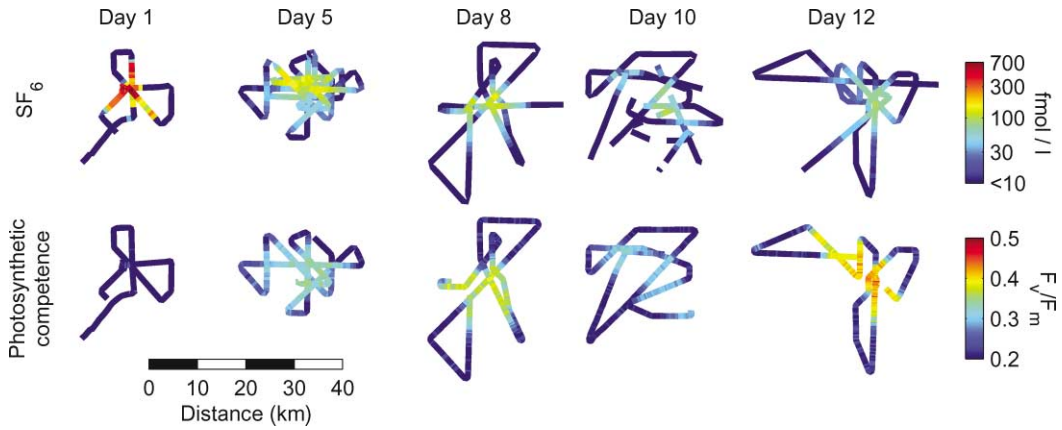

Fig. 4. Underway maps of SF_6 levels (fmol/l) and F_v/F_m during the daily mapping of the iron-fertilised patch on day 1 (February 10); day 5 (February 14); day 8 (February 17); day 10 (February 19) and day 12 (February 21). The ribbon plots denote the vessel's track during each survey. The F_v/F_m plots show data collected between 1000 and 1800 UTC, during which time F_v/F_m shows little diel variation (see Fig. 9).

(doubling) of F_v/F_m at iron levels greater than 0.2 nM (Fig. 6). This relationship shows that the patch of enhanced F_v/F_m is restricted to water that has a dissolved iron concentration of 0.2 nM or more. The non-linear response of the phytoplankton to dissolved iron levels is also seen, to a lesser extent, in variables such as pCO_2 (Bakker et al., 2001).

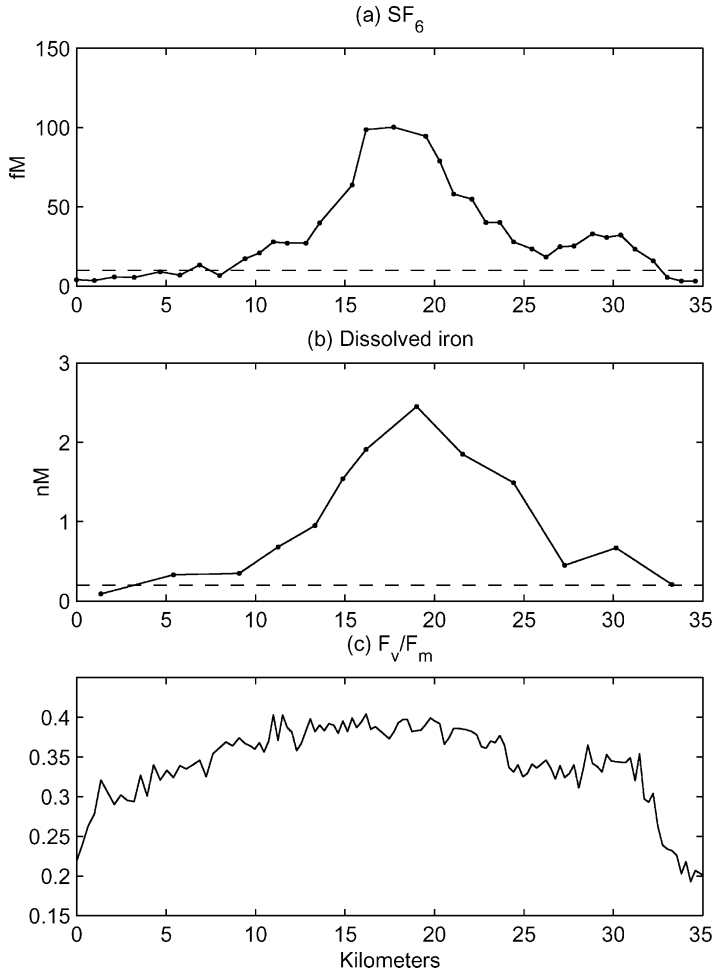

Fig. 5. Underway data (5 m depth) from a transect along the long axis of the fertilised patch (an ellipsoid) on day 9 (February 18), showing (a) SF_6 (b) dissolved iron and (c) F_v/F_m. The dashed lines show (a) the 10 fM SF_6 concentration and (b) the 0.2 nM dissolved iron concentration.

3.4. *Underway sampling* (*30 m*)

FRRF data obtained underway from the tow-body (day 11) indicate that the levels of F_v/F_m at 30 m (Fig. 7) were consistently higher than those sampled underway at 5 m within the patch. This trend was not apparent in the surrounding HNLC waters (Fig. 2b). As most of the underway sampling took place at night and as the surface samples had been dark-adapted, it is unlikely that such differences in the magnitude of F_v/F_m were due to quenching (see Kolber et al., 1998). Increases in F_v/F_m with depth also were observed in the CTD vertical profiles during the experiment (see below). The areal extent of waters chacterised by elevated F_v/F_m at 30 m depth on day 11 was similar to that for surface waters from underway sampling (5 m), with no evidence of

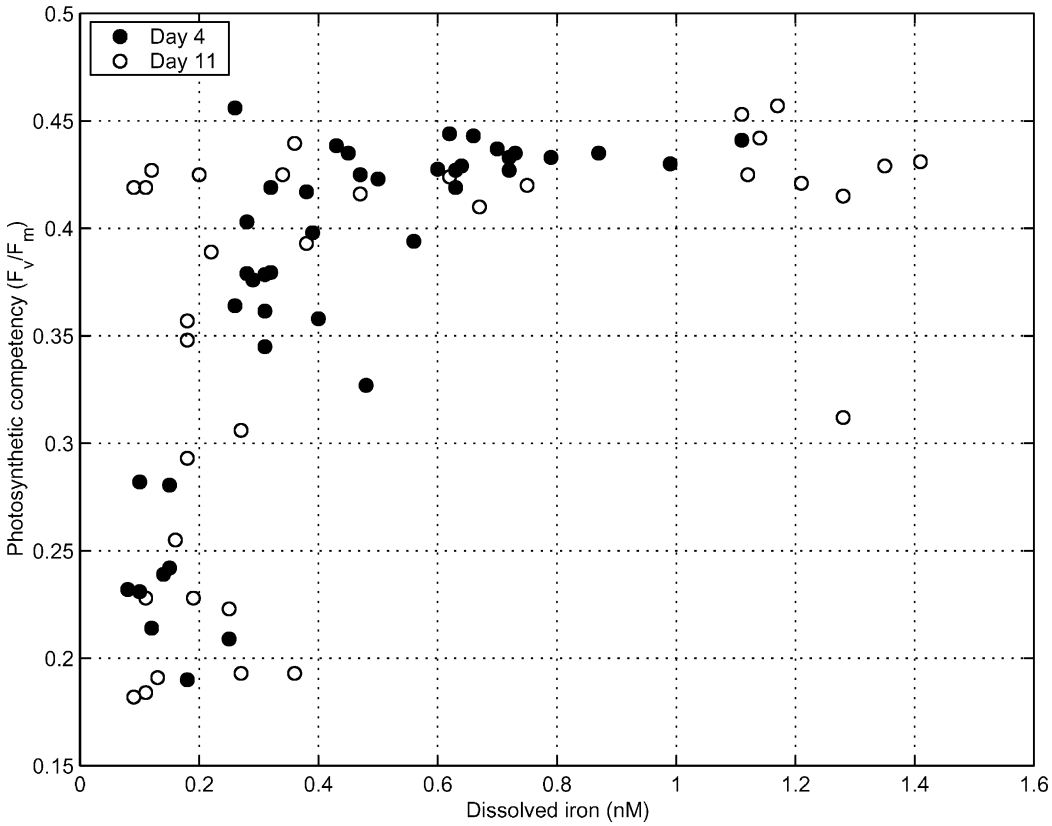

Fig. 6. Underway F_v/F_m versus concurrently sampled dissolved iron concentrations during mapping on day 4 (filled symbols) and day 11 (open symbols) of SOIREE.

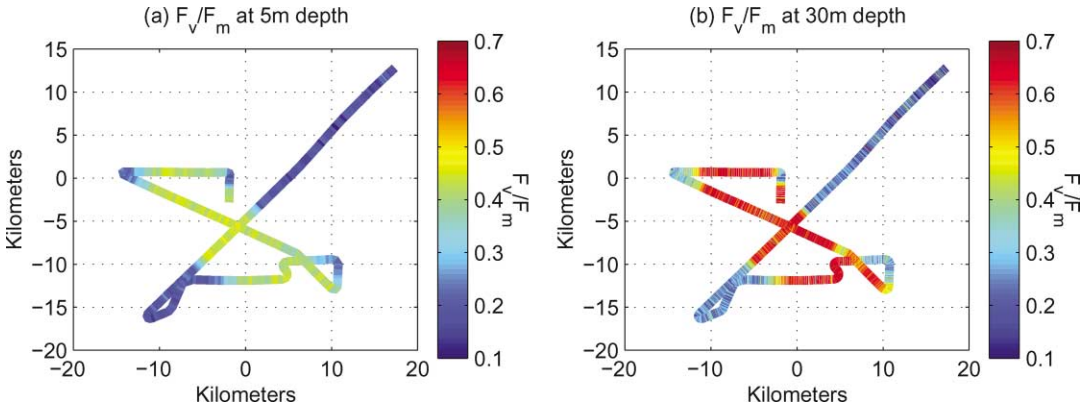

Fig. 7. Underway map of F_v/F_m on day 11 (20 February 1999), between 1100 and 1700 h UTC (a) in the surface waters and (b) from a towbody at 30 m depth. The patch is vertically coherent.

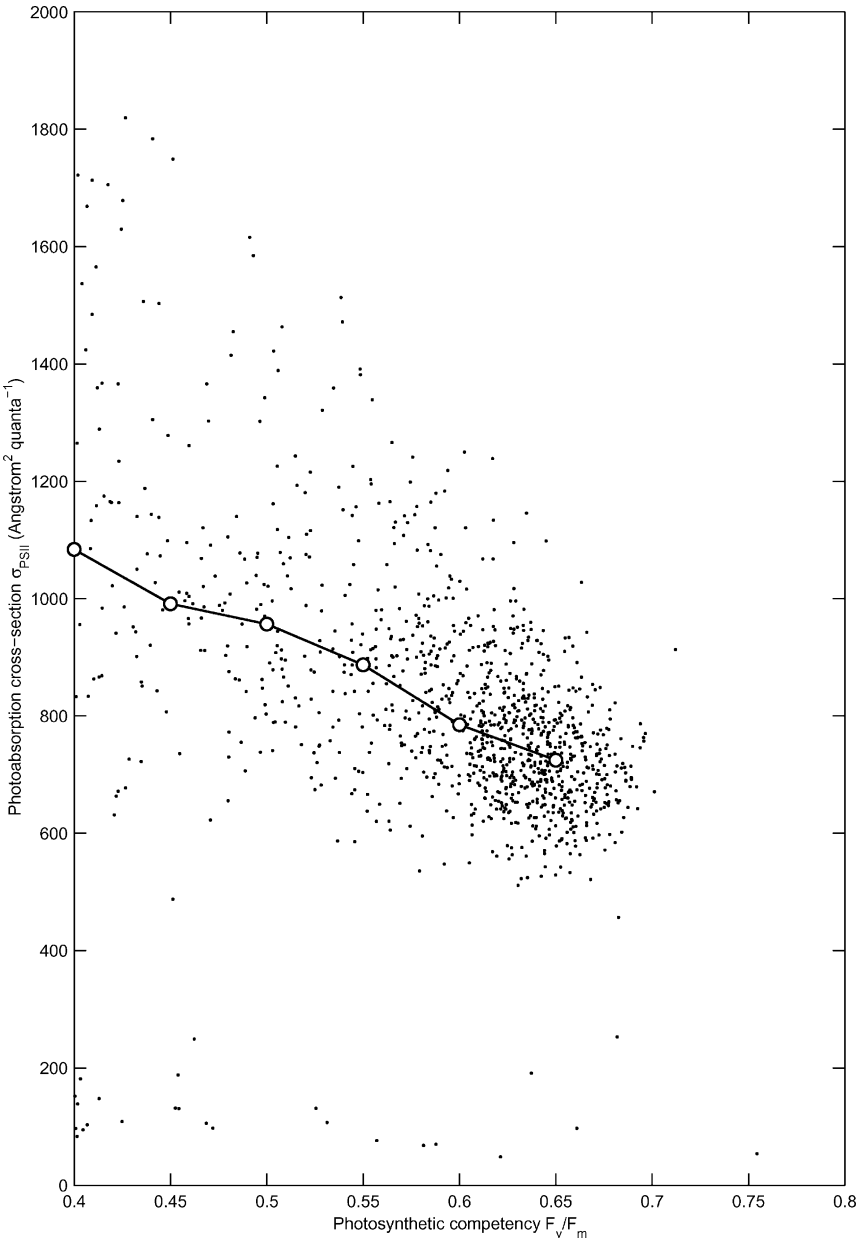

Fig. 8. Data from the towbody (30 m) survey showing the relationship between F_v/F_m and σ. Towards the periphery of the patch F_v/F_m is lower and σ is higher. Estimates of σ from the FRRF become unreliable at low F_v/F_m, so only data with $F_v/F_m > 0.4$ are shown. The dots show all the data, and the circles show the median value of sigma in 0.05 long F_v/F_m bins.

vertical shear. Trends in σ data from the towbody FRRF indicated a 30% decrease within the patch (see Discussion) relative to the surrounding waters (Fig. 8), although, due to low F_v/F_m, an accurate determination of σ in the waters outside the patch was not obtained.

3.5. Diel variability in F_v/F_m

The underway FRRF surveys, in addition to yielding an estimate of the spatial variability of F_v/F_m within the iron-fertilised waters, provided the opportunity to examine diel changes in F_v/F_m. In the HNLC waters at 61°S 140°E prior to and during the experiment, there was a depression in F_v/F_m during daylight hours followed by an increase towards dusk in F_v/F_m (Fig. 9a). This trend was also evident within the patch, with depressed daytime values of F_v/F_m relative to those during the night being recorded for up to 12 h periods, and on a number of days during the SOIREE bloom evolution (Fig. 9b). The mid-day F_v/F_m was, on average, reduced to 60% of the night-time value (with a standard deviation of 18% and a range of 38–96%, over 11 days). As for the surrounding waters, F_v/F_m increased late in the day in the patch and reached constant values around dusk (this may have implications for the photoadaptation times employed, see Methods). The level of F_v/F_m remained approximately constant during the next 6 h or more of darkness, before exhibiting a pronounced increase around dawn (the average increase was 22%, with a standard deviation of 22% and a range of 0–66%, over 11 days). The surface F_v/F_m then dropped rapidly during the morning as the light intensity increased.

3.6. Vertical FRRF profiles

Early in SOIREE, vertical profiles displayed no variations in the magnitude of F_v/F_m over the mixed layer (Fig. 10A), with values of around 0.3 inside the patch, reflecting the trends observed in the underway (5 m) data (see Fig. 2b). However, after day 5 the likely influence of the transient thermal stratification on F_v/F_m was observed, with lower values in the upper 15 m of the water column, relative to those at depth (Fig. 10). This trend was particularly marked on the last day of sampling (day 13) during two comprehensive CTD surveys through the patch (Fig. 11), and this pattern is consistent with that from the towbody and underway mapping (5 and 30 m) data sets.

During the experiment a deep chlorophyll-*a* maximum (DCM) developed (or was advected into) the surrounding HNLC waters (Boyd et al., 2000). Despite higher chlorophyll *a* levels at depth, there was no increase in F_v/F_m (which would indicate a healthy population of phytoplankton) in the DCM at the base of the seasonal mixed layer. The evolution of the SOIREE bloom resulted in a shoaling of the photic depth (defined arbitrarily as the 1% incident light level) from > 70 to 45 m due to increased light attenuation associated with elevated chlorophyll *a* levels (Gall et al., 2001b). The cells at depths > 45 m (i.e. in the aphotic zone) exhibited higher F_v/F_m levels than those between 20–40 m (i.e. in the photic zone, but away from the surface 0–20 m layer); the reasons for this trend are discussed later.

The quantity F_v/F_o may be derived from F_v/F_m ($F_v/F_o = F_v/F_m/(1 - F_v/F_m)$) and has values between 0 and 2. The effect of light climate on F_v/F_o has been discussed previously (Behrenfeld et al., 1999), with low values signifying photoinhibition. Vertical profiles of F_v/F_o on day 13 indicate that cells trapped in the upper ocean in the 0–20 m layer have values of 0.5 during daylight hours (0523 h UTC), which rapidly increase to around 1 at depths > 20 m (data not shown). Based on F_v/F_o, the cells in the upper 20 m appear to have partially recovered from photoinhibition by dusk (1100 h UTC), with F_v/F_o around 1.0 throughout the upper 20 m of the water column.

The temporal changes in F_v/F_m of cells within four algal size classes are presented in Table 1. All size classes had cells with low F_v/F_m early in the experiment (in the waters outside the patch), and

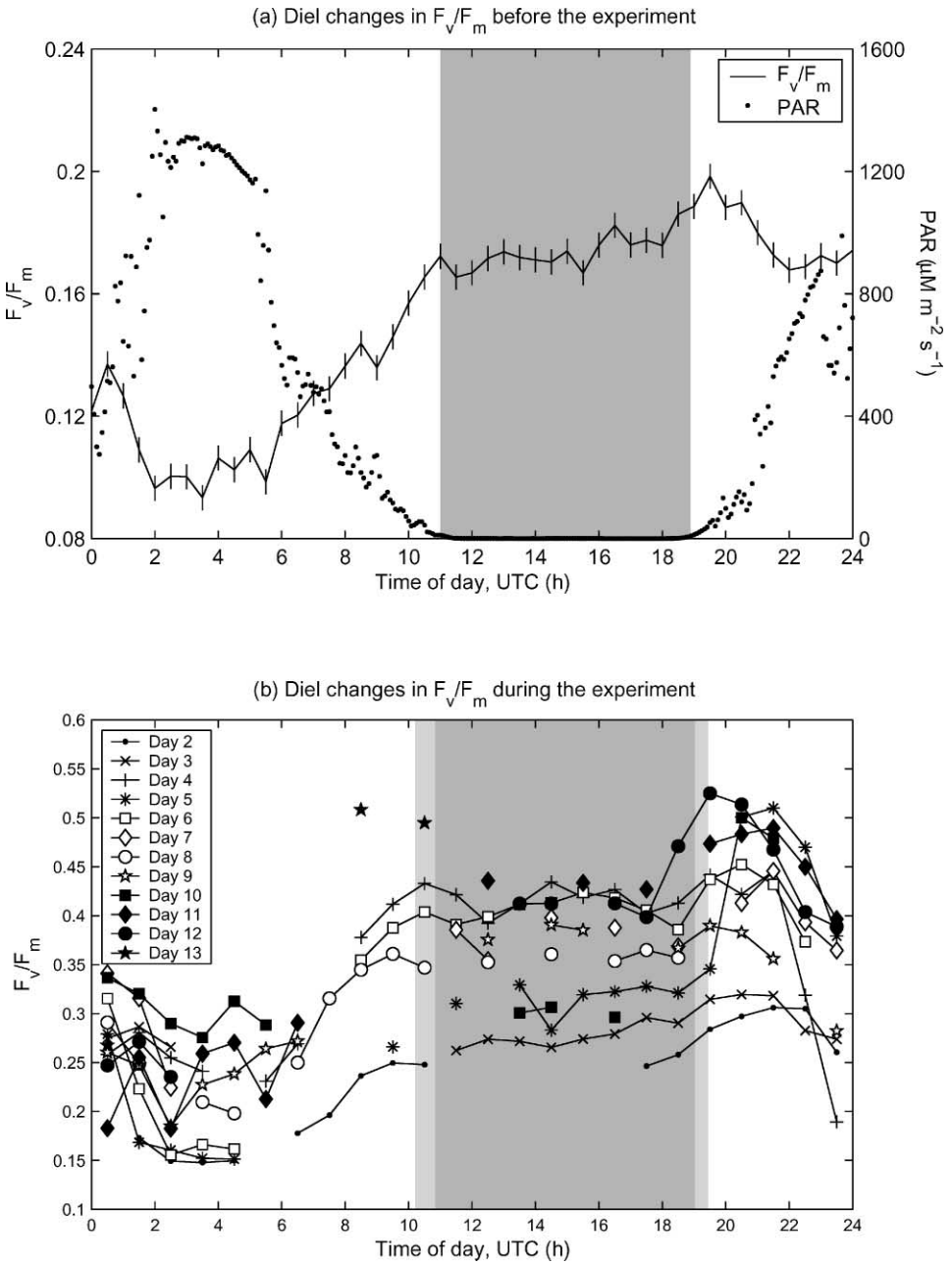

Fig. 9. Diel variations in F_v/F_m: (a) Changes in F_v/F_m at 5 m depth prior to SOIREE (8 February, 1999), when the vessel was in the vicinity of the release site. The underway data are binned into half hour intervals and the mean and standard error of the data in each bin are shown. Incident irradiance, as measured by a PAR sensor mounted high on the ship, is shown by the dots. The shading indicates the time period between sunset and sunrise; (b) Changes in F_v/F_m at 5 m depth within the patch during SOIREE. All the underway data for which the SF_6 concentration was greater than 50 fM have been binned into hour long intervals. The night lengthened during SOIREE and the dark and light shading in (b) shows the hours of between sunset and sunrise at the beginning and the end of the experiment, respectively.

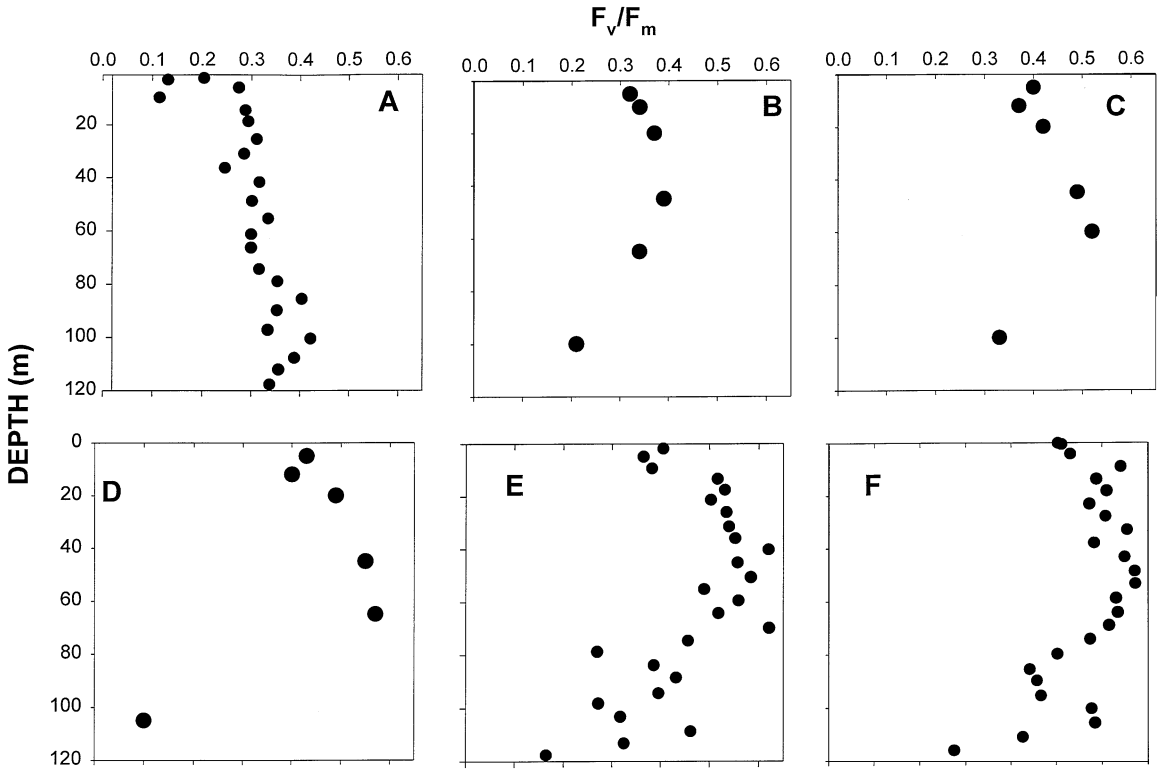

Fig. 10. A time-series of vertical profiles of F_v/F_m over the 13 d SOIREE for iron-fertilised waters. (a) denotes day 4; (b) day 5; (c) day 6; (d) day 8; (e) day 11; and (f) day 13. Data presented in panels b, c and d were derived from discrete samples (Niskin bottles, FRRF run in benchtop mode, casts around local noon), and those in panels a, e and f are from FRRF vertical profiles made around local noon.

the cells in all size classes display iron-mediated increases in F_v/F_m during SOIREE. However, insufficient measurements were made to ascertain whether there were significant differences in the response of each algal size class to iron-enrichment. Cells $> 20\,\mu m$ were mainly large chain-forming diatoms, those 5–20 μm were mainly autotrophic flagellates (and some autotrophic dinoflagellates), while those 2–5 μm and $< 2\,\mu m$ were small autotrophic flagellates and pico-eukaryotes, respectively (Gall et al., 2001b).

4. Discussion

4.1. The temporal evolution of the bloom

The addition of iron to Southern Ocean waters at the SOIREE site resulted in increased photochemical energy conversion efficiency (F_v/F_m) of the resident phytoplankton community. These changes in F_v/F_m were the first indications of a response by the algal assemblage to iron enrichment, and occurred several days prior to other increases in phytoplankton properties such as

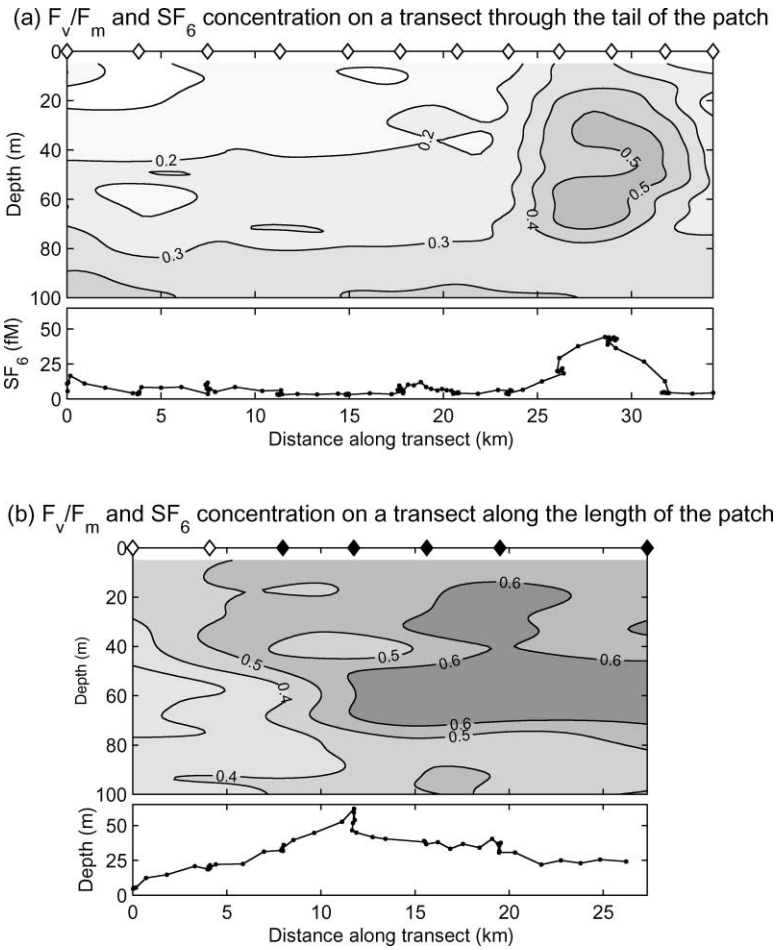

Fig. 11. Contoured sections of smoothed F_v/F_m data versus depth (2 m bins), from a high resolution spatial CTD survey conducted on February 22 1999 (Day 13). (a) from SW to NE across the tail of the patch (b) from SE to NW along the length of the patch. Diamonds show the positions of all CTD casts, with filled diamonds showing casts taken during the night. The lower panel in both (a) and (b) shows the surface SF_6 concentration along the transects.

chlorophyll *a*, growth rate, or cell size (see Gall et al., 2001a,b). The increases in F_v/F_m were subsequent to the first three iron infusions, with evidence of slight decreases in F_v/F_m within 24 h of an infusion as observed during IronEx II (Behrenfeld et al., 1996; see later). A steady increase of F_v/F_m towards maximal values was seen at depth, but the surface values were variable, as they were affected by the changing near-surface stratification. The observed temporal trends for F_v/F_m differ from those recorded by other proxies for algal iron stress such as the flavodoxin levels in diatoms — which decreased from day 5 until day 8, then began to increase (see below).

The low spatial variability in F_v/F_m across the iron-enriched patch (the 'top-hat' effect) was interpreted as being due to the observed relationship between F_v/F_m and dissolved iron concentrations, with a pronounced threshold in F_v/F_m (doubling at this threshold) being observed at around 0.2 nM. In order for this relation to have been seen, the response of F_v/F_m must have been

Table 1
F_v/F_m of cells (sampled from 20 m) with algal size classes during SOIREE. The standard error of the mean on three pseudo-replicates from the 20 m sample was $< \pm 0.04$ in all cases. 'Total' denotes unfiltered samples. IN and OUT denote the iron-fertilised and the surrounding HNLC waters, respectively

	F_v/F_m				
DAY (IN or OUT)	Total	$> 20\,\mu m$	$< 20\,\mu m$	$< 5\,\mu m$	$< 2\,\mu m$
5 (OUT)	0.25	0.19	0.26	0.24	0.17
6 (IN)	0.46	0.33	0.39	0.29	0.34
8 (IN)	0.56	0.41	0.37	0.35	0.41
11 (IN)	0.53	0.42	0.37	0.33	0.36

sufficiently rapid that horizontal mixing did not erode the sharp boundary between the high and low F_v/F_m waters. Olson et al. (2000) report a threshold for marked increases in F_v/F_m of around 0.15 nM dissolved iron — derived from the relationship between ambient dissolved iron levels and F_v/F_m — for the resident cells at stations south of the PF (along the 170°W meridian). Olson et al. (2000) also observed no significant iron-mediated increases in F_v/F_m during deckboard iron-enrichments of phytoplankton from waters characterised by dissolved iron levels greater than 0.15 nM. Coale et al. (1996) report a threshold for iron limitation of 0.15–0.2 nM dissolved iron from quasi-Michaelis-Menten iron-uptake kinetic experiments in HNLC Equatorial Pacific waters. The SOIREE results are therefore consistent with those from other HNLC regions, suggesting that this threshold response may be applicable to all HNLC waters.

4.2. Development of thermal transients and UV damage

The FRRF data from the underway and CTD instruments display differences in the magnitude of F_v/F_m, which can be attributed to the development of the transient thermal stratification. The isolation of cells in the upper ocean in a 0–20 m layer (after day 5) probably resulted in increased photoinhibition by visible and ultraviolet radiation (the E_k of the resident cells in the patch ranged from 30–60 μmol quanta $m^{-2} s^{-1}$ in the upper 40 m (R. Strzepek, unpublished data)). Modelling (Neale et al., 1998a) and laboratory studies of resident cells in the Weddell Sea (Neale et al., 1998b) point to marked increases in UV dosage after the sudden development of shallow layers within a deep seasonal mixed layer, suggesting that photoinhibition caused the depression of near-surface F_v/F_m during the SOIREE site occupation. Although the mixing of the upper waters on day 10 may have been expected to bring cells with higher F_v/F_m to the surface, a pronounced decrease was seen in F_v/F_m. This was presumably caused by bringing low-light-adapted cells up to the surface where they are exposed to higher mean irradiances, resulting in photoinhibition.

Behrenfeld et al. (1999) used F_v/F_o as a proxy for photoinhibition and reported two-fold decreases in F_v/F_o in tropical Pacific waters during 12 h deckboard experiments, from around 1 early in the day to 0.5 by midday (1500 μmol quanta $m^{-2} s^{-1}$). Although, the SOIREE site was characterised by lower incident irradiance levels (< 1000 μmol quanta $m^{-2} s^{-1}$, at local noon) similar trends were observed in F_v/F_o (and in F_v/F_m) in the upper layer (0–20 m).

During SOIREE, the response of F_v/F_m to changes in irradiance was consistent with the existence of several time-scales for recovery from photoinhibition — a fast response (greater than 5 min but less than 60 min), which permitted F_v/F_m to increase as the light decreased between midday and dusk (see Fig. 9), and a slow response (12 h or more), which meant that cells exposed to high irradiances during the day did not fully recover over the night, but retained F_v/F_m values that were lower than those of phytoplankton from depth. The dramatic decrease in F_v/F_m on day 10 (see Fig. 2; due to a mixing event) suggested that the response of F_v/F_m to changing light depends on the previous light-history of the phytoplankton cells. F_v/F_m is mainly referred to as a proxy for nutrient stress (see Geider et al., 1993b), but the complexity of the algal response to changes in irradiance means that this interpretation of F_v/F_m at times will be confounded.

On day 13, phytoplankton were isolated within 3 discrete strata, yet high values of F_v/F_m (0.65, the theoretical maximum, Kolber and Falkowski, 1993) were recorded at 50–60 m (see Fig. 10) in the aphotic portion of the water column ($K_d > 0.10\,m^{-1}$). Dissolved iron levels at 50–60 m depth were similar to those observed in the surface waters of the patch (see Bowie et al., 2001). Algal iron requirements are reported to increase under low light conditions (Raven, 1990; Sunda and Huntsman, 1997; Maldonado et al., 1999), and thus it is puzzling that maximal values of F_v/F_m were recorded under aphotic conditions during SOIREE. Berges and Falkowski (1998) in a lab culture study report that F_v/F_m declined slightly for the diatom *Thalassiosira weissflogii* during prolonged exposure to darkness (14 days). This trend also was observed recently for the lab-cutured diatoms *Skeletonema costatum* and *T. pseudonana*, while the F_v/F_m of other diatom species (*Phaeodactylum tricornutum*) was affected more strongly by prolonged exposure to darkness (J.A. Berges, pers. comm.). In the HNLC waters surrounding the patch, there was no discernible increase in F_v/F_m within the DCM at the base of the seasonal mixed layer. Parslow et al. (2001) investigated the reasons for the existence of such DCM in sub-polar and polar waters just north of the SOIREE site and were unable to provide any satisfactory mechanism to explain the development and persistence of such a feature.

4.3. Algal community structure and diel variability in F_v/F_m

Phytoplankton stocks in the surrounding HNLC waters were initially dominated by pico-eukaryotes, and during the evolution of SOIREE there were transient increases in pico-eukaryote and autotrophic flagellate stocks, but sustained increases only in diatom biomass (Gall et al., 2001b). Size-fractionated F_v/F_m data suggested that all algal classes displayed sub-optimal photosynthetic efficiencies at the onset of the experiment, with increases in F_v/F_m for all size classes upon iron enrichment. Although the community structure in the polar Southern Ocean is different to that in the equatorial Pacific (for example no *Prochlorococcus* or *Synechococcus*) the observed trends for all taxa (as inferred from the size class data) are similar to that observed during IronEx I (Kolber et al., 1994).

There was no evidence in the waters surrounding the SOIREE patch of the distinct diel fluorescence patterns reported by Behrenfeld and Kolber (1999) in the South Pacific Gyre (i.e. night-time decreases in F_v/F_m—due to prokaryotes under iron-limitation being susceptible to the influence of strong state transitions). One explanation for this is the absence of prokaryotic picoplankton in the polar Southern Ocean (Marchant et al., 1987), with none reported at the SOIREE site (Hall and Safi, 2001). The fluorescence signature of state transitions so far has only

been observed in prokaryotic algae (Behrenfeld and Kolber, 1999) as, unlike eukaryotes, they have some common electron carrier components for both photosynthesis and respiration. Other differences between the polar and tropical waters include algal growth rates (0.2 d^{-1} in the SOIREE bloom (Gall et al., 2001a) compared with 1.0 d^{-1} in tropical waters (Behrenfeld and Kolber, 1999). Diel patterns in F_v/F_m were observed during SOIREE (Fig. 9), and in particular there was a marked dawn increase in F_v/F_m, followed by a rapid decrease. This was not observed in the Equatorial Pacific IronEx II experiment (see Fig. 2C in Behrenfeld and Kolber, 1999), and the reason for such a 'shift-up' is not presently known. Similar dawn shift-up trends have been observed in other intrinsic algal biochemical properties — such as Nitrate Reductase activity in Californian coastal waters (see Berges et al., 1995).

4.4. Trends in other physiological proxies for algal Fe stress

During SOIREE, iron-mediated changes in algal physiological status also were monitored using other techniques, such as the flavodoxin assay (LaRoche et al., 1996), which considered together provide insights into the allocation of resources within algal cells upon iron-enrichment. The resident diatoms prior to the experiment were iron-stressed (see Boyd et al., 2000), based on the single cell flavodoxin immunofluorescence assay (LaRoche et al., 1996). This supports the relatively low values of F_v/F_m observed prior to SOIREE. Upon iron enrichment there was a detectable increase in F_v/F_m after 24 h, whereas the alleviation of algal iron stress in diatoms (based on flavodoxin assay) was not evident until after day 5 (see Fig. 12). Similarly, decreases in sinking rates of large cells, a proxy for the alleviation of iron limitation (Muggli et al., 1996), were not recorded until day 5 (Waite and Nodder, 2001). Thus photosynthetic competence (F_v/F_m) was the first property to respond to iron supply.

Conversely, F_v/F_m remained close to maximal on day 13 when trends in other proxies indicated the onset of algal iron stress, for example flavodoxin levels in diatoms (see Fig. 12) and algal sinking rates were approaching initial values (Fig. 12). Additional evidence for the onset of algal iron stress was provided from observations of the uptake of organically bound iron (a proxy for algal physiological status, Maldonado and Price, 1999), which decreased by day 5 and then, by day 13, increased to rates comparable with those at the onset of SOIREE (Maldonado et al., 2001). The elevated iron stress towards the end of the experiment may have resulted from changes in the partitioning of iron between the inorganic and organic pools (Croot et al., submitted; Maldonado et al., in press).

F_v/F_m is a non-linear function of growth rate and does not decline significantly until algal growth rates drop to 50% or less of μ_{max} (Kolber et al., 1988; Graziano et al., 1996), whereas other proxies are more sensitive indicators of iron stress (McKay et al., 1997; Erdner, 1998). Indeed, McKay et al. reported flavodoxin expression in cultured diatoms at 90% of maximum algal growth rates. The highest estimated diatom growth rate during SOIREE was 0.6 div d^{-1} (below the theoretical maximum at 2.5°C ambient water temperatures, see Banse, 1991) and this had declined to 0.4 div d^{-1} by the end of the experiment, but still remained above 0.5 μ_{max}. This suggests that a significant decrease in F_v/F_m would not have occurred by day 13. It is thought that any iron-mediated reduction in F_v/F_m is delayed until all other mechanisms to reduce cellular iron requirements have been exploited (McKay et al., 1997). This would appear to have been the case during the experiment, since the SOIREE bloom

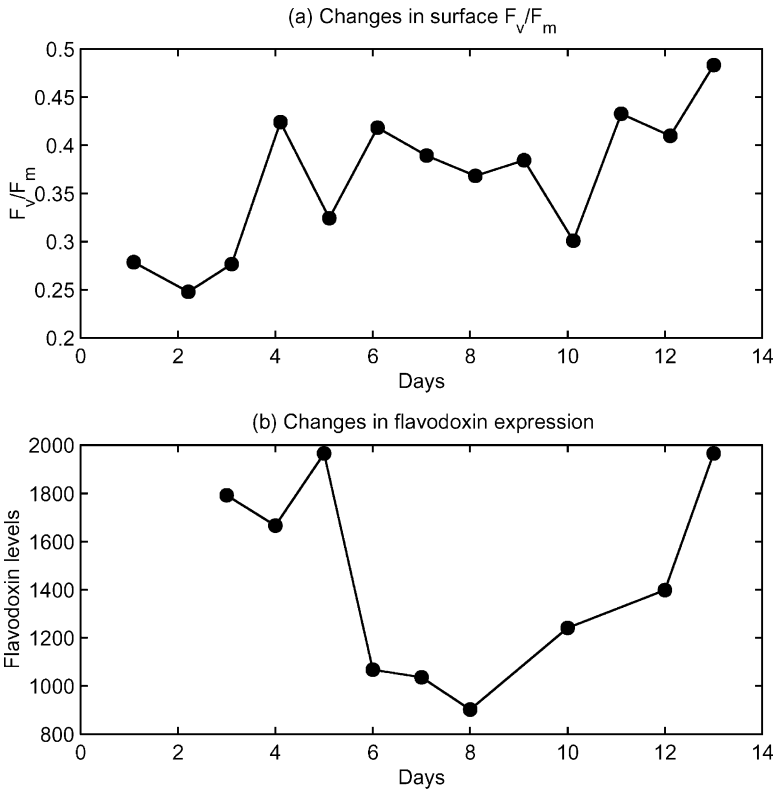

Fig. 12. The temporal evolution (a) of F_v/F_m (5 m, underway, in patch; redrawn from Fig. 2b) and (b) flavodoxin levels in diatoms (0–10 m, in patch, data courtesy of Julie LaRoche) during SOIREE.

was observed from space more than 40 days after the initial enrichment (i.e. during mid March 1999; see Abraham et al., 2000).

4.5. Comparison with other Fe enrichment studies

One of the main findings of SOIREE — that of iron-mediated increases in F_v/F_m of the resident phytoplankton — was observed during both IronEx in situ enrichments in the Equatorial Pacific (Kolber et al., 1994; Behrenfeld et al., 1996). Although the general trends observed in SOIREE are similar to those in IronEx I (Kolber et al., 1994; iron-mediated increases in F_v/F_m for all size fractions) and II (Behrenfeld et al., 1996; increase in F_v/F_m after iron addition, with slight decreases in F_v/F_m between additions), there were also significant differences between the studies, particularly in the timing of the increases in F_v/F_m. During SOIREE (based on samples from 30 m depth) F_v/F_m had doubled by day 7 (0.25–0.53), and subsequently increased linearly, attaining the theoretical maximum on day 10/11. In contrast, during IronEx I F_v/F_m had increased 70% (and exponentially) within 24 h and peaked (0.63) after 48 h (Kolber et al., 1994). Similarly, during Ironex II, F_v/F_m increased exponentially over an initial 25-h period from 0.25 to 0.50. In the NE subarctic Pacific, Boyd et al. (1998) reported that F_v/F_m increased to maximal values within 36 h of iron enrichment (deckboard, water temperature 10°C, May 1995).

There have been several deployments of FRRF instruments in the polar Southern Ocean (Strutton et al., 1997, 2000; Olson et al., 2000), but only the latter study has examined the influence of iron enrichment on F_v/F_m. Olson et al. (2001) report that a 4–6 day incubation period was required for F_v/F_m to increase from ambient levels (0.25) to maximum levels (0.66). As for SOIREE, this time period was considerably slower than those reported for equatorial and subarctic Pacific waters, suggesting that temperature plays a key role in determining the time scale of response of F_v/F_m to iron enrichment, as it does for other physiological processes (Banse, 1991). The response times observed by Olson et al. (2000) are slightly faster than observed in SOIREE, but were conducted under conditions of incident irradiance (i.e. with no screening, Ross Sea experiments, 4-day response time), or with some screening (details not provided by Olson et al.) for experiments conducted south of the PF (5–6 day response time).

The data set for the cross-sectional area of photosystem II, σ, was noisier than that for F_v/F_m during SOIREE, but there was a slight decrease in σ towards the center of the patch (less than 800 $Å^2$ quanta^{-1} inside, compared with approximately 1000 $Å^2$ quanta^{-1} outside). During IronEx I, σ decreased two-fold, whereas during IronEx II there was a doubling in σ over an initial 25-h period after the enrichment. The reasons for the different trends for σ in the IronEx studies is not known. Cells may respond to changes in environmental factors by either altering σ (and not changing the number of reaction centres) or by creating more reaction centres with similar cross sections (Behrenfeld et al., 1999). The slight decrease in σ within the SOIREE patch may be due to the resident cells in the HNLC waters having relatively few reaction centres in the pigment beds. Then, upon iron enrichment, the cells increased the number of reaction centers rapidly, relative to increases in their light-harvesting pigments (see Discussion in Behrenfeld et al., 1999). There appears to be no published information on the response of σ in phytoplankton to iron-enrichment within the deep mixed layers that characterise much of the Southern Ocean.

4.6. Comparison with other Southern Ocean studies

The values of F_v/F_m (0.2) observed at the onset of SOIREE and during the pre-site oceanographic survey were similar to those observed south of the PF (170°W) and in the Ross Sea in February/March 1998 (Olson et al., 2000). However, Olson et al. reported values of F_v/F_m of 0.4–0.5, at several stations close to the PF that were characterised by elevated dissolved iron levels. The PF, in the Atlantic sector, has elevated iron levels associated with an iron-rich frontal jet (de Baar et al., 1995). The levels observed during SOIREE are also similar to those from the study of Strutton et al. (1997, 2000) in the waters (both open-ocean and coastal) south of the SOIREE site in the vicinity of the E. Antarctic land mass in summer.

5. Conclusions

(i) F_v/F_m of the resident cells increased upon iron enrichment, and reached maximum levels after 10 days. This was considerably slower than reported for equatorial and subarctic Pacific waters. The slower response time may be related to low water temperature, and/or possibly to the presence of deep mixed layers in the Southern Ocean.

(ii) All algal taxa responded to iron-enrichment during SOIREE, which also was observed in the IronEx I experiment.
(iii) There was evidence on several occasions during the time-course of the SOIREE bloom of marked dawn increases in F_v/F_m, followed by a pronounced decrease in F_v/F_m after dawn due to increasing light levels.
(iv) Phytoplankton near the surface had lower values of F_v/F_m than phytoplankton at depth, and changes in water column structure had a strong effect on surface values of F_v/F_m. This suggests that there is a multi-timescale response of F_v/F_m to changing light and that care must be taken in interpreting depressed surface F_v/F_m solely to algal nutrient stress.

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Times of sunset and sunrise were calculated using routines made available by the United States Naval Observatory over the world-wide web (http://aa.usno.navy.mil/AA/)

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