Exceptional growth rates of phytoplankton species under iron-replete conditions

Philipp Assmy¹, Christine Klaas¹, Joachim Henjes¹, Marina Montresor², Ilka Peeken³, Rüdiger Röttgers⁴, Dieter Wolf-Gladrow¹ & Victor Smetacek¹

¹Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
²Stazione Zoologica 'A. Dohrn', Villa Comunale, 80121 Napoli, Italy
³Leibniz Institute for Marine Sciences, IFM-GEOMAR, West Shore Campus, Düsternbrooker Weg 20, 24105 Kiel, Germany
⁴Institute for Coastal Research, GKSS Research Center Geesthacht, Max-Planck Strasse 1, 21502 Geesthacht, Germany

Introduction

All iron fertilization experiments conducted so far have shown that iron is a limiting factor for phytoplankton growth in HNLC areas. Model studies and a recent comparison of all iron fertilization experiments have suggested that the deep mixed layers occurring in the Southern Ocean, might constrain the build-up of phytoplankton biomass and iron utilization below the levels found in other oceanic areas with stratified regimes. Here we report growth rates of phytoplankton species and biomass accumulation from two fertilization experiments carried out in the Southern Ocean (EisenEx and EIFEX). We show that despite deep mixed layers (>40 to about 100 m depth) dominant species showed high growth rates that argue against the importance of light limitation in controlling biomass accumulation in the Southern Ocean.

Iron-induced blooms

During both EisenEx and EIFEX massive phytoplankton blooms developed in deeply mixed surface layers (Fig. 1).

**Figure 1:** Bloom development in µg Chl a m⁻³ over the duration of both experiments for the upper 200 m of the water column. Note the different time scales for both experiments. The red line indicates the bottom of the mixed layer.

**Species-specific response**

Detailed microscopic analysis of the phytoplankton assemblage during the two iron-fertilization experiments revealed characteristic patterns of net accumulation (without patch dilution and mortality) of phytoplankton species populations (Fig. 2). *Pseudo-nitzschia lineola* and *Chaetoceros debilis* showed the highest net accumulation rates of 0.2 d⁻¹. Other species (e.g. *Fragilariopsis kerguelensis*) increased population size at a linear rate whereas some species such as *Emiliania huxleyi* decreased in abundance.

**Figure 2:** Temporal development of 80 m-depth integrated abundance of *Pseudo-nitzschia lineola*, *Chaetoceros debilis*, *Fragilariopsis kerguelensis* and *Emiliania huxleyi* during EisenEx. Symbols indicate samples taken inside (solid diamonds) and outside (open squares) the fertilized patch. The thin line represents the running average over three temporally adjacent in-patch stations.

**Mortality estimates**

Mortality rates were estimated from dark incubation experiments (Fig. 3A) and accumulation of empty and broken diatom frustules (Fig. 3B). Mortality estimates derived from empty and broken frustules were up to an order of magnitude lower as those calculated from the dark incubations because we could not account for losses due to sinking and dissolution and for the fraction of frustules incorporated into fecal pellets.

**Figure 3:** A) Mortality rates derived from dark incubation experiments for five diatom species and the coccolithophore *Emiliania huxleyi*. The average mortality rate is indicated by the black line. B) Mortality rates derived from accumulation of empty and broken frustules of four diatom species over the time course of EisenEx. The black arrow indicates the average mortality rate derived from dark incubations.

**In-situ growth rate estimates**

The model combines net accumulation rates from cell counts with mortality rates derived from dark incubation experiments and patch dilution. Patch dilution was derived from horizontal and vertical diffusion of the inert tracer SF₆. The evolution of phytoplankton species in the mixed layer (e.g. *Fragilariopsis kerguelensis*, Fig. 4) within the patch could therefore be expressed as the sum of diffusive terms, accumulation terms, and mortality.

**Figure 4:** The red dotted line represents the temporal evolution of growth rates of *Fragilariopsis kerguelensis* during EisenEx. The solid black line depicts the general deepening of the mixed layer during EisenEx whereas the red line indicates the maximum growth rate for *F. kerguelensis* given in the literature.

Conclusions

- With our model we could show that during EisenEx loss terms accounted for roughly 60% of growth and that mixing and mortality contributed equally to the losses.
- Furthermore our model indicates that light limitation due to deep mixed layers did not severely control build-up of bloom biomass.
- *Fragilariopsis kerguelensis* growth was close to the maximum growth given in the literature.
- Estimates of growth rates are strongly dependent on our knowledge of mortality rates.

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