Resource colimitation drives competition between phytoplankton and bacteria in the Southern Ocean

Lavenia Ratnarajah, Stéphane Blain, Philip W Boyd, Marion Fourquez, Ingrid Obernosterer, Alessandro Tagliabue

Resource colimitation drives competition between phytoplankton and bacteria in the Southern Ocean

Lavenia Ratnarajah[1], Stéphane Blain[2], Philip W. Boyd[3], Marion Fourquez[4,3], Ingrid Obernosterer[2], Alessandro Tagliabue[1]

1. Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom
2. Sorbonne Université, CNRS, Laboratoire d'Océanographie Microbienne (LOMIC), Observatoire Océanologique de Banyuls, 66650 Banyuls sur mer, France
3. Institute for Marine and Antarctic Studies, University of Tasmania, Tasmania, Australia
4. Aix Marseille Univ., Universite de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille, France

Corresponding author:
Lavenia Ratnarajah (L.Ratnarajah@liverpool.ac.uk)

Keywords: Iron, Phytoplankton, Bacteria, Competition, Southern Ocean

Key points: (140 characters)

1. Competition for iron between phytoplankton and bacteria is modulated by the colimiting effects of light and dissolved organic carbon
2. When enough labile dissolved organic carbon is present, bacteria can outcompete phytoplankton for iron
3. Phytoplankton exudation may be insufficient to stimulate bacterial dominance in the absence of other dissolved organic carbon sources

Abstract (150 words)

Across the Southern Ocean, phytoplankton growth is governed by iron and light, whilst bacterial growth is regulated by iron and labile dissolved organic carbon (LDOC). We use a mechanistic model to examine how competition for iron between phytoplankton and bacteria responds to changes in iron, light and LDOC. Consistent with experimental evidence, increasing iron and light encourages phytoplankton dominance, whilst increasing LDOC and decreasing light favours bacterial dominance. Under elevated LDOC, bacteria can outcompete phytoplankton for iron, most easily under lower iron. Simulations reveal that bacteria are major iron consumers, and suggest that luxury storage plays a key role in competitive iron uptake. Under seasonal conditions typical of the Southern Ocean, sources of LDOC besides phytoplankton exudation modulate the strength of competitive interactions. Continued investigations on the competitive fitness of bacteria in driving changes in primary production in iron-limited systems will be invaluable in refining these results.

Plain summary

In large areas of the Southern Ocean, phytoplankton growth is controlled by the availability of iron and light whilst bacterial growth is controlled by the availability of iron and labile dissolved organic carbon (LDOC). We developed a mechanistic model to examine how phytoplankton and bacteria compete for iron under different light levels and LDOC supply. We find that phytoplankton dominate as iron and light increases while increasing LDOC and decreasing light favours bacterial dominance. If enough LDOC is present, bacteria can outcompete phytoplankton for iron. More broadly, we find that while bacteria are a major consumer of iron in the Southern Ocean, seasonal changes in light drive phytoplankton dominance over bacteria, unless LDOC is supplied by other sources such as viral lysis, excretion etc., which strengthen competitive interactions.

Introduction

Phytoplankton growth in large areas of the Southern Ocean is regulated by the micronutrient iron (Fe) (Martin et al. 1994, Blain et al. 2007, Boyd et al. 2007), with seasonal co-limitation by light (Mitchell et al. 1991, Strzepek et al. 2012) due to the deep mixed layers and ice cover that are prevalent in early spring, autumn and winter. The low rates of primary production and large-scale upwelling of deep water containing low dissolved organic carbon (DOC) concentrations lead to some of the lowest surface DOC concentrations in the global ocean (~40 – 50 μM, Hansell et al. 2012). While low surface dissolved Fe and DOC is thought to restrict heterotrophic bacterial (hereafter bacteria) growth in the Southern Ocean (Church et al. 2000, Obernosterer et al. 2015), studies from Fe-limited regions have demonstrated that bacteria may also be significant consumers of dissolved Fe and can exhibit greater cellular Fe quotas than phytoplankton (Tortell et al. 1996, 1999, Boyd et al. 2012, Fourquez et al. 2015, 2020). High bacterial Fe demand and uptake rates compared to phytoplankton suggest that bacteria could be significant competitors for dissolved Fe in the Southern Ocean (Fourquez et al., 2015, 2020, Mazzotta et al. 2020).

Theoretically, two species competing for the same limiting resource cannot coexist at constant population levels (Hardin 1960). However, colimitation can lead to stable coexistence (Burson et al. 2018) or alternative stable states, depending on ambient environmental factors (e.g. resource supply and lability, temperature, light and mortality) and the traits of the competing species (Tilman 1982, Brauer et al. 2012) that affect resource uptake and growth (Hutchinson 1953, Titman 1976). In the Southern Ocean, the distinct seasonal light cycle regulates the timing of phytoplankton blooms, whereas Fe controls the magnitude of growth. While phytoplankton productivity then fluctuates according to season and location (Ardyna et al. 2017), the implications of changes in Fe, DOC and light over the seasonal cycle on phytoplankton-bacterial interactions are poorly understood. Upwelling of deep water is generally considered to supply a relatively refractory pool of DOC (Hansell et al. 2013). However, the release of labile DOC via phytoplankton exudation (Larsson and Hagström 1979, Wood and Van Valen 1990) or by other biotic processes commonly linked to phytoplankton production, such as sloppy feeding and faecal production by predators (Lampitt et al 1990, Møller et al. 2003, Møller 2007), viral lysis (Bratbak et al. 1993, Middleboe et al. 2002, Gobler et al. 2003, Poorvin et al. 2004) and phytoplankton cell mortality (Veldhuis et al. 2001) suggests that seasonal changes in phytoplankton production

may facilitate phytoplankton and bacterial coexistence in the Southern Ocean by supplying labile DOC. While labile DOC is often rapidly utilised within hours (Fourquez et al. 2014, Obernosterer et al 2015), seasonal accumulation of DOC has been observed in the Bermuda Atlantic Time Series (BATS) site possibly due to phosphorus limitation of bacterioplankton growth (Cotner et al. 1997, Rivkin and Anderson 1997) or the accumulation of recalcitrant DOC that prevents rapid utilisation (Legendre and Le Fevre 1995, Carlson and Ducklow 1996, Carlson et al. 1998, Cherrier et al. 1996, Søndergaard et al. 2000). The turnover time for recalcitrant DOC ranges from months (semi-labile) – 40,000 years (ultra-refractory) (Carlson and Ducklow 1995, Cherrier et al. 1996, Hansell et al. 2012, 2013, Lønborg et al. 2018).

At a cellular level, phytoplankton can use mechanisms such as Fe storage protein (i.e. ferritin) and vacuolar storage that enable them to stockpile Fe for use when ambient Fe levels are low (e.g., Lampe et al. 2018, Marchetti et al. 2009, Cohen et al. 2018). A more limited set of observations indicates that although bacteria possess two types of ferritin-like molecules, the bacterial ferritins and bacterioferritin (Andrews et al. 2003, Rivera 2017, Debeljak et al. 2019), the regulation of the bacterioferritin gene is unclear (Carrondo 2003). Nevertheless, the higher Fe quotas observed in bacteria, relative to phytoplankton (Fourquez et al., 2015, 2020, Mazzotta et al. 2020, Tortell et al. 1996, Sarthou et al. 2008, Boyd et al. 2012) suggest that bacteria may require more Fe, or have the capacity for luxury Fe uptake, and hence may compete with phytoplankton for Fe. The parallel impact of other environmental regulatory factors, such as light or labile DOC, on the outcome of such a competition are unclear.

In this study, we develop a mechanistic model to examine the competitive interactions between phytoplankton and bacteria in response to Fe, light and DOC colimitation. Our model was designed to assess the mechanisms behind these competitive interactions in an idealised setting and to explore the implications of these interactions on seasonal bloom dynamics in the Southern Ocean. We find resource competition influences the magnitude of phytoplankton and bacterial biomass and rates of Fe uptake, growth and carbon fixation - which depend on secondary factors affecting the growth and biomass accumulation of phytoplankton and bacteria, such as light, DOC and luxury Fe uptake.

2. Methods

2.1 Biogeochemical model

The rate of change in phytoplankton carbon, chlorophyll-a and dissolved Fe is based on the Pelagic Integration Scheme for Carbon and Ecosystem studies (PISCES-v2, Aumont et al. 2015) model, which is commonly used as part of global studies of ocean Fe biogeochemistry (e.g. Tagliabue et al., 2016). Here, we also explicitly account for the change in bacterial carbon and Fe biomass. Changes in phytoplankton and bacterial carbon and Fe biomass, as well as phytoplankton cellular chlorophyll-a are driven by rates of growth, carbon fixation, chlorophyll synthesis and Fe uptake in response to Fe, light (modelled here as the photosynthetic available radiation, PAR) and labile DOC (Fig. 1). We identify two sources of labile DOC: phytoplankton exudation and additional biotic sources which can be supplied via grazing processes (excretion, sloppy feeding), viral lysis etc. Detailed equations and specific parameterisations are described in the supplementary material (Supp. methods and Supp. Table 1). Here we briefly describe the underlying processes considered and their dependencies.

Fe uptake by both phytoplankton and bacteria is modelled as a function of external Fe availability, including luxury Fe uptake and is down regulated when maximum cellular Fe quotas are reached. For simplicity, we assume phytoplankton and bacteria have the same maximum cellular Fe quota of 80 μmol Fe:mol C. This is based on the maximum phytoplankton cellular Fe quota used in PISCES-v2 (Aumont et al. 2015) and maximum bacterial cellular Fe quota from a laboratory experiment under Fe-replete conditions (Mazzotta et al. 2020). Labile DOC uptake by bacteria is modelled as a function of the temperature dependant maximum specific growth rate and bacterial Fe limitation. Light limitation of phytoplankton is identical to the PISCES-v2 model, explicitly accounting for phytoplankton carbon production and chlorophyll synthesis. Resource limitation for both phytoplankton and bacteria follow the quota model approach for Fe used in PISCES-v2 and a Monod style limitation form for labile DOC. Phytoplankton carbon fixation is then a function of the temperature dependant maximum growth rate and light and Fe limitation. DOC is cycled via exudation and mortality and Fe is cycled via mortality (Fig. 1). DOC exudation is a fixed proportion of phytoplankton carbon fixation (10%; Aumont et al. 2015). A quadratic mortality drives the recycling of cellular Fe, carbon and chlorophyll.

2.2 Experimental design

Using our model, we explore the role of Fe-light and Fe-DOC co-regulation of phytoplankton and bacteria using two sets of model simulations at a constant temperature of 1°C. We first

run a set of simulations with phytoplankton alone, across a range of light and Fe levels (from 1 W m^{-2} to 40 W m^{-2} and 0 to 1 nM for PAR and Fe, respectively) and bacteria alone, across a range of labile DOC and Fe levels (from 0 to 100 μM and 0 to 1 nM for total DOC and total Fe, respectively). These initial experiments allow us to explore the separate responses of phytoplankton and bacteria to changing light, Fe and DOC levels. We then run a second set of experiments with both phytoplankton and bacteria competing under varying light and Fe (Fe-PAR), with a fixed DOC level of 5 μM (broadly representative of typical labile DOC levels, Hansell et al. 2009), and varying Fe and DOC (Fe-DOC), with a fixed light level of 20 W m^{-2} (broadly representative of typical mixed layer average Southern Ocean light levels). To specifically address the potential role played by luxury Fe uptake in bacteria, we run a parallel simulation with variable cellular Fe quota for phytoplankton, but fixed the Fe quota for bacteria at a constant 10 μmol Fe:mol C (Aumont et al. 2015). We use the model results after 35 days of integration (by which time the model has reached quasi steady state) in our analysis.

3. Results and Discussion

3.1 Response to resource co-limitation in the absence of competitive interactions

Increasing Fe and light leads to an expected increase in phytoplankton carbon biomass (Fig. 2a), with the phytoplankton cellular Fe quota (Fe:C ratio) increasing as ambient Fe concentration increases (Fig. 2b). However as light increases in parallel to Fe, phytoplankton accumulate less cellular Fe relative to carbon because of high rates of growth and carbon fixation (Fig. 2b, c). Increasing Fe and DOC similarly leads to an increase in carbon biomass of bacteria (Fig. 2d). Although bacteria reach their maximum cellular Fe quota in all our simulations, bacterial growth remained restricted at low DOC concentrations due to DOC limitation which leads to high Fe:C ratios due to low rates of C assimilation (Fig. 2e). Increasing Fe and DOC in parallel results in a 7-fold increase in bacterial growth rate (Fig. 2f).

3.2 How does iron-light influence phytoplankton-bacterial interactions?

Competition for Fe between phytoplankton and bacteria affects growth rates, production and Fe uptake, which influences the relative accumulation of biomass. Under varying Fe and light, but fixed DOC, competition with bacteria decreases phytoplankton biomass by 3 – 60% (Fig. 3a) relative to the simulations with only phytoplankton due to bacterial Fe uptake, with greatest change observed at the lowest Fe levels across all light levels. We denote the 1:1-line

(i.e. region where phytoplankton biomass equals bacteria biomass), which separates regions of phytoplankton (blue) and bacterial (red) biomass dominance as the 'line of coexistence'. This line of coexistence when defined in terms of carbon biomass is very similar to that defined from the specific growth rate (d^{-1}, orange dash) and carbon production rate (orange solid) (Fig. 3b), due to their fundamental role in driving biomass accumulation in our model. Below the line of coexistence (red area), bacteria are dominant, but their biomass remains low as low levels of phytoplankton productivity results in insufficient DOC supply from phytoplankton exudation. Above this line of coexistence (blue area), increasing light and Fe increases phytoplankton growth rate and carbon production resulting in overall phytoplankton dominance as they outcompete bacteria for Fe. As phytoplankton biomass increases, the DOC inventory increases via exudation, which stimulates bacterial growth in parallel, but bacterial biomass remains less than phytoplankton biomass (Supp. Fig. 1a, b). This is because the exudation of DOC by phytoplankton at the start of the experiment is insufficient for bacteria to outcompete phytoplankton. The low DOC levels allow phytoplankton to respond more strongly in general by increasing growth rates, carbon production and biomass (Supp. Fig. 1a, b and 2a, b).

The difference in the rates of Fe uptake between phytoplankton and bacteria (Fig. 3c) show a slightly different form to that seen for biomass, growth and carbon fixation at low Fe and light. Bacteria consume up to 50% of the ambient Fe pool at low Fe (< 0.2 nM) and light (<8 W m^{-2}) levels due to low phytoplankton biomass levels and higher Fe uptake efficiency (i.e. lower bacterial half saturation constant for Fe uptake, Supp. Table 1), but increasing Fe and light causes greater phytoplankton biomass to accumulate (Fig. 3c). We find that phytoplankton can outcompete bacteria for Fe uptake at high light and Fe (Fig. 3c) due to their higher biomass and growth rate (Supp. Fig. 1a and 2a, b). In contrast, when bacteria rely solely on phytoplankton exudation as a DOC source, bacteria become relatively poor competitors for available Fe across these experiments.

3.3 How does iron-DOC influence phytoplankton-bacterial interactions?

Under varying Fe and DOC, but fixed light, bacteria receive two sources of DOC; DOC from phytoplankton exudation and DOC from additional biotic processes. In the natural environment, zooplankton excretion, viral lysis and sloppy feeding represent additional biotic sources of DOC as well as Fe. Whilst there are limited quantitative estimates on the contribution from each component, Antarctic krill were shown to excrete 188 – 560 µM

239 labile DOC that was rapidly utilised by the bacterial community within the 140 – 160 hour
240 experimental duration leading to an increase in bacterial biomass and production (Arístegui et
241 al. 2014).
242
243 In contrast to the Fe-PAR simulation (where the only DOC was from phytoplankton
244 exudation), phytoplankton-bacterial competition increases bacterial biomass ('+', Fig. 3d)
245 more substantially (by up to 90% at low DOC levels), relative to the simulations with bacteria
246 alone. The increase in bacterial biomass is driven by high phytoplankton biomass growth
247 rates and carbon production (Supp. Fig. 1c, d and 2d, d) which adds to the DOC inventory via
248 phytoplankton exudation thereby facilitating bacterial growth (Fig. 3d, e). An exception is at
249 high DOC and low Fe where competitive Fe uptake by phytoplankton results in a small
250 (<6%) decrease in bacterial biomass ('-', Fig. 3d). Greater DOC levels increasingly shift the
251 dominance from phytoplankton to bacteria throughout this experiment, pointing to the
252 importance of DOC in driving the competitive fitness of bacteria. The biomass line of
253 coexistence is similar to the 1:1 line for carbon production (orange solid), but phytoplankton
254 growth rate at this point is ~10% greater than bacterial growth rate (Fig. 3e, Supp. Fig. 2). Fe
255 uptake is decoupled from biomass levels and carbon production rates (Fig. 3f versus 3e).
256 Bacteria consume between 50 – 80% of the ambient Fe pool except at low DOC (Fig. 3f).
257 While the Fe-PAR simulation suggests that bacteria are poor competitors for available Fe
258 when they rely solely on phytoplankton exudation as a source of DOC, we find that bacteria
259 are more effective competitors for Fe as total (phytoplankton exudation + additional biotic
260 processes) DOC increases.
261
262 At the extremes, our simulations show phytoplankton dominance under increasing light and
263 Fe (Fig. 3b and Supp. Fig. 1a and 3b), but bacterial dominance under increasing total DOC
264 and decreasing light (Fig. 3e and Supp. Fig. 1b, d and 3a, b). We find that under moderate
265 light levels (20 W m^{-2}), coexistence between phytoplankton and bacteria can be facilitated
266 when labile DOC increases in tandem with Fe up to around 20 – 30 μM DOC. However,
267 stable coexistence is only found in our simulations at low biomass levels where colimitation
268 constrains both phytoplankton and bacterial populations (Fig. 3b, e). Overall, our simulations
269 show that in the presence of sufficient labile DOC, bacteria are effective competitors with
270 phytoplankton for Fe, exacerbating phytoplankton Fe limitation, most notably under
271 moderate light levels.
272

Our model suggests that bacteria are an important consumer of Fe (Fig. 3c, f), in line with the field studies that demonstrated higher Fe uptake by bacteria compared to phytoplankton (Tortell et al. 1996, Sarthou et al. 2008, Boyd et al. 2012, Fourquez et al. 2015, 2020). Furthermore, we find that bacteria are unable to sustain high growth rates in the absence of luxury Fe uptake (Supp. Fig. 4). If phytoplankton were the only organisms undertaking luxury Fe uptake in our model, then phytoplankton would outcompete bacteria everywhere above the lowest light levels (2 W m^{-2}) required to sustain phytoplankton growth, even at very high labile DOC levels (100 μM) as phytoplankton are able to rapidly consume and store any available Fe (Supp. Fig 4a – d). This highlights the importance of bacterial Fe storage in shaping the competition between phytoplankton and bacteria for Fe and is consistent with other approaches based on metalloproteins (Mazzatto et al. 2020).

3.4 Impact of covariance in Fe, PAR and DOC over the Southern Ocean seasonal cycle

There are two distinct regions within the Southern Ocean; the sub Antarctic zone (SAZ) and polar zone (PZ) which each encounter 4 different seasonal regimes; Winter (June – August), Spring (September – November), Summer (December – February), and Autumn (March – May). The availability of Fe, DOC and PAR is likely to vary between these 4 regimes and between the SAZ and PZ. We use satellite estimates of PAR (NASA Ocean Colour Data, VIIRS OBPG 2019) coupled with Fe fluxes from observations and modelling studies (Fig. 4) and the assumption that labile DOC exudation is ~10% of phytoplankton primary production, to initialise our model and examine the strength of phytoplankton-bacterial interactions in each seasonal regime.

In winter, deep mixed layers and ice cover results in complete darkness in the PZ, while PAR levels remain around 2 – 7 W m^{-2} in the SAZ (Fig. 4). As the supply of deep Fe will be maximal at this time, dissolved Fe levels in seawater will be expected to reach their seasonal maxima of around 0.9 nM in the surface open ocean (Tagliabue et al. 2014) and perhaps >1 nM closer to the shelf (Tagliabue et al. 2012). At this time of year, there is only a deep source of refractory DOC in large areas of the open ocean (Hansell et al. 2013). Under these conditions, we find that phytoplankton and bacterial biomass are low in the SAZ where there is low light. Yet the very low biomass of phytoplankton take up ~98% of the Fe pool and deplete its concentration from 0.9 nM to 0.3 only after 35 days. Over this time, phytoplankton biomass can increase to from 0.1 to 6 μmol C L^{-1} but we observe no sustained increase in bacterial biomass despite a build-up of 1 μM of DOC in our experiment from phytoplankton

307 exudation. Phytoplankton outcompeted bacteria because the low labile DOC at the onset of
308 the experiment constrained bacterial growth, and instead allowed phytoplankton to drawdown
309 Fe and moderately increase in biomass despite the apparent light limitation. To maintain
310 seawater dissolved Fe levels of >0.7 nM throughout winter in the SAZ, either Fe must be
311 continuously supplied via deep winter mixing (Tagliabue et al. 2014) or >50% of the
312 particulate Fe in phytoplankton and bacteria needs to be rapidly recycled. In the PZ, despite
313 the darkness, grazing by the resident zooplankton community (e.g. Antarctic krill, Walsh et
314 al. 2020) under the winter ice can lead to the coupled release of Fe and DOC potentially
315 driving competition between bacteria and low-light acclimated ice algae, a community of
316 phytoplankton not modelled in this study.
317
318 In spring, PAR levels increase to 20 W m^{-2} in the PZ and 30 W m^{-2} in the SAZ (Fig. 4).
319 Shoaling of the mixed layer maintains high dissolved Fe stock of ~0.9 nM at the onset of
320 spring (Tagliabue et al. 2014). Initialising our model under these high Fe and light levels,
321 coupled with the 1 μM of DOC that built up over the winter period, we find that
322 phytoplankton outcompete bacteria at a ratio of 100:1 and consume >98% of the dissolved Fe
323 pool within 13 (PAR 30 W m^{-2}) to 15 (PAR 20 W m^{-2}) days because the low DOC at the
324 onset of spring allows phytoplankton to outcompete bacteria. PAR continues to increase to
325 the seasonal maximum of 30 W m^{-2} in the PZ and 40 W m^{-2} in the SAZ during summer, but
326 dissolved Fe concentrations tend to decrease to ~0.15 nM in the surface open ocean as
327 phytoplankton have depleted the winter stock and recycling turns over the dissolved Fe stock
328 rapidly (Strzepek et al. 2005, Boyd et al. 2012, Tagliabue et al. 2014). Under low Fe and high
329 light conditions, and assuming a labile DOC stock of ~5 μM in addition to continual DOC
330 exudation (10% of primary production) (Hansell et al. 2009), phytoplankton take up ~80% of
331 the ambient Fe and phytoplankton biomass ~16 times greater than bacteria. From late
332 summer into autumn the mixed layer starts to deepen, PAR decreases from 20 to 0 W m^{-2}
333 (Fig. 4) and Fe is at its seasonal minimum (~0.1 nM, Tagliabue et al. 2012). Here
334 phytoplankton take up ~55% of the Fe and phytoplankton biomass is ~6 times greater than
335 bacteria.
336
337 The low standing stocks of Fe in spring/summer do not preclude fast recycling via
338 bacterivory and herbivory coupled with rapid utilisation (Strzepek et al. 2005). Bacterivory
339 and herbivory would lead to the coupled release of Fe and DOC. If we assume greater levels
340 of Fe and labile DOC, that might be representative of the greater recycling (e.g. bacterivory;

Strzepek et al. 2005), then the competitive fitness of bacteria is enhanced. Our results suggest that the amount of DOC necessary to switch the dominance from phytoplankton to bacteria varies as a non-linear function of Fe (black line in Fig 3e). At the low Fe levels typical of summer as little as 20-30 μM DOC would alter the competitive outcome, while at higher Fe levels typical of earlier in the bloom phase more DOC is needed (Fig 3e).

Our analysis suggests that decreasing light and Fe, coupled with a small DOC inventory (5 μM) facilitates Fe uptake by bacteria, but microbial Fe uptake is decoupled from carbon production. Phytoplankton biomass is consistently greater than bacterial biomass across all seasons. Bacteria require >50 μM of labile DOC to outcompete phytoplankton biomass in spring. This decreases to 40 μM in summer, 15 μM in autumn and 8 μM in winter. Bacteria require less DOC as the season progresses because of the colimiting effects of Fe and light on phytoplankton growth. This suggests that sources such as ice, dust, sediments, recycling etc. with varying Fe and DOC levels may influence different components of the microbial community, with the strength of the interaction further compounded by seasonal effects on phytoplankton growth.

4. Competition under changing climate: uncertainties and future work

There is a strong interest in understanding the response of phytoplankton to a changing climate due to its role in the global carbon cycle and supporting ocean fisheries. Southern Ocean surface seawater is predicted to warm by 2 – 3°C by the year 2100. Both phytoplankton and bacterial metabolism respond positively with an increase in temperature (Rivkin et al. 1996, Pomeroy and Wiebe 2001, Deppeler and Davidson 2016, Toseland et al. 2013). But there is substantial disagreement on how temperature could regulate phytoplankton-bacterial interactions and DOC production and stimulation. Bacterial production could follow an increase in primary production and not temperature (Kirchman et al. 1995, Morán et al. 2006) or respond to an increase in temperature and not primary production (Hoppe et al. 2008). Our analysis finds that bacteria can outcompete phytoplankton leading to a decrease in phytoplankton biomass if sufficient labile DOC is available which can be found in regions of high recycling (Ruiz-Halpern et al. 2011, Arístegui et al. 2014) and ice melt (Norman et al. 2010, Underwood et al. 2010), where there is also concurrent release of Fe, a concept that has previously not been considered in our understanding of the Fe cycle in the Southern Ocean (Tagliabue et al., 2014). As ice melt

increases with rising temperatures, the increase in Fe and DOC supply coupled with an increase in temperature may stimulate bacterial communities at the expense of phytoplankton. Furthermore, increased temperature can lead to increased DOC exudation by phytoplankton (Zlotnik and Dubinsky 1989) and greater microbial degradation of recalcitrant DOC (Lønborg et al. 2018), which suggests the potential for greater DOC availability under warmer climate. However, ice melt can strongly stratify the surface water, thereby relieving phytoplankton light limitation and strengthening competition with bacteria.

Additional feedbacks, not explored in this study, are the interactions around the bacterial production of siderophores in response to Fe scarcity (e.g. Boiteau et al., 2016) and the weaker Fe binding agents associated with phytoplankton exudates, such as saccharides (Hassler et al., 2011) or heme groups (Louropoulou et al., 2020), or the role of bacterivory in recycling the Fe stored in bacteria (Tortell et al. 1996, Strzepek et al. 2005, Boyd et al. 2012, Boyd et al. 2015, Mazzotta et al. 2020). Furthermore, along the coastal Antarctic sea-ice edge communities, phytoplankton are limited by cobalamin (vitamin B_{12}) and Fe (Bertrand et al. 2015). As cobalamin is only produced by bacteria and archaea, this suggest that phytoplankton-bacterial interactions mediate micronutrient colimitation for nutrients other than Fe as well. As such, more experimental-modelling work is required to gain a better mechanistic understanding of how the competitive interactions between phytoplankton and bacteria could change in response to multiple concurrent environmental changes.

5. Conclusions

Overall, we find that resource co-limitation and competition alters the response of phytoplankton and bacteria. Phytoplankton growth rate decreases due to competition for Fe uptake by bacteria. In contrast, the increase in DOC supplied via phytoplankton exudation leads to an increase in bacterial growth rate but is insufficient to stimulate bacterial biomass to an extent that bacteria outcompete phytoplankton. If additional DOC is supplied, for instance from recycling or sea ice melting, then bacteria can successfully outcompete phytoplankton for Fe and depress rates of phytoplankton productivity. As large areas of the Southern Ocean are characterised by low dissolved Fe-low labile DOC, the seasonal cycle of light and ensuing exudation, grazing, viral lysis and cell death which increases DOC inventory ultimately regulates phytoplankton-bacterial interactions.

Acknowledgements

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant agreement No. 724289). The model used in this study is based on the global 3D biogeochemical model PISCES as described in Aumont et al. 2015 and freely available as part of the NEMO modelling platform. The NEMO code is available from https://www.nemo-ocean.eu. The equations and parameters used in this study are provided in the supplementary material. Mixed layer depth data was sourced from deBoyer-Montegut et al. 2004 (http://www.ifremer.fr/cerweb/deboyer/mld/Surface_Mixed_Layer_Depth.php) and PAR was sourced from NASA Ocean Color (VIIRS monthly climatological data at 4km resolution https://oceancolor.gsfc.nasa.gov/l3/).

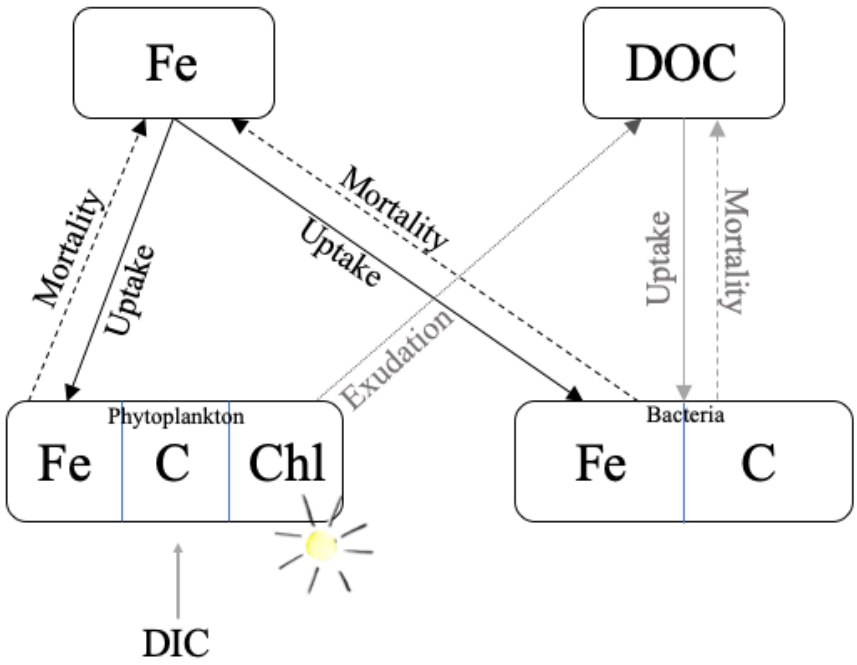


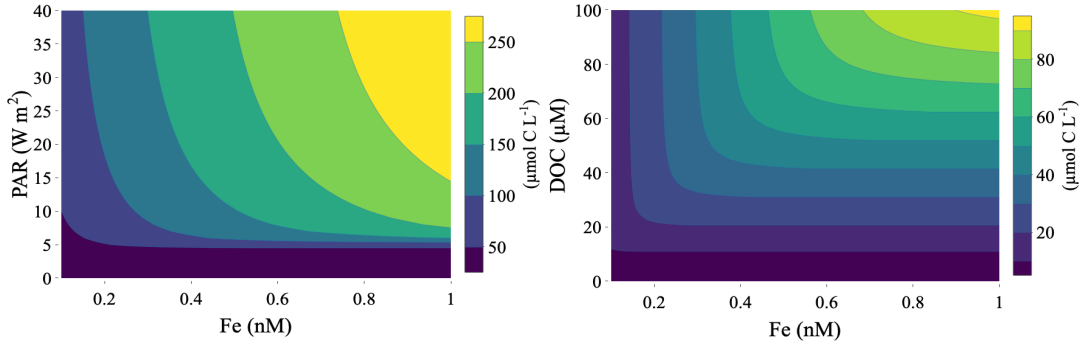
Figure 1: Schematic of model configuration with 2 biological pools – phytoplankton and bacteria, and 3 resources –dissolved iron (Fe), light and dissolved organic carbon (DOC). Fe and DOC are taken up by phytoplankton and bacteria (solid lines) and recycled via mortality (dashed lines) and phytoplankton exudation (dotted).

Fe-PAR **Fe-DOC**

Phytoplankton Bacteria

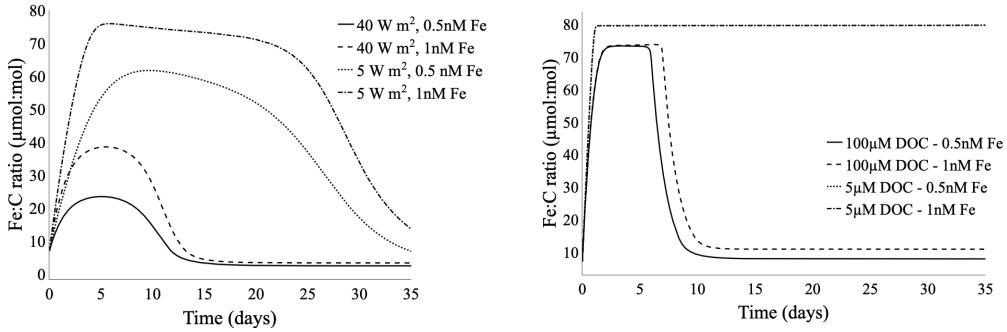
Biomass

a) d)



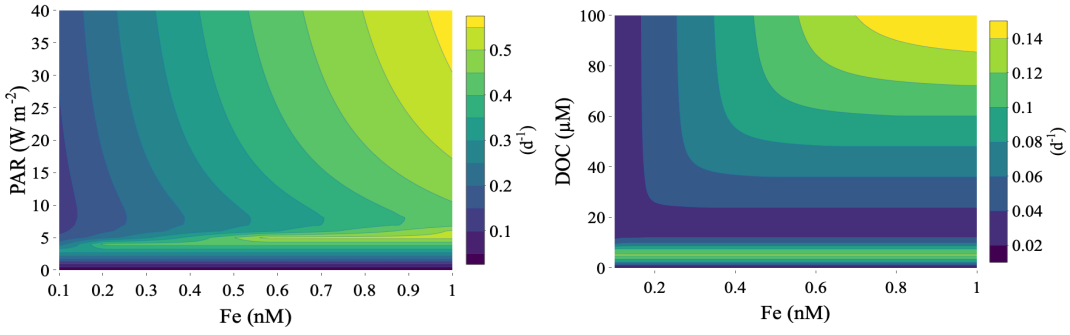
Fe:C ratio

b) e)



Growth rate

c) f)



433

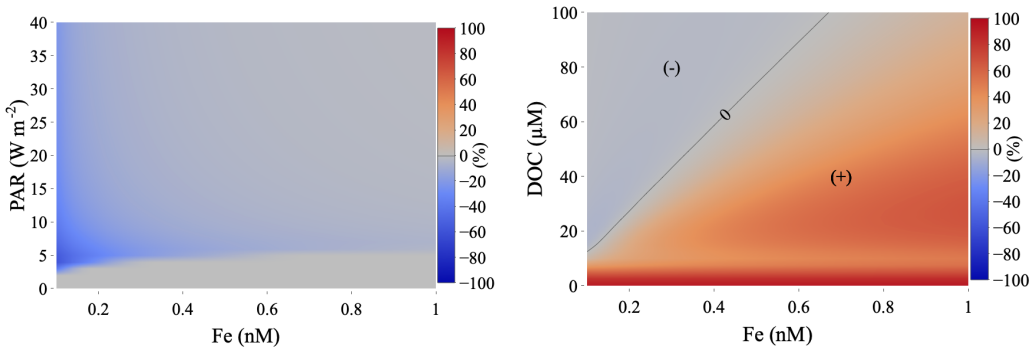
434

Figure 2: Steady state response of phytoplankton under iron (Fe) and light (PAR) colimitation (a – c) and bacteria under Fe and dissolved organic carbon (DOC) colimitation (d – f) in the absence of competitive interactions. Changes in carbon biomass (a, d), cellular Fe quota (b, e) and growth rate (c, f). Note that the response of Fe:C ratios (2e) in the 5 µM DOC, 0.5 nM Fe (dotted line) treatment is hidden behind the 5 µM DOC, 1.0 nM Fe (dot dash) treatment.

Fe-PAR **Fe-DOC**

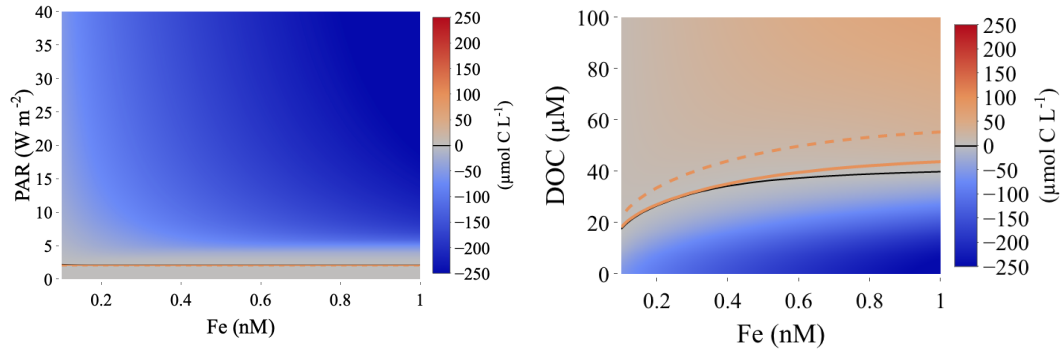
Changes in biomass compared to reference simulation

a) d)



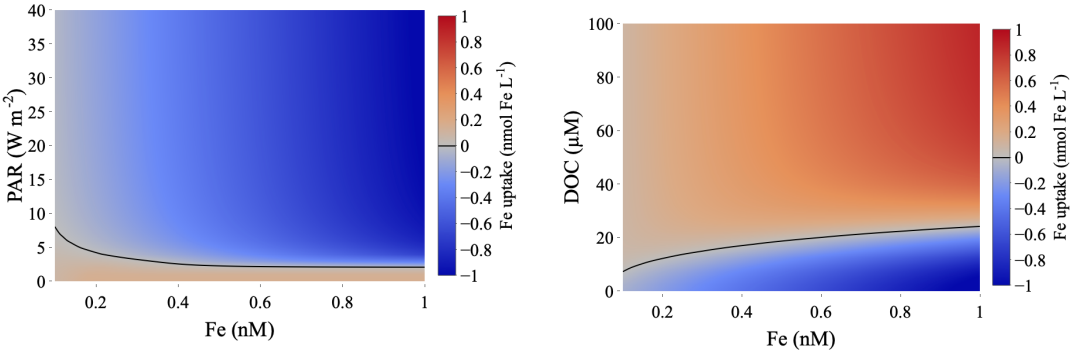
Competitive outcome for biomass, carbon production and growth rate

b) e)



Relative iron uptake

c) f)



442

443

Figure 3: Steady state response of phytoplankton and bacteria as they compete for iron (Fe) under Fe – light (PAR) (a – c) and Fe – dissolved organic carbon (DOC) colimitation (d – f). Carbon biomass relative to no competition simulation (a, d). Difference in biomass (black), growth rate (orange dash) and carbon production rate (orange solid) between phytoplankton and bacteria (b, e). Difference in Fe uptake rate between phytoplankton and bacteria (c, f). All lines denote regions where phytoplankton and bacteria are equal and separate regions of phytoplankton (blue) and bacterial (red) dominance.

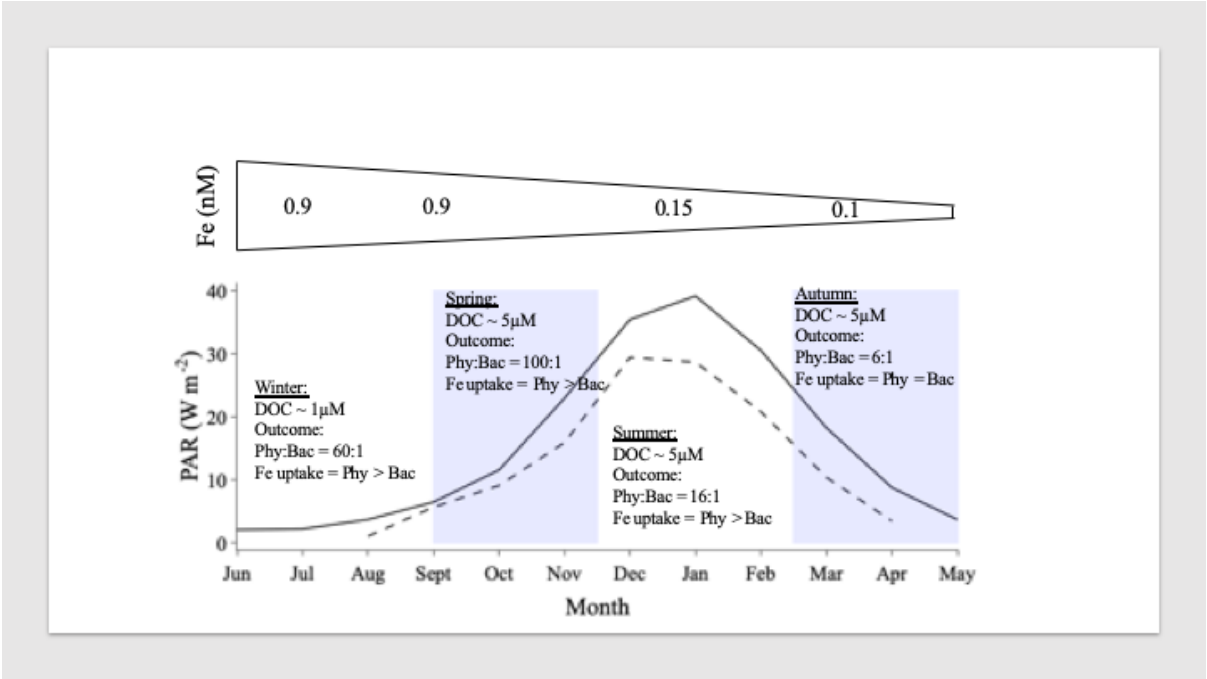


Figure 4: Top panel represents dissolved iron (Fe) fluxes from observations and modelling studies. Bottom panel demonstrates average mixed layer depth integrated light (PAR; based on VIIRS Ocean Colour Data, Ocean Biology Processing Group 2019 and de Boyer Montegut 2004) for the subAntarctic (solid line) and polar (dashed line) zones and assumptions of labile dissolved organic carbon (DOC) available for bacteria used to initialise the model. Highlighted rectangular regions represent austral spring and autumn.

References

1. Andrews SC, Robinson AK and Rodríguez-Quiñones (2003) Bacterial iron homeostasis. FEMS Microbiology Reviews 27(2-3): 215-237

2. Ardnya M, Claustre H, Sallée JB, D'Ovidio F, Gentili B, D'Ortenzio F and Arrigo K (2017) Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean. Geophysical Research Letters 5016 – 5024

3. Arístegui J, Duarte CM, Reche I and Gómez-Pinchetti JL (2014) Krill excretion boosts microbial activity in the Southern Ocean. PLoS One 9(2)

4. Aumont O, Ethé C, Tagliabue A, Bopp L and Gehlen M (2015) PISCES-v2: an ocean biogeochemical model for carbon and ecosystem studies. Geoscientific Model Development 8: 2465 – 2513

5. Bertrand E, McCow JP, Moustafa A, Zheng H, McQuaid JB, Delmont TO, Post AF, Sipler RE, Spackeen JL, Xu K, Bronk DA, Hutchins DA and Allen AE (2015) Phytoplankton-bacterial interactions mediate micronutrient co-limitation at the coastal Antarctic sea ice edge. Proceedings of the National Academy of Sciences 112 (32) 9938 – 9943

6. Blain S, Quéguiner B, Armand L, Belviso S, Bombled L, Bopp L, Bowie A, Brunet C, Brussard C, Carlotti F, Christaki U, Corbière A, Durand I, Ebersbach F, Fuda, J-L, Garcia N, Gerringa L, Griffiths B, Guigue C, Guillerm C, Jacquet , Jeandel C, Laan P, Lefèvre, D, Monaco CL, Malits A, Mosseri J, Obernosterer I, Park Y-H, Picheral M, Pondaven P, Remenyi T, Sandroni V, Sarthou G, Savoye N, Scouarnec L, Souhaut M, Thuiller D, Timmermans K, Trull T, Uitz J, van Beek P, Veldhuis M, Vincent E, Viollier E, Vong L and Wagener T (2007) Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. Nature 446: 1070 – 1074

7. Boiteau RM, Mende DR, Hawco NJ, McIllwin MR, Fitzsimmons JN, Saito MA, Sedwick PN, DeLong EF and Repeta DJ (2016) Siderophore-based microbial adaptations to

500 iron scarcity across the eastern Pacific Ocean. Proceedings of the Natural Academy of
501 Science 113(50): 14237-14242
502
503 8. Boyd PW, Jickells T, Law CS, Blain S, Boyle EA, Buesseler KO, Coale KH, Cullen
504 JJ, de Baar HJW, Follows M, Harvey M, Lancelot C, Levasseur M, Owens NPJ, Pollard R,
505 Rivkin RB, Sarmiento J., Schoemann V, Smetacek V, Takeda S, Tsuda A, Turner S and
506 Watson AJ (2007) Mesoscale iron enrichment experiments 1993-2005: synthesis and future
507 directions. Science 315: 612 – 617
508
509 9. Boyd PW, Strzepek R, Chiswell S, Chang H, DeBruyn JM, Ellwood M, Keenan S,
510 King AL, Maas EW, Nodder S, Sander SG, Sutton P, Twining B, Wilhelm SW and Hutchins
511 D (2012) Microbial control of diatom bloom dynamics in the open ocean. Geophysical
512 Research Letters 39 (18): 1 – 6
513
514 10. Bratbak G, Egge JK and Heldal M (1993) Viral mortality of the marine alga *Emiliana*
515 *huxleyi* (Haptophycaea) and termination of algal blooms. Marine Ecology Progress Series 93:
516 39 – 48
517
518 11. Brauer VS, Stomp M and Huisman J (2012) The Nutrient-Load Hypothesis: Patterns
519 of Resource Limitation and Community Structure Driven by Competition for Nutrients and
520 Light. The America Naturalist 179 (6): 721 – 740
521
522 12. Burson A, Stomp M, Greenwell E, Grosse J and Huisman J (2018) Competition for
523 nutrients and light: testing advances in resource competition with a natural phytoplankton
524 community. Ecology 99 (5): 1109 – 1118
525
526 13. Carlson CA and Ducklow HW (1995) Dissolved organic carbon in the upper ocean of
527 the central Equatorial Pacific, 1992: Daily and finescale vertical variations. Deep-Sea
528 Research II 42: 639 – 656
529
530 14. Carlson CA and Ducklow HW (1996) Growth of bacterioplankton and consumption
531 of dissolved organic carbon in the Sargasso Sea. Aquatic Microbial Ecology 10:69–85
532

15. Carlson CA, Ducklow HW, Hansell DA and Smith WO (1998) Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea Polynya and the Sargasso Sea. Limnology and Oceanography 43:375–386

16. Carrondo MA (2003) Ferritins, iron uptake and storage from the bacterioferritin viewpoint. The EMBO Journal 22: 1959–1968.

17. Cherrier J, Bauer JE and Druffel ERM (1996) Utilization and turnover of labile dissolved organic matter by bacterial heterotrophs in eastern North Pacific surface waters. Marine Ecology Progress Series 139:267–279

18. Church MJ, Hutchins, DA and Ducklow HW (2000) Limitation of bacterial growth by dissolved organic matter and iron in the Southern Ocean. Applied and Environmental Microbiology 66 (2):455-466

19. Cohen NR, Mann E, Stemple B, Morena CM, Rauschenberg S, Jacquot JE, Sunda WG, Twining BS and Marchetti A (2018) Iron storage capacities and associated ferritin gene expression among marine diatoms. Limnology and Oceanography 63 (4): 1677-1691

20. Cotner JB, Ammerman JW, Peele ER and Bentzen E (1997) Phosphorus-limited bacterioplankton growth in the Sargasso Sea. Aquatic Microbial Ecology 13:141–149

21. De Boyer Montegut C, Madec G, Fischer AS, Lazar A and Iudicone, D. (2004) Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. Journal of Geophysical Research 109, C12003

22. Debeljak P, Toulza E, Beier S, Blain S and Obernosterer I (2019) Microbial iron metabolism as revealed by gene expression profiles in contrasted Southern Ocean regimes. Environmental Microbiology 21(7): 2360–2374

23. Deppeler SL and Davidson AT (2017) Southern Ocean phytoplankton in a changing climate. Frontiers in Marine Science

24. Fourquez M, Devez A, Schaumann A, Guéneuguès A, Jouenne T, Obernosterer I, and Blain S (2014) Effects of iron limitation on growth and carbon metabolism in oceanic and coastal heterotrophic bacteria. Limnology and Oceanography 59: 349 – 360.

25. Fourquez, M, Bressac, M, Deppeler, SL, Ellwood, M, Obernosterer, I, Trull, TW and Boyd, PW (2020) Microbial Competition in the Subpolar Southern Ocean: An Fe–C Co-limitation Experiment. Frontiers in Marine Science.

26. Fourquez, M, Obernosterer, I, Davies, DM, Trull, TW and Blain, S. (2015). Microbial iron uptake in the naturally fertilized waters in the vicinity of the Kerguelen Islands: phytoplankton–bacteria interactions. Biogeosciences. doi:10.5194/bg-12-1893-2015.

27. Gobler CJ, Hutchins DA, Fisher NS, Cosper EM and Sańudo-Wilhelmy SA (2003) Release and bioavailability of C, N, P, Se and Fe following viral lysis of a marine chrysophyte. Limnology and Oceanography 42 (7): 1492 – 1504

28. Hansell DA, Carlson CA, Repeta, DJ and Schlitzer R. (2009) Dissolved organic matter in the ocean: A controversy stimulates new insights. Oceanography 22: 202–211

29. Hansell DA, Carlson CA and Schlitzer R (2012) Net removal of major marine dissolved organic carbon fractions in the subsurface ocean. Global Biogeochemical Cycles 26 (1): 1 – 9

30. Hansell DA (2013) Recalcitrant Dissolved Organic Carbon Fractions. Annual Reviews 5: 421 – 445

31. Hardin G (1960) The competitive exclusion principle. Science 131 (3409): 1392 – 1297

32. Hassler CS, Schoemann V, Nichols CM, Butler ECV and Boyd PW (2011) Saccharides enhance iron bioavalability to Southern Ocean phytoplankton. Proceesings of the Natural Academy of Science 108(3): 1076-1081

599 33. Hoppe HG, Breithaupt P, Walther K, Koppe R, Bleck S, Sommer U and Jürgens K
600 (2008) Climate warming in winter affects the coupling between phytoplankton and bacteria
601 during the spring bloom: a mesocosm study. Aquatic Microbial Ecology 51: 105-115
602
603 34. Hutchinson E (1953) The concept of pattern in ecology. Proceedings of the Natural
604 Academy of Science 105: 1 – 12
605
606 35. Kirchman DL, Rich JH and Barber RT (1995) Biomass and biomass production of
607 heterotrophic bacteria along 140°W in the equatorial Pacific: Effect of temperature on the
608 microbial loop. Deep Sea Research Part II: Topical Studies in Oceanography 42(2-3): 603-
609 619
610
611 36. Lampe RH, Mann EL, Cohen NR, Till CP, Thamatrakoln K, Brzezinski, MA, Bruland
612 KW, Twining BS and Marchetti A (2018) Different iron storage strategies among bloom-
613 forming diatoms. Proceedings of the National Academy of Sciences. 115 (52): 12275 –
614 12284
615
616 37. Lampitt RS, Noji T and von Bodungen B (1990) What happens to zooplankton faecal
617 pellets? Implications for material flux. Marine Biology 104 (1): 15 – 23
618
619 38. Larsson U and Hagström A (1979) Phytoplankton exudate release as an energy source
620 for the growth of pelagic bacteria. Marine Biology 52 (3): 199 – 206
621
622 39. Legendre L and Le Fevre J (1995) Microbial food webs and the export of biogenic
623 carbon in oceans. Aquatic Microbial Ecology 9: 69–77
624
625 40. Louropoulou E, Gledhill M, Achterberg EP, Browning TJ, Honey DJ, Schmitz RZ
626 and Tagliabue A (2020) Heme *b* distributions through the Atlantic Ocean: evidence for
627 “anemic” phytoplankton populations. Scientific Reports 10(4551)
628
629 41. Lønborg C, Álvarez-Salgado XA, Letscher RT and Hansell DA (2018) Large
630 stimulation of recalcitrant dissolved organic carbon degradation by increasing ocean
631 temperature. Frontiers in Marine Science

42. Marchetti A, Parker MS, Moccia LP, Lin EO, Arrieta AL, Ribalet F, Murphy MEP, Maldonado MT and Armbrust, EV (2009) Ferritin is used for iron storage in bloom-forming marine pennate diatoms. Nature 457: 467-470

43. Martin JH, Fitzwater SE and Gorgon MR (1994) Iron deficiency limits phytoplankton growth in Antarctic waters. Global Biogeochemical Cycles 4 (1) 5 – 12

44. Mazzotta MG, McIIvin MR and Saito MA (2020) Characterization of the Fe Metalloproteome of a Ubiquitous Marine Heterotroph, Pseudoalteromonas (BB2-AT2): Multiple Bacterioferritin Copies enable significant Fe Storage

45. Middelboe M and Lyck PG (2002) Regeneration of dissolved organic matter by viral lysis in marine microbial communities. Aquatic Microbial Ecology 27:187–194

46. Mitchell BG, Brody EA, Holm-Hansen O, McClain C and Bishop J (1991) Light limitation of phytoplankton biomass and macronutrient utilization in the Southern Ocean. Limnology and Oceanography 36 (8): 1662 – 1677

47. Morán XAG, Sebastián M, Pedrís-Alií C and Estrada M (2006) Response of Southern Ocean phytoplankton and bacterioplankton production to short-term experimental warming. Limnology and Oceanography 51(4): 1791-1800

48. Møller EF, Thor P and Nielsen TG (2003) Production of DOC by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* through sloppy feeding and leakage from fecal pellets. Marine Ecology Progress Series 262:185 – 191

49. Møller EF (2007) Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus*, and *Temora longicornis*. Limnology and Oceanography 52 (1): 79 – 84

50. NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group; (2019): Visible Infrared Imaging Radiometer Suite (VIIRS). Maintained

665 by NASA Ocean Biology Distributed Active Archive Centre (OB. DAAC), Goddard Space
666 Flight Centre, Greenbelt MD.
667
668 51. Norman L, Thomas DN, Stedmon CA, Granskog MA, Papadimitriou S, Krapp RH,
669 Meiners KM, Lannuzel D van der Merwe P and Dieckmann GS (2010) The characteristics of
670 dissolved organic matter (DOM) and chromophoric dissolved organic matter (CDOM) in
671 Antarctic sea ice. Deep-Sea Research II 58: 1075-1091
672
673 52. Obernosterer I, Fourquez M and Blain S (2015) Fe and C co-limitation of
674 heterotrophic bacteria in the naturally fertilized region off the Kerguelen Islands.
675 Biogeosciences 12 (6): 1983-1992
676
677 53. Pomeroy LR and Wiebe WJ (2001) Temperature and Substrates as Interactive
678 Limiting Factors for Marine Heterotrophic Bacteria. Aquatic Microbial Ecology 23: 187-204.
679
680 54. Poorvin L, Rinta-Kanto JM, Hutchins DA and Wilhelm SW (2004) Viral release of
681 iron and its bioavailability to marine plankton 49(5): 1734-1741
682
683 55. Rivera M (2017) Bacterioferritin: Structure, Dynamics, and Protein-Protein
684 Interactions at Play in Iron Storage and Mobilization. Accounts of Chemical Research 50(2):
685 331–340
686
687 56. Rivkin RB, Anderson MR and Lajzerowicz C (1996) Microbial processes in cold
688 oceans. I. Relationship between temperature and bacterial growth rate. Aquatic Microbial
689 Ecology 10: 243-254
690
691 57. Rivkin RB and Anderson MR (1997) Inorganic nutrient limitation of oceanic
692 bacterioplankton. Limnology and Oceanography 42:730 – 740
693
694 58. Ruiz Halpern S, Duarte CM, Tovar-Sanchez A, Pastor M, Horstkotte B, Lasternas S
695 and Agustí S (2011) Antarctic krill as a source of dissolved organic carbon to the Antarctic
696 ecosystem. Limnology and Oceanography 56: 521-528.
697

59. Sarthou G, Vincent D, Christaki U, Obernosterer I, Timmermans KR and Brussaard CPD (2008) The fate of biogenic iron during a phytoplankton bloom induced by natural fertilisation: impact of copepod grazing. Deep- Sea Research II Topical Studies in Oceanogrraphy 55: 734 – 751.

60. Søndergaard M, Williams PJleB, Cauwet G, Riemann B, Robinson C, Terzic S, Woodward EMS and Worm J (2000) Net accumulation and flux of dissolved organic carbon and dissolved organic nitrogen in marine plankton communi- ties. Limnol Oceanogr 45(5):1097–1111

61. Strzepek RF, Maldonado MT, Higgins JL, Hall J, Safi K, Wilhelm SW and Boyd PW (2005) Spinning the "Ferrous Wheel": The importance of the microbial community in an iron budget during the FeCycle experiment. Global Biogeochemical Cycles 19: 1-14

62. Strzepek RF, Hunter KA, Frew RD, Harrison PJ and Boyd PW (2012) Iron-light interctions differ in Southern Ocean phytoplankton. Limnology and Oceanography 57 (4): 1182 – 1200

63. Tagliabue A, Mtshali T, Aumont O, Bowie AR, Klunder MB, Roychoudhury AN and Swart S (2012) A global compilation of dissolved iron measurements: focus on distributions and processes in the Southern Ocean. Biogeosciences 9: 2333-2349

64. Tagliabue A, Sallée JB, Bowie AR, Lévy M, Swart S and Boyd P.W (2014) Surface-water iron supplies in the Southern Ocean sustained by deep winter mixing. Nature Geoscience 7: 314 – 320

65. Tagliabue A, Aumont O, Death R, Dunne JP, Dutkiewicz S, Galbraith E, Misumi K, Moore JK, Ridgwell A, Sherman E, Stock C, Vichi M, Völker C and Yool A (2016) How well do global ocean biogeochemistry models simulate dissolved iron distributions? Global Biogeochemical Cycles 30(2): 149-174

66. Tilman DG (1982) Resource competition and community structure. Monographs in population biology 17: 1 – 296

67. Titman D (1976) Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192 (4238): 463 – 465

68. Tortell PD, Maldonado MT and Price NM (1996) The role of heterotrophic bacteria in iron-limited ocean ecosystems. Nature 383: 330–332

69. Tortell PD, Maldonado MT, Granger J and Price NM (1999) Marine bacteria and biogeochemical cycling of iron in the oceans FEMS Microbiology Ecology 29(1): 1-11

70. Toseland A, Daines, S.J, Clark, J.R, Kirckham A, Strauss J, Uhlig C, Lenton T.M, Valentin K, Pearson GA, Moulton V and Mock T (2013) The impact of temperature on marine phytoplankton resource allocation and metabolism. Nature Climate Change 3: 979-984

71. Underwood GJC, Fietz S, Papadimitriou S, Thomas DN and Dieckman GS (2010) Distribution and composition of dissolved extracellular polymeric substances (EPS) in Antarctic sea ice. Marine Ecology Progress Series 404: 1-19

72. Veldhuis M, Kraay G and Timmermans K (2001) Cell death in phytoplankton: correlation between changes in membrane permeability, photosynthetic activity, pigmentation and growth. European Journal of Phycology 36 (2): 167 – 177

73. Walsh J, Reiss CS and Watters GM (2020) Flexibility in Antarctic krill *Euphausia superba* decouples diet and recruitment from overwinter sea ice conditions in the northern Antarctic Peninsula. Marine Ecology Progress Series 642: 1-19

74. Wood AM and Van Valen LM (1990). Paradox lost? On the release of energy-rich compounds by phytoplankton. Marine Microbial Food Webs 4: 103–116.

75. Zlotnik I and Dubinsky Z (1989) The effect of light and temperature on DOC excretion by phytoplankton. Limnology and Oceanography 34(5): 831-839

767