

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

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35

36 **Key points: (140 characters)**

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

43

44 **Abstract (150 words)**

45 Across the Southern Ocean, phytoplankton growth is governed by iron and light, whilst

46 bacterial growth is regulated by iron and labile dissolved organic carbon (LDOC). We use a

47 mechanistic model to examine how competition for iron between phytoplankton and bacteria

48 responds to changes in iron, light and LDOC. Consistent with experimental evidence,

49 increasing iron and light encourages phytoplankton dominance, whilst increasing LDOC and

50 decreasing light favours bacterial dominance. Under elevated LDOC, bacteria can

51 outcompete phytoplankton for iron, most easily under lower iron. Simulations reveal that

52 bacteria are major iron consumers, and suggest that luxury storage plays a key role in

53 competitive iron uptake. Under seasonal conditions typical of the Southern Ocean, sources of

54 LDOC besides phytoplankton exudation modulate the strength of competitive interactions.

55 Continued investigations on the competitive fitness of bacteria in driving changes in primary

56 production in iron-limited systems will be invaluable in refining these results.

57

58 **Plain summary**

59 In large areas of the Southern Ocean, phytoplankton growth is controlled by the availability

60 of iron and light whilst bacterial growth is controlled by the availability of iron and labile

61 dissolved organic carbon (LDOC). We developed a mechanistic model to examine how

62 phytoplankton and bacteria compete for iron under different light levels and LDOC supply.

63 We find that phytoplankton dominate as iron and light increases while increasing LDOC and

64 decreasing light favours bacterial dominance. If enough LDOC is present, bacteria can

65 outcompete phytoplankton for iron. More broadly, we find that while bacteria are a major

66 consumer of iron in the Southern Ocean, seasonal changes in light drive phytoplankton

67 dominance over bacteria, unless LDOC is supplied by other sources such as viral lysis,

68 excretion etc., which strengthen competitive interactions.

69

70 ***Introduction***

71 Phytoplankton growth in large areas of the Southern Ocean is regulated by the micronutrient
72 iron (Fe) (Martin et al. 1994, Blain et al. 2007, Boyd et al. 2007), with seasonal co-limitation
73 by light (Mitchell et al. 1991, Strzepek et al. 2012) due to the deep mixed layers and ice cover
74 that are prevalent in early spring, autumn and winter. The low rates of primary production
75 and large-scale upwelling of deep water containing low dissolved organic carbon (DOC)
76 concentrations lead to some of the lowest surface DOC concentrations in the global ocean
77 (~40 – 50 μM , Hansell et al. 2012). While low surface dissolved Fe and DOC is thought to
78 restrict heterotrophic bacterial (hereafter bacteria) growth in the Southern Ocean (Church et
79 al. 2000, Obernosterer et al. 2015), studies from Fe-limited regions have demonstrated that
80 bacteria may also be significant consumers of dissolved Fe and can exhibit greater cellular Fe
81 quotas than phytoplankton (Tortell et al. 1996, 1999, Boyd et al. 2012, Fourquez et al. 2015,
82 2020). High bacterial Fe demand and uptake rates compared to phytoplankton suggest that
83 bacteria could be significant competitors for dissolved Fe in the Southern Ocean (Fourquez et
84 al., 2015, 2020, Mazzotta et al. 2020).

85

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

103 may facilitate phytoplankton and bacterial coexistence in the Southern Ocean by supplying
104 labile DOC. While labile DOC is often rapidly utilised within hours (Fourquez et al. 2014,
105 Obernosterer et al 2015), seasonal accumulation of DOC has been observed in the Bermuda
106 Atlantic Time Series (BATS) site possibly due to phosphorus limitation of bacterioplankton
107 growth (Cotner et al. 1997, Rivkin and Anderson 1997) or the accumulation of recalcitrant
108 DOC that prevents rapid utilisation (Legendre and Le Fevre 1995, Carlson and Ducklow
109 1996, Carlson et al. 1998, Cherrier et al. 1996, Søndergaard et al. 2000). The turnover time
110 for recalcitrant DOC ranges from months (semi-labile) – 40,000 years (ultra-refractory)
111 (Carlson and Ducklow 1995, Cherrier et al. 1996, Hansell et al. 2012, 2013, Lønborg et al.
112 2018).

113

114 At a cellular level, phytoplankton can use mechanisms such as Fe storage protein (i.e.
115 ferritin) and vacuolar storage that enable them to stockpile Fe for use when ambient Fe levels
116 are low (e.g., Lampe et al. 2018, Marchetti et al. 2009, Cohen et al. 2018). A more limited set
117 of observations indicates that although bacteria possess two types of ferritin-like molecules,
118 the bacterial ferritins and bacterioferritin (Andrews et al. 2003, Rivera 2017, Debeljak et al.
119 2019), the regulation of the bacterioferritin gene is unclear (Carrondo 2003). Nevertheless,
120 the higher Fe quotas observed in bacteria, relative to phytoplankton (Fourquez et al., 2015,
121 2020, Mazzotta et al. 2020, Tortell et al. 1996, Sarthou et al. 2008, Boyd et al. 2012) suggest
122 that bacteria may require more Fe, or have the capacity for luxury Fe uptake, and hence may
123 compete with phytoplankton for Fe. The parallel impact of other environmental regulatory
124 factors, such as light or labile DOC, on the outcome of such a competition are unclear.

125

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

134

135 **2. Methods**

136 **2.1 Biogeochemical model**

137 The rate of change in phytoplankton carbon, chlorophyll-a and dissolved Fe is based on the
138 Pelagic Integration Scheme for Carbon and Ecosystem studies (PISCES-v2, Aumont et al.
139 2015) model, which is commonly used as part of global studies of ocean Fe biogeochemistry
140 (e.g. Tagliabue et al., 2016). Here, we also explicitly account for the change in bacterial
141 carbon and Fe biomass. Changes in phytoplankton and bacterial carbon and Fe biomass, as
142 well as phytoplankton cellular chlorophyll-a are driven by rates of growth, carbon fixation,
143 chlorophyll synthesis and Fe uptake in response to Fe, light (modelled here as the
144 photosynthetic available radiation, PAR) and labile DOC (Fig. 1). We identify two sources of
145 labile DOC: phytoplankton exudation and additional biotic sources which can be supplied via
146 grazing processes (excretion, sloppy feeding), viral lysis etc. Detailed equations and specific
147 parameterisations are described in the supplementary material (Supp. methods and Supp.
148 Table 1). Here we briefly describe the underlying processes considered and their
149 dependencies.

150

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

167

168 ***2.2 Experimental design***

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

171 run a set of simulations with phytoplankton alone, across a range of light and Fe levels (from
172 1 W m^{-2} to 40 W m^{-2} and 0 to 1 nM for PAR and Fe, respectively) and bacteria alone, across
173 a range of labile DOC and Fe levels (from 0 to 100 μM and 0 to 1 nM for total DOC and total
174 Fe, respectively). These initial experiments allow us to explore the separate responses of
175 phytoplankton and bacteria to changing light, Fe and DOC levels. We then run a second set
176 of experiments with both phytoplankton and bacteria competing under varying light and Fe
177 (Fe-PAR), with a fixed DOC level of 5 μM (broadly representative of typical labile DOC
178 levels, Hansell et al. 2009), and varying Fe and DOC (Fe-DOC), with a fixed light level of 20
179 W m^{-2} (broadly representative of typical mixed layer average Southern Ocean light levels).
180 To specifically address the potential role played by luxury Fe uptake in bacteria, we run a
181 parallel simulation with variable cellular Fe quota for phytoplankton, but fixed the Fe quota
182 for bacteria at a constant 10 $\mu\text{mol Fe:mol C}$ (Aumont et al. 2015). We use the model results
183 after 35 days of integration (by which time the model has reached quasi steady state) in our
184 analysis.

185

186 **3. Results and Discussion**

187 ***3.1 Response to resource co-limitation in the absence of competitive interactions***

188 Increasing Fe and light leads to an expected increase in phytoplankton carbon biomass (Fig.
189 2a), with the phytoplankton cellular Fe quota (Fe:C ratio) increasing as ambient Fe
190 concentration increases (Fig. 2b). However as light increases in parallel to Fe, phytoplankton
191 accumulate less cellular Fe relative to carbon because of high rates of growth and carbon
192 fixation (Fig. 2b, c). Increasing Fe and DOC similarly leads to an increase in carbon biomass
193 of bacteria (Fig. 2d). Although bacteria reach their maximum cellular Fe quota in all our
194 simulations, bacterial growth remained restricted at low DOC concentrations due to DOC
195 limitation which leads to high Fe:C ratios due to low rates of C assimilation (Fig. 2e).
196 Increasing Fe and DOC in parallel results in a 7-fold increase in bacterial growth rate (Fig.
197 2f).

198

199 ***3.2 How does iron-light influence phytoplankton-bacterial interactions?***

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

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

221

222 The difference in the rates of Fe uptake between phytoplankton and bacteria (Fig. 3c) show a
223 slightly different form to that seen for biomass, growth and carbon fixation at low Fe and
224 light. Bacteria consume up to 50% of the ambient Fe pool at low Fe (< 0.2 nM) and light (< 8
225 $W m^{-2}$) levels due to low phytoplankton biomass levels and higher Fe uptake efficiency (i.e.
226 lower bacterial half saturation constant for Fe uptake, Supp. Table 1), but increasing Fe and
227 light causes greater phytoplankton biomass to accumulate (Fig. 3c). We find that
228 phytoplankton can outcompete bacteria for Fe uptake at high light and Fe (Fig. 3c) due to
229 their higher biomass and growth rate (Supp. Fig. 1a and 2a, b). In contrast, when bacteria rely
230 solely on phytoplankton exudation as a DOC source, bacteria become relatively poor
231 competitors for available Fe across these experiments.

232

233 ***3.3 How does iron-DOC influence phytoplankton-bacterial interactions?***

234 Under varying Fe and DOC, but fixed light, bacteria receive two sources of DOC; DOC from
235 phytoplankton exudation and DOC from additional biotic processes. In the natural
236 environment, zooplankton excretion, viral lysis and sloppy feeding represent additional biotic
237 sources of DOC as well as Fe. Whilst there are limited quantitative estimates on the
238 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 (Aristegui 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

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

284

285 ***3.4 Impact of covariance in Fe, PAR and DOC over the Southern Ocean seasonal cycle***

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

295

296 In winter, deep mixed layers and ice cover results in complete darkness in the PZ, while PAR
297 levels remain around $2 - 7 \text{ W m}^{-2}$ in the SAZ (Fig. 4). As the supply of deep Fe will be
298 maximal at this time, dissolved Fe levels in seawater will be expected to reach their seasonal
299 maxima of around 0.9 nM in the surface open ocean (Tagliabue et al. 2014) and perhaps >1
300 nM closer to the shelf (Tagliabue et al. 2012). At this time of year, there is only a deep source
301 of refractory DOC in large areas of the open ocean (Hansell et al. 2013). Under these
302 conditions, we find that phytoplankton and bacterial biomass are low in the SAZ where there
303 is low light. Yet the very low biomass of phytoplankton take up $\sim 98\%$ of the Fe pool and
304 deplete its concentration from 0.9 nM to 0.3 only after 35 days. Over this time, phytoplankton
305 biomass can increase to from 0.1 to $6 \text{ }\mu\text{mol C L}^{-1}$ but we observe no sustained increase in
306 bacterial biomass despite a build-up of $1 \text{ }\mu\text{M}$ 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 $1 \mu\text{M}$ 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 $\sim 5 \mu\text{M}$ in addition to continual DOC
330 exudation (10% of primary production) (Hansell et al. 2009), phytoplankton take up $\sim 80\%$ 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 $\sim 55\%$ 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;

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

346

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

357

358 ***4. Competition under changing climate: uncertainties and future work***

359 There is a strong interest in understanding the response of phytoplankton to a changing
360 climate due to its role in the global carbon cycle and supporting ocean fisheries. Southern
361 Ocean surface seawater is predicted to warm by 2 – 3°C by the year 2100. Both
362 phytoplankton and bacterial metabolism respond positively with an increase in temperature
363 (Rivkin et al. 1996, Pomeroy and Wiebe 2001, Deppeler and Davidson 2016, Toseland et al.
364 2013). But there is substantial disagreement on how temperature could regulate
365 phytoplankton-bacterial interactions and DOC production and stimulation. Bacterial
366 production could follow an increase in primary production and not temperature (Kirchman et
367 al. 1995, Morán et al. 2006) or respond to an increase in temperature and not primary
368 production (Hoppe et al. 2008). Our analysis finds that bacteria can outcompete
369 phytoplankton leading to a decrease in phytoplankton biomass if sufficient labile DOC is
370 available which can be found in regions of high recycling (Ruiz-Halpern et al. 2011,
371 Arístegui et al. 2014) and ice melt (Norman et al. 2010, Underwood et al. 2010), where there
372 is also concurrent release of Fe, a concept that has previously not been considered in our
373 understanding of the Fe cycle in the Southern Ocean (Tagliabue et al., 2014). As ice melt

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

381

382 Additional feedbacks, not explored in this study, are the interactions around the bacterial
383 production of siderophores in response to Fe scarcity (e.g. Boiteau et al., 2016) and the
384 weaker Fe binding agents associated with phytoplankton exudates, such as saccharides
385 (Hassler et al., 2011) or heme groups (Louropoulou et al., 2020), or the role of bacterivory in
386 recycling the Fe stored in bacteria (Tortell et al. 1996, Strzepek et al. 2005, Boyd et al. 2012,
387 Boyd et al. 2015, Mazzotta et al. 2020). Furthermore, along the coastal Antarctic sea-ice edge
388 communities, phytoplankton are limited by cobalamin (vitamin B₁₂) and Fe (Bertrand et al.
389 2015). As cobalamin is only produced by bacteria and archaea, this suggest that
390 phytoplankton-bacterial interactions mediate micronutrient colimitation for nutrients other
391 than Fe as well. As such, more experimental-modelling work is required to gain a better
392 mechanistic understanding of how the competitive interactions between phytoplankton and
393 bacteria could change in response to multiple concurrent environmental changes.

394

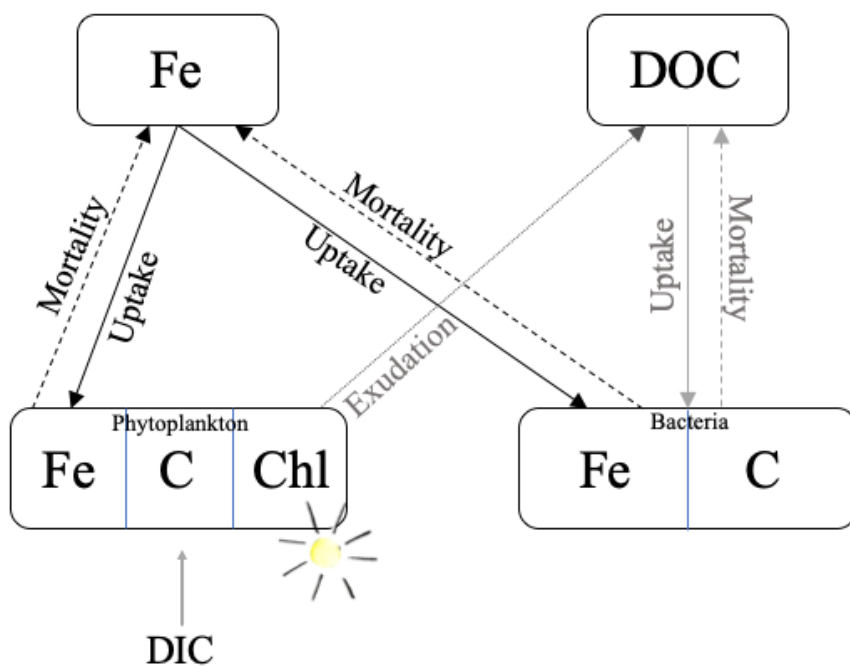
395 **5. Conclusions**

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

406

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 411 PISCES as described in Aumont et al. 2015 and freely available as part of the NEMO
 412 modelling platform. The NEMO code is available from <https://www.nemo-ocean.eu>. The
 413 equations and parameters used in this study are provided in the supplementary material.
 414 Mixed layer depth data was sourced from deBoyer-Montegut et al. 2004 (
 415 http://www.ifremer.fr/cerweb/deboyer/mlD/Surface_Mixed_Layer_Depth.php) and PAR was
 416 sourced from NASA Ocean Color (VIIRS monthly climatological data at 4km resolution
 417 <https://oceancolor.gsfc.nasa.gov/l3/>).
 418



419
 420 Figure 1: Schematic of model configuration with 2 biological pools – phytoplankton and
 421 bacteria, and 3 resources –dissolved iron (Fe), light and dissolved organic carbon (DOC). Fe
 422 and DOC are taken up by phytoplankton and bacteria (solid lines) and recycled via mortality
 423 (dashed lines) and phytoplankton exudation (dotted).
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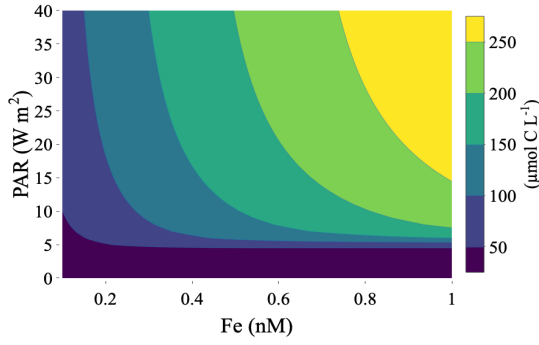
432

Fe-PAR
Phytoplankton

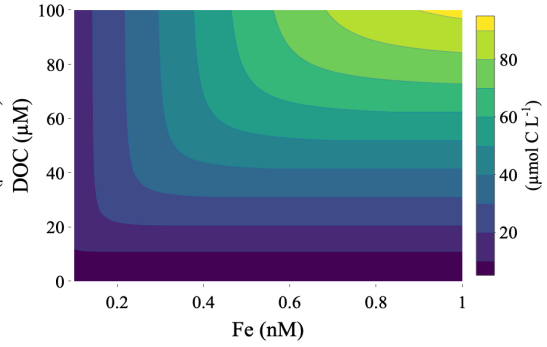
Fe-DOC
Bacteria

Biomass

a)

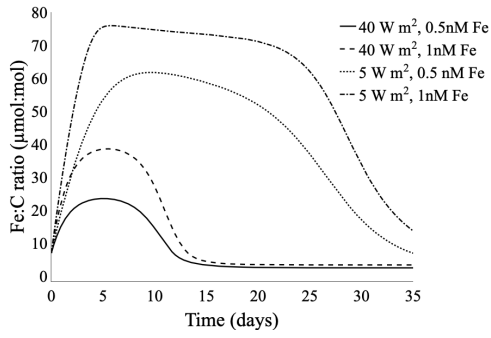


d)

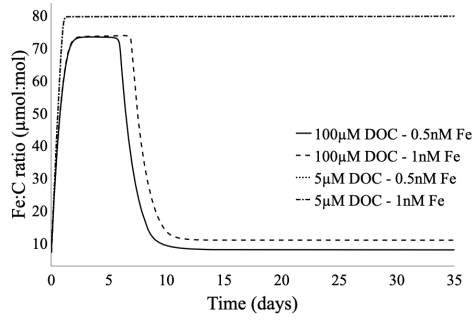


Fe:C ratio

b)

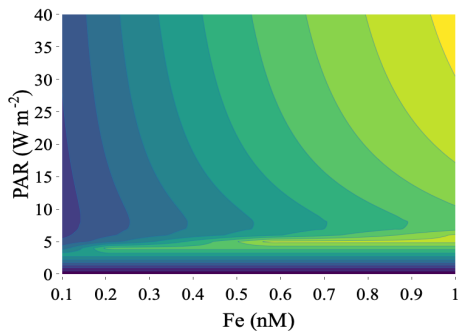


e)

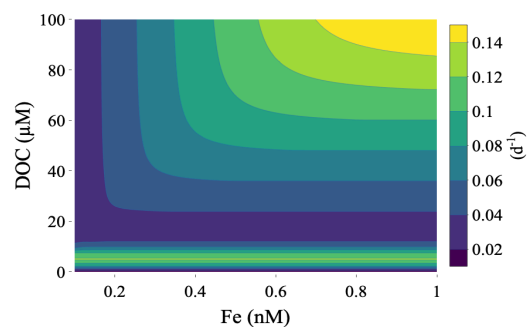


Growth rate

c)



f)



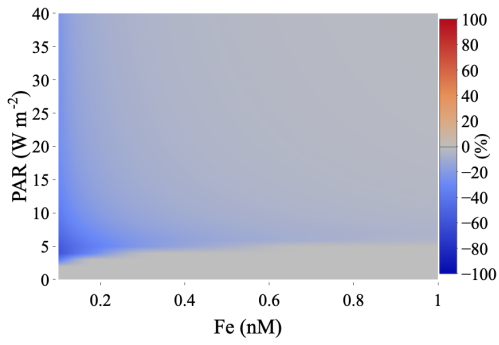
435 Figure 2: Steady state response of phytoplankton under iron (Fe) and light (PAR)
436 colimitation (a – c) and bacteria under Fe and dissolved organic carbon (DOC) colimitation
437 (d – f) in the absence of competitive interactions. Changes in carbon biomass (a, d), cellular
438 Fe quota (b, e) and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

441

Fe-PAR

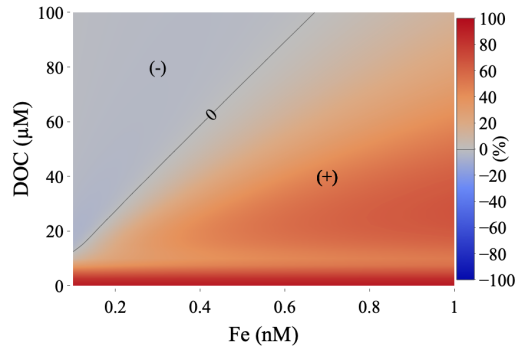
Changes in biomass compared to reference simulation

a)



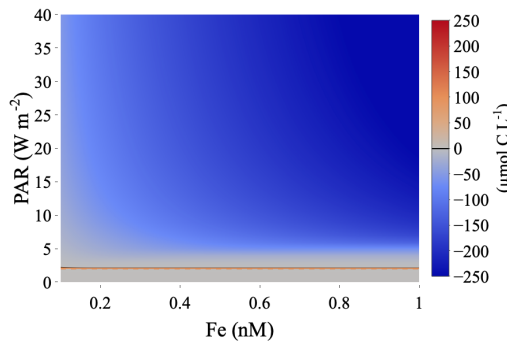
Fe-DOC

d)

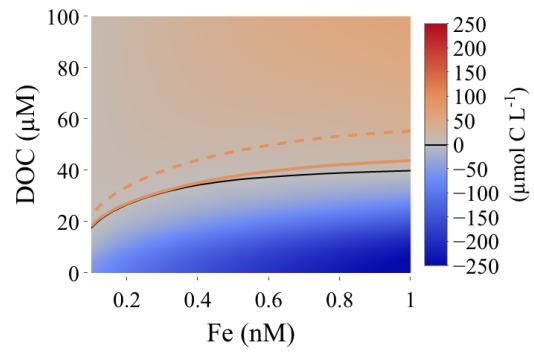


Competitive outcome for biomass, carbon production and growth rate

b)

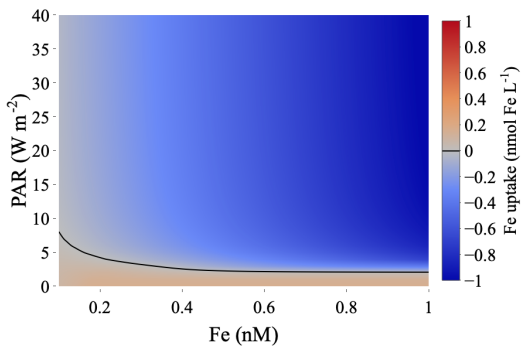


e)

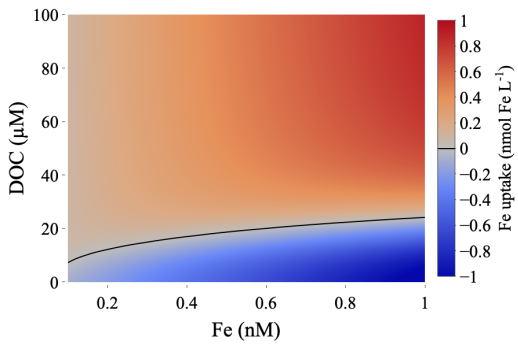


Relative iron uptake

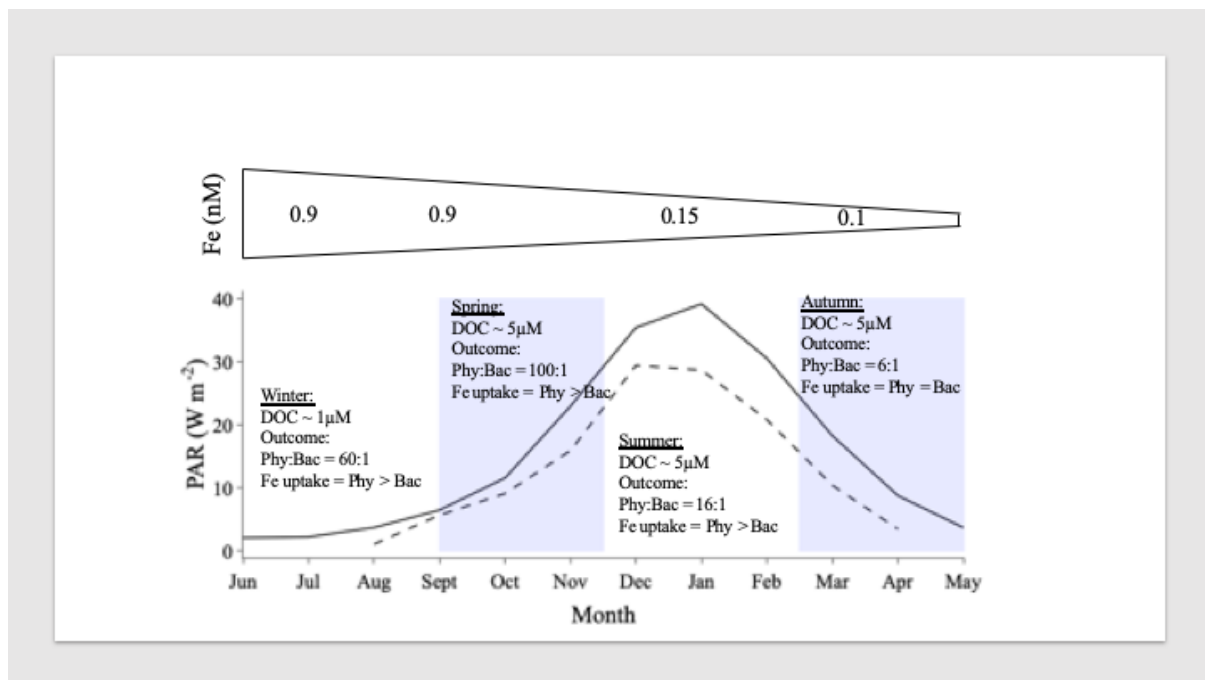
c)



f)



444 Figure 3: Steady state response of phytoplankton and bacteria as they compete for iron (Fe)
 445 under Fe – light (PAR) (a – c) and Fe – dissolved organic carbon (DOC) colimitation (d – f).
 446 Carbon biomass relative to no competition simulation (a, d). Difference in biomass (black),
 447 growth rate (orange dash) and carbon production rate (orange solid) between phytoplankton
 448 and bacteria (b, e). Difference in Fe uptake rate between phytoplankton and bacteria (c, f).
 449 All lines denote regions where phytoplankton and bacteria are equal and separate regions of
 450 phytoplankton (blue) and bacterial (red) dominance.
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 455 Figure 4: Top panel represents dissolved iron (Fe) fluxes from observations and modelling
 456 studies. Bottom panel demonstrates average mixed layer depth integrated light (PAR; based
 457 on VIIRS Ocean Colour Data, Ocean Biology Processing Group 2019 and de Boyer
 458 Montegut 2004) for the subAntarctic (solid line) and polar (dashed line) zones and
 459 assumptions of labile dissolved organic carbon (DOC) available for bacteria used to initialise
 460 the model. Highlighted rectangular regions represent austral spring and autumn.
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