

1 **Impact of Lagrangian Sea Surface Temperature Variability on Southern Ocean**
2 **Phytoplankton Community Growth Rates**

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13 **Key Points:**

- 14 • Sea surface temperature (SST) variability differs between the Lagrangian and Eulerian
15 reference frames
- 16 • SST variability on timescales of days to weeks encountered by advecting phytoplankton
17 decreases phytoplankton community growth rates
- 18 • The commonly used Eppley curve or Q_{10} growth model do not capture the effects of sea
19 surface temperature variability on phytoplankton growth

20

21

22 **Abstract**

23 Ocean phytoplankton play a critical role in the global carbon cycle, contributing ~50% of global
24 photosynthesis. As planktonic organisms, phytoplankton encounter significant environmental
25 variability as they are advected throughout the ocean. How this variability impacts
26 phytoplankton growth rates and population dynamics remains unclear. Here, we systematically
27 investigated the impact of different rates and magnitudes of sea surface temperature (SST)
28 variability on phytoplankton community growth rates using surface drifter observations from the
29 Southern Ocean (> 30°S) and a phenotype-based ecosystem model. Short-term SST variability
30 (<7 days) had a minimal impact on phytoplankton community growth rates. Moderate SST
31 changes of 3-5°C over 7-21 days produced a large time lag between the temperature change and
32 the biological response. The impact of SST variability on community growth rates was nonlinear
33 and a function of the rate and magnitude of change. Additionally, the nature of variability
34 generated in a Lagrangian reference frame (following trajectories of surface water parcels) was
35 larger than that within an Eulerian reference frame (fixed point), which initiated different
36 phytoplankton responses between the two reference frames. Finally, we found that these
37 dynamics were not captured by the Eppley growth model commonly used in global
38 biogeochemical models and resulted in an overestimation of community growth rates,
39 particularly in dynamic, strong frontal regions of the Southern Ocean. This work demonstrates
40 that the timescale for environmental selection (community replacement) is a critical factor in
41 determining community composition and takes a first step towards including the impact of
42 variability and biological response times into biogeochemical models.

43

44 **Plain Language Summary**

45 Ocean phytoplankton are fundamental to the global carbon cycle. However, it remains unclear
46 how environmental variability impacts phytoplankton growth, and thus, the global carbon cycle.
47 Phytoplankton encounter environmental variability (e.g., sea surface temperature (SST) changes)
48 as they are transported throughout the oceans by surface currents. Here, we quantified this
49 variability (i.e., in a Lagrangian reference frame) using surface drifters and investigated the
50 impact of this variability on phytoplankton community growth rates using an ecosystem model.
51 We also compared the Lagrangian SST to the SST variability of a fixed point (e.g., a buoy)
52 where ocean currents flow past (i.e., the Eulerian reference frame) using high-resolution satellite
53 data. We found larger SST changes in the Lagrangian than in the Eulerian reference frame and
54 discovered that this difference impacted phytoplankton community structure and growth rates.
55 The impact of SST variability was not captured by the growth model that is typically used by
56 global biogeochemical models. Our results provide an important extension on the classic
57 principle that “everything is everywhere: but the environment selects” (Hutchinson, 1961). Even
58 when ‘everything is everywhere’, we show that the timescale for environmental selection
59 (community replacement) is a critical factor in determining community composition
60

61

62 **1. Introduction**

63 Phytoplankton are a fundamental part of the global carbon cycle accounting for nearly 50% of all
64 photosynthesis globally (Falkowski et al., 2008). Phytoplankton also serve as the base of the
65 marine food web and drive the ocean biological carbon pump, which acts to sequester carbon in
66 the deep ocean. Understanding the impact of rising global temperatures on phytoplankton
67 communities is therefore critical for predicting the influence of anthropogenic warming on ocean
68 ecosystems and the global carbon cycle (Doney, 1999; Quéré et al., 2005). Currently, the
69 parameterization of temperature-dependent growth rates is one of the main sources of uncertainty
70 for future carbon cycle predictions among global biogeochemical models (Laufkötter et al.,
71 2015). Due to their planktonic nature, phytoplankton will encounter anthropogenic warming in
72 two ways: 1) as a general warming overlain on top of significant temperature variability due to
73 advection; and 2) as changes in variability driven by large-scale shifts in ocean physics (Boyd et
74 al., 2016; Fu et al., 2016; Lomas et al., 2010). Both of these processes will shift the type and
75 magnitude of temperature variability experienced by phytoplankton. Therefore, an improved
76 understanding of the impact of temperature variability on phytoplankton growth rates is
77 necessary in order to mechanistically incorporate phytoplankton growth dynamics into
78 biogeochemical ecosystem models and to generate robust predictions of future changes.
79

80 Accurately assessing the type of temperature variability (rate and magnitude of change)
81 encountered by phytoplankton in the ocean requires the correct reference frame. For
82 phytoplankton, the correct reference frame is Lagrangian (along trajectory) rather than an
83 Eulerian (fixed location) reference frame (Figure 1). Modeling studies have demonstrated that
84 both mean conditions and variability (magnitude and rate of change) can differ markedly
85 between the two reference frames (e.g. Doblin & van Sebille, 2016). Here we quantify the nature
86 of the variability experienced by phytoplankton along Lagrangian trajectories using *in situ* data
87 from the Southern Ocean – a region where global climate models lack a consensus on the impact
88 of anthropogenic warming on phytoplankton growth (Bopp et al, 2013). This analysis allows us

89 to constrain realistic rates and magnitudes of temperature changes experienced by Southern
90 Ocean communities and determine the impact of this variability on population growth rates.

91
92 The response of a phytoplankton community to changes in temperature is driven by individual
93 phytoplankter dynamics. Growth rate as a function of temperature (reaction norm) for an
94 individual phytoplankter is unimodal and tends to be asymmetric, often with skewed tails
95 towards lower temperatures (Boyd, 2019). Therefore, the growth response for an individual
96 phytoplankter to a change in sea surface temperature (SST) depends on the starting SST relative
97 to the optimum growth temperature (T_{opt} , the temperature with the highest growth rate) and
98 whether the SST change is increasing or decreasing (Figure 2). The rate of change in growth rate
99 will depend on the acclimation rate (how fast the phytoplankter adjusts to the new temperature)
100 and type of acclimation of the phytoplankter (Kremer et al., 2018). When SST changes are
101 slower than the phytoplankter acclimation rate, the instantaneous growth rate will be equivalent
102 to the acclimated growth rate (i.e., the phytoplankter is able to keep up with the rate of
103 temperature change). When the rate of SST change is faster than the rate of acclimation, the
104 instantaneous growth rates could be higher or lower than the acclimated growth rate, depending
105 on the type of response, detrimental or beneficial, respectively (Kremer et al., 2018).

106
107 Laboratory based experiments on the impact of temperature variability on phytoplankton growth
108 have produced conflicting results. Some studies found an overall decrease in growth rates in a
109 thermally variable environment relative to a stable environment (Bernhardt et al., 2018; Qu et al.,
110 2019; Wang et al., 2019), while others found higher growth rates under variable conditions
111 (Schaum et al., 2018), and some found that thermal variability did not impact community
112 growth rates (Kling et al., 2019; Qu et al., 2019). The lack of consensus concerning the impact of
113 variability on phytoplankton growth rates may be due to the different magnitudes and rates of
114 change used by the different studies, which ranged from $\sim 1.5^{\circ}\text{C}/\text{day}$ (Schaum et al., 2018) to as
115 high as $10^{\circ}\text{C}/\text{day}$ (Bernhardt et al., 2018).

116
117 Understanding how an *in situ* population of phytoplankton will respond to temperature
118 fluctuations is further complicated by phenotype and strain diversity. Multiple phenotypes can
119 co-occur within a population of phytoplankton each with different optimal temperatures (T_{opt} ,
120 e.g., Webb et al., 2009). As such, the temperature response of a population is often modeled
121 using an Eppley curve (αe^{bT} , Eppley, 1972) where growth rate increases exponentially with
122 temperature rather than as a unimodal relationship (Bopp et al., 2013). In essence, this assumes
123 rapid phenotypic shifts within the community such that, as the temperature changes, the
124 community rapidly shifts its optimal growth temperature (Fig. 3b). Previous work has
125 demonstrated that representing phytoplankton growth using an Eppley curve results in an over-
126 estimation of phytoplankton community growth rates (Moisan et al., 2002). In addition, the
127 advection of communities across large temperature gradients, such as those along a western
128 boundary current, can result in considerable differences between the optimum growth
129 temperature (T_{opt}) for the community and the *in situ* temperature (Hellweger et al. 2016). Here
130 we build upon these studies and use a model to assess phenotypic shifts within a population in
131 response to different types of temperature fluctuations and the resulting impact on population (or
132 community) level growth rates.

133

134 In this study, we systematically assessed the effect of different magnitudes and rates of change of
 135 temperature on phytoplankton community growth rates in the Southern Ocean (south of 30°S)
 136 using *in situ* SST data and a numerical ecosystem model. This southern hemisphere region
 137 encompasses some of the lowest (0.2°C) and highest (1.6-2.0°C) long-term mean SST
 138 variability globally (Deser et al., 2010; Maheshwari et al., 2013). We found that relatively small
 139 changes (< 2 °C over 7-90 days) did not substantially impact community growth rates and that
 140 moderate changes (4-6°C over 21-45 days) had the largest and longest lasting effect on
 141 community growth rates. These moderate changes resulted in a temporary decrease in
 142 community growth rate, that lasted up to 20 generations, as the community responded to the new
 143 temperature. The response of community growth rate to variable temperatures was non-linear
 144 and so could not easily be accounted for with an adjustment to the Eppley curve. Finally, we
 145 found that the impact of temperature variability on phytoplankton community growth rates was
 146 present everywhere in Southern Ocean with the largest impact occurring in regions dominated by
 147 meso- and sub-mesoscale activity.

148

149 **2. Methods**

150 The impact of SST variability on phytoplankton community growth rates was studied by
 151 combining SST observations, both *in situ* and from remote sensing products, and a phenotype-
 152 based ecosystem model. Here, we focused on the impact of mixed layer SST variability on
 153 phytoplankton community growth rates and therefore did not consider growth limitations due to
 154 other sources of variability such as nutrients, light, and mixed layer depth (e.g., Rohr et al.,
 155 2020a, 2020b). We tested the impact of co-limitation by temperature and nitrate and found that
 156 the results were generally consistent with the findings presented here (Supplement S6). Further
 157 work is needed to investigate the impact of multiple un-correlated environmental drivers.

158

159 *2.1 Southern Ocean drifter profiles*

160 Lagrangian SST data were obtained from 422 Southern Ocean surface drifters from the Global
 161 Drifter Program with 6-hourly SST data. Float data south of 30°S from July 1999 – April 2016
 162 was downloaded from the Drifter Data Centre at the Atlantic Oceanographic and Meteorological
 163 Laboratory (accessed 11/2018). The lifetime of the drifters ranged from 91 days to 5.8 years
 164 with a median duration of 521 days. Each drifter was segmented into 90-day trajectories to
 165 provide consistency in the dataset. We used only segments that had less than 10% of missing
 166 data. This resulted in 2,190 90-day trajectories (Figure 3a).

167

168 To estimate the magnitude of Lagrangian variability in our study region, we calculated the range
 169 of SSTs ($\Delta\text{SST}_{\text{max}}$) and the time (Δt_{max}) over which the temperature change occurred using
 170 moving windows of 1 to 90 days (in 1-day increments). We then assessed the distribution of
 171 variability across different window sizes by aggregating the data into 1°C bins for $\Delta\text{SST}_{\text{max}}$ and 1
 172 day Δt_{max} bins. For example, a 2.4°C change that occurred over 14 days was recorded in the 2-
 173 3°C and 14-day bin. To investigate the potential impact of small-scale noise, we also created
 174 smoothed splines of each of the 90-day SST profiles using a cubic smoothing spline (*csaps* in
 175 Matlab with a smoothing parameter of 0.00001). The splines filter out 25% of the variability on a
 176 1-day timescale up to 95% at the 90-day window (Figure S1). We then repeated the $\Delta\text{SST}_{\text{max}}$ and
 177 Δt_{max} analysis on the spline data.

178

179 *2.2 Remote sensing SST*

180 To compare the SST variability in the Lagrangian reference frame to the variability that would
 181 be captured in the Eulerian reference frame, we used high-resolution (0.01° horizontal resolution
 182 and 1-day temporal resolution) satellite SST data from GHRSSST Level 4 MUR Global
 183 Foundation Sea Surface Temperature Analysis (v4.1) (JPL MUR MEaSURES Project, 2015;
 184 accessed Oct. 2018). This dataset spanned 2003-2014 which overlaps with 71% of our 90-day
 185 drifter segments. For each 90-day drifter segment between 2003-2014, we extracted 90 days of
 186 satellite SST data for the latitude and longitude of the final location of the drifter, where the 90
 187 days corresponded to the dates of the drifter segment. We then also extracted the satellite SST
 188 along the drifter trajectories to provide a direct comparison between the Eulerian and Lagrangian
 189 reference frames in terms of the temporal and spatial resolution of the datasets. We performed
 190 the same $\Delta\text{SST}_{\text{max}}$ and Δt_{max} variability analyses for the satellite data as the surface drifter
 191 trajectories (described in Section 2.1).

192

193 *2.3 Idealized SST trajectories*

194 We complemented the observed SST trajectories with idealized SST trajectories to
 195 mechanistically understand the impact of the rate and magnitude of SST change on community
 196 growth rates. Specifically, a suite of trajectories ($N = 64$) was generated with both increasing and
 197 decreasing SST trends ranging from $\Delta\text{SST} = 2^\circ$ to $\Delta\text{SST} = 9^\circ\text{C}$ (in increments of 1°C) over 7, 21,
 198 45, and 90 days. These ΔSST values and durations were chosen based on our Lagrangian
 199 variability analysis. To minimize initialization bias, SST was held constant for the first 30 days
 200 before increasing/decreasing. After the SST change, the SST was again held constant until the
 201 200th day. The final temperature for all idealized trajectories was 15°C . The impact of the final
 202 temperature on the model results was analyzed with a set of sensitivity experiments. The final
 203 SST had no significant impact on the results when the results were reported in terms of the
 204 doubling time (generation), rather than absolute days as this normalized the effect of higher
 205 growth rates at warmer temperatures (Supplemental Material S1). Generation time was
 206 calculated as $\ln 2 / \mu_{SS}$, where μ_{SS} is the stabilized community growth rate. With a final SST of
 207 15°C , the generation time was approximately 1.37 days.

208

209 *2.4 Phenotype-based Ecosystem Model*

210 To estimate the impact of variable temperature on phytoplankton community growth rates, we
 211 used a phenotype-based ecosystem model. The model consisted of 319 phytoplankton
 212 phenotypes that were identical in all aspects (i.e. model parameters) other than the optimal
 213 growth temperature (T_{opt}). Temperature dependent growth rate (μ , day^{-1}) was defined as a
 214 function of T ($^\circ\text{C}$) (Thomas et al., 2012):

$$215 \quad \mu(T) = ae^{bT} \left[1 - \left(\frac{T - T_{opt}}{w/2} \right)^2 \right] \quad \text{Eq. 1}$$

216

217 where T_{opt} was the optimal growth temperature. The value of b controlled the shape of the
 218 reaction norm, a (day^{-1}) scaled the reaction norm, and w ($^\circ\text{C}$) defined the width of the reaction
 219 norm (the difference between the maximum (T_{max}) and minimum (T_{min}) growth temperatures).
 220 We ran the model with two sets of reaction norms: a symmetrical, or broad, curve where $b = 0$
 221 ($^\circ\text{C}^{-1}$) and a skewed reaction norm where $b = 0.3$ ($^\circ\text{C}^{-1}$). Both reaction norms had a width of 14°C
 222 ($w = 20$ $^\circ\text{C}$), consistent with observed reaction norms for many polar species (Boyd, 2019).
 223 Sensitivity tests were performed with reaction norm widths of 10.5°C ($w = 15$ $^\circ\text{C}$) and 20.5°C (w

224 = 29 °C) (Supplemental Material S2). The results from these sensitivity tests did not differ
 225 substantially from the simulations with a reaction norm width of 14 °C.

226

227 The parameter a scaled the reaction norms at T_{opt} to the Eppley curve (Eppley, 1972) where
 228 maximum growth rates ranged between 0.28 day⁻¹ at -1.8 °C to 1.0 day⁻¹ at 30 °C, consistent with
 229 experimental data (Boyd, 2019). Specifically, a_i was defined for each phenotype i as:

$$230 \quad a_i = 0.2963e^{0.0405T_{opt}} \quad \text{Eq. 2}$$

231 This resulted in an increase of ~1.5x in growth rate for every 10 degrees (i.e. a Q₁₀ relationship
 232 of 1.5, *see Discussion*). We generated 319 phenotype curves for both the broad and skewed
 233 reaction norms with T_{opt} ranging from -1.8 °C to 30 °C increasing by 0.1 °C (Figure 3a).

234

235 The biomass of each phytoplankton phenotype P_i was calculated at each time-step as the integral
 236 of:

$$237 \quad \frac{dP_i}{dt} = \mu_i(T)P_i - m(T)P_i^2 \quad \text{Eq. 3}$$

238 where $\mu_i(T)$ was the temperature-dependent growth rate for phenotype i from Equation 1. $m(T)$
 239 was the temperature-dependent quadratic mortality rate (m³ mmol C⁻¹ day⁻¹) where:

$$240 \quad m(T) = 0.35 * a \quad \text{Eq. 4}$$

241 Here we used the same temperature dependent Eppley curve (Eq. 2) to scale mortality with
 242 temperature using SST instead of T_{opt} where $a = 1$ day⁻¹ for SST = 30 °C. We imposed a
 243 minimum biomass (0.001 mmol C m⁻³) so that no phenotype went locally extinct, akin to the
 244 “everything is everywhere” principle (Hutchinson, 1961). Sensitivity tests were performed with
 245 the minimum biomass set to 0.0001 mmol C m⁻³. The minimum biomass threshold did not
 246 affect the overall patterns but did increase both the magnitude of the difference from the
 247 community growth rates obtained using the Eppley growth model and the time to acclimation
 248 (memory length, Section 3.2) for both broad and skewed reaction norms (Supplemental Material
 249 S.3). Imposing this minimum biomass purposefully introduced mass into the system which was
 250 accounted for by adjusting the biomass of each phenotype to keep the total community biomass
 251 at the concentration it would have been without the minimum biomass criteria. Specifically, the
 252 total change in biomass without the minimum biomass phenotypes was calculated using the
 253 biomass weighted community growth rate (λ) in place of $\mu(T)$ in Eq. 3, where λ was defined as:

$$254 \quad \lambda = \sum \mu_{i,t} \frac{P_{i,t}}{P} \quad \text{Eq. 5}$$

255 where, $\mu_{i,t}$ was the growth rate of the i th phenotype at time t for all phenotypes with biomass
 256 greater than the minimum, $P_{i,t}$ was the biomass of the i th phenotype whose biomass was greater
 257 than the minimum at time t , P was the sum of the biomass of all phenotypes with biomass greater
 258 than the minimum at time t .

259

260 Several different models for mortality and grazing were tested including linear mortality,
 261 constant mortality, a dynamic zooplankton population, and a simple ecosystem model with
 262 constant grazing pressure (see section S.4 in Supplemental Material). All model versions resulted
 263 in qualitatively similar results which demonstrated that the community dynamics were not
 264 particularly sensitive to the top-down control formulation in the model (Section S.4 in
 265 Supplemental Material). Here, we present the quadratic mortality as it was the simplest model
 266 with smooth (non-oscillatory) solutions.

267

268 The ecosystem model was forced with each of the 2,190 drifter segments (see Figure 3c-e for
 269 examples), the corresponding smoothed splines, the idealized SST trajectories, and the satellite-
 270 derived SSTs. The initial biomass of phenotypes with a T_{opt} within $\pm 2.5^\circ\text{C}$ of the starting SST
 271 value were randomized to simulate previously accumulated biomass with phenotypes outside this
 272 range set to the minimum biomass. Simulations that used idealized SST trajectories were
 273 performed 100 times with different initial biomass conditions to account for stochasticity in the
 274 model initialization.

275

276 *2.5 Acclimation Rate*

277 To test the impact of different acclimation timescales, we performed sensitivity tests in which we
 278 incorporated a linear acclimation rate for all phenotypes in the model. Specifically, we
 279 incorporated a timescale over which an individual phenotype could change its growth rate in
 280 response to a temperature change. For example, if SST rapidly changed from 15°C to 16°C , a
 281 phenotype with an acclimation timescale of $0.2^\circ\text{C day}^{-1}$ would move from the growth rate at
 282 15°C to the growth rate at 15.2°C in one day. If the SST then held constant at 16°C , the
 283 phenotype would acclimate by the end of the fifth day. We tested acclimation rates ranging from
 284 $0.2^\circ\text{C day}^{-1}$ to $0.6^\circ\text{C day}^{-1}$ in increments of $0.1^\circ\text{C day}^{-1}$ which are consistent with acclimation
 285 rates determined for the Southern Ocean diatom *F. cylindrus* (see Table S2). The model with
 286 acclimation was forced with the idealized SST trajectories for a $\Delta\text{SST} = 2^\circ\text{C}$ in 7 days (0.29°C
 287 day^{-1}), 3°C in 7 days ($0.43^\circ\text{C day}^{-1}$), 4°C in 7 days ($0.57^\circ\text{C day}^{-1}$) and 5°C in 21 days (0.24°C
 288 day^{-1}). These intervals corresponded to the magnitudes and rates of change most commonly
 289 experienced by the drifter trajectories (see Section 3.1) for which the rate of change was greater
 290 than $0.2^\circ\text{C day}^{-1}$.

291

292

293 **3. Results**

294 *3.1 SST variability*

295 We characterized *in situ* SST variability experienced by phytoplankton (i.e., in a Lagrangian
 296 reference frame) using the surface drifter SST data. Seasonal dynamics were not filtered out as
 297 they were important sources of SST variability encountered by phytoplankton. While the surface
 298 drifters may have been subjected to some physical movements that phytoplankton do not
 299 encounter (e.g., lateral transfer across fronts due to wind rather than subduction and mixing),
 300 they provided the best *in situ* dataset for studying Lagrangian variability in surface temperature.
 301 However, to minimize the impact of unrealistic fluctuations in the drifter dataset, we limited our
 302 subsequent analyses to the most frequently measured scales of variability within the drifter
 303 record. The average $\Delta\text{SST}_{\text{max}}$ values ranged from $0.9^\circ\text{C} \pm 0.7^\circ\text{C}$ (1σ) for the 7-day window,
 304 which corresponded to 0.13°C/day change over the 7 days, to $4.2^\circ\text{C} \pm 2.0^\circ\text{C}$ (1σ) for the 90-day
 305 window or 0.05°C/day change (Figure S12, Table S1). The latter was consistent with the
 306 expected seasonal SST cycle for the Southern Ocean (Reynolds & Smith, 1994). The SST
 307 variability of the drifters (standard deviation over the window) was highly correlated with
 308 $\Delta\text{SST}_{\text{max}}$ ($R^2 = 0.92$, $p < 0.01$, Figure S13).

309

310 Using the $\Delta\text{SST}_{\text{max}}$ analysis, we were able to quantify the most common types of variability
 311 encountered *in situ* in terms of both the magnitude of change and the rate of change (Figure 4).
 312 Due to the difference in the number of data points generated by the moving windows, we
 313 assessed the frequency of each $\Delta\text{SST}_{\text{max}}$ within a given window length (y-axis) such that the

314 highest value across the row indicates the most likely $\Delta\text{SST}_{\text{max}}$ for that window length. The
 315 $\Delta\text{SST}_{\text{max}}$ bins sum to 100% across the row. Overall, there is a trend of increasing $\Delta\text{SST}_{\text{max}}$ with
 316 increasing window length, as expected. We selected four representative window lengths, 7 days,
 317 21 days, 45 days, and 90 days, as illustrative examples though the results are not dependent on
 318 these selections. A 7-day window was most likely to have a $\Delta\text{SST}_{\text{max}}$ of 2°C or less (82%), and
 319 ~3% of the trajectories recorded a $\Delta\text{SST}_{\text{max}}$ of 4 °C. Over a 21-day window, most trajectories had
 320 a $\Delta\text{SST}_{\text{max}}$ of 2-3°C (combined accounting for 86% of data) and ~10% of the trajectories had a
 321 $\Delta\text{SST}_{\text{max}}$ of 4-5°C. $\Delta\text{SST}_{\text{max}}$ reached as high as 9°C for the 90-day windows but accounted for
 322 only 2.5% of the data in that window.

323
 324 A comparison of Lagrangian and Eulerian reference frames demonstrated that, while the overall
 325 patterns of variability were similar, the Lagrangian reference frame was more likely to capture
 326 large $\Delta\text{SST}_{\text{max}}$ (Figure S14). This was true for both the drifter and satellite derived Lagrangian
 327 trajectories when compared to the satellite SST in the Eulerian reference frame. For example,
 328 within a time-frame of 21 to 30 days, a $\Delta\text{SST}_{\text{max}}$ greater than 3°C was more likely to occur in
 329 both the drifter and satellite derived Lagrangian (17%) trajectories than in the Eulerian (11%).
 330 Similarly, for the 51-day to 60-day windows, $\Delta\text{SST}_{\text{max}}$ of 2-4 °C were common in both reference
 331 frames, but changes >4°C were more common in the satellite derived Lagrangian trajectories
 332 (24%) and the drifter Lagrangian trajectories (23%) than the satellite Eulerian data (16%). This
 333 same pattern was consistently observed for all windows from 1 to 90 days. The impact of these
 334 differences in SST changes on phytoplankton community growth rates are discussed below (see
 335 Sections 3.2 and 3.3).

336
 337 For most of the SST data recorded by the drifters, the rate of SST change was slower than the
 338 expected phytoplankton acclimation rates. Acclimation rates for the Southern Ocean diatom *F.*
 339 *cylindrus* are on average 0.3°C/day (Table S2). For the drifter trajectories, only 8% of the 1-day
 340 bins ($n = 197,100$ days) recorded rates of SST change greater than 0.3°C/day and less than 2% of
 341 the daily bins recorded rates of change greater than 0.6°C/day (Figure S15). Because SST rates of
 342 change were typically slower than the phytoplankton acclimation rate, we hypothesize that, for
 343 the majority of the Southern Ocean, the rate of acclimation will not play a major role in the
 344 community response. Therefore, to simplify model dynamics, we ran our model with rapid
 345 acclimation such that each phenotype responded directly to SST changes. See Section 4.1 for
 346 discussion about situations in which acclimation may be important.

347 348 *3.2 Impact of variable SSTs on community growth rates*

349 We used idealized simulations to develop a mechanistic understanding of how variability
 350 impacts community growth rates. For small, gradual SST changes of less than 2-3°C in 45-90
 351 days (0.02-0.07 °C/day), the community growth rates changed linearly with the SST changes
 352 during the period of SST transition and then stabilized once SST stopped changing. When the
 353 rate of change was slow, the distribution of phenotypes within the community changed at the
 354 same rate as the SST such that the T_{opt} of the most dominate phenotype closely matched the SST.
 355 As a result, the temporal response in the community growth rate from the phenotype model was
 356 similar to the growth rate from a null model using an Eppley curve parameterization.

357
 358 For SST rates of change larger than 2-3°C in 45-90 days (0.02-0.07 °C/day), community growth
 359 rates initially increased or decreased depending on the sign of the SST change, but then began to

360 decrease rapidly (see Figure S16 for example). Once SSTs stabilized at the final value,
361 community growth rates increased and eventually stabilized. Out of the environmentally relevant
362 rates of SST change, 4°C in 7 days (0.57°C/day) resulted in the largest change 70% ±1% (1σ)
363 during the low growth period (Figure 5a). While the absolute percent change in growth rate was
364 sensitive to model formulation and parameter values, the qualitative relationships presented here
365 were robust (Figure S8).

366
367 The impact of temperature variability on community growth rates is a function of both changes
368 in the growth rates of individual phenotypes (i.e. shifts along a reaction norm) and shifts in the
369 community composition (i.e. abundance of different phenotypes). The low growth phase after a
370 shift in SST (either increasing or decreasing) was caused by the SSTs extending beyond the
371 thermal optimum of the initial community such that the bulk of the biomass was growing slowly.
372 During this period, the individual phenotypes with elevated growth rates only made up a small
373 fraction of the community and so did not contribute significantly to the community growth rate.
374 The community growth rates then rebounded as these high growth phenotypes increased their
375 biomass and eventually became the dominate biomass group. Faster rates of SST change moved
376 the community out of the thermal optimum of the initial community more quickly than smaller
377 rates of change, and therefore larger and faster ΔSSTs resulted in greater decreases in community
378 growth rates. However, the high growth individuals were able to dominate the community more
379 quickly due to the high loss rates for the slow (or no) growth individuals and so the community
380 growth rates rebounded more quickly for rapid relative to moderate rates of SST change. For
381 rapid SST changes, the rate and type of acclimation response could potentially play a role in the
382 shifts in community growth rates depending on the nature of the plastic response (see
383 *Discussion*).

384
385 An Eppley curve was unable to capture the impact of variability in SST on community growth
386 rates due to the non-linear phenotype dynamics. Community growth rates derived directly using
387 the Eppley curve model were always larger than those simulated by the phenotype model,
388 consistent with previous work (Moisan et al. 2002; Bernhardt et al. 2018). The difference
389 between the phenotype modeled growth rates and the Eppley curve estimates varied as a function
390 of SST variability (Figures 5b, S18). As the ΔSST increased over a given window length, so did
391 the difference between the phenotype model and the Eppley curve estimate. The largest
392 departures occurred for ΔSSTs of 4°C and 5 °C over 7 and 21 days, respectively, with up to 80%
393 lower simulated community growth rates for the phenotype model. Generally, larger ΔSSTs and
394 faster rates of change (changes occurring over a few generations) resulted in larger differences
395 between the models.

396
397 Although we focus on the impact of temperature-limitation on phytoplankton growth in this
398 study, nutrient limitation also plays an important role in co-limiting phytoplankton growth in the
399 Southern Ocean (Cochlan, 2008). While a full analysis of the impact of fluctuating co-limitation
400 is beyond the scope of this study, we conducted a set of model simulations to test the impact of
401 temperature and nitrate limitation on the observed dynamics (Supplemental Material S6). Given
402 the non-linear formulation of nutrient limitation and the relatively low half-saturation values for
403 the uptake of nitrate, for the majority of the Southern Ocean the model results with co-limitation
404 are similar to those from simulations with temperature limitation only. This is because the

405 variation in nutrient limitation was small compared to the variation in temperature limitation (at
406 the level of individual phenotypes).

407

408 *3.3 Memory Effect*

409 The timescales of the biological response to temperature fluctuations varied as a function of the
410 overall magnitude and direction (increasing or decreasing) of SST change, the duration of the
411 SST change, and shape of the reaction norm (broad vs skewed) for the individuals within the
412 population. Here we define the timescale of biological response as the “memory effect” – the
413 time for the community growth rate to stabilize ($\pm 5\%$ of the stable value). Here we present the
414 memory effect in terms of generations calculated using the final stable growth rate. This allowed
415 us to understand the relative impact of temperature change on phytoplankton using a common
416 currency such that our results are not growth rate dependent.

417

418 The most common Δ SST changes (Figure 4) were associated with the longest memory effects
419 (Figures 5b, S19). Nearly all of the environmentally relevant Δ SST values were sufficient to
420 create a memory effect of longer than 2 generations. Moderate changes of 3-4°C over 7-45 days
421 or 4-28 generations (0.07-0.57 °C/day) resulted in the longest memory effects of up to up to 22
422 generations for both reaction norm shapes (Figure 5c, Figure S19). This biological response time
423 is nearly five times longer than the duration of the temperature change. Larger SST changes (5-6
424 °C) that occurred over 45 or 90 days or 28-57 generations (0.06-0.13 °C/day) tended to have
425 shorter memory effects (~8-19 generations) than moderate changes that occurred over the same
426 time frame, but this difference was not statistically significant. Longer memory effects for
427 moderate SST changes resulted from dominant phenotypes in the previously acclimated
428 community being able to grow in the new environment, albeit at a reduced rate. This increased
429 the time required for the phenotypes optimally suited for the new environment to dominate the
430 community, which resulted in larger memory effects.

431

432 The sign of the SST change also impacted the response time of the community. Decreasing
433 Δ SSTs had longer memory effects by an average of 7 generations compared to increasing Δ SSTs
434 (t-test, 95% CI) for the skewed shaped reaction norms. The longer memory effect was due to the
435 long tail on the decreasing side of the reaction norm, which allowed the phenotypes in the initial
436 community to grow during decreasing SST conditions (Figure S19). For reaction norms that
437 were symmetrical about the optimum growth temperature, the direction of Δ SST did not matter,
438 and the memory lengths were not statistically different for increasing and decreasing Δ SSTs (t-
439 test, 95% CI) (Figure S19).

440

441 *3.4 Southern Ocean Drifter Trajectories*

442 The idealized simulations allowed for a mechanistic characterization of how phytoplankton
443 community growth rates vary as a function of rate and magnitude of SST change (*sections 3.2 &*
444 *3.3*). However, in the ocean, SST change is much more complicated as phytoplankton are
445 exposed to a large variety of rates and durations of SST changes. We used Southern Ocean
446 drifter trajectories to investigate the impact of *in situ* SST variability on community growth rates.
447 When phenotypic diversity was considered (phenotype model), variable SST resulted in lower
448 average community growth rates compared to the Eppley curve approximation (Figure 6).
449 Though nutrient and light limitation were not explicitly included in the phenotype model, the
450 simulated growth rates were consistent with *in situ* (Buitenhuis et al., 2013), remote-sensed

451 based (Arteaga et al., 2020), and incubation derived growth rates (Boyd, 2019; Boyd et al.,
452 2013), and therefore reasonably captured growth dynamics. As drifter SST variability increased,
453 so did the difference between the phenotype model and the Eppley curve approximation,
454 consistent with the idealized simulation results. The mean percent difference between the
455 phenotype model and the Eppley curve approximation over the 90-day trajectories ranged
456 between -142% to -11.5% with a mean of -25.8% ($\pm 16.6\%$ 1σ) for the skewed reaction norms. A
457 similar pattern was observed for the broad shaped reaction norms, but the magnitude of the
458 difference was smaller and ranged from just -1.3% to -53.2% different with a mean of -6.1%
459 ($\pm 5\%$ 1σ) (Figure S20). Trajectories with higher mean SSTs were affected less by SST
460 variability than trajectories with lower SSTs because faster growth rates at higher temperatures
461 allowed quicker responses to SST changes.

462

463 To isolate the impact that short-term variability may have on community growth rates relative to
464 longer-term shifts, we compared the 90-day mean biomass-weighted community growth rate of
465 the drifter trajectories to the smoothed splines derived from the trajectories. Removing short-
466 term variability had no significant impact on community growth rates (t-test, 95% CI; Figure
467 S21).

468

469 **4. Discussion**

470 *4.1 Impact of Acclimation*

471 As ocean surface temperature shifts, two processes occur simultaneously: 1) individual
472 phytoplankton phenotypes respond to the change in temperature (acclimation), and 2) phenotype
473 abundance within the community shifts towards individuals with higher maximum growth rates
474 at the new temperature. In this study, we investigated the impact of these individual-level
475 dynamics on community-level growth. We demonstrate that shifts in phenotype abundance are
476 the primary drivers of community growth rate dynamics. This is in large part due to *in situ* rates
477 of SST changes being slower than the rates of individual acclimation (based on laboratory
478 estimates), even for the dynamic Southern Ocean. When individual acclimation rates were
479 slower than the rate of SST change, we observed a delay in the low growth phase and a smaller
480 magnitude decrease in community growth rates (Figure S22). The memory effect increased
481 linearly as individual acclimation rates decreased (longer acclimation time) (Figures 7 and S23).

482

483 The representation of phenotype acclimation in the model was a simplistic representation of
484 phenotypic plasticity (*see Methods*). In reality, plastic responses are much more complex and
485 nonlinear and most likely vary among species (Kremer et al., 2018). Additional work is needed
486 to better constrain both the range of acclimation timescales and the mechanisms of phenotypic
487 plasticity. However, our results suggest that these dynamics will only become important under
488 rapid temperature changes which are infrequent in the ocean.

489

490 *4.2 Implications for in-situ community composition*

491 Our findings support the important role of thermal history in shaping the response of
492 phytoplankton communities to changes in temperature. We have shown that SST variability can
493 lower community growth rates for tens of generations following SST perturbation. This indicates
494 that, for many regions of the ocean, the phytoplankton community will not be fully acclimated to
495 local conditions as a result of the mismatch between timescales of physical variability and
496 biological response. This mismatch in timescales will be a function of the rate and magnitude of

497 SST variability that phytoplankton in the water mass were previously exposed to and may be
498 reflected in physiological properties such as optimum growth temperature or overall community
499 growth rate.

500

501 Our results also provide an important extension on the classic principle that “everything is
502 everywhere: but the environment selects” (Hutchinson, 1961). Even when ‘everything is
503 everywhere’, we show that the timescale for environmental selection (community replacement)
504 is a critical factor in determining community composition. Specifically, we hypothesize that even
505 when the ‘optimal’ organism is present in an environment, environmental variability generated
506 by local physics, lateral advection, and seasonal trends can delay or prevent that organism from
507 dominating the community. This hypothesis is supported by previous modeling work that has
508 shown a time-lag on the order of weeks to a month in the phytoplankton community growth
509 response to SST changes due to lateral advection and seasonal trends (Moisan, et al., 2002;
510 Hellweger et al. 2016). Here, we have quantified the relationship between varying rates of SST
511 variability and the timescale required for community replacement to impact the community
512 composition.

513

514 We tested the impact of Eulerian versus Lagrangian variability on community growth rates and
515 demonstrated significant differences for locations in which SST variability differed in the two
516 reference frames. Specifically, while the final SST of the drifter segments and satellite data were
517 not statistically different (t-test, 95% CI, Figure S24), differences in the nature of variability in
518 the proceeding 90 days resulted in a significant difference between the final SST and the T_{opt} of
519 the most abundant phenotype (t-test, 95% CI, Figures 8 and S25). The magnitude of the offset
520 between SST and T_{opt} depended on the timing of SST changes throughout the 90-day profiles.
521 When SST changes were slow, the offset between SST and the T_{opt} of the most abundant
522 phenotype were negligible (Figure S26 for an example). Large SST changes that occurred early
523 in the 90-day segment allowed sufficient time for the community to respond (e.g. Figure S26).
524 When SST changes occurred later in the 90-days, the community did not have sufficient time to
525 respond which caused a larger offset between the SST at day 90 and the T_{opt} of the community
526 (e.g., Figure S27). Different phenotype distributions for the Eulerian versus Lagrangian reference
527 frames is consistent with previous results that showed advection of phytoplankton communities
528 was a key process in shaping phytoplankton diversity (Barton et al., 2010; Clayton et al., 2013;
529 Lévy et al., 2014).

530

531 The shape of the reaction norm impacts the community response to temperature variability and
532 phenotype competitive advantage. Under decreasing temperatures, a phenotype with a skewed
533 reaction norm (T_{opt} closer to T_{max} than T_{min}) has a competitive advantage over a phenotype with a
534 broad reaction norm (T_{opt} at the center of T_{max} and T_{min}), given the same reaction norm width and
535 T_{opt} . A skewed reaction norm provides a larger range of temperatures $<T_{opt}$ under which the
536 phenotype can grow. Therefore, organisms with skewed reaction norms should be adapted to
537 have T_{opt} values close to maximum encountered temperatures not only due to the rapid decline in
538 growth rates for temperatures greater than T_{opt} but also due to the competitive advantage under
539 temperatures less than T_{opt} . Conversely, broad reaction norms are favored when temperatures are
540 warming, as expected, or when temperatures are more variable. In a highly variable region such
541 as the Southern Ocean, there should be selective pressure for either broad reaction norms with

542 large growth ranges beyond T_{opt} (Moisan et al., 2002) or skewed reaction norms where T_{opt} is
 543 higher than mean SSTs (Thomas et al., 2012).

544

545

546 *4.3 Implications for simulating community growth rates in global biogeochemical models*

547 A form of the Eppley curve Q_{10} temperature-growth response ($\mu = \mu_0 Q_{10}^{\frac{T-T_0}{10}}$) is widely used in
 548 global biogeochemical models (Bopp et al., 2013), where typical model Q_{10} values range
 549 between 1.5-2 (Sherman et al. 2016). The premise behind employing a Q_{10} growth equation is
 550 that each modeled functional group encompasses many species or strains and so the Eppley
 551 curve may be a reasonable representation of the group dynamics. However, as we have
 552 demonstrated, community growth rates (or functional group growth rates in the model
 553 framework) will depend on the underlying phenotype dynamics, which are a function of the rate,
 554 magnitude, and direction of temperature change and the shape of the species/strains' thermal
 555 response curve. As a result, the Q_{10} temperature-growth response not only underestimates
 556 temperature-limitation on community growth rates (i.e., overestimates growth rates) but does so
 557 as a function of SST, SST variability, and reaction norm shape. Our work indicates that adjusting
 558 the Q_{10} relationship to use a lower exponent as previously suggested (Sherman et al., 2016) will
 559 only partially capture realistic dynamics. Because phytoplankton play a key role in sequestering
 560 carbon dioxide from the Earth's atmosphere, by overestimating phytoplankton growth rates, and
 561 thus overestimating carbon uptake, biogeochemical models may be underestimating the extent of
 562 future anthropogenic warming.

563

564 To predict changes in phytoplankton community growth rates robustly, models must also
 565 consider the impact of different types of SST variability and the appropriate reference frame for
 566 this variability. Specifically, we have shown that SST variability can differ markedly between
 567 the Eulerian reference frame and the Lagrangian reference frame (Figure S14). While the spatial
 568 patterns of SST variability in the Southern Ocean were similar between Eulerian and Lagrangian
 569 reference frames (Figure 9a-c), the Eulerian reference frame exhibited substantially less
 570 variability. Consequentially, the offset between Eppley curve approximation and the phenotype
 571 model was substantially less for the Eulerian relative to the Lagrangian reference frame (Figure
 572 9d-f). This pattern was consistent for both the drifter Lagrangian trajectories and the satellite
 573 derived trajectories.

574

575 Models such as DARWIN (Follows et al., 2007) resolve phenotypes with a range of thermal
 576 reaction norms and so will capture the community growth rate dynamics presented here.
 577 However, additional work is needed to compare the variability encountered by functional group
 578 phenotypes in large-scale models integrated in an Eulerian framework to true Lagrangian
 579 variability.

580

581 Improving the parameterized temperature-growth relationship is particularly important in the
 582 Southern Ocean given the uncertainty of future primary productivity in this ocean basin (Bopp et
 583 al., 2013). We used our model results to identify key regions within the Southern Ocean that
 584 might be most strongly impacted by temperature variability. Three particular regions stand out
 585 that exhibited the most SST variability and had the largest relative deviations from the Eppley
 586 curve (Q_{10}) approximation: the Malvinas-Brazil confluence zone; the Agulhas Retroflexion
 587 region; and downstream from these two along the Subtropical Front near $\sim 45^\circ\text{S}$, 60°E (Figures

588 9a-c). All three regions were previously identified as highly dynamic, strong frontal regions
589 (Artana et al., 2019; Beal et al., 2015; Graham & Boer, 2013) and shown to be important hot-
590 spots for phytoplankton diversity (Barton et al., 2010; Clayton et al., 2013; d'Ovidio et al., 2010;
591 Soccodato et al., 2016). It is possible that in these highly dynamic frontal regions the floats were
592 subjected to physical movements across the fronts that was previously thought to elude
593 phytoplankton movements. However, recent field and modeling studies have shown that cross-
594 front transfer and diapycnal mixing can occur due to the fine-scale physics associated with these
595 strong fronts (Clayton et al., 2017; Mahadevan, 2016; Wenegrat et al., 2020). Our results also
596 showed that large SST changes were not required for temperature variations to have a lasting
597 impact on community growth rates. Regions of the Southern Ocean with moderate (1-2 °C, 1 σ)
598 SST variability also recorded equally large differences in community growth rate, often at least
599 30% smaller than Eppley curve approximations and up to $\geq 80\%$ smaller than Eppley curve
600 approximations.

601

602 **5. Conclusions**

603 We utilized idealized SST simulations and SST data from ocean surface drifters to show that
604 synoptic SST variability on timescales of a few days to a few weeks decreases phytoplankton
605 community growth rates, while higher frequency variability has little impact. The time taken for
606 the community growth rate to reflect the new environment was dependent upon the rate and
607 magnitude of temperature change, the direction of change, and the shape of the thermal response
608 curve. The largest memory effects resulted from moderate changes in SST that occurred over 1-3
609 weeks. This impact of SST variability can cause a large offset between a phenotype-based
610 temperature-dependent community growth rate and an Eppley curve-based approximation and
611 suggests that phytoplankton communities sampled *in situ* may often not be adjusted to local
612 conditions. Given the highly variable nature of the ocean and importance of environmental
613 variability for phytoplankton physiology, it is critical to consider the appropriate reference frame
614 and the magnitude and duration of variability when studying phytoplankton dynamics. Here we
615 demonstrated that variability captured in the Lagrangian reference frame (by drifters) was, in
616 many instances, different from variability in the Eulerian frame and that this had significant
617 impacts for estimating phytoplankton growth rates. These findings have potentially far-reaching
618 implications for how temperature-dependent phytoplankton growth is represented in global
619 biogeochemical models.

620

621

622

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631 Data Centre at the Atlantic Oceanographic and Meteorological Laboratory
632 (<https://www.aoml.noaa.gov/phod/gdp/>) and satellite data are available from the GHRSSST Level

633 4 MUR Global Foundation Sea Surface Temperature Analysis
634 (<https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>).

635
 636 Figure 1. Lagrangian versus Eulerian reference frames. Lagrangian reference frames follow the
 637 water parcel itself through time. The Eulerian reference frame refers to a fixed point in space
 638 (e.g. buoys or mooring stations) where advection of water parcels floating past the fixed point
 639 generates temporal variability. Panels (a), (b), and (c) depict three different water masses (grey,
 640 blue, and green) as they each pass through the fixed Eulerian location (red dot) at times t_1 , t_2 , and
 641 t_3 . Panel (d) shows the temperature of each water mass through time (grey, blue, and green lines)
 642 as well as the temperature recorded at the Eulerian location (red line). Note in panel (d) that
 643 overall temperature variability in the Lagrangian reference frame (grey, blue and green lines) is
 644 much greater than that in the Eulerian reference frame (red dots) though this may not always be
 645 the case.

646
 647 Figure 2. The impact of SST variability on individual phenotype growth rate. (a) The
 648 temperature related growth response for a phenotype with a skewed shaped reaction norm. The
 649 values for the optimum growth temperature (T_{opt}) and the corresponding maximum growth rate
 650 (μ_{max}) are shown with dashed lines. (b) The 90-day SST profile of an example drifter trajectory
 651 (black) and the associated changes in phenotype growth rate (blue). The orange and red arrows in
 652 the top panel indicate the change in the phenotype growth rate associated with the corresponding
 653 changes in SST in the bottom panel.

654
 655 Figure 3. a) Map of all 90-day drifter trajectories ($n = 2190$) colored by SST. Two example
 656 trajectories are highlighted in purple and magenta. b) Reaction norms for each of the 319
 657 phenotypes in the ecosystem model. The grey lines represent all the phenotype reaction norms
 658 and the green lines are example phenotypes to highlight the reaction norm shape. c and d)
 659 Example trajectories and their resulting model outputs. The top panels show the SST (colors), the
 660 community growth rate estimated using the Eppley curve (dashed line), and the community
 661 growth rate from our phenotype-based model as calculated using Eq. 5 (solid line). The bottom
 662 panel shows the biomass through time of each phenotype (grey lines). The blue line follows the
 663 phenotype with the highest initial biomass, the red dashed line follows the phenotype that has the
 664 highest biomass at the end of the 90 days, and the green line follows the phenotype that has a T_{opt}
 665 equal to the mean SST of the trajectory.

667
 668 Figure 4. SST variability analysis. The frequency of ΔSST_{max} changes from the drifter segments
 669 over different window lengths are shown. Data are presented as total percent of data that fall
 670 within that window length such that each row sums to 100%. There is a general pattern of
 671 increasing magnitudes of ΔSST_{max} over longer window lengths.

672
 673 Figure 5. Simulated response of phytoplankton community with skewed shaped reaction norm to
 674 increasing ΔSST (see Supplemental Material for decreasing ΔSST conditions and broad reaction
 675 norm results). Panel (a) plots the decline in community growth rate in the phenotype model that
 676 results from the SST moving out of the thermal niche of the original population (see Methods

677 and Figure S16). Data that are greyed out represent Δ SST and window length combinations that
678 were not supported by the results from Figure 3. Panel (b) shows the percent difference between
679 the Eppley growth model approximation and the phenotype modeled community growth rates at
680 the point where SST stabilizes (see Figure S16 for example). Panel (c) plots the memory effect
681 length associated with SST changes in the idealized simulations. This represents the time it takes
682 for the community growth rate to be within 5% of the steady state growth rate at the final SST
683 from the first time-step that SST is constant (See Figure S16 for example).

684
685 Figure 6. Impact of SST variability on community growth rate. The average percent difference in
686 community growth rate between the phenotype model and the Eppley growth model from the 90-
687 day drifter segments are plotted against the standard deviation (1σ) of the drifter SST. Each
688 segment is colored by the mean SST. Results from the idealized trajectories are shown as black
689 diamonds with filled circles denoting increasing SST trajectories and open circles denoting
690 decreasing SSTs. Pink triangles represent the two example trajectories from Figure 3. Results
691 shown here are for skewed shaped reaction norms, see Figure S20 for results for the broad
692 shaped reaction norms.

693
694 Figure 7. The impact of acclimation on the number of generations for which the effect persists
695 (memory length). Acclimation rates that were slower than the rate of SST change resulted in
696 longer memory lengths than for simulations in which acclimation rate was equal to or faster than
697 the SST rate of change.

698 Figure 8. The impact of Lagrangian and Eulerian variability on community composition. Here
699 we plot the difference between the T_{opt} of the most abundant phenotype at the end of each 90-day
700 trajectory and the final SST for the drifter trajectory (x-axis) and the satellite data (y-axis). The
701 final SSTs for the drifter and satellite data are not statistically different (t-test, 95% CI).
702 Therefore, deviations from the 1:1 line demonstrate the impact of a Lagrangian versus Eulerian
703 reference frame on community composition.

704 Figure 9. Distribution of SST variability (a-c) and the deviation in community growth rate from
705 the Eppley growth model (d-f) over the Southern Ocean ($>30^{\circ}$ S). Only those drifters which
706 overlap in space and time with the satellite data are shown. For full results, see Figure S29. Three
707 key regions of high SST variability stand out: Malvinas-Brazil confluence zone, the Agulhas
708 Retroflection, and the Subtropical front. These regions have enhanced SST variability in all
709 datasets but higher variability in the Lagrangian trajectories. These high variability regions
710 correspond to large differences between the phenotype model growth rates and the Eppley
711 approximation of growth, a pattern consistent across all three sets of simulations.

712

- 713 Artana, C., Provost, C., Lellouche, J., Rio, M., Ferrari, R., & Sennéchaël, N. (2019). The
714 Malvinas Current at the Confluence With the Brazil Current: Inferences From 25 Years
715 of Mercator Ocean Reanalysis. *Journal of Geophysical Research: Oceans*, *124*(10),
716 7178–7200. <https://doi.org/10.1029/2019JC015289>
- 717 Arteaga, L. A., Boss, E., Behrenfeld, M. J., Westberry, T. K., & Sarmiento, J. L. (2020).
718 Seasonal modulation of phytoplankton biomass in the Southern Ocean. *Nature*
719 *Communications*, *11*(1), 5364. <https://doi.org/10.1038/s41467-020-19157-2>
- 720 Barton, A. D., Dutkiewicz, S., Flierl, G., Bragg, J., & Follows, M. J. (2010). Patterns of
721 Diversity in Marine Phytoplankton. *Science*, *327*(5972), 1509–1511.
722 <https://doi.org/10.1126/science.1184961>
- 723 Beal, L. M., Elipot, S., Houk, A., & Leber, G. M. (2015). Capturing the Transport Variability of
724 a Western Boundary Jet: Results from the Agulhas Current Time-Series Experiment
725 (ACT). *Journal of Physical Oceanography*, *45*(5), 1302–1324.
726 <https://doi.org/10.1175/JPO-D-14-0119.1>
- 727 Bernhardt, J. R., Sunday, J. M., Thompson, P. L., & O'Connor, M. I. (2018). Nonlinear
728 averaging of thermal experience predicts population growth rates in a thermally variable
729 environment. *Proceedings of the Royal Society B: Biological Sciences*, *285*(20181076),
730 10.
- 731 Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze,
732 C., Ilyina, T., Séférian, R., Tjiputra, J., & Vichi, M. (2013). Multiple stressors of ocean
733 ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences*, *10*(10),
734 6225–6245. <https://doi.org/10.5194/bg-10-6225-2013>

- 735 Boyd, P. W. (2019). Physiology and iron modulate diverse responses of diatoms to a warming
736 Southern Ocean. *Nature Climate Change*, 9(2), 148–152. [https://doi.org/10.1038/s41558-](https://doi.org/10.1038/s41558-018-0389-1)
737 018-0389-1
- 738 Boyd, P. W., Cornwall, C. E., Davison, A., Doney, S. C., Fourquez, M., Hurd, C. L., Lima, I. D.,
739 & McMinn, A. (2016). Biological responses to environmental heterogeneity under future
740 ocean conditions. *Global Change Biology*, 22(8), 2633–2650.
741 <https://doi.org/10.1111/gcb.13287>
- 742 Boyd, P. W., Rynearson, T. A., Armstrong, E. A., Fu, F., Hayashi, K., Hu, Z., Hutchins, D. A.,
743 Kudela, R. M., Litchman, E., Mulholland, M. R., Passow, U., Strzepek, R. F., Whittaker,
744 K. A., Yu, E., & Thomas, M. K. (2013). Marine Phytoplankton Temperature versus
745 Growth Responses from Polar to Tropical Waters – Outcome of a Scientific Community-
746 Wide Study. *PLoS ONE*, 8(5), e63091. <https://doi.org/10.1371/journal.pone.0063091>
- 747 Buitenhuis, E. T., Hashioka, T., & Quéré, C. L. (2013). Combined constraints on global ocean
748 primary production using observations and models. *Global Biogeochemical Cycles*,
749 27(3), 847–858. <https://doi.org/10.1002/gbc.20074>
- 750 Clayton, S., Dutkiewicz, S., Jahn, O., & Follows, M. J. (2013). Dispersal, eddies, and the
751 diversity of marine phytoplankton. *Limnology and Oceanography: Fluids and*
752 *Environments*, 3(1), 182–197. <https://doi.org/10.1215/21573689-2373515>
- 753 Clayton, S., Lin, Y.-C., Follows, M. J., & Worden, A. Z. (2017). Co-existence of distinct
754 *Ostreococcus* ecotypes at an oceanic front. *Limnology and Oceanography*, 62(1), 75–88.
755 <https://doi.org/10.1002/lno.10373>
- 756 Cochlan, W. (2008). *Nitrogen Uptake in the Southern Ocean* (pp. 569–596).

- 757 d'Ovidio, F., De Monte, S., Alvain, S., Dandonneau, Y., & Levy, M. (2010). Fluid dynamical
758 niches of phytoplankton types. *Proceedings of the National Academy of Sciences*,
759 *107*(43), 18366–18370. <https://doi.org/10.1073/pnas.1004620107>
- 760 Deser, C., Alexander, M. A., Xie, S.-P., & Phillips, A. S. (2010). Sea Surface Temperature
761 Variability: Patterns and Mechanisms. *Annual Review of Marine Science*, *2*(1), 115–143.
762 <https://doi.org/10.1146/annurev-marine-120408-151453>
- 763 Doblin, M. A., & van Sebille, E. (2016). Drift in ocean currents impacts intergenerational
764 microbial exposure to temperature. *Proceedings of the National Academy of Sciences*,
765 *113*(20), 5700–5705. <https://doi.org/10.1073/pnas.1521093113>
- 766 Doney, S. C. (1999). Major challenges confronting marine biogeochemical modeling. *Global*
767 *Biogeochemical Cycles*, *13*(3), 705–714. <https://doi.org/10.1029/1999GB900039>
- 768 Eppley, R. (1972). Temperature and phytoplankton growth in the sea. *Fishery Bulliten*, *70*(4),
769 1063–1085.
- 770 Falkowski, P. G., Fenchel, T., & Delong, E. F. (2008). The Microbial Engines That Drive Earth's
771 Biogeochemical Cycles. *Science*, *320*(5879), 1034–1039.
772 <https://doi.org/10.1126/science.1153213>
- 773 Follows, M. J., Dutkiewicz, S., Grant, S., & Chisholm, S. W. (2007). Emergent Biogeography of
774 Microbial Communities in a Model Ocean. *Science*, *315*(5820), 1843–1846.
775 <https://doi.org/10.1126/science.1138544>
- 776 Fu, W., Randerson, J. T., & Moore, J. K. (2016). Climate change impacts on net primary
777 production (NPP) and export production(EP) regulated by increasing stratification and
778 phytoplankton communitystructure in the CMIP5 models. *Biogeosciences*, *13*(18), 5151–
779 5170. <https://doi.org/10.5194/bg-13-5151-2016>

- 780 Graham, R. M., & Boer, A. M. D. (2013). The Dynamical Subtropical Front. *Journal of*
781 *Geophysical Research: Oceans*, *118*(10), 5676–5685. <https://doi.org/10.1002/jgrc.20408>
- 782 Hellweger, F. L., van Sebille, E., Calfee, B. C., Chandler, J. W., Zinser, E. R., Swan, B. K., &
783 Fredrick, N. D. (2016). The Role of Ocean Currents in the Temperature Selection of
784 Plankton: Insights from an Individual-Based Model. *PLOS ONE*, *11*(12), e0167010.
785 <https://doi.org/10.1371/journal.pone.0167010>
- 786 Hutchinson, G. E. (1961). The Paradox of the Plankton. *The American Naturalist*, *95*(882), 137–
787 145. <https://doi.org/10.1086/282171>
- 788 Kling, J. D., Lee, M. D., Fu, F., Phan, M. D., Wang, X., Qu, P., & Hutchins, D. A. (2019).
789 Transient exposure to novel high temperatures reshapes coastal phytoplankton
790 communities. *The ISME Journal*. <https://doi.org/10.1038/s41396-019-0525-6>
- 791 Kremer, C. T., Fey, S. B., Arellano, A. A., & Vasseur, D. A. (2018). Gradual plasticity alters
792 population dynamics in variable environments: Thermal acclimation in the green alga
793 *Chlamydomonas reinhardtii*. *Proceedings of the Royal Society B: Biological Sciences*,
794 *285*(1870), 20171942. <https://doi.org/10.1098/rspb.2017.1942>
- 795 Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E.,
796 Doney, S. C., Dunne, J., Hashioka, T., Hauck, J., Hirata, T., John, J., Le Quéré, C., Lima,
797 I. D., Nakano, H., Seferian, R., Totterdell, I., Vichi, M., & Völker, C. (2015). Drivers and
798 uncertainties of future global marine primary production in marine ecosystem models.
799 *Biogeosciences*, *12*(23), 6955–6984. <https://doi.org/10.5194/bg-12-6955-2015>
- 800 Lévy, M., Jahn, O., Dutkiewicz, S., & Follows, M. J. (2014). Phytoplankton diversity and
801 community structure affected by oceanic dispersal and mesoscale turbulence. *Limnology*

- 802 *and Oceanography: Fluids and Environments*, 4(1), 67–84.
803 <https://doi.org/10.1215/21573689-2768549>
- 804 Lomas, M. W., Steinberg, D. K., Dickey, T., Carlson, C. A., Nelson, N. B., Condon, R. H., &
805 Bates, N. R. (2010). Increased ocean carbon export in the Sargasso Sea linked to climate
806 variability is countered by its enhanced mesopelagic attenuation. *Biogeosciences*, 7(1),
807 57–70. <https://doi.org/10.5194/bg-7-57-2010>
- 808 Mahadevan, A. (2016). The Impact of Submesoscale Physics on Primary Productivity of
809 Plankton. *Annual Review of Marine Science*, 8(1), 161–184.
810 <https://doi.org/10.1146/annurev-marine-010814-015912>
- 811 Maheshwari, M., Singh, R. K., Oza, S. R., & Kumar, R. (2013). An Investigation of the Southern
812 Ocean Surface Temperature Variability Using Long-Term Optimum Interpolation SST
813 Data. *ISRN Oceanography*, 2013, 1–9. <https://doi.org/10.5402/2013/392632>
- 814 Moisan, J. R., Moisan, T. A., & Abbott, M. R. (2002). Modelling the effect of temperature on the
815 maximum growth rates of phytoplankton populations. *Ecological Modelling*, 153(3),
816 197–215. [https://doi.org/10.1016/S0304-3800\(02\)00008-X](https://doi.org/10.1016/S0304-3800(02)00008-X)
- 817 Qu, P., Fu, F.-X., Kling, J. D., Huh, M., Wang, X., & Hutchins, D. A. (2019). Distinct Responses
818 of the Nitrogen-Fixing Marine Cyanobacterium *Trichodesmium* to a Thermally Variable
819 Environment as a Function of Phosphorus Availability. *Frontiers in Microbiology*, 10,
820 1282. <https://doi.org/10.3389/fmicb.2019.01282>
- 821 Quéré, C. L., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre,
822 H., Cunha, L. C. D., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L.,
823 Manizza, M., Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, A. J., & Wolf-
824 Gladrow, D. (2005). Ecosystem dynamics based on plankton functional types for global

- 825 ocean biogeochemistry models. *Global Change Biology*, 11(11), 2016–2040.
826 <https://doi.org/10.1111/j.1365-2486.2005.1004.x>
- 827 Reynolds, R. W., & Smith, T. M. (1994). Improved Global Sea Surface Temperature Analyses
828 Using Optimum Interpolation. *Journal of Climate*, 7(6), 929–948.
829 [https://doi.org/10.1175/1520-0442\(1994\)007<0929:IGSSTA>2.0.CO;2](https://doi.org/10.1175/1520-0442(1994)007<0929:IGSSTA>2.0.CO;2)
- 830 Rohr, T., Harrison, C., Long, M. C., Gaube, P., & Doney, S. C. (2020a). Eddy-Modified Iron,
831 Light, and Phytoplankton Cell Division Rates in the Simulated Southern Ocean. *Global*
832 *Biogeochemical Cycles*, 34(6), e2019GB006380. <https://doi.org/10.1029/2019GB006380>
- 833 Rohr, T., Harrison, C., Long, M. C., Gaube, P., & Doney, S. C. (2020b). The Simulated
834 Biological Response to Southern Ocean Eddies via Biological Rate Modification and
835 Physical Transport. *Global Biogeochemical Cycles*, 34(6), e2019GB006385.
836 <https://doi.org/10.1029/2019GB006385>
- 837 Schaum, C.-E., Buckling, A., Smirnov, N., Studholme, D. J., & Yvon-Durocher, G. (2018).
838 Environmental fluctuations accelerate molecular evolution of thermal tolerance in a
839 marine diatom. *Nature Communications*, 9(1), 1719. [https://doi.org/10.1038/s41467-018-](https://doi.org/10.1038/s41467-018-03906-5)
840 [03906-5](https://doi.org/10.1038/s41467-018-03906-5)
- 841 Sherman, E., Moore, J. K., Primeau, F., & Tanouye, D. (2016). Temperature influence on
842 phytoplankton community growth rates. *Global Biogeochemical Cycles*, 30(4), 550–559.
843 <https://doi.org/10.1002/2015GB005272>
- 844 Soccodato, A., d'Ovidio, F., Lévy, M., Jahn, O., Follows, M. J., & De Monte, S. (2016).
845 Estimating planktonic diversity through spatial dominance patterns in a model ocean.
846 *Marine Genomics*, 29, 9–17. <https://doi.org/10.1016/j.margen.2016.04.015>

- 847 Thomas, M. K., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2012). A Global Pattern of
848 Thermal Adaptation in Marine Phytoplankton. *Science*, 338(6110), 1085–1088.
849 <https://doi.org/10.1126/science.1224836>
- 850
851 Wang, X., Fu, F., Qu, P., Kling, J. D., Jiang, H., Gao, Y., & Hutchins, D. A. (2019). How will
852 the key marine calcifier <i>Emiliana huxleyi</i> respond to a warmer and
853 more thermally variable ocean? *Biogeosciences*, 16(22), 4393–4409.
854 <https://doi.org/10.5194/bg-16-4393-2019>
- 855 Webb, E. A., Ehrenreich, I. M., Brown, S. L., Valois, F. W., & Waterbury, J. B. (2009).
856 Phenotypic and genotypic characterization of multiple strains of the diazotrophic
857 cyanobacterium, *Crocospaera watsonii*, isolated from the open ocean. *Environmental*
858 *Microbiology*, 11(2), 338–348. <https://doi.org/10.1111/j.1462-2920.2008.01771.x>
- 859 Wenegrat, J. O., Thomas, L. N., Sundermeyer, M. A., Taylor, J. R., D’Asaro, E. A., Klymak, J.
860 M., Shearman, R. K., & Lee, C. M. (2020). Enhanced mixing across the gyre boundary at
861 the Gulf Stream front. *Proceedings of the National Academy of Sciences*.
862 <https://doi.org/10.1073/pnas.2005558117>
- 863