

1 **Title: Drift in ocean currents impacts intergenerational microbial exposure to**
2 **temperature**

3
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16
17 **Abstract**

18
19 Microbes are the foundation of marine ecosystems (Falkowski *et al.* 2008 The microbial
20 engines that drive Earth's biogeochemical cycles. *Science* 320:1034-1039). Until now, the
21 analytical framework for understanding the implications of ocean warming on microbes has
22 not considered thermal exposure during transport in dynamic seascapes, implying that our
23 current view of change for these critical organisms may be inaccurate. Here we show that
24 upper ocean microbes experience along-trajectory temperature variability up to 10°C greater
25 than seasonal fluctuations estimated in a static frame, and that this variability depends
26 strongly on location. These findings demonstrate that drift in ocean currents can increase the
27 thermal exposure of microbes and suggests that microbial populations with broad thermal
28 tolerance will survive transport to distant regions of the ocean and invade new habitats. Our
29 findings also suggest that advection has the capacity to influence microbial community
30 assemblies such that regions with strong currents and large thermal fluctuations select for
31 communities with greatest plasticity and evolvability, and communities with narrow thermal
32 performance are found where ocean currents are weak or along-trajectory temperature
33 variation is low. Given that fluctuating environments select for individual plasticity in
34 microbial lineages and that physiological plasticity of ancestors can predict the magnitude of
35 evolutionary responses of subsequent generations to environmental change (Schaum and

36 Collins 2014 Plasticity predicts evolution in a marine alga. Proc. R. Soc. B 281: 20141486),
37 our findings suggest that microbial populations in the sub-Antarctic (~40°S), North Pacific
38 and North Atlantic, will have most capacity to adapt to contemporary ocean warming.

39

40 **Significance Statement**

41 Our current understanding of how marine biota are adapted to magnitudes, trends and
42 temporal patterns of variability in sea surface temperature has arisen from examining long-
43 term records at key ocean locations. However, floating plankton have a different perception
44 of their habitat because they drift in ocean currents. Here we show that upper ocean microbes
45 can be advected up to 3,500 km in latitude in 500 days, and that their operational
46 temperatures exceed the *in situ* Eulerian temperature range by up to 10 °C, even in locations
47 with strong seasonality. This result revises the present view of thermal exposure in the upper
48 ocean, and provides a new framework for investigating climate change impacts on planktonic
49 organisms.

50 \body

51 **Introduction**

52

53 Photosynthetic marine microbes, otherwise known as phytoplankton, underpin all of the
54 production-based ocean ecosystem services, and impact on human health and wellbeing
55 through their regulation of climate (1), formation of harmful algal blooms (2) and support of
56 biodiversity at multiple dimensions and trophic levels (3). Heterotrophic microbes, including
57 bacteria, archaea and eukaryotes, are also critical for ocean functioning, being the dominant
58 remineralisers of organic matter and key players in the Earth's biogeochemical cycles (1,4).
59 Depending on the CO₂ emissions scenario, the surface ocean is predicted to warm 2–4°C on
60 average by 2100 (5). Because microbes demonstrate a steep decline in growth at temperatures
61 exceeding their optimum (6,7,8,9,10), such warming has the potential to affect the
62 distribution and diversity of marine microbes through exceedance of thermal limits and
63 changes in fitness, with cascading impacts to ecosystem services (11,12).

64

65 However, by virtue of their large population sizes, relatively rapid reproduction, and high
66 diversity, microbes have considerable potential to mitigate negative consequences of past and
67 present ocean change through phenotypic plasticity (acclimation) and adaptive evolution
68 (genetic change). Until now, our understanding of how microbial communities will be

69 reorganized under contemporary ocean change has developed from empirical studies
70 involving examination of the current geographic distribution of microbial taxa and their
71 relationships with temperature and other environmental parameters (8,10,13), laboratory
72 investigations that measure performance of microbial ecotypes (thought to be representative
73 of populations) under different conditions (6,7,9,14), and modelling studies which use
74 microbial traits describing resource (e.g., nutrients, light) utilization to estimate fitness and
75 predict future distributions of microbes under projected ocean change (15,16,17). The
76 limitation of these studies is that microbial traits are assumed to be constant during model
77 runs, so the microbes themselves are not responding to changes in their environment (18).
78 However, there is increasing evidence that photosynthetic microbes are altering their realized
79 niches in response to contemporary changes in ocean temperature and irradiance (19), and
80 that the geographic origin of microbial ecotypes influences their plasticity (capacity for
81 physiological acclimation) (9,20), as well as adaptation (21) at the population level
82 (potentially via increased rate of mitotic mutations) (22), with some ecotypes tolerant of a
83 broad range of temperature, and others more thermally specialized (7). Microbes generally
84 experience the ocean as a viscous medium (23), and their motion is therefore predominantly
85 determined by drift with ocean currents (noting that some taxa are motile or regulate their
86 buoyancy) (24). As a result, their habitat temperatures are highly dynamic and cannot be
87 described assuming a fixed location. This means there currently is no clear global estimate of
88 the thermal history of marine microbes, making it difficult to understand their realised
89 thermal niche and relate this to their performance under controlled (typically stable)
90 experimental conditions, let alone predict the impact of a 2–4°C projected rise in mean ocean
91 temperature.

92

93 Thus, in order to advance our understanding of marine microbial acclimation and adaptation,
94 and to determine which microbes can keep pace with rates of contemporary ocean change, a
95 spatially explicit understanding of temperature exposure from the perspective of the moving
96 organism is critical (25). This requires examining the temperature experienced by marine
97 microbes in a Lagrangian (drift) framework.

98

99 **Results**

100

101 We used a global three-dimensional circulation model OFES (Ocean model for the Earth
102 Simulator) with a $1/10^\circ$ horizontal resolution to characterise the inter-generational
103 temperature exposure of upper ocean microbes. This model has previously been used to study
104 neutral evolution of bacteria (26) and drift of foraminifera (27). Virtual microbes were
105 released across the global ocean on a $2^\circ \times 2^\circ$ grid at a depth of 10 m every month for the years
106 1981–2007, for a total of 2.9 million particles (360 particles per grid cell). Their position in
107 the ocean was tracked (backwards in time) for 500 days prior to their arrival at their
108 destination grid, and their thermal histories were averaged for analysis, using the well-
109 established and open-source Connectivity Modeling System (28). This software has been
110 extensively validated (e.g., in ‘physical oceanography mode’ the amount of water carried by
111 particles through the Indonesian Throughflow very closely resembles the Eulerian flux
112 through the straits; 29) and is widely used in both physical oceanography and marine ecology
113 and biology studies (30,31,32). We compared the magnitude of virtual particle velocities,
114 based on the trajectories at each grid cell, with observed drifters in the ocean (33). Comparing
115 our trajectories and that of actual drifters, we find good agreement, both in the magnitude of
116 speeds, as well as their locations (i.e., low velocities in the middle of the gyres as well as high
117 velocities in the western boundary currents; figure S1). A random selection of trajectories is
118 illustrated in figure S2.

119

120 Our rationale for backtracking to 500 days is that the adaptation capacity of microbes to
121 future ocean conditions has been examined *in vitro* for up to 500 generations (21) and the
122 average reproductive rate (i.e., timescale of one generation) of a unicellular alga is in the
123 order of one vegetative cell division per day at 20°C (34). For comparison, we also
124 undertook the analysis for 50, 150 and 250 days. In each analysis, the thermal history of a
125 microbial population is therefore between 50 and 500 days, with only one cell out of each
126 generation needing to survive and reproduce. There are two implications of advection: (i)
127 that during its path, a microbial genotype which undergoes a temperature shift beyond its
128 upper or lower thermal limit may be adversely impacted due to a shortfall in physiological
129 plasticity or inability to produce phenotypes across multiple environments (i.e., is a thermal
130 specialist); and (ii) that a microbe retrieved from the ocean is adapted not for the local
131 environmental circumstance, but rather to the circumstances experienced during its upstream
132 trajectory (while noting that microbes in some regions of the global ocean undergo mainly
133 zonal rather than meridional transport, and therefore experience more limited thermal

134 fluctuations. Here, we will show what impact this may have on the thermal life strategy of
135 ocean microbes.

136

137 Our results demonstrate that virtual microbes are advected up to 3,500 km in latitude in 500
138 days, with particles that arrive in the extensions of the western boundary currents in the
139 subtropics having moved the greatest distances (figure 1a; see figure S3 for other measures of
140 drift distance). As expected, the longer the time frame, the greater the range of temperature
141 experienced (figure S4). However, our analysis also reveals that in some regions (e.g., eastern
142 Pacific, eastern Indian, Benguela and Canary Upwellings) the thermal exposure is higher in a
143 Lagrangian compared to Eulerian frame, at all time scales analysed (figure S4). This
144 advection means that the distribution of different microbial genotypes (and phenotypes within
145 species) spans a large range, and that the temperature experienced by drifting microbes can
146 be significantly different from simple location-specific predictions, with microbes arriving in
147 the extensions of the western boundary currents exposed to an average temperature up to 6°C
148 warmer than the local *in situ* temperature (figure 1b). In contrast, microbes on the northern
149 flank of the Antarctic Circumpolar Current have an average temperature exposure of up to
150 6°C colder than the local *in situ* temperature. Both these offsets can be explained by
151 advection in ocean currents. Western boundary currents transport tropical microbes poleward,
152 so that their mean temperature exposure is higher than the local latitudinally predicted *in situ*
153 temperature. In contrast, the Ekman transport in the Antarctic Circumpolar Current pushes
154 polar microbes equatorward and consequently their mean temperature exposure is lower than
155 the local *in situ* temperature.

156

157 Given that the rates and modes of acclimation or adaptation for biota are determined not by
158 average environmental conditions, but by the extent of environmental variability (35,36)
159 (along with longevity, life-history and other traits), our Lagrangian analysis also reveals that
160 the temperature fluctuation for microbes along a 500 day trajectory (figure 2b) can be
161 significantly different from the *in situ* Eulerian temperature range (i.e., compared to if they
162 didn't move; figure 2a), suggesting that the realised thermal niche (as well as geographic
163 range) of microbial ecotypes may be broader than currently estimated. Figure 2c shows that
164 the temperature fluctuations experienced by 500-day advected microbes significantly exceed
165 the annual range of temperature almost everywhere, even in locations with strong seasonality
166 (e.g., North Atlantic Ocean). Thermal variability is up to 10°C higher for microbes in a ~10°

167 latitudinal band from 40°S to 50°S in the Southern Ocean and the North Atlantic, and up to
168 4°C in the tropics and on the eastern sides of the subtropical gyres. Analyses over shorter
169 time frames reveal greater patchiness, with smaller differences in thermal exposure between
170 fixed and moving particles (figure S4). Nonetheless, the inter-generational exposure of
171 microbes over 500 days indicates that thermal histories of microbes exceed seasonal ranges
172 by 10°C in some locations, a result that revises our present view of thermal exposure in the
173 surface ocean, and suggests that for the majority of ocean locations, projected changes in
174 thermal regimes are within the range of temperatures already experienced by drifting
175 microbes. We therefore anticipate this result will shift current thinking about risks of ocean
176 warming and that consideration of drift trajectories will advance understanding of direct
177 temperature effects on microbes and other plankton. Because all enzymatic rates are affected
178 by temperature, thermal tolerance of advected organisms is not lineage-specific, and likely
179 involves genome-wide changes, with growth in a new thermal regime requiring maintenance
180 of critical cellular processes. Furthermore, for microbes, temperature adaptation is distinct
181 from adaptation to other environmental variables, whereby a horizontally transferred gene or
182 operon could allow acquisition of new resources (10).

183

184 Combining the distance travelled with the fluctuation in temperature along microbial
185 trajectories, we then build a global view of microbial habitats in the surface ocean. Figure 3
186 shows that microbes arriving in the low latitudes are advected long distances (> 1,240 km of
187 latitude in 500 days, the global median) but experience relatively low thermal variation (<
188 6.5°C, the global median of temperature range). Similarly, microbes south of the Antarctic
189 Circumpolar Current in the Southern Ocean experience low thermal variation but travel
190 relatively short distances, as they mostly get recirculated in the Ross and Weddell gyres.
191 However, in most of the mid latitudes, temperature variability is relatively high (> 6.5°C)
192 with microbes having the potential to travel more than 1,240 km in 500 days. Evidently,
193 microbes experience both heating and cooling along their trajectories (figure S5), at variable
194 rates depending on their location (figure S6). Across the 2.9 million trajectories in our study,
195 the most rapid heating and cooling (at more than 4°C per day, sustained over a 5 day period)
196 was for microbes arriving in the North Atlantic (figure S7), with a strong spatial agreement
197 between regions of strong air-sea heat fluxes (37) and rapid cooling and warming. To our
198 knowledge, there have been no experiments to date that examine fitness of microbes under
199 such rapid, but transient, temperature changes.

200

201 **Discussion**

202

203 The thermal trajectories of microbes do more than contextualise the projected 2–4°C rise in
204 mean ocean temperature during the next century. Our results reshape the present view of
205 temperature experienced by upper ocean microbes, indicating that realized thermal niches are
206 wider than previously thought. Furthermore, the along-trajectory temperature exposure of
207 microbes has important implications for microbial life strategies and the assembly of
208 microbial communities. Drifting communities experiencing large variations in temperature
209 are under selection to be plastic (genotypes produce variable phenotypes in response to
210 environmental conditions) or generalists (entrained genotypes produce invariable phenotypes
211 over multiple environments), resulting in broad thermal tolerance compared to communities
212 from stable environments that are more likely to be thermal specialists (36,38). Based on
213 empirical evidence from laboratory experiments, plasticity in an ancestral population is a
214 good predictor of eventual evolutionary responses in subsequent generations, suggesting that
215 populations in fluctuating environments are also more adaptable (35).

216

217 While there have been previous studies of microbes using Lagrangian floats and profilers (39,
218 40, 41), this is the first to provide a spatially explicit understanding of temperature exposure
219 of pelagic microbes in the context of plastic and evolutionary responses to contemporary
220 ocean change. Our analysis shows that the proportion of the global ocean showing greater
221 thermal exposure of drifting versus stationary microbes increases with time (figure S4). At
222 500 days, there are only a few locations (e.g., Southern Ocean centered around 60°S,
223 northwestern Pacific and Atlantic) that show more limited thermal exposure of microbes in a
224 Lagrangian compared to Eulerian frame (figure 2). It also reveals that thermal trajectories are
225 complex (figure S6)—they don't monotonically increase or decrease, rather they fluctuate,
226 some with high variability and others with low variability (figure 3). Thus, as microbes are
227 transported through this variable seascape, they are effectively under selection because
228 populations must be able to deal with temperature fluctuation—if it exceeds their capacity,
229 they die. We make no assumptions about other losses (e.g., grazing) or whether cooling or
230 warming thermal histories (represented as skewness in figure S5) results in better outcomes
231 with respect to microbial fitness, only that if a population has dealt with temperature
232 variability in the past, then it has a greater capacity to deal with future temperature change.

233 Tolerance of temperature variability in microbial populations arises through constituent
234 genotypes being plastic or because entrained microbial genotypes produce phenotypes across
235 multiple environments (i.e., are generalists). Both mechanisms could operate to shape
236 microbial communities and would apply to phototrophs, grazers and other plankton drifting
237 in the surface ocean, provided they remain suspended in the upper mixed layer.

238

239 Considering that numerical models are resolving planktonic community composition by the
240 representation of microbial traits or ecotypes (42), figure 3 therefore suggests the global
241 ocean can be partitioned into thermal generalist (plastic with relatively high evolutionary
242 potential) versus thermal specialist selection regimes (high vs low temperature fluctuations,
243 respectively), and hence provide a guide for where microbial communities will be most or
244 least stable in the future. Given the distinct thermal optima of polar versus tropical microbes
245 (7), the global ocean could be further partitioned on the basis of variation around different
246 mean temperatures, yielding low/high temperature specialists/generalists (table 1). Studies on
247 macroscopic marine biota indicate that organisms with broad temperature tolerance are more
248 likely to establish in new habitats (43), suggesting that temperature generalists may become
249 more prevalent in regions influenced by strong ocean currents. A good example of this is in
250 western boundary currents, which are intensifying and increasing their polewards extension
251 with global warming (44). A corollary of this is that thermal specialists with narrower
252 thermal histories are more vulnerable to temperature change.

253

254 Previous studies have compared the thermal responses of microbial ecotypes according to the
255 average temperature of their isolation location (6,7,14) and concluded that some microbes are
256 at greater risk of reduced fitness under future ocean warming because their thermal optima
257 are closer to their habitat temperature. This is because thermal response curves are
258 asymmetric, with a sharper decline in fitness at supraoptimal temperature compared to
259 suboptimal temperature (6,7). However, this study indicates that microbes may experience
260 large thermal fluctuations as they are being advected in the ocean before they reach their
261 potential isolation location, suggesting that estimates of microbial fitness in a future ocean
262 need to consider not only the direction, asymmetry and magnitude of temperature variation
263 from the thermal optimum, but also the time scale of temperature excursions. Given that *in-*
264 *vitro* evolution experiments indicate more plastic individuals evolve more (35), our analysis
265 provides a framework to test whether natural communities of microbes in the mid latitudes
266 (figure 3) have greater plasticity and evolutionary potential versus communities from the low

267 and high latitudes. Studies on the mechanisms promoting diversity of microbes in the ocean
268 (45,46) show some consistency with our analysis, supporting the notion that to understand the
269 assembly of communities at the local scale, it is not enough to understand local resource
270 availability—transport of populations must be accounted for. Furthermore, this Lagrangian
271 perspective of planktonic thermal exposure suggests that ocean warming not only has a direct
272 impact on microbes by influencing metabolism and growth, but also through changes in
273 ocean circulation which could lead to new transport corridors and the potential for novel
274 thermal trajectories.

275

276 **Materials and Methods**

277 The OFES model (47) is an eddy-resolving model based on the MOM3 ocean code and
278 forced with NCEP winds. It has a $1/10^\circ$ horizontal resolution and 54 vertical levels and spans
279 the global ocean from 75°S to 75°N , and is available on three-day resolution from 1980 to
280 2010. Virtual microbes were released at 10 m depth every month for the years 1981–2007 on
281 a $2^\circ \times 2^\circ$ regular grid, yielding a total of 2.9 million particles. These particles were then
282 tracked backwards in time using the Connectivity Modelling System v1.1 (28). The
283 Connectivity Modelling System has been extensively tested and widely applied in
284 oceanographic and biological studies (30,31). In particular, its trajectories have been
285 explicitly validated in the tropical Pacific (29). The virtual microbes were advected using
286 only the horizontal velocity fields, and thus did not change depth over the integration. Both
287 the geographical and local sea surface temperature information was stored on daily temporal
288 resolution. Maps were produced using the average of the 360 particles released at each grid
289 location.

290

291 The temperature variation along trajectories was described by computing the average, range,
292 variability and skewness of local sea surface temperature experienced along their trajectories
293 by microbes arriving in each grid cell. These along-trajectory temperatures (Lagrangian
294 temperatures) could then be compared against the average, range and variability of the
295 temperature within the grid cell (Eulerian temperatures). Distance travelled was also
296 calculated by computing the path length over the daily locations from the start and end
297 location of the trajectory.

298

299 To visualise a subset of relevant thermal trajectories (figure S6), we used the isolation
300 locations of strains in a global compilation of thermal performance curves as our destination

301 points (n = 85) (6). Average along-trajectory temperature was plotted over time to illustrate
302 thermal trajectories of virtual microbes arriving to grid cells.

303

304 Examination of the range of temperature variation (i.e. difference between minimum and
305 maximum temperature along each trajectory) and distance travelled allowed us to partition
306 the global dataset into grids containing microbes that had experienced relatively high/low
307 temperature fluctuation along long/short transport distances. Our temperature and distance
308 thresholds were chosen using the median values of thermal variation and distance travelled.
309 This yielded a relatively even number of grid cells split across all categories, but nevertheless
310 highlights that in absolute terms, microbes experience a large gradient in thermal variation
311 when they are transported variable distances in ocean currents.

312

313

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323 Infrastructure (NCI); *url to come*.

324

325 *The authors declare no conflict of interest.*

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328 **References**

- 329 1. Falkowski P, Fenchel T, De Long E (2008) The microbial engines that drive Earth's
330 biogeochemical cycles. *Science* 320:1034-1039. doi: 10.1126/science.1153213.
- 331 2. Anderson DA, Glibert PM, Burkholder JM (2002) Harmful algal blooms and eutrophication:
332 Nutrient sources, composition, and consequences. *Estuaries* 25: 704–726.
- 333 3. Chassot E, Bonhommeau S, Dulvy NK, Mélin F, Watson R, Gascuel D, Le Pape O (2010) Global
334 marine primary production constrains fisheries catches. *Ecology Letters* 13: 495–505.
- 335 4. Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The Ecological Role of
336 Water-Column Microbes in the sea. *Marine Ecology Progress Series* Vol. 10: 257-263.
- 337 5. IPCC (2013) *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group
338 I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker,
339 TF, D Qin, GK Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex and PM Midgley

- (eds.]). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324.
6. Thomas MK, Kremer CT, Klausmeier CA and Litchman E (2012) A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085-8. doi: 10.1126/science.1224836.
 7. Boyd PW, Rynearson TA, Armstrong EA, Fu F, Hayashi K (2013) Marine phytoplankton temperature versus growth responses from polar to tropical waters – Outcome of a Scientific Community-Wide Study. *PLoS ONE* 8(5): e63091. doi:10.1371/journal.pone.0063091.
 8. Flombaum P, Gallegos JL, Gordillo RA, Rincón J, Zabala LL, Jiao N, Karl DM, Li WKW, Lomas MW, Veneziano D, Vera CS, Vrugt JA, Martiny AC (2013) Present and future global distributions of the marine Cyanobacteria *Prochlorococcus* and *Synechococcus*. *PNAS* 110: 9824–9829.
 9. Pittera J, Humily F, Thorel M, Grulois D, Garczarek L, Six C (2014) Connecting thermal physiology and latitudinal niche partitioning in marine *Synechococcus*. *The ISME Journal* 8: 1221–1236.
 10. Yung C, Vereen MK, Herbert A, Davis KM, Yang J, Kantorowska A, Ward CS, Wernegreen JJ, Johnson ZI, Hunt DE (2015) Thermally adaptive tradeoffs in closely related marine bacterial strains. *Environmental Microbiology* 17: 2421–2429.
 11. Costanza R, dArge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, Oneill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
 12. Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. *Global Environmental Change* 26: 152–158.
 13. Irwin AJ, Nelles AM, Finkel ZV (2012) Phytoplankton niches estimated from field data. *Limnology and Oceanography* 57:787–797.
 14. Mackey KRM, Paytan A, Caldeira K, Grossman AR, Moran D, McIlvin M, and Saito MA (2013) Effect of temperature on photosynthesis and growth in marine *Synechococcus* spp. *Plant Physiology* 163: 815–829.
 15. Steinacher M, Joos F, Frölicher TL, Bopp L, Cadule P, Cocco V, Doney SC, Gehlen M, Lindsay K, Moore JK, Schneider V, Segschneider J (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7: 979–1005.
 16. Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, Heinze C, Ilyina T, Séférian R, Tjiputra J, Vichi M (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10: 6225–6245.
 17. Dutkiewicz S, Scott JR, Follows MJ (2013) Winners and losers: Ecological and biogeochemical changes in a warming ocean. *Global Biogeochemical Cycles* 27: 463 - 477, doi:10.1002/gbc.20042.
 18. Woods JD (2005) The Lagrangian Ensemble metamodel for simulating plankton ecosystems. *Progress in Oceanography* 67: 84-159.
 19. Irwin AJ, Finkel ZV, Müller-Karger FE, Troccoli Ghinaglia L (2015) Phytoplankton adapt to changing ocean environments. *Proceedings National Academy of Science* 112: 5762–5766.
 20. Schaum E, Rost B, Miller AJ and Collins S (2013) Variation in plastic responses of a globally distributed picoplankton species to ocean acidification. *Nature Climate Change* doi: 10.1038/NCLIMATE1774.

- 385 21. Schlüter L, Lohbeck KT, Gutowska MA, Gröer JP, Riebesell U, Reusch TBH (2014) Adaptation
386 of a globally important coccolithophore to ocean warming and acidification. *Nature Climate*
387 *Change* doi:10.1038/NCLIMATE2379.
- 388 22. Plough HH, Ives PT (1934) Induction of mutations by high temperature in *Drosophila*.
389 *Genetics* 20: 42-69.
- 390 23. Purcell EM (1977) Life at low Reynolds number. *American Journal of Physics* 45:3-11.
- 391 24. Raven JA, Doblin MA (2014) Active water transport in unicellular algae: where, why and how.
392 *Journal of Experimental Botany* 65: 6279–6292..
- 393 25. Helmuth, B, Broitman B, Yamane L, Gilman SE, Mach K, Mislán KAS, Denny MW (2010)
394 Organismal climatology: analyzing variability at scales relevant to physiological stress.
395 *Journal of Experimental Biology* 213: 995-1003.
- 396 26. Hellweger FL, van Sebille E, Fredrick ND (2014) Biogeographic patterns in ocean microbes
397 emerge in a neutral agent-based model. *Science* 345: 1346-1349.
- 398 27. Van Sebille E, Scussolini P, Durgadoo JV, Peeters FJC, Biastoch A, Weijer W, Turney C, Paris
399 CB, and Zahn R (2015) Ocean currents generate large footprints in marine palaeoclimate
400 proxies. *Nature Communications* 6: 6521. doi: 10.1038/ncomms7521.
- 401 28. Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity Modeling System: A
402 probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the
403 ocean. *Environ Modell Software* 42: 47-54, doi:10.1016/j.envsoft.2012.12.006.
- 404 29. Van Sebille E, Sprintall J, Schwarzkopf FU, Sen Gupta A, Santoso A, England MH, Biastoch A,
405 Böning CW (2014) Pacific-to-Indian Ocean connectivity: Tasman leakage, Indonesian
406 Throughflow, and the role of ENSO, *Journal of Geophysical Research: Oceans* 119: 1365-
407 1382.
- 408 30. Kough AS, Paris CB, Butler MJ IV (2013) Larval Connectivity and the International
409 Management of Fisheries. *PLoS ONE* 8(6): e64970. doi:10.1371/journal.pone.0064970.
- 410 31. Snyder RE, Paris CB, Vaz AC (2014) How Much Do Marine Connectivity Fluctuations
411 Matter? *The American Naturalist* 184: 523–530.
- 412 32. Sala I, Harrison CS, Caldeira RMA (2016) The role of the Azores Archipelago in capturing and
413 retaining incoming particles. *Journal of Marine Systems* 154: 146-156.
- 414 33. Lumpkin R, Johnson GC (2013) Global Ocean Surface Velocities from Drifters: Mean,
415 Variance, ENSO Response, and Seasonal Cycle. *Journal Geophysical Research-Oceans* 118:
416 2992-3006, doi:10.1002/jgrc.20210..
- 417 34. Eppley RW (1972) Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70:
418 1063-1085.
- 419 35. Schaum CE, Collins S (2014) Plasticity predicts evolution in a marine alga. *Proc. R. Soc. B* 281:
420 20141486. <http://dx.doi.org/10.1098/rspb.2014.1486>.
- 421 36. Gilchrist GW (1995) Specialists and generalists in changing environments. I. Fitness
422 landscapes of thermal sensitivity. *The American Naturalist* 146: 252-270.
- 423 37. Yu L, Weller RA (2007) Objectively analyzed air–sea heat fluxes for the global ice-free oceans
424 (1981–2005). *Bull. Amer. Meteor. Soc.* 88: 527-539. doi: [http://dx.doi.org/10.1175/BAMS-](http://dx.doi.org/10.1175/BAMS-88-4-527)
425 88-4-527.
- 426 38. Reboud X, Bell G (1997) Experimental evolution in *Chlamydomonas*. III. Evolution of specialist
427 and generalist types in environments that vary in space and time. *Heredity* 78: 507-514.

- 428 39. Abbott MR, Brink KH, Booth CR, Blasco D, Codispoti LA, Niiler PP, Ramp SR (1990)
 429 Observations of phytoplankton and nutrients from a Lagrangian drifter off Northern
 430 California. *Journal of Geophysical Research* 95: 9393-9409.
- 431 40. Alkire MB, D'Asaro E, Lee C, Perry M, Gray A, Cetinic I, Briggs N, Rehma E, Kallin E, Kaiser J,
 432 González-Posada A (2012) Estimates of net community production and export using high-
 433 resolution, Lagrangian measurements of O₂, NO₃ and POC through the evolution of a spring
 434 diatom bloom in the North Atlantic. *Deep-Sea Research I* 64: 157–174.
- 435 41. Ottesen EA, Young CR, Gifford SM, Eppley JM, Marin R, Schuster SC, Scholin CA, DeLong EF
 436 (2014) Multispecies diel transcriptional oscillations in open ocean heterotrophic bacterial
 437 assemblages. *Science* 345: 207–212.
- 438 42. Follows MJ, Dutkiewicz S, Grant S, Chisholm SW (2007), Emergent biogeography of microbial
 439 communities in a model ocean. *Science* 315: 1843-1846. doi: [10.1126/science.1138544](https://doi.org/10.1126/science.1138544).
- 440 Bates AE, McKelvie CM, Sorte CJB, Morley SA, Jones NAR, Mondon JA, Bird TJ, Quinn G
 441 (2013) Geographical range, heat tolerance and invasion success in aquatic species. *Proc R*
 442 *Soc B* 280: 20131958. <http://dx.doi.org/10.1098/rspb.2013.1958>.
- 443 43. Wu L, Cai W, Zhang L, Nakamura H, Timmermann A, Joyce T, McPhaden MJ, Alexander M,
 444 Qiu B, Visbeck M, Chang P, Giese B (2012) Enhanced warming over the global subtropical
 445 western boundary currents. *Nature Climate Change* 2: 161-166.
- 446 44. Clayton S, Dutkiewicz S, Jahn O, Follows MJ (2014) Dispersal, eddies, and the diversity of
 447 marine phytoplankton. *Limnology and Oceanography: Fluids and Environments* 3: 182–197.
 448 doi: 10.1215/21573689-2373515.\
- 449 45. Lévy M, Jahn O, Dutkiewicz S, Follows MJ (2014) Phytoplankton diversity and community
 450 structure affected by oceanic dispersal and mesoscale turbulence. *Limnology and*
 451 *Oceanography: Fluids and Environments* 4: 67–84. doi: 10.1215/21573689-2768549.
- 452 46. Masumoto Y, Sasaki H, Kagimoto T, Komori N, Ishida A, Sasai Y, Miyama T, Motoi T,
 453 Mitsudera H, Takahashi K, Sakuma H, Yamagata T (2004) A fifty-year eddy-resolving
 454 simulation of the world ocean - Preliminary outcomes of OFES (OGCM for the Earth
 455 Simulator). *J Earth Simul*, 1: 35-56.

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Figure Legends

459 **Figure 1. Advection of microbial genotypes by ocean currents.** (a) The average meridional
 460 (latitudinal) distance travelled by 500-day microbial genotypes. While microbes can be
 461 advected for thousands of kilometres in the global ocean, they are most likely to experience
 462 changes in temperature through meridional rather than zonal (longitudinal) transport. (b) The
 463 offset between the along-trajectory average temperature experienced by the microbes as they
 464 have traveled for 500 days and the local temperature at each grid location. The poleward
 465 flowing western boundary currents carry microbes that have provenances in much warmer
 466 water than where they are found. In contrast, microbes on the northern flank of the Antarctic
 467 Circumpolar Current originate from the cold water close to Antarctica and have been carried
 468 northward by the Ekman transport.

469

470 **Figure 2. Analysis of the temperature variability experienced by microbes.** (a) The
471 average range of temperatures (difference between minimum and maximum) experienced by
472 microbial genotypes over 500 days if they did not move (i.e. were ‘Eulerian microbes’). The
473 largest variability, up to 20°C, is seen in the north-western Pacific and Atlantic Ocean. (b)
474 The average range of temperatures experienced by Lagrangian microbes along their 500-day
475 trajectories. (c) The difference between panel (b) and panel (a) showing in red/blue the
476 regions where microbes carried by currents experience greater/lesser temperature variability
477 compared to stationary microbes.

478

479 **Figure 3. Thermal variability and transport distance of microbes in the ocean.** Locations
480 are partitioned based on median temperature range (6.5°C) and median meridional travel
481 distance (1,240km) to reflect the magnitude of variation in temperature and distance travelled
482 by microbes advected for 500 days. Map constructed using 2 x 2° grid cells as in the global
483 ocean circulation model.

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