

1 **Uncertain response of ocean biological carbon export in a changing world**

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DRAFT

30 **Abstract**

31 The export flux of organic carbon from the upper ocean is the starting point of the
32 transfer and long term storage of photosynthetically-fixed carbon in the deep ocean.
33 This “biological carbon pump” is a significant component of the global carbon cycle,
34 reducing atmospheric CO₂ levels by ~ 200 ppm. Carbon exported out of the upper
35 ocean also fuels the productivity of the mesopelagic zone, including significant
36 fisheries. Here we show that, despite its importance, export flux is poorly constrained
37 in Earth System Models, with the modelled range in projected future global-mean
38 changes due to climate change spanning +1.8 to -41%. Fundamental constraints to
39 understanding export flux arise because a myriad of interconnected processes make
40 the biological carbon pump challenging to both observe and model. Our synthesis
41 prioritises the processes likely to be most important to include in modern-day
42 estimates (particle fragmentation and zooplankton vertical migration) and future
43 projections (phytoplankton and particle size spectra, and temperature-dependent
44 remineralisation) of export. We also identify the observations required to achieve more
45 robust characterisation, and hence improved model parameterization, of export flux,
46 and thus decrease uncertainties in current and future estimates of this important
47 planetary carbon flux.

48

49 **Main text:**

50 Biological activity in the upper ocean takes up 50-60 GtC from the atmosphere
51 annually, of which ~ 10% sinks out of the surface ocean¹. This 'exported' carbon fuels
52 the biological carbon pump and hence plays a central role in storing carbon in the
53 ocean on climatically-relevant timescales². Because of the complexity of the

54 processes that drive export flux, estimates of both the present-day and future
55 magnitude of this important planetary carbon flux are poorly constrained³⁻⁵.

56

57 Despite its importance, global climate models, such as those used in IPCC
58 assessments, evince vastly different estimates of export flux (as well as primary
59 production and export ratio^{6,7}). Our analysis shows that the most recent generation of
60 climate models project changes in particulate organic carbon (POC) export by 2100 of
61 between +0.16 to -1.98 GtC yr⁻¹ at 100m depth (+1.8 to -41%; Fig. 1a, b; SSP5-8.5
62 scenario). Even the direction of change in export flux is uncertain: for 84% of the
63 ocean, the models disagree on whether export will increase or decrease by the year
64 2100 (Fig. 1c). In addition, the differences among models in present-day export flux
65 far exceed the projected changes by 2100 (Supplementary Fig. 1). This casts doubt
66 on the reliability of the modelled particle export flux, and its response and feedback to
67 climate change.

68

69 The key processes that influence present-day export flux, and which may determine
70 the sensitivity of export flux to future climate change, are summarized in Table 1.
71 Currently, several processes are missing from state-of-the-art climate models, partly
72 due to a lack of understanding of their role in export flux and/or a paucity of suitable
73 observations from which to derive parsimonious parameterisations (Supplementary
74 Tables 1, 2). Here, we attempt to prioritise the currently missing processes that may
75 be of most significance to improving understanding of both present-day and future
76 export flux.

77

78 **Uncertainties in present-day export flux processes**

79 Gravitational sinking of particles plays a key role in export flux⁸, and is represented in
80 all climate models with a marine biogeochemistry module. However, the treatment of
81 sinking particle generation and transformation varies widely (Table 1). The
82 gravitational flux of carbon to depth by sinking particles is affected by (Fig. 2): a) the
83 rate of particle sinking, which is influenced by particle size, density, shape^{9–11} and
84 composition, as mineral ballasting^{12–14} or association with Transparent Exopolymer
85 Particles (TEP) and other biological ‘glues’ can alter sinking speed^{15,16}; b) the
86 temperature-dependent viscosity of the water the particles are sinking through^{17,18}; c)
87 the rate at which microbes remineralise the sinking particles, which can be influenced
88 by temperature, oxygen and resource availability^{19–21}; d) zooplankton consumption
89 and fragmentation of particles^{22,23}; and e) the ability of microbes to access carbon
90 within the particles^{24,25}. For many of these processes, it is relatively uncertain how
91 significantly they would affect present-day export fluxes if incorporated into a model,
92 or even in which direction they would drive the global export estimates (Table 1). Here
93 we focus discussion on those processes for which sufficient understanding exists to
94 quantify their contribution to export flux (albeit with high uncertainty in some cases).

95
96 Fragmentation from large to small particles, both physically and biologically mediated,
97 promotes microbial colonisation and POC remineralisation, due to the larger ratio of
98 surface area to volume of small particles^{22,26}. Recent observations from the
99 biogeochemical-Argo float array suggest that fragmentation could drive up to 50% of
100 mid-water remineralisation²³. Fragmentation is included in only one of the current
101 climate models (Table 1) due to a lack of understanding of its drivers and lack of
102 observations to constrain it.

103

104 Migration by zooplankton and nekton is a significant component of flux, as carbon is
105 transported from the upper ocean directly to the mesopelagic where the organisms
106 excrete, egest, respire and sometimes die^{27,28}. Vertical migration is not included in any
107 of the current climate models (Table 1) due to uncertain mechanistic drivers. Inclusion
108 of vertical migration of zooplankton and nekton could increase model estimates of
109 present-day export by anywhere from 14-40% globally²⁹⁻³¹ and potentially even more
110 at specific locations³². Although currently poorly constrained by observations, the
111 contribution to carbon flux by vertically migrating fish may contribute up to 16% of
112 global export fluxes³³. Note that specifics of the plankton community structure are not
113 considered here, e.g. contribution to flux by gelatinous zooplankton³⁴ or mixotrophs³⁵,
114 as we conduct our analysis on coupled climate models which do not include explicit
115 representation of plankton types (typically these models simulate 2-3 phytoplankton
116 and 1-2 zooplankton classes). Although a new class of models which attempt to
117 mechanistically model plankton community structure exist (e.g. ³⁶), these models have
118 not been used to conduct coupled climate runs as the computational expense of
119 adding many more tracers (in some cases, hundreds more) to centuries-long coupled
120 runs is prohibitive.

121
122 Finally, some processes have been quantified, but their contribution to total export flux
123 is expected to be small. Small-scale physical transport of both particulate and
124 dissolved organic matter to depth^{8,37} is missing from climate models as the spatial
125 resolution is too coarse to resolve (sub)mesoscales. The effect of unresolved
126 mesoscale processes could have a large effect on export at local scales, but is unlikely
127 to have a substantial impact on globally integrated export flux³⁸ (< 2%). Warmer water

128 has reduced viscosity, thus potentially enabling particles to sink more rapidly, however
129 incorporating this effect into climate models is likely to have a small effect¹⁸ (~ 3%).

130

131 It is relatively uncertain how much and in which direction other processes assessed
132 here (temperature-dependent remineralization, oxygen-dependent remineralization,
133 phytoplankton size effect on sinking, mineral ballasting, mineral protection and TEP
134 production; Table 1) would affect modelled modern-day global export. For instance,
135 in the case of mineral ballasting, increased dissolved inorganic carbon in the oceans
136 may increase coccolithophore abundance and export, but at the same time
137 acidification reduces calcification and hence ballasting potential³⁹. Including the
138 effects of seawater viscosity on particle sinking speed and small-scale physical
139 transport are unlikely to significantly improve modern-day export estimates.
140 Therefore, fragmentation may be the most important currently unaccounted for
141 process for improving modern-day export flux simulations, followed by zooplankton
142 vertical migration.

143

144 **Uncertainties in response of export flux to climate change**

145 The climate change response of export flux is likely to be sensitive to somewhat
146 different processes than present-day export (Table 1, Supplementary Table 2). For
147 all processes, simulating a response to climate change requires its drivers to be
148 understood and themselves modelled, otherwise the process will not respond to
149 changing forcing. Projected climate change-driven shifts in phytoplankton size and
150 resultant sinking particle size are highly variable across simulations, however they are
151 often a particularly strong driver of export decrease^{5,40,41}. Projected decreases in

152 global export due to warming-driven increases in temperature-dependent
153 remineralization are also wide-ranging, but may be as high as ~20%^{20,42,43}.

154

155 Incorporating the effects of mineral ballasting^{44,45}, seawater viscosity¹⁸ and changing
156 stoichiometry of sinking particles⁴⁶ will likely have a lesser, though non-negligible,
157 influence on projections of future carbon export. Decreases in remineralization rates
158 due to reduced oxygen availability should increase future export, but the size of this
159 effect is not well quantified. The effect of predicted increases in compounds that
160 promote aggregation (e.g. TEP) is also not well quantified, with studies disagreeing on
161 the direction of the effect on export^{15,16,47}. On the other hand, resolving the effects of
162 future changes in mineral protection and eddy pump strength, no matter their direction,
163 are likely to be relatively less important due to their smaller overall contributions to
164 export globally^{38,48}. The remaining processes examined here (fragmentation, and
165 zooplankton and fish vertical migration) fall into the “known unknown” category, as
166 there is great uncertainty as to how much and in which direction these may change
167 with future warming (Supplementary Table 2), and therefore the importance of
168 modelling these processes for projections of future export flux is unknown. We thus
169 conclude that, within the limits of our current understanding, inclusion of dynamic
170 phytoplankton and sinking particle sizes, along with temperature-dependent
171 remineralisation, are likely to have the most significant effect on modelled future export
172 flux.

173

174 **Uncertainties in feedbacks between export and climate change**

175 Climate-driven changes in all of these processes can result in feedbacks to climate
176 change (Fig. 3). The magnitude, and sometimes even direction, of these feedbacks

177 are poorly known. An example of a positive feedback to climate (i.e. an initial climate-
178 driven change ultimately results in more climate change) occurs when warming
179 increases ocean vertical temperature gradients and stratification, thus decreasing
180 nutrient supply from the deep ocean to the euphotic zone (Fig. 3a). Lower nutrient
181 availability favours smaller phytoplankton which results in smaller particles that sink
182 more slowly and thus reduce export flux, potentially ultimately reducing ocean carbon
183 storage. An example of a negative feedback to climate arises from decreased
184 seawater viscosity due to ocean warming, leading to increased particle sinking speed
185 and enhanced export fluxes that may result in greater ocean carbon sequestration
186 (Fig. 3b). Another negative feedback is driven by increased upper ocean stratification,
187 which decreases the depth of wintertime ventilation and along with it the depth that
188 sinking particles must reach to contribute to long-term carbon sequestration. For other
189 feedbacks, even the direction of the potential feedback effect is not readily inferred
190 (Fig. 3c). For example, if zooplankton migrations become less frequent, export fluxes
191 may be substantially reduced, possibly resulting in a positive feedback. If, on the other
192 hand, future ocean conditions favour increased zooplankton biomass or more frequent
193 migrations, this could result in enhanced export flux and a negative feedback on
194 climate. Export flux is also influenced by processes occurring deeper in the water
195 column. For example, if particles are remineralised more shallowly or zooplankton do
196 not migrate as deeply in the future, more nutrients will be retained in the upper ocean,
197 which could fuel phytoplankton growth and enhance export, thus partially cancelling
198 out the initial decreases^{30,41}. Greater understanding of these feedbacks is therefore
199 also likely to contribute to improved model representation of mesopelagic
200 remineralisation and sequestration flux. The uncertainties in the climate-export
201 feedbacks highlighted here further emphasise the need for improved mechanistic

202 understanding and modelling of export processes, as these feedbacks are likely
203 important for robustly quantifying global climate sensitivities.

204

205 **A bright future for understanding export processes**

206 Owing to the vastness of the ocean, many observations of export processes are
207 sparse and biased towards regions and seasons that are convenient to sample (e.g.
208 the North Atlantic during summer). However, the recent rapid increase in deployments
209 of autonomous platforms such as moorings, floats, gliders and surface vehicles, plus
210 development of new sensors, is fuelling a significant increase in observations with the
211 potential to provide insights into many of the export processes identified here
212 (Supplementary Table 3).

213

214 To predict the response to a changing environment, the knowledge of states such as
215 chlorophyll or POC concentration, is insufficient: we need to understand the
216 relationship between the different processes. For example, how do zooplankton
217 interact with and fragment particles, and how does community size structure relate to
218 sinking particle size spectra? While laboratory experiments have provided some
219 insights, it is generally uncertain how these translate into the interactions occurring in
220 the open ocean. Moreover, such experiments cannot provide data on the large spatial
221 and temporal scales needed to understand the present-day magnitude and climate
222 response of export processes. The rise of autonomous platforms offers a potential
223 solution, as frequent and semi-Lagrangian sampling of state variables over time can
224 be used to estimate rates, including carbon export and vertical sinking fluxes^{49,50},
225 primary production and community respiration^{51,52}, and particle fragmentation²³.
226 Additionally, multi-sensor sampling from the biogeochemical-Argo float initiative⁵³,

227 deployment of uncrewed surface vehicles⁵⁴, and time-series programmes which
228 integrate moored platforms and autonomous vehicles⁵⁵, are driving an exponential
229 increase in data availability. In parallel, the development of new sensors is opening up
230 new avenues of research, such as small, energy-efficient camera systems with the
231 ability to image particles and plankton *in situ* at similar spatiotemporal scales and
232 hence deduct abundance, distribution and composition of particles and plankton
233 communities^{56–58}.

234
235 Synthesizing the information from these observations, made across a wide range of
236 environmental conditions and spatio-temporal scales, into robust mechanistic
237 parameterisations that can be implemented in global models, or into global validation
238 datasets suitable to compare with model output, remains a challenge. Sparseness of
239 data, particularly with sufficient spatial and temporal coverage, lack of information on
240 episodic fluxes, and inconsistencies across different observational datasets (e.g. in
241 the choice of export depth horizon^{59,60}, definition of sinking particles, or treatment of
242 dissolved organic matter) continue to hinder integration with model development.
243 These efforts will benefit in coming years from simultaneous development of novel
244 techniques and sensors, continuation of ship-based studies to observe export flux
245 processes in great detail at a single location and time period, expansion of the global
246 biogeochemical-Argo array and deployments of other autonomous platforms, and new
247 remote sensing capabilities. Improved process understanding from exploitation of
248 ever-increasing observational datasets should be carried out hand-in-hand with model
249 development. Including many additional tracers in a coupled climate model, as used
250 in IPCC simulations, is typically unfeasible and so simplified parameterisations should
251 be developed where possible that ‘plug-and-play’ with tracers already common in

252 models (e.g. temperature or primary production). New parameterisations should also
253 be tested in a simplified 1-D framework or semi-empirical model initially, and
254 potentially also in a computationally efficient 3-D framework, such as a transport
255 matrix, e.g. ^{61,62}. Only if the additional processes are then shown to significantly alter
256 modern-day export flux estimates should they then be implemented in a full climate
257 model to make projections of the future magnitude and efficiency of the biological
258 carbon pump.

259

260 **Conclusion**

261 This Perspective identifies 12 processes that are likely to have the greatest impact on
262 present-day and future projections of export flux, of which 10 are currently missing
263 from the majority of climate models. These processes: a) are significant contributors
264 to export flux and/or its climate feedback, b) have the potential for technology and
265 platform developments to generate sufficient data to act as a robust model constraint
266 and/or develop new parameterisations, c) are computationally tractable (i.e. the
267 process can be incorporated in a model without hugely increasing its complexity, and
268 therefore run time), and d) can be applied on the centennial, global scale of climate
269 models. We are poised on the edge of a new era in biological carbon pump studies.
270 As a community, there is now a potential route to reducing uncertainties in export flux,
271 via common data sharing platforms, enhanced networks of ocean observations and
272 synthesis activities (e.g. JETZON, Joint Exploration of the Twilight Zone Ocean
273 Network⁶³), the development of new technologies and platforms to overcome gaps in
274 process understanding, and collaboration with modellers on developing the next
275 generation of biogeochemical models.

276

277 **Author contributions**

278 SH conceived the manuscript, and all authors contributed extensively to the work
279 presented in this paper.

280

281 **Data availability**

282 All CMIP6 model output used in our analysis is freely available from [https://esgf-](https://esgf-node.llnl.gov/projects/cmip6/)
283 [node.llnl.gov/projects/cmip6/](https://esgf-node.llnl.gov/projects/cmip6/)

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285 **References**

286 1. De La Rocha, C. L. The biological pump. in *Treatise on Geochemistry (Second*
287 *Edition)* 83–111 (Pergamon, 2006).

288 2. Kwon, E. Y., Primeau, F. & Sarmiento, J. L. The impact of remineralization
289 depth on the air-sea carbon balance. *Nat. Geosci.* **2**, 630–635 (2009).

290 3. Henson, S. A., Sanders, R. & Madsen, E. Global patterns in efficiency of
291 particulate organic carbon export and transfer to the deep ocean. *Global*
292 *Biogeochem. Cycles* **26**, n/a-n/a (2012).

293 4. Marsay, C. M. *et al.* Attenuation of sinking particulate organic carbon flux
294 through the mesopelagic ocean. *Proc. Natl. Acad. Sci.* **112**, 1089–1094 (2015).

295 5. Laufkötter, C. *et al.* Projected decreases in future marine export production:
296 the role of the carbon flux through the upper ocean ecosystem.
297 *Biogeosciences* **13**, 4023–4047 (2016).

298 6. Séférian, R. *et al.* Tracking Improvement in Simulated Marine Biogeochemistry
299 Between CMIP5 and CMIP6. *Curr. Clim. Chang. Reports* **6**, 95–119 (2020).

300 7. Kwiatkowski, L. *et al.* Twenty-first century ocean warming, acidification,
301 deoxygenation, and upper-ocean nutrient and primary production decline from

- 302 CMIP6 model projections. *Biogeosciences* **17**, 3439–3470 (2020).
- 303 8. Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A. & Weber, T. Multi-faceted
304 particle pumps drive carbon sequestration in the ocean. *Nature* **568**, 327–335
305 (2019).
- 306 9. Waite, A., Fisher, A., Thompson, P. & Harrison, P. Sinking rate versus cell
307 volume relationships illuminate sinking rate control mechanisms in marine
308 diatoms. *Mar. Ecol. Prog. Ser.* **157**, 97–108 (1997).
- 309 10. Iversen, M. H. & Lampitt, R. S. Size does not matter after all: No evidence for a
310 size-sinking relationship for marine snow. *Prog. Oceanogr.* **189**, 102445
311 (2020).
- 312 11. McDonnell, A. M. P. & Buesseler, K. O. Variability in the average sinking
313 velocity of marine particles. *Limnol. Oceanogr.* **55**, 2085–2096 (2010).
- 314 12. Francois, R., Honjo, S., Krishfield, R. & Manganini, S. Factors controlling the
315 flux of organic carbon to the bathypelagic zone of the ocean. *Global*
316 *Biogeochem. Cycles* **16**, 34-1-34–20 (2002).
- 317 13. Le Moigne, F. A. C., Pabortsava, K., Marcinko, C. L. J., Martin, P. & Sanders,
318 R. J. Where is mineral ballast important for surface export of particulate
319 organic carbon in the ocean? *Geophys. Res. Lett.* **41**, 8460–8468 (2014).
- 320 14. Maerz, J., Six, K. D., Stemmler, I., Ahmerkamp, S. & Ilyina, T. Microstructure
321 and composition of marine aggregates as co-determinants for vertical
322 particulate organic carbon transfer in the global ocean. *Biogeosciences* **17**,
323 1765–1803 (2020).
- 324 15. Seebah, S., Fairfield, C., Ullrich, M. S. & Passow, U. Aggregation and
325 Sedimentation of *Thalassiosira weissflogii* (diatom) in a Warmer and More
326 Acidified Future Ocean. *PLoS One* **9**, e112379 (2014).

- 327 16. Mari, X., Passow, U., Migon, C., Burd, A. B. & Legendre, L. Transparent
328 exopolymer particles: Effects on carbon cycling in the ocean. *Prog. Oceanogr.*
329 **151**, 13–37 (2017).
- 330 17. Bach, L. T. *et al.* An approach for particle sinking velocity measurements in the
331 3–400 μm size range and considerations on the effect of temperature on
332 sinking rates. *Mar. Biol.* **159**, 1853–1864 (2012).
- 333 18. Taucher, J., Bach, L. T., Riebesell, U. & Oschlies, A. The viscosity effect on
334 marine particle flux: A climate relevant feedback mechanism. *Global*
335 *Biogeochem. Cycles* **28**, 415–422 (2014).
- 336 19. Devol, A. H. & Hartnett, H. E. Role of the oxygen-deficient zone in transfer of
337 organic carbon to the deep ocean. *Limnol. Oceanogr.* **46**, 1684–1690 (2001).
- 338 20. Laufkötter, C., John, J. G., Stock, C. A. & Dunne, J. P. Temperature and
339 oxygen dependence of the remineralization of organic matter. *Global*
340 *Biogeochem. Cycles* **31**, 1038–1050 (2017).
- 341 21. López-Urrutia, Á. & Morán, X. A. G. RESOURCE LIMITATION OF
342 BACTERIAL PRODUCTION DISTORTS THE TEMPERATURE
343 DEPENDENCE OF OCEANIC CARBON CYCLING. *Ecology* **88**, 817–822
344 (2007).
- 345 22. Cavan, E. L., Henson, S. A., Belcher, A. & Sanders, R. Role of zooplankton in
346 determining the efficiency of the biological carbon pump. *Biogeosciences* **14**,
347 177–186 (2017).
- 348 23. Briggs, N., Dall’Olmo, G. & Claustre, H. Major role of particle fragmentation in
349 regulating biological sequestration of CO₂ by the oceans. *Science (80-.)*. **367**,
350 791–793 (2020).
- 351 24. Belcher, A. *et al.* The role of particle associated microbes in remineralization of

- 352 fecal pellets in the upper mesopelagic of the Scotia Sea, Antarctica. *Limnol.*
353 *Oceanogr.* **61**, 1049–1064 (2016).
- 354 25. Herndl, G. J. & Reinthaler, T. Microbial control of the dark end of the biological
355 pump. *Nat. Geosci.* **6**, 718–724 (2013).
- 356 26. Burd, A. B. & Jackson, G. A. Particle Aggregation. *Ann. Rev. Mar. Sci.* **1**, 65–
357 90 (2009).
- 358 27. Steinberg, D. K. & Landry, M. R. Zooplankton and the Ocean Carbon Cycle.
359 *Ann. Rev. Mar. Sci.* **9**, 413–444 (2017).
- 360 28. Jónasdóttir, S. H., Visser, A. W., Richardson, K. & Heath, M. R. Seasonal
361 copepod lipid pump promotes carbon sequestration in the deep North Atlantic.
362 *Proc. Natl. Acad. Sci.* **112**, 12122–12126 (2015).
- 363 29. Archibald, K. M., Siegel, D. A. & Doney, S. C. Modeling the Impact of
364 Zooplankton Diel Vertical Migration on the Carbon Export Flux of the Biological
365 Pump. *Global Biogeochem. Cycles* **33**, 181–199 (2019).
- 366 30. Gorgues, T., Aumont, O. & Memery, L. Simulated Changes in the Particulate
367 Carbon Export Efficiency due to Diel Vertical Migration of Zooplankton in the
368 North Atlantic. *Geophys. Res. Lett.* **46**, 5387–5395 (2019).
- 369 31. Aumont, O., Maury, O., Lefort, S. & Bopp, L. Evaluating the Potential Impacts
370 of the Diurnal Vertical Migration by Marine Organisms on Marine
371 Biogeochemistry. *Global Biogeochem. Cycles* **32**, 1622–1643 (2018).
- 372 32. Stukel, M., Ohman, M., Benitez-Nelson, C. & Landry, M. Contributions of
373 mesozooplankton to vertical carbon export in a coastal upwelling system. *Mar.*
374 *Ecol. Prog. Ser.* **491**, 47–65 (2013).
- 375 33. Saba, G. K. *et al.* Toward a better understanding of fish-based contribution to
376 ocean carbon flux. *Limnol. Oceanogr.* Ino.11709 (2021). doi:10.1002/Ino.11709

- 377 34. Luo, J. Y. *et al.* Gelatinous Zooplankton-Mediated Carbon Flows in the Global
378 Oceans: A Data-Driven Modeling Study. *Global Biogeochem. Cycles* **34**,
379 (2020).
- 380 35. Ward, B. A. & Follows, M. J. Marine mixotrophy increases trophic transfer
381 efficiency, mean organism size, and vertical carbon flux. *Proc. Natl. Acad. Sci.*
382 **113**, 2958–2963 (2016).
- 383 36. Dutkiewicz, S. *et al.* Dimensions of marine phytoplankton diversity.
384 *Biogeosciences* **17**, 609–634 (2020).
- 385 37. Dever, M., Nicholson, D., Omand, M. M. & Mahadevan, A. Size-Differentiated
386 Export Flux in Different Dynamical Regimes in the Ocean. *Global Biogeochem.*
387 *Cycles* **35**, (2021).
- 388 38. Harrison, C. S., Long, M. C., Lovenduski, N. S. & Moore, J. K. Mesoscale
389 Effects on Carbon Export: A Global Perspective. *Global Biogeochem. Cycles*
390 **32**, 680–703 (2018).
- 391 39. Krumhardt, K. M. *et al.* Coccolithophore Growth and Calcification in an
392 Acidified Ocean: Insights From Community Earth System Model Simulations.
393 *J. Adv. Model. Earth Syst.* **11**, 1418–1437 (2019).
- 394 40. Bopp, L., Aumont, O., Cadule, P., Alvain, S. & Gehlen, M. Response of
395 diatoms distribution to global warming and potential implications: A global
396 model study. *Geophys. Res. Lett.* **32**, n/a-n/a (2005).
- 397 41. Leung, S. W., Weber, T., Cram, J. A. & Deutsch, C. Variable particle size
398 distributions reduce the sensitivity of global export flux to climate change.
399 *Biogeosciences* **18**, 229–250 (2021).
- 400 42. Cavan, E. & Boyd, P. Effect of anthropogenic warming on microbial respiration
401 and particulate organic carbon export rates in the sub-Antarctic Southern

- 402 Ocean. *Aquat. Microb. Ecol.* **82**, 111–127 (2018).
- 403 43. Cavan, E. L., Henson, S. A. & Boyd, P. W. The Sensitivity of Subsurface
404 Microbes to Ocean Warming Accentuates Future Declines in Particulate
405 Carbon Export. *Front. Ecol. Evol.* **6**, (2019).
- 406 44. Heinze, C. Simulating oceanic CaCO₃ export production in the greenhouse.
407 *Geophys. Res. Lett.* **31**, (2004).
- 408 45. Hofmann, M. & Schellnhuber, H.-J. Oceanic acidification affects marine carbon
409 pump and triggers extended marine oxygen holes. *Proc. Natl. Acad. Sci. U. S.*
410 *A.* **106**, 3017–3022 (2009).
- 411 46. Tanioka, T. & Matsumoto, K. Buffering of Ocean Export Production by Flexible
412 Elemental Stoichiometry of Particulate Organic Matter. *Global Biogeochem.*
413 *Cycles* **31**, 1528–1542 (2017).
- 414 47. Wohlers, J. *et al.* Changes in biogenic carbon flow in response to sea surface
415 warming. *Proc. Natl. Acad. Sci.* **106**, 7067–7072 (2009).
- 416 48. Iversen, M. H. & Ploug, H. Temperature effects on carbon-specific respiration
417 rate and sinking velocity of diatom aggregates – potential implications for deep
418 ocean export processes. *Biogeosciences* **10**, 4073–4085 (2013).
- 419 49. Briggs, N. *et al.* High-resolution observations of aggregate flux during a sub-
420 polar North Atlantic spring bloom. *Deep Sea Res. Part I Oceanogr. Res. Pap.*
421 **58**, 1031–1039 (2011).
- 422 50. Estapa, M. L., Feen, M. L. & Breves, E. Direct Observations of Biological
423 Carbon Export From Profiling Floats in the Subtropical North Atlantic. *Global*
424 *Biogeochem. Cycles* **33**, 282–300 (2019).
- 425 51. Gordon, C., Fennel, K., Richards, C., Shay, L. K. & Brewster, J. K. Can ocean
426 community production and respiration be determined by measuring high-

- 427 frequency oxygen profiles from autonomous floats? *Biogeosciences* **17**, 4119–
428 4134 (2020).
- 429 52. Yang, B. *et al.* In Situ Estimates of Net Primary Production in the Western
430 North Atlantic With Argo Profiling Floats. *J. Geophys. Res. Biogeosciences*
431 **126**, (2021).
- 432 53. Claustre, H., Johnson, K. S. & Takeshita, Y. Observing the Global Ocean with
433 Biogeochemical-Argo. *Ann. Rev. Mar. Sci.* **12**, 23–48 (2020).
- 434 54. Meinig, C. *et al.* Public–Private Partnerships to Advance Regional Ocean-
435 Observing Capabilities: A Saildrone and NOAA-PMEL Case Study and Future
436 Considerations to Expand to Global Scale Observing. *Front. Mar. Sci.* **6**,
437 (2019).
- 438 55. Trowbridge, J. *et al.* The Ocean Observatories Initiative. *Front. Mar. Sci.* **6**,
439 (2019).
- 440 56. Lombard, F. *et al.* Globally Consistent Quantitative Observations of Planktonic
441 Ecosystems. *Front. Mar. Sci.* **6**, (2019).
- 442 57. Giering, S. L. C. *et al.* Sinking Organic Particles in the Ocean—Flux Estimates
443 From in situ Optical Devices. *Front. Mar. Sci.* **6**, (2020).
- 444 58. Cram, J. A. *et al.* Slow particle remineralization, rather than suppressed
445 disaggregation, drives efficient flux transfer through the Eastern Tropical North
446 Pacific Oxygen Deficient Zone. *Global Biogeochem. Cycles*
447 doi:10.1002/essoar.10507130.4
- 448 59. Palevsky, H. I. & Doney, S. C. Sensitivity of 21st Century Ocean Carbon
449 Export Flux Projections to the Choice of Export Depth Horizon. *Global*
450 *Biogeochem. Cycles* **35**, (2021).
- 451 60. Buesseler, K. O., Boyd, P. W., Black, E. E. & Siegel, D. A. Metrics that matter

- 452 for assessing the ocean biological carbon pump. *Proc. Natl. Acad. Sci.* **117**,
453 9679–9687 (2020).
- 454 61. Mayor, D. J., Gentleman, W. C. & Anderson, T. R. Ocean carbon
455 sequestration: Particle fragmentation by copepods as a significant
456 unrecognised factor?: Explicitly representing the role of copepods in
457 biogeochemical models may fundamentally improve understanding of future
458 ocean carbon storage. *BioEssays* **42**, (2020).
- 459 62. Tanioka, T., Matsumoto, K. & Lomas, M. W. Drawdown of Atmospheric pCO₂
460 via Variable Particle Flux Stoichiometry in the Ocean Twilight Zone. *Geophys.*
461 *Res. Lett.* (2021). doi:10.1029/2021GL094924
- 462 63. Martin, A. *et al.* The oceans' twilight zone must be studied now, before it is too
463 late. *Nature* **580**, 26–28 (2020).
- 464 64. Giering, S. L. C. *et al.* Reconciliation of the carbon budget in the ocean's
465 twilight zone. *Nature* **507**, 480–483 (2014).
- 466 65. Boyd, P. W. Toward quantifying the response of the oceans' biological pump to
467 climate change. *Front. Mar. Sci.* **2**, (2015).
- 468 66. Kriest, I. & Oschlies, A. On the treatment of particulate organic matter sinking
469 in large-scale models of marine biogeochemical cycles. *Biogeosciences* **5**, 55–
470 72 (2008).
- 471 67. Weber, T. & Bianchi, D. Efficient Particle Transfer to Depth in Oxygen
472 Minimum Zones of the Pacific and Indian Oceans. *Front. Earth Sci.* **8**, (2020).
- 473 68. Wilson, J. D., Barker, S. & Ridgwell, A. Assessment of the spatial variability in
474 particulate organic matter and mineral sinking fluxes in the ocean interior:
475 Implications for the ballast hypothesis. *Global Biogeochem. Cycles* **26**, n/a-n/a
476 (2012).

- 477 69. Iversen, M. H. & Robert, M. L. Ballasting effects of smectite on aggregate
478 formation and export from a natural plankton community. *Mar. Chem.* **175**, 18–
479 27 (2015).
- 480 70. Resplandy, L., Lévy, M. & McGillicuddy, D. J. Effects of Eddy-Driven
481 Subduction on Ocean Biological Carbon Pump. *Global Biogeochem. Cycles*
482 **33**, 1071–1084 (2019).
- 483 71. Riebesell, U. *et al.* Enhanced biological carbon consumption in a high CO₂
484 ocean. *Nature* **450**, 545–548 (2007).
- 485 72. Taucher, J. *et al.* Enhanced carbon overconsumption in response to increasing
486 temperatures during a mesocosm experiment. *Biogeosciences* **9**, 3531–3545
487 (2012).

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489 **Figure Legends**

490 **Figure 1: Uncertain response of export flux to climate change.** (a) Percent
491 change in export flux and (b) absolute change (Gt C yr⁻¹) in export flux in 19 coupled
492 climate models in the CMIP6 archive, forced with the SSP5-8.5 scenario. Percent
493 change is calculated with respect to the mean of years 1850-1900 for each model.
494 Multi-model mean is shown as a thick black line. (c) Multi-model mean change in
495 export flux (gC m⁻² yr⁻¹) between the 2080-2100 average and the 1850-1900
496 average. Hatching indicates where 90% of models (i.e. at least 17 of 19) agree on
497 the sign of the change in export flux.

498

499 **Figure 2: Potential response of export processes to climate change.** Export will
500 change in response to increasing temperature, decreasing oxygen concentration and
501 ocean acidification. Potential responses in: (a) phytoplankton size, (b) primary

502 production, (c) rate of microbial remineralization, (d) zooplankton abundance and
503 size, (e) water viscosity, (f) mineral ballast are depicted. However, there are high
504 uncertainties in both the direction of many of these responses and the effect on
505 export flux due to complex feedbacks.

506

507 **Figure 3: Feedbacks between changing export flux mechanisms and climate.**

508 Mechanisms are separated into those which are likely to have a positive, negative or
509 uncertain feedback to climate.

510

DRAFT

511 **Table 1: Influence of omitting specific mechanisms on modelled present-day**
 512 **and future export flux.** We surveyed the IPCC CMIP6 archive for global climate
 513 models which incorporate explicit marine biogeochemistry (total of 19; Supplementary
 514 Table 4). The model structure was examined to determine whether the processes we
 515 identify as important to export flux are included. We also assess the direction of bias
 516 in present-day model estimates of export flux if processes are excluded, and the
 517 direction of change in future global export flux due to the same processes. Full details
 518 of the model assessment are in Supplementary Table 1, and the detailed rationale for
 519 our prioritisation is in Supplementary Table 2.

520
521

Process	Summary of climate model structure (*1)	Bias in present-day modelled global export without this process (*2)	Direction of change in future global export due to this process (*3)	Key references for this process
Fragmentation	 18  1			23,64
Zooplankton vertical migration	 19  0			29-31
Phytoplankton size effect on sinking (*4)	 13  6			5,41,65,66
Temperature dependent remineralisation	 8  11			4,20
Oxygen dependent remineralisation	 9  10			19,20,67
Viscosity of seawater	 18  1			18
Mineral ballasting	 14  5			13,45,68
Mineral protection	 14  5			48,69
Eddy pump (*5)	 19  0			8,38,70
Fish vertical migration	 19  0			33

Particle stickiness (including transparent exopolymers)	 19  0	?	?	15,16,47
Variable stoichiometry in sinking particles	 18  1	?		46,71,72

522

523

524 (*1) Summary of the 19 climate models included in the IPCC CMIP6 archive which include a
525 marine biogeochemistry component.

526 (*2) Plus (minus) symbols indicate models likely overestimate (underestimate) export flux if
527 this process is missing, with the size of the symbol indicating the potential influence of the
528 missing process. Question marks indicate that either the global-scale effect, or the size of
529 the effect, is unknown.

530 (*3) Up (down) arrows indicate that this process is likely to increase (decrease) future export
531 flux, with the size of the symbol indicating the possible influence of the missing process.

532 Question marks indicate that either the global-scale effect, or the size of the effect, is
533 unknown.

534 (*4) If sinking speed does not change with phytoplankton community composition, the model
535 is classed as a "No" for this category.

536 (*5) Model resolution varies from $\frac{1}{4}$ - 1 degree, and therefore none of the models are eddy-
537 resolving.

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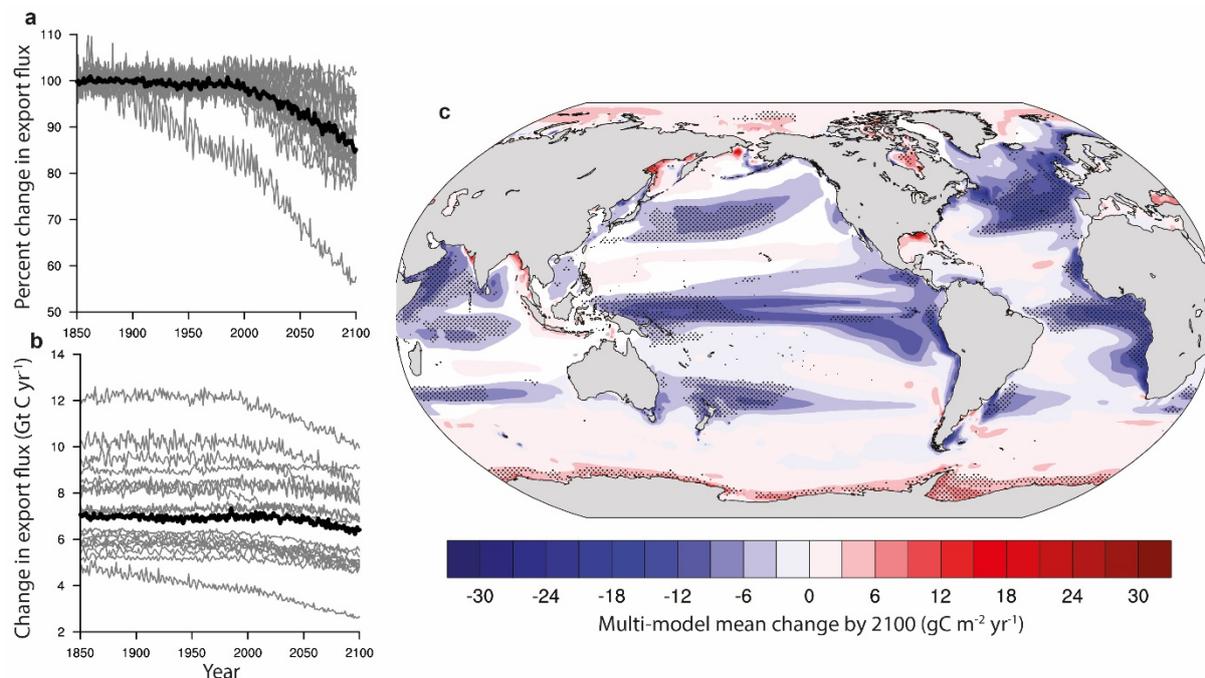


Figure 1: Uncertain response of export flux to climate change. (a) Percent change in export flux and (b) absolute change (Gt C yr⁻¹) in export flux in 19 coupled climate models in the CMIP6 archive, forced with the SSP5-8.5 scenario. Percent change is calculated with respect to the mean of years 1850-1900 for each model. Multi-model mean is shown as a thick black line. (c) Multi-model mean change in export flux (gC m⁻² yr⁻¹) between the 2080-2100 average and the 1850-1900 average. Hatching indicates where 90% of models (i.e. at least 17 of 19) agree on the sign of the change in export flux.

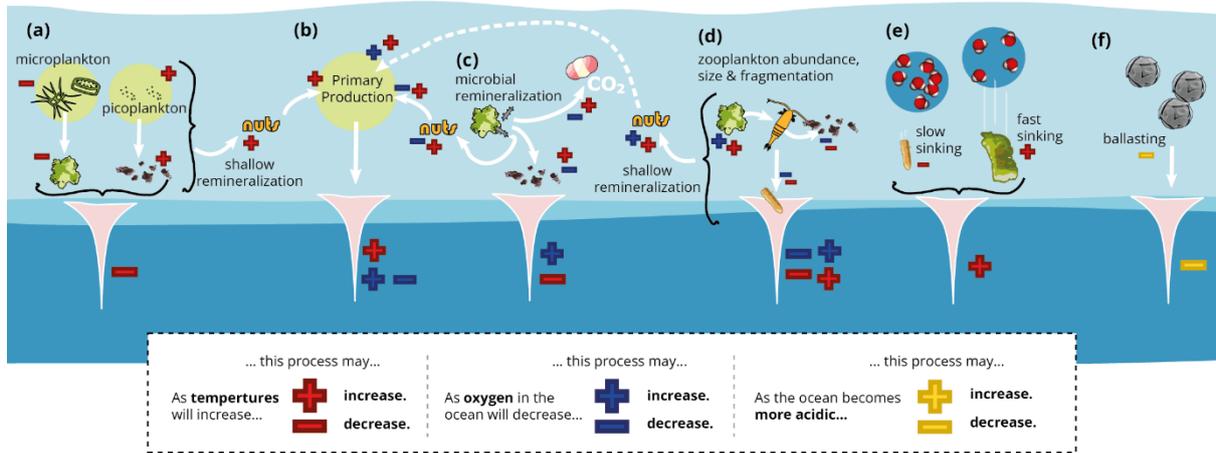


Figure 2: Potential response of export processes to climate change. Export will change in response to increasing temperature, decreasing oxygen concentration and ocean acidification. Potential responses in: (a) phytoplankton size, (b) primary production, (c) rate of microbial remineralization, (d) zooplankton abundance and size, (e) water viscosity, (f) mineral ballast are depicted. However, there are high uncertainties in both the direction of many of these responses and the effect on export flux due to complex feedbacks.

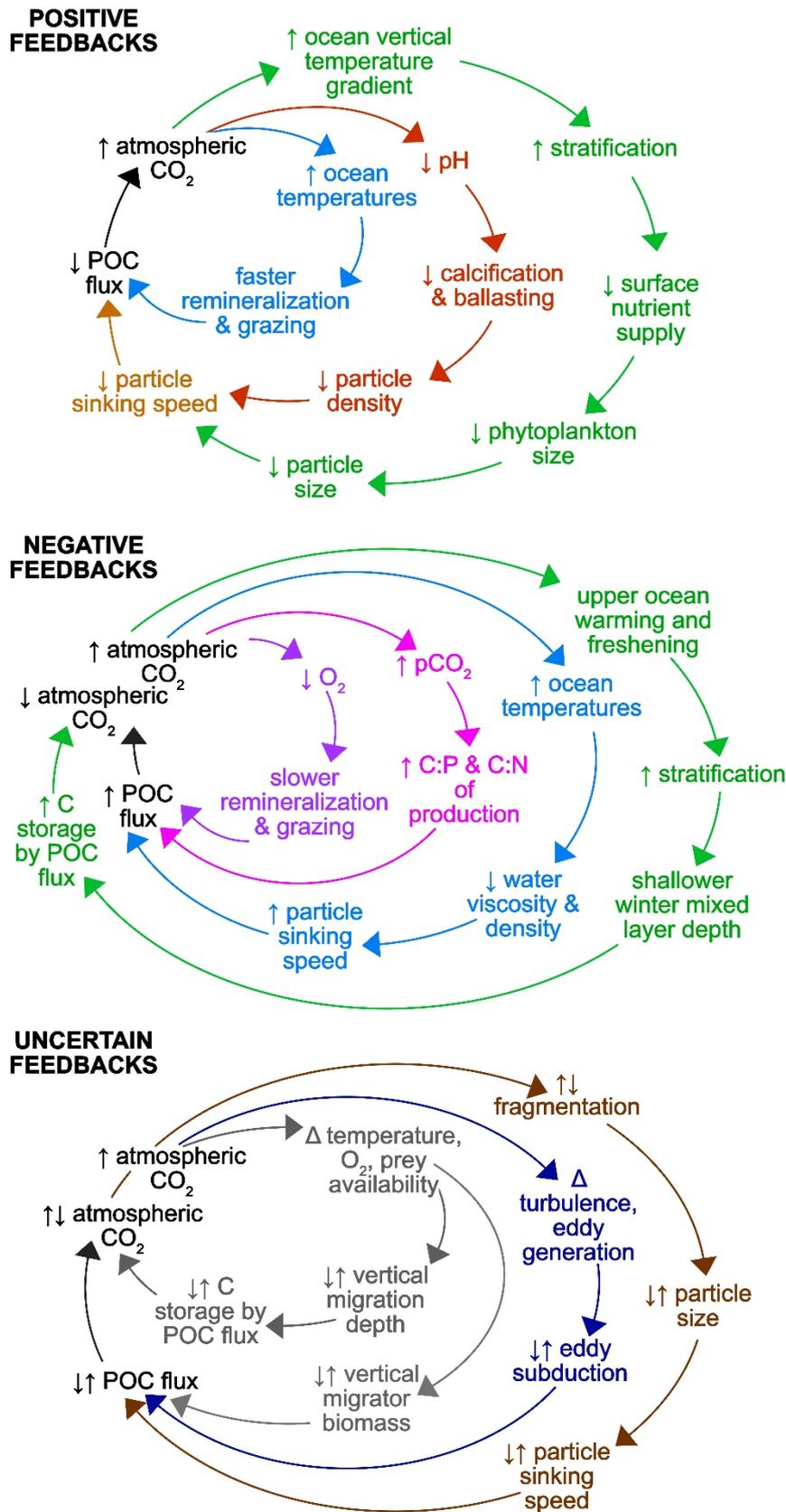


Figure 3: Feedbacks between changing export flux mechanisms and climate. Mechanisms are separated into those which are likely to have a positive, negative or uncertain feedback to climate.