

1 **What the flux? Uncertain response of ocean biological carbon export in a changing**
2 **world**

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19 **Abstract**

20 The export flux of organic carbon from the upper ocean is the starting point of the transfer and
21 long term storage of photosynthetically-fixed carbon in the deep ocean. This “biological carbon
22 pump” is a significant component of the global carbon cycle, reducing atmospheric CO₂ levels
23 by ~ 50%. Carbon exported out of the upper ocean also fuels the productivity of the
24 mesopelagic zone, including significant fisheries. Despite its importance, export flux is poorly
25 constrained in Earth System Models, with the modelled range in projected future global-mean
26 changes due to climate warming spanning +1.8 to -41%. Fundamental constraints to
27 understanding export flux arise because a myriad of interconnected processes make the
28 biological carbon pump challenging to both observe and model. Our synthesis prioritises the
29 processes likely to be most important to include in modern-day estimates and future
30 projections of export, as well as identifying the observations and model developments required
31 to achieve more robust characterisation of this important planetary carbon flux. We identify
32 particle fragmentation and zooplankton vertical migration as the mechanisms most likely to
33 substantially influence the magnitude of present-day modelled export flux. Of the processes
34 sufficiently understood to allow implementation in climate models, projections of future export
35 flux and feedbacks to climate are likely to be most sensitive to changes in phytoplankton and
36 particle size spectra, and to temperature-dependent remineralisation. “Known unknown”
37 processes which are not currently represented in models and will have an uncertain impact on
38 future projections include particle stickiness and fish vertical migration. With the advent of
39 new observational technologies, such as biogeochemical-Argo floats and miniaturised camera
40 systems, we will be able to better parameterize models and thus decrease uncertainties in
41 current and future export flux.

42

43 **Main text:**

44 Biological activity in the upper ocean takes up 50-60 GtC from the atmosphere annually, of
45 which ~ 10% sinks out of the surface ocean¹. This 'exported' carbon is the starting point of the
46 biological carbon pump and hence plays a central role in storing carbon in the ocean on
47 climatically-relevant timescales². Because of the complexity of the processes that drive export
48 flux, estimates of both the present-day and future magnitude of this important planetary carbon
49 flux are poorly constrained³⁻⁵.

50

51 Despite its importance, global climate models (such as those used in IPCC assessments)
52 evince vastly different estimates of export flux. Our analysis shows that the most recent
53 generation of climate models project changes in particulate organic carbon (POC) export by
54 2100 of between +0.16 to -1.98 GtC yr⁻¹ at 100m depth (Fig. 1a; SSP5-8.5 scenario). Even
55 the direction of change in export flux is uncertain: for 84% of the ocean, the models disagree

56 on whether export will increase or decrease by the year 2100 (Fig. 1b). In addition, the
57 differences among models in present-day export flux far exceed the projected changes by
58 2100 (Supplementary Fig. S1). This casts doubt on the reliability of the modelled particle
59 export flux, and its response and feedback to climate change.

60

61 The key processes that influence present-day export flux, and which may determine the
62 sensitivity of export flux to future climate change, are summarized in Table 1. Currently,
63 several processes are missing from state-of-the-art climate models, partly due to a lack of
64 process understanding of their role in export flux and/or a paucity of suitable observations from
65 which to derive parameterisations, and partly due to computational constraints
66 (Supplementary Tables S1, S2). Here, we attempt to prioritise the currently missing processes
67 that may be of most significance to improving understanding of both present-day and future
68 export flux.

69

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

71 Gravitational sinking of particles plays a key role in export flux⁶, and is represented in all
72 climate models with a marine biogeochemistry module. However, the treatment of sinking
73 particle generation and transformation varies widely (Supplementary Table S1). The
74 gravitational flux of carbon to depth by sinking particles is affected by (Fig. 2): a) the rate of
75 particle sinking, which is influenced by particle size, density, shape⁷⁻⁹ and composition, as
76 mineral ballasting^{10,11} or association with Transparent Exopolymer Particles (TEP) and other
77 biological 'glues' can alter sinking speed^{12,13}; b) the temperature-dependent viscosity of the
78 water the particles are sinking through^{14,15}; c) the rate at which microbes remineralise the
79 sinking particles, which can be influenced by temperature, oxygen and resource availability¹⁶⁻
80 ¹⁸; and d) the ability of microbes to access carbon within the particles^{19,20}. For many of these
81 processes, it is relatively uncertain how significantly they would affect present-day export
82 fluxes if incorporated into a model, or even in which direction they would drive the global export
83 estimates (Table 1).

84

85 Fragmentation from large to small particles, both physically and biologically mediated,
86 promotes microbial colonisation and POC remineralisation, due to the larger ratio of surface
87 area to volume of small particles^{21,22}. Recent observations from the biogeochemical-Argo float
88 array suggest that fragmentation could drive up to 50% of mid-water remineralisation²³.
89 Fragmentation is not included in any of the current climate models (Table 1) due to a lack of
90 understanding of its drivers and lack of observations to constrain it.

91

92 Migration by zooplankton and nekton is a significant component of flux, as carbon is
93 transported from the upper ocean directly to the mesopelagic where the organisms excrete,
94 egest, respire and sometimes die^{24,25}. Vertical migration is not included in any of the current
95 climate models (Table 1) due to uncertain mechanistic drivers. Inclusion of vertical migration
96 of zooplankton and nekton could increase model estimates of present-day export by anywhere
97 from 14-40% globally²⁶⁻²⁸ and potentially even more at specific locations²⁹. Although currently
98 poorly constrained by observations, the contribution to carbon flux by vertically migrating fish
99 may contribute up to 16% of global export fluxes³⁰.

100

101 Finally, small-scale physical transport of both particulate and dissolved organic matter to
102 depth^{6,31} is missing from climate models as the spatial resolution is too coarse to resolve
103 (sub)mesoscales. The effect of unresolved mesoscale processes could have a large effect on
104 export at local scales, but is unlikely to have a substantial impact on globally integrated export
105 flux³² (< 2%).

106

107 Taking all of the above into account, fragmentation may be the most important currently
108 unaccounted for process for improving modern-day export flux simulations, followed by
109 zooplankton, and potentially fish, vertical migration. Including the effects of seawater viscosity
110 on particle sinking speed, small-scale physical transport, and mineral protection are less likely
111 to significantly improve modern-day export estimates. It is relatively uncertain how much and
112 in which direction other processes assessed here (temperature-dependent remineralization,
113 oxygen-dependent remineralization, phytoplankton size effect on sinking, mineral ballasting,
114 and TEP production; Table 1) would affect modelled modern-day global export.

115

116 **Uncertainties in response of export flux to future climate change**

117 The climate change response of export flux is likely to be sensitive to somewhat different
118 processes than present-day export (Table 1, Supplementary Table S2). For all processes,
119 simulating a response to climate change requires its drivers to be understood and themselves
120 modelled, otherwise the process will not respond to changing forcing. Projected climate
121 change-driven shifts in phytoplankton size and resultant sinking particle size are highly
122 variable across simulations, however they are often a particularly strong driver of export
123 decrease³³⁻³⁵. Projected decreases in global export due to warming-driven increases in
124 temperature-dependent remineralization are also wide-ranging, but may be as high as ~20%
125 ^{17,36,37}. We thus conclude that inclusion of dynamic phytoplankton and sinking particle sizes,
126 along with temperature-dependent remineralisation, are likely to have the most significant
127 effect on modelled future export flux.

128

129 Incorporating the effects of mineral ballasting^{38,39}, seawater viscosity¹⁵ and changing
130 stoichiometry of sinking particles⁴⁰ will likely have a lesser, though non-negligible, influence
131 on projections of future carbon export. Decreases in remineralization rates due to reduced
132 oxygen availability should increase future export, but the size of this effect is not well
133 quantified. The effect of predicted increases in compounds that promote aggregation (e.g.
134 TEP) is also not well quantified, with studies disagreeing on the direction of the effect on
135 export^{12,13,41}. On the other hand, resolving the effects of future changes in mineral protection
136 and eddy pump strength, no matter their direction, are likely to be relatively less important due
137 to their smaller overall contributions to export globally. For the remaining processes examined
138 here (fragmentation, and zooplankton and fish vertical migration; Table 1), there is great
139 uncertainty as to how much and in which direction these may change with future warming, and
140 therefore the importance of modelling these processes for projections of future export flux is
141 unknown.

142

143 **Uncertainties in feedbacks between export flux and climate change**

144 Climate-driven changes in all of these processes can result in feedbacks to climate change
145 (Fig. 3). The magnitude, and sometimes even direction, of these feedbacks are poorly known.
146 An example of a positive feedback to climate (i.e. an initial climate-driven change ultimately
147 results in more climate change) occurs when warming increases ocean vertical temperature
148 gradients and stratification, thus decreasing nutrient supply from the deep ocean to the
149 euphotic zone (Fig. 3a). Lower nutrient availability favours smaller phytoplankton which results
150 in smaller particles that sink more slowly and thus reduce export flux, potentially ultimately
151 reducing ocean carbon storage. An example of a negative feedback to climate arises from
152 decreased seawater viscosity due to ocean warming, leading to increased particle sinking
153 speed and enhanced export fluxes that may result in greater ocean carbon sequestration (Fig.
154 3b). For other feedbacks, even the direction of the potential feedback effect is not readily
155 inferred (Fig. 3c). For example, if zooplankton migrations become less frequent, export fluxes
156 may be substantially reduced, possibly resulting in a positive feedback. If, on the other hand,
157 future ocean conditions favour increased zooplankton biomass or more frequent migrations,
158 this could result in enhanced export flux and a negative feedback on climate. Export flux is
159 also influenced by processes occurring deeper in the water column. For example, if particles
160 are remineralised more shallowly or zooplankton do not migrate as deeply in the future, more
161 nutrients will be retained in the upper ocean, which could fuel phytoplankton growth and
162 enhance export, thus partially cancelling out the initial decreases^{27,35}. The uncertainties in
163 these climate-export feedbacks further emphasise the need for improved mechanistic
164 understanding and modelling of export processes, as these feedbacks are likely important for
165 robustly quantifying global climate sensitivities.

166

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

168 Owing to the vastness of the ocean, many observations of export processes are sparse and
169 biased towards regions and seasons that are convenient to sample (e.g. the North Atlantic
170 during summer). However, the recent rapid increase in deployments of autonomous platforms
171 such as moorings, floats, gliders and surface vehicles, plus development of new sensors, is
172 fuelling a significant increase in observations with the potential to provide insights into many
173 of the export processes identified here (Supplementary Table S3).

174

175 To predict the response to a changing environment, the knowledge of states such as
176 chlorophyll or POC concentration, is insufficient: we need to understand the relationship
177 between the different processes. For example, how do zooplankton interact with and fragment
178 particles, and how does community size structure relate to sinking particle size spectra? While
179 laboratory experiments have provided some insights, it is generally uncertain how these
180 translate into the interactions occurring in the open ocean. Moreover, such experiments cannot
181 provide data on the large spatial and temporal scales needed to understand the present-day
182 magnitude and climate response of export processes. The rise of autonomous platforms offers
183 a potential solution, as frequent and semi-Lagrangian sampling of state variables over time
184 can be used to estimate rates, including carbon export and vertical sinking fluxes^{42,43}, primary
185 production and community respiration^{44,45}, and particle fragmentation²³. Additionally, multi-
186 sensor sampling from the biogeochemical-Argo float initiative⁴⁶, deployment of uncrewed
187 surface vehicles⁴⁷, and time-series programmes which integrate moored platforms and
188 autonomous vehicles⁴⁸, are driving an exponential increase in data availability. In parallel, the
189 development of new sensors is opening up new avenues of research, such as small, energy-
190 efficient camera systems with the ability to image particles and plankton *in situ* at similar
191 spatiotemporal scales and hence deduct abundance, distribution and composition of particles
192 and plankton communities^{49,50}.

193

194 Synthesizing the information from these observations, made across a wide range of
195 environmental conditions and spatio-temporal scales, into robust mechanistic
196 parameterisations that can be implemented in global models, or into global validation datasets
197 suitable to compare with model output, remains a challenge. Sparseness of data, particularly
198 with sufficient spatial and temporal coverage, lack of information on episodic fluxes, and
199 inconsistencies across different observational datasets (e.g. in the choice of export depth
200 horizon^{51,52}, definition of sinking particles, or treatment of dissolved organic matter) continue
201 to hinder integration with model development. These efforts will benefit in coming years from
202 simultaneous development of novel techniques and sensors, continuation of ship-based

203 studies to observe export flux processes in great detail at a single location and time period,
204 expansion of the global biogeochemical-Argo array and deployments of other autonomous
205 platforms, and new remote sensing capabilities.

206

207 **Conclusion**

208 This Perspective identifies 12 processes that are likely to have the greatest impact on present-
209 day and future projections of export flux, of which 10 are currently missing from the majority
210 of climate models. These processes: a) are significant contributors to export flux and/or its
211 climate feedback, b) have the potential for technology and platform developments to generate
212 sufficient data to act as a robust model constraint and/or develop new parameterisations, c)
213 are computationally tractable, and d) can be applied on the centennial, global scale of climate
214 models. We are poised on the edge of a new era in biological carbon pump studies. As a
215 community, there is now a potential route to reducing uncertainties in export flux, via data
216 synthesis activities (e.g. JETZON, Joint Exploration of the Twilight Zone Ocean Network⁵³),
217 the development of new technologies and platforms to overcome gaps in process
218 understanding, and collaboration with modellers on developing the next generation of
219 biogeochemical models.

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222 **Acknowledgements**

223 This work was supported by a European Research Council Consolidator grant (GOCART,
224 agreement number 724416) to SAH. SAH and SCLG received funding from the Natural
225 Environment Research Council through the COMICS project (Controls over Ocean
226 Mesopelagic Interior Carbon Storage; NE/M020835/1). CL acknowledges support from the
227 Swiss National Science Foundation under grant 174124. HIP acknowledges support from the
228 U.S. National Science Foundation (Award #1946072). ELC was supported by an Imperial
229 College Research Fellowship, funded by Imperial College London.

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232 **References**

- 233 1. De La Rocha, C. L. The biological pump. in *Treatise on Geochemistry (Second*
234 *Edition)* 83–111 (Pergamon, 2006).
- 235 2. Kwon, E. Y., Primeau, F. & Sarmiento, J. L. The impact of remineralization depth on
236 the air-sea carbon balance. *Nat. Geosci.* **2**, 630–635 (2009).
- 237 3. Henson, S. A., Sanders, R. & Madsen, E. Global patterns in efficiency of particulate
238 organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles* **26**,
239 n/a-n/a (2012).

- 240 4. Marsay, C. M. *et al.* Attenuation of sinking particulate organic carbon flux through the
241 mesopelagic ocean. *Proc. Natl. Acad. Sci.* **112**, 1089–1094 (2015).
- 242 5. Laufkötter, C. *et al.* Projected decreases in future marine export production: the role of
243 the carbon flux through the upper ocean ecosystem. *Biogeosciences* **13**, 4023–4047
244 (2016).
- 245 6. Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A. & Weber, T. Multi-faceted particle
246 pumps drive carbon sequestration in the ocean. *Nature* **568**, 327–335 (2019).
- 247 7. Waite, A., Fisher, A., Thompson, P. & Harrison, P. Sinking rate versus cell volume
248 relationships illuminate sinking rate control mechanisms in marine diatoms. *Mar. Ecol.*
249 *Prog. Ser.* **157**, 97–108 (1997).
- 250 8. Iversen, M. H. & Lampitt, R. S. Size does not matter after all: No evidence for a size-
251 sinking relationship for marine snow. *Prog. Oceanogr.* **189**, 102445 (2020).
- 252 9. McDonnell, A. M. P. & Buesseler, K. O. Variability in the average sinking velocity of
253 marine particles. *Limnol. Oceanogr.* **55**, 2085–2096 (2010).
- 254 10. Francois, R., Honjo, S., Krishfield, R. & Manganini, S. Factors controlling the flux of
255 organic carbon to the bathypelagic zone of the ocean. *Global Biogeochem. Cycles* **16**,
256 34-1-34–20 (2002).
- 257 11. Le Moigne, F. A. C., Pabortsava, K., Marcinko, C. L. J., Martin, P. & Sanders, R. J.
258 Where is mineral ballast important for surface export of particulate organic carbon in
259 the ocean? *Geophys. Res. Lett.* **41**, 8460–8468 (2014).
- 260 12. Seebah, S., Fairfield, C., Ullrich, M. S. & Passow, U. Aggregation and Sedimentation
261 of *Thalassiosira weissflogii* (diatom) in a Warmer and More Acidified Future Ocean.
262 *PLoS One* **9**, e112379 (2014).
- 263 13. Mari, X., Passow, U., Migon, C., Burd, A. B. & Legendre, L. Transparent exopolymer
264 particles: Effects on carbon cycling in the ocean. *Prog. Oceanogr.* **151**, 13–37 (2017).
- 265 14. Bach, L. T. *et al.* An approach for particle sinking velocity measurements in the 3-400
266 μm size range and considerations on the effect of temperature on sinking rates. *Mar.*
267 *Biol.* **159**, 1853–1864 (2012).
- 268 15. Taucher, J., Bach, L. T., Riebesell, U. & Oschlies, A. The viscosity effect on marine
269 particle flux: A climate relevant feedback mechanism. *Global Biogeochem. Cycles* **28**,
270 415–422 (2014).
- 271 16. Devol, A. H. & Hartnett, H. E. Role of the oxygen-deficient zone in transfer of organic
272 carbon to the deep ocean. *Limnol. Oceanogr.* **46**, 1684–1690 (2001).
- 273 17. Laufkötter, C., John, J. G., Stock, C. A. & Dunne, J. P. Temperature and oxygen
274 dependence of the remineralization of organic matter. *Global Biogeochem. Cycles* **31**,
275 1038–1050 (2017).
- 276 18. López-Urrutia, Á. & Morán, X. A. G. RESOURCE LIMITATION OF BACTERIAL

- 277 PRODUCTION DISTORTS THE TEMPERATURE DEPENDENCE OF OCEANIC
278 CARBON CYCLING. *Ecology* **88**, 817–822 (2007).
- 279 19. Belcher, A. *et al.* The role of particle associated microbes in remineralization of fecal
280 pellets in the upper mesopelagic of the Scotia Sea, Antarctica. *Limnol. Oceanogr.* **61**,
281 1049–1064 (2016).
- 282 20. Herndl, G. J. & Reinthaler, T. Microbial control of the dark end of the biological pump.
283 *Nat. Geosci.* **6**, 718–724 (2013).
- 284 21. Burd, A. B. & Jackson, G. A. Particle Aggregation. *Ann. Rev. Mar. Sci.* **1**, 65–90
285 (2009).
- 286 22. Cavan, E. L., Henson, S. A., Belcher, A. & Sanders, R. Role of zooplankton in
287 determining the efficiency of the biological carbon pump. *Biogeosciences* **14**, 177–186
288 (2017).
- 289 23. Briggs, N., Dall’Olmo, G. & Claustre, H. Major role of particle fragmentation in
290 regulating biological sequestration of CO₂ by the oceans. *Science (80-.)*. **367**, 791–
291 793 (2020).
- 292 24. Steinberg, D. K. & Landry, M. R. Zooplankton and the Ocean Carbon Cycle. *Ann.*
293 *Rev. Mar. Sci.* **9**, 413–444 (2017).
- 294 25. Jónasdóttir, S. H., Visser, A. W., Richardson, K. & Heath, M. R. Seasonal copepod
295 lipid pump promotes carbon sequestration in the deep North Atlantic. *Proc. Natl.*
296 *Acad. Sci.* **112**, 12122–12126 (2015).
- 297 26. Archibald, K. M., Siegel, D. A. & Doney, S. C. Modeling the Impact of Zooplankton
298 Diel Vertical Migration on the Carbon Export Flux of the Biological Pump. *Global*
299 *Biogeochem. Cycles* **33**, 181–199 (2019).
- 300 27. Gorgues, T., Aumont, O. & Memery, L. Simulated Changes in the Particulate Carbon
301 Export Efficiency due to Diel Vertical Migration of Zooplankton in the North Atlantic.
302 *Geophys. Res. Lett.* **46**, 5387–5395 (2019).
- 303 28. Aumont, O., Maury, O., Lefort, S. & Bopp, L. Evaluating the Potential Impacts of the
304 Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. *Global*
305 *Biogeochem. Cycles* **32**, 1622–1643 (2018).
- 306 29. Stukel, M., Ohman, M., Benitez-Nelson, C. & Landry, M. Contributions of
307 mesozooplankton to vertical carbon export in a coastal upwelling system. *Mar. Ecol.*
308 *Prog. Ser.* **491**, 47–65 (2013).
- 309 30. Saba, G. K. *et al.* Toward a better understanding of fish-based contribution to ocean
310 carbon flux. *Limnol. Oceanogr.* Ino.11709 (2021). doi:10.1002/Ino.11709
- 311 31. Dever, M., Nicholson, D., Omand, M. M. & Mahadevan, A. Size-Differentiated Export
312 Flux in Different Dynamical Regimes in the Ocean. *Global Biogeochem. Cycles* **35**,
313 (2021).

- 314 32. Harrison, C. S., Long, M. C., Lovenduski, N. S. & Moore, J. K. Mesoscale Effects on
315 Carbon Export: A Global Perspective. *Global Biogeochem. Cycles* **32**, 680–703
316 (2018).
- 317 33. Bopp, L., Aumont, O., Cadule, P., Alvain, S. & Gehlen, M. Response of diatoms
318 distribution to global warming and potential implications: A global model study.
319 *Geophys. Res. Lett.* **32**, n/a-n/a (2005).
- 320 34. Laufkötter, C. *et al.* Projected decreases in future marine export production: the role of
321 the carbon flux through the upper ocean ecosystem. *Biogeosciences* **13**, 4023–4047
322 (2016).
- 323 35. Leung, S. W., Weber, T., Cram, J. A. & Deutsch, C. Variable particle size distributions
324 reduce the sensitivity of global export flux to climate change. *Biogeosciences* **18**,
325 229–250 (2021).
- 326 36. Cavan, E. & Boyd, P. Effect of anthropogenic warming on microbial respiration and
327 particulate organic carbon export rates in the sub-Antarctic Southern Ocean. *Aquat.*
328 *Microb. Ecol.* **82**, 111–127 (2018).
- 329 37. Cavan, E. L., Henson, S. A. & Boyd, P. W. The Sensitivity of Subsurface Microbes to
330 Ocean Warming Accentuates Future Declines in Particulate Carbon Export. *Front.*
331 *Ecol. Evol.* **6**, (2019).
- 332 38. Heinze, C. Simulating oceanic CaCO₃ export production in the greenhouse. *Geophys.*
333 *Res. Lett.* **31**, (2004).
- 334 39. Hofmann, M. & Schellnhuber, H.-J. Oceanic acidification affects marine carbon pump
335 and triggers extended marine oxygen holes. *Proc. Natl. Acad. Sci. U. S. A.* **106**,
336 3017–3022 (2009).
- 337 40. Tanioka, T. & Matsumoto, K. Buffering of Ocean Export Production by Flexible
338 Elemental Stoichiometry of Particulate Organic Matter. *Global Biogeochem. Cycles*
339 **31**, 1528–1542 (2017).
- 340 41. Wohlers, J. *et al.* Changes in biogenic carbon flow in response to sea surface
341 warming. *Proc. Natl. Acad. Sci.* **106**, 7067–7072 (2009).
- 342 42. Briggs, N. *et al.* High-resolution observations of aggregate flux during a sub-polar
343 North Atlantic spring bloom. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **58**, 1031–
344 1039 (2011).
- 345 43. Estapa, M. L., Feen, M. L. & Breves, E. Direct Observations of Biological Carbon
346 Export From Profiling Floats in the Subtropical North Atlantic. *Global Biogeochem.*
347 *Cycles* **33**, 282–300 (2019).
- 348 44. Gordon, C., Fennel, K., Richards, C., Shay, L. K. & Brewster, J. K. Can ocean
349 community production and respiration be determined by measuring high-frequency
350 oxygen profiles from autonomous floats? *Biogeosciences* **17**, 4119–4134 (2020).

- 351 45. Yang, B. *et al.* In Situ Estimates of Net Primary Production in the Western North
352 Atlantic With Argo Profiling Floats. *J. Geophys. Res. Biogeosciences* **126**, (2021).
- 353 46. Claustre, H., Johnson, K. S. & Takeshita, Y. Observing the Global Ocean with
354 Biogeochemical-Argo. *Ann. Rev. Mar. Sci.* **12**, 23–48 (2020).
- 355 47. Meinig, C. *et al.* Public–Private Partnerships to Advance Regional Ocean-Observing
356 Capabilities: A Saildrone and NOAA-PMEL Case Study and Future Considerations to
357 Expand to Global Scale Observing. *Front. Mar. Sci.* **6**, (2019).
- 358 48. Trowbridge, J. *et al.* The Ocean Observatories Initiative. *Front. Mar. Sci.* **6**, (2019).
- 359 49. Lombard, F. *et al.* Globally Consistent Quantitative Observations of Planktonic
360 Ecosystems. *Front. Mar. Sci.* **6**, (2019).
- 361 50. Giering, S. L. C. *et al.* Sinking Organic Particles in the Ocean—Flux Estimates From
362 in situ Optical Devices. *Front. Mar. Sci.* **6**, (2020).
- 363 51. Palevsky, H. I. & Doney, S. C. Sensitivity of 21st Century Ocean Carbon Export Flux
364 Projections to the Choice of Export Depth Horizon. *Global Biogeochem. Cycles* **35**,
365 (2021).
- 366 52. Buesseler, K. O., Boyd, P. W., Black, E. E. & Siegel, D. A. Metrics that matter for
367 assessing the ocean biological carbon pump. *Proc. Natl. Acad. Sci.* **117**, 9679–9687
368 (2020).
- 369 53. Martin, A. *et al.* The oceans’ twilight zone must be studied now, before it is too late.
370 *Nature* **580**, 26–28 (2020).
- 371 54. Giering, S. L. C. *et al.* Reconciliation of the carbon budget in the ocean’s twilight zone.
372 *Nature* **507**, 480–483 (2014).
- 373 55. Boyd, P. W. Toward quantifying the response of the oceans’ biological pump to
374 climate change. *Front. Mar. Sci.* **2**, (2015).
- 375 56. Weber, T. & Bianchi, D. Efficient Particle Transfer to Depth in Oxygen Minimum Zones
376 of the Pacific and Indian Oceans. *Front. Earth Sci.* **8**, (2020).
- 377 57. Wilson, J. D., Barker, S. & Ridgwell, A. Assessment of the spatial variability in
378 particulate organic matter and mineral sinking fluxes in the ocean interior: Implications
379 for the ballast hypothesis. *Global Biogeochem. Cycles* **26**, n/a-n/a (2012).
- 380 58. Iversen, M. H. & Ploug, H. Temperature effects on carbon-specific respiration rate and
381 sinking velocity of diatom aggregates – potential implications for deep ocean export
382 processes. *Biogeosciences* **10**, 4073–4085 (2013).
- 383 59. Resplandy, L., Lévy, M. & McGillicuddy, D. J. Effects of Eddy-Driven Subduction on
384 Ocean Biological Carbon Pump. *Global Biogeochem. Cycles* **33**, 1071–1084 (2019).
- 385 60. Riebesell, U. *et al.* Enhanced biological carbon consumption in a high CO₂ ocean.
386 *Nature* **450**, 545–548 (2007).
- 387 61. Taucher, J. *et al.* Enhanced carbon overconsumption in response to increasing

388 temperatures during a mesocosm experiment. *Biogeosciences* **9**, 3531–3545 (2012).

389

390 **Figure Legends**

391 **Figure 1: Uncertain response of export flux to climate change.** (Left) Percent change in
392 export flux in 19 coupled climate models in the CMIP6 archive, forced with the SSP5-8.5
393 scenario. Percent change is calculated with respect to the mean of years 1850-1900 for
394 each model, and ranges from +1.8 to -41%. Multi-model mean is shown as a thick black
395 line. (Right) Multi-model mean change in export flux ($\text{gC m}^{-2} \text{ yr}^{-1}$) between the 2080-2100
396 average and the 1850-1900 average. Hatching indicates where 90% of models (i.e. at least
397 17 of 19) agree on the sign of the change in export flux.

398

399 **Figure 2: Potential response of export processes to climate change.** Export will change
400 in response to increasing temperature, decreasing oxygen concentration and ocean
401 acidification. (a) A shift to smaller phytoplankton species may lead to smaller particles and
402 less export. (b) Higher primary production may allow higher export flux, though complex
403 feedbacks, e.g. via nutrient recycling, lead to high uncertainties for predicted export. (c) The
404 rate of microbial remineralization, which produces smaller particles that are less likely to be
405 exported, should increase due to warming, yet may decrease owing to less oxygen
406 availability. (d) Smaller zooplankton that produce smaller, slower sinking faecal pellets are
407 expected to become more prevalent, hence likely leading to a decrease in export.
408 Alternatively, the expected decrease in zooplankton abundance will lead to less particle
409 fragmentation, which may result in more large particles that are more likely to be exported.
410 (e) Water density is expected to decrease, allowing particles to sink faster, hence leading to
411 higher export rates. (f) Ocean acidification is expected to reduce the abundance of mineral
412 ballast-producing species, such as coccolithophores, which in turn may result in less dense
413 particles that sink more slowly and are less likely to be exported.

414

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

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

418

419 **Table 1: Influence of omitting specific mechanisms on modelled present-day and future**
 420 **export flux.** We surveyed the IPCC CMIP6 archive for global climate models which
 421 incorporate explicit marine biogeochemistry (total of 19; Supplementary Table S4). The model
 422 structure was examined to determine whether the processes we identify as important to export
 423 flux are included. We also assess the direction of bias in present-day model estimates of
 424 export flux if processes are excluded, and the direction of change in future global export flux
 425 due to the same processes. Full details of the model assessment are in Supplementary Table
 426 S1, and the detailed rationale for our prioritisation is in Supplementary Table S2.

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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			23,54
Zooplankton vertical migration	 19  0			26–28
Phytoplankton size effect on sinking (*4)	 13  6			34,35,55
Temperature dependent remineralisation	 8  11			4,17
Oxygen dependent remineralisation	 9  10			16,17,56
Viscosity of seawater	 18  1			15
Mineral ballasting	 14  5			11,39,57
Mineral protection	 14  5			58
Eddy pump (*5)	 19  0			6,32,59
Fish vertical migration	 19  0			30
Particle stickiness (including transparent exopolymers)	 19  0			12,13,41
Variable stoichiometry in sinking particles	 18  1			40,60,61

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

433 (*2) Plus (minus) symbols indicate models likely overestimate (underestimate) export flux if
434 this process is missing, with the size of the symbol indicating the potential influence of the
435 missing process. Question marks indicate that either the global-scale effect, or the size of
436 the effect, is unknown.
437 (*3) Up (down) arrows indicate that this process is likely to increase (decrease) future export
438 flux, with the size of the symbol indicating the possible influence of the missing process.
439 Question marks indicate that either the global-scale effect, or the size of the effect, is
440 unknown.
441 (*4) If sinking speed does not change with phytoplankton community composition, the model
442 is classed as a “No” for this category.
443 (*5) Model resolution varies from $\frac{1}{4}$ - 1 degree, and therefore none of the models are eddy-
444 resolving.
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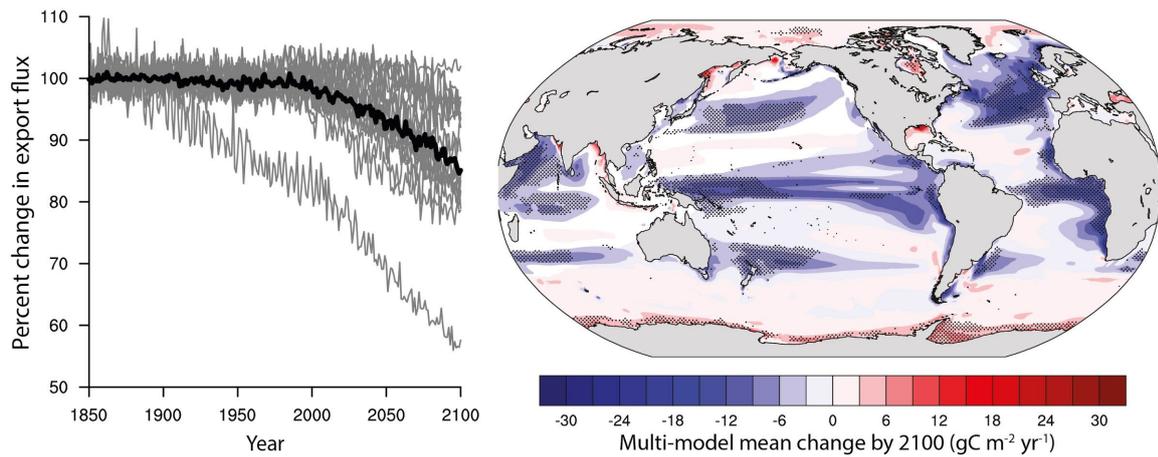


Figure 1: Uncertain response of export flux to climate change. (Left) Percent change in export flux in 19 coupled climate models in the CMIP6 archive, forced with the SSP5-8.5 scenario. Percent change is calculated with respect to the mean of years 1850-1900 for each model, and ranges from +1.8 to -41%. Multi-model mean is shown as a thick black line. (Right) Multi-model mean change in export flux ($\text{gC m}^{-2} \text{ yr}^{-1}$) 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.

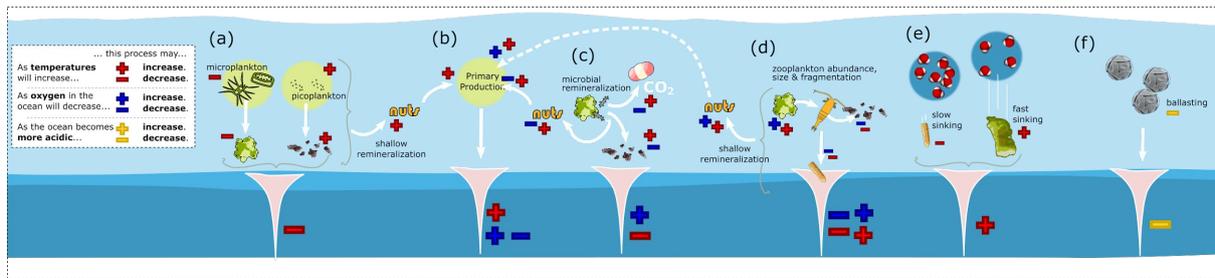


Figure 2: Potential response of export processes to climate change. Export will change in response to increasing temperature, decreasing oxygen concentration and ocean acidification. (a) A shift to smaller phytoplankton species may lead to smaller particles and less export. (b) Higher primary production may allow higher export flux, though complex feedbacks, e.g. via nutrient recycling, lead to high uncertainties for predicted export. (c) The rate of microbial remineralization, which produces smaller particles that are less likely to be exported, should increase due to warming, yet may decrease owing to less oxygen availability. (d) Smaller zooplankton that produce smaller, slower sinking faecal pellets are expected to become more prevalent, hence likely leading to a decrease in export. Alternatively, the expected decrease in zooplankton abundance will lead to less particle fragmentation, which may result in more large particles that are more likely to be exported. (e) Water density is expected to decrease, allowing particles to sink faster, hence leading to higher export rates. (f) Ocean acidification is expected to reduce the abundance of mineral ballast-producing species, such as coccolithophores, which in turn may result in less dense particles that sink more slowly and are less likely to be exported.

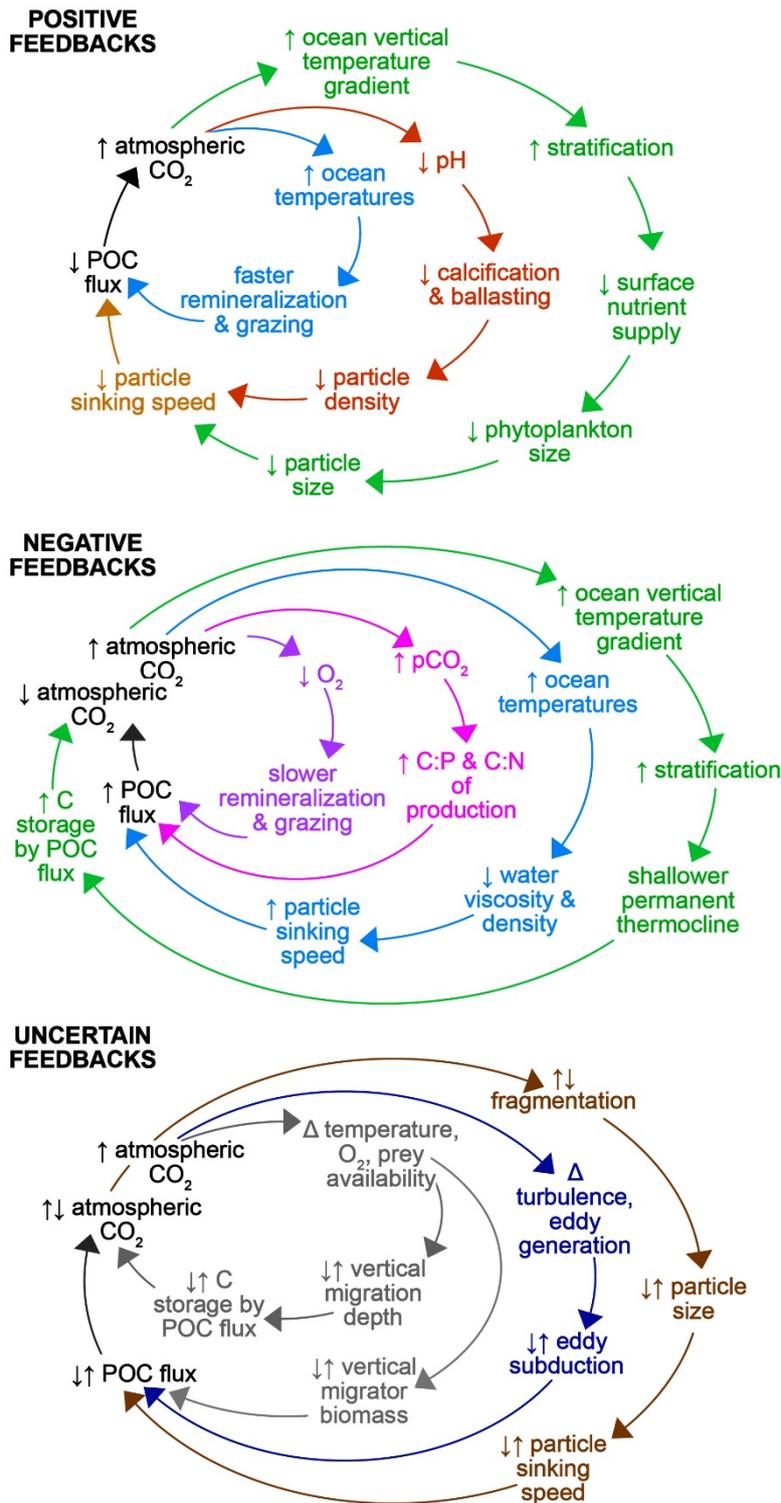


Figure 3: Feedbacks between changing export flux mechanisms and climate. Mechanisms are separated into those which are likely to have a positive, negative or uncertain feedback to climate.