

Uncertain response of ocean biological carbon export in a changing world

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Abstract

The transfer of organic carbon from the upper to the deep ocean by particulate export flux is the starting point for the long term storage of photosynthetically-fixed carbon. This “biological carbon pump” is a critical component of the global carbon cycle, reducing atmospheric CO₂ levels by ~ 200 ppm relative to a world without export flux. This carbon flux also fuels the productivity of the mesopelagic zone, including significant fisheries. Here we show that, despite its importance for understanding future ocean carbon cycling, that Earth System Models disagree on the projected response of the global export flux to climate change, with estimates ranging from -41% to +1.8%. Fundamental constraints to understanding export flux arise because a myriad of interconnected processes make the biological carbon pump challenging to both observe and model. Our synthesis prioritises the processes likely to be most important to include in modern-day estimates (particle fragmentation and zooplankton vertical migration) and future projections (phytoplankton and particle size spectra, and temperature-dependent remineralization) of export. We also identify the observations required to achieve more robust characterisation, and hence improved model parameterization, of export flux, and thus reduce uncertainties in current and future estimates in the overall cycling of carbon in the ocean.

Main text:

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

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

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

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

Uncertainties in present-day export flux processes

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

Fragmentation from large to small particles, both physically and biologically mediated, promotes microbial colonisation and POC remineralization, due to the larger ratio of surface area to volume of small particles^{22,26}. Recent observations from the biogeochemical-Argo float array suggest that fragmentation could drive up to 50% of mid-water remineralization²³. Fragmentation is included in only one of the current climate models (Table 1) due to a lack of understanding of its drivers and lack of observations to constrain it.

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

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

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

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

Uncertainties in response of export flux to climate change

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

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

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

Uncertainties in feedbacks between export and climate change

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

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

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

A bright future for understanding export processes

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

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

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

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

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

Conclusion

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

Competing Interests Statement

The authors declare no competing interests.

Author contributions

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

Data availability

All CMIP6 model output used in our analysis is freely available from <https://esgf-data.dkrz.de/projects/cmip6-dkrz/>

References

1. De La Rocha, C. L. The biological pump. in *Treatise on Geochemistry (Second Edition)* 83–111 (Pergamon, 2006).
2. Kwon, E. Y., Primeau, F. & Sarmiento, J. L. The impact of remineralization depth on the air-sea carbon balance. *Nat. Geosci.* **2**, 630–635 (2009).
3. Henson, S. A., Sanders, R. & Madsen, E. Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles* **26**, n/a-n/a (2012).
4. Marsay, C. M. *et al.* Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci.* **112**, 1089–1094 (2015).
5. Laufkötter, C. *et al.* Projected decreases in future marine export production: the role of the carbon flux through the upper ocean ecosystem. *Biogeosciences* **13**, 4023–4047 (2016).
6. Séférian, R. *et al.* Tracking Improvement in Simulated Marine Biogeochemistry

- Between CMIP5 and CMIP6. *Curr. Clim. Chang. Reports* **6**, 95–119 (2020).
7. Kwiatkowski, L. *et al.* Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* **17**, 3439–3470 (2020).
 8. Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A. & Weber, T. Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* **568**, 327–335 (2019).
 9. Waite, A., Fisher, A., Thompson, P. & Harrison, P. Sinking rate versus cell volume relationships illuminate sinking rate control mechanisms in marine diatoms. *Mar. Ecol. Prog. Ser.* **157**, 97–108 (1997).
 10. Iversen, M. H. & Lampitt, R. S. Size does not matter after all: No evidence for a size-sinking relationship for marine snow. *Prog. Oceanogr.* **189**, 102445 (2020).
 11. McDonnell, A. M. P. & Buesseler, K. O. Variability in the average sinking velocity of marine particles. *Limnol. Oceanogr.* **55**, 2085–2096 (2010).
 12. Francois, R., Honjo, S., Krishfield, R. & Manganini, S. Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. *Global Biogeochem. Cycles* **16**, 34-1-34–20 (2002).
 13. Le Moigne, F. A. C., Pabortsava, K., Marcinko, C. L. J., Martin, P. & Sanders, R. J. Where is mineral ballast important for surface export of particulate organic carbon in the ocean? *Geophys. Res. Lett.* **41**, 8460–8468 (2014).
 14. Maerz, J., Six, K. D., Stemmler, I., Ahmerkamp, S. & Ilyina, T. Microstructure and composition of marine aggregates as co-determinants for vertical particulate organic carbon transfer in the global ocean. *Biogeosciences* **17**, 1765–1803 (2020).

15. Seebah, S., Fairfield, C., Ullrich, M. S. & Passow, U. Aggregation and Sedimentation of *Thalassiosira weissflogii* (diatom) in a Warmer and More Acidified Future Ocean. *PLoS One* **9**, e112379 (2014).
16. Mari, X., Passow, U., Migon, C., Burd, A. B. & Legendre, L. Transparent exopolymer particles: Effects on carbon cycling in the ocean. *Prog. Oceanogr.* **151**, 13–37 (2017).
17. Bach, L. T. *et al.* An approach for particle sinking velocity measurements in the 3–400 μm size range and considerations on the effect of temperature on sinking rates. *Mar. Biol.* **159**, 1853–1864 (2012).
18. Taucher, J., Bach, L. T., Riebesell, U. & Oschlies, A. The viscosity effect on marine particle flux: A climate relevant feedback mechanism. *Global Biogeochem. Cycles* **28**, 415–422 (2014).
19. Devol, A. H. & Hartnett, H. E. Role of the oxygen-deficient zone in transfer of organic carbon to the deep ocean. *Limnol. Oceanogr.* **46**, 1684–1690 (2001).
20. Laufkötter, C., John, J. G., Stock, C. A. & Dunne, J. P. Temperature and oxygen dependence of the remineralization of organic matter. *Global Biogeochem. Cycles* **31**, 1038–1050 (2017).
21. López-Urrutia, Á. & Morán, X. A. G. RESOURCE LIMITATION OF BACTERIAL PRODUCTION DISTORTS THE TEMPERATURE DEPENDENCE OF OCEANIC CARBON CYCLING. *Ecology* **88**, 817–822 (2007).
22. Cavan, E. L., Henson, S. A., Belcher, A. & Sanders, R. Role of zooplankton in determining the efficiency of the biological carbon pump. *Biogeosciences* **14**, 177–186 (2017).
23. Briggs, N., Dall’Olmo, G. & Claustre, H. Major role of particle fragmentation in

- regulating biological sequestration of CO₂ by the oceans. *Science* (80-.). **367**, 791–793 (2020).
24. Belcher, A. *et al.* The role of particle associated microbes in remineralization of fecal pellets in the upper mesopelagic of the Scotia Sea, Antarctica. *Limnol. Oceanogr.* **61**, 1049–1064 (2016).
 25. Herndl, G. J. & Reinthaler, T. Microbial control of the dark end of the biological pump. *Nat. Geosci.* **6**, 718–724 (2013).
 26. Burd, A. B. & Jackson, G. A. Particle Aggregation. *Ann. Rev. Mar. Sci.* **1**, 65–90 (2009).
 27. Steinberg, D. K. & Landry, M. R. Zooplankton and the Ocean Carbon Cycle. *Ann. Rev. Mar. Sci.* **9**, 413–444 (2017).
 28. Jónasdóttir, S. H., Visser, A. W., Richardson, K. & Heath, M. R. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proc. Natl. Acad. Sci.* **112**, 12122–12126 (2015).
 29. Archibald, K. M., Siegel, D. A. & Doney, S. C. Modeling the Impact of Zooplankton Diel Vertical Migration on the Carbon Export Flux of the Biological Pump. *Global Biogeochem. Cycles* **33**, 181–199 (2019).
 30. Gorgues, T., Aumont, O. & Memery, L. Simulated Changes in the Particulate Carbon Export Efficiency due to Diel Vertical Migration of Zooplankton in the North Atlantic. *Geophys. Res. Lett.* **46**, 5387–5395 (2019).
 31. Aumont, O., Maury, O., Lefort, S. & Bopp, L. Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. *Global Biogeochem. Cycles* **32**, 1622–1643 (2018).
 32. Stukel, M., Ohman, M., Benitez-Nelson, C. & Landry, M. Contributions of mesozooplankton to vertical carbon export in a coastal upwelling system. *Mar.*

- Ecol. Prog. Ser.* **491**, 47–65 (2013).
33. Saba, G. K. *et al.* Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* Ino.11709 (2021). doi:10.1002/Ino.11709
 34. Luo, J. Y. *et al.* Gelatinous Zooplankton-Mediated Carbon Flows in the Global Oceans: A Data-Driven Modeling Study. *Global Biogeochem. Cycles* **34**, (2020).
 35. Ward, B. A. & Follows, M. J. Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux. *Proc. Natl. Acad. Sci.* **113**, 2958–2963 (2016).
 36. Dutkiewicz, S. *et al.* Dimensions of marine phytoplankton diversity. *Biogeosciences* **17**, 609–634 (2020).
 37. Dever, M., Nicholson, D., Omand, M. M. & Mahadevan, A. Size-Differentiated Export Flux in Different Dynamical Regimes in the Ocean. *Global Biogeochem. Cycles* **35**, (2021).
 38. Harrison, C. S., Long, M. C., Lovenduski, N. S. & Moore, J. K. Mesoscale Effects on Carbon Export: A Global Perspective. *Global Biogeochem. Cycles* **32**, 680–703 (2018).
 39. Krumhardt, K. M. *et al.* Coccolithophore Growth and Calcification in an Acidified Ocean: Insights From Community Earth System Model Simulations. *J. Adv. Model. Earth Syst.* **11**, 1418–1437 (2019).
 40. Bopp, L., Aumont, O., Cadule, P., Alvain, S. & Gehlen, M. Response of diatoms distribution to global warming and potential implications: A global model study. *Geophys. Res. Lett.* **32**, n/a-n/a (2005).
 41. Leung, S. W., Weber, T., Cram, J. A. & Deutsch, C. Variable particle size distributions reduce the sensitivity of global export flux to climate change.

- Biogeosciences* **18**, 229–250 (2021).
42. Cavan, E. & Boyd, P. Effect of anthropogenic warming on microbial respiration and particulate organic carbon export rates in the sub-Antarctic Southern Ocean. *Aquat. Microb. Ecol.* **82**, 111–127 (2018).
 43. Cavan, E. L., Henson, S. A. & Boyd, P. W. The Sensitivity of Subsurface Microbes to Ocean Warming Accentuates Future Declines in Particulate Carbon Export. *Front. Ecol. Evol.* **6**, (2019).
 44. Heinze, C. Simulating oceanic CaCO₃ export production in the greenhouse. *Geophys. Res. Lett.* **31**, (2004).
 45. Hofmann, M. & Schellnhuber, H.-J. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 3017–3022 (2009).
 46. Tanioka, T. & Matsumoto, K. Buffering of Ocean Export Production by Flexible Elemental Stoichiometry of Particulate Organic Matter. *Global Biogeochem. Cycles* **31**, 1528–1542 (2017).
 47. Wohlers, J. *et al.* Changes in biogenic carbon flow in response to sea surface warming. *Proc. Natl. Acad. Sci.* **106**, 7067–7072 (2009).
 48. Iversen, M. H. & Ploug, H. Temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates – potential implications for deep ocean export processes. *Biogeosciences* **10**, 4073–4085 (2013).
 49. Briggs, N. *et al.* High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **58**, 1031–1039 (2011).
 50. Estapa, M. L., Feen, M. L. & Breves, E. Direct Observations of Biological Carbon Export From Profiling Floats in the Subtropical North Atlantic. *Global*

- Biogeochem. Cycles* **33**, 282–300 (2019).
51. Gordon, C., Fennel, K., Richards, C., Shay, L. K. & Brewster, J. K. Can ocean community production and respiration be determined by measuring high-frequency oxygen profiles from autonomous floats? *Biogeosciences* **17**, 4119–4134 (2020).
 52. Yang, B. *et al.* In Situ Estimates of Net Primary Production in the Western North Atlantic With Argo Profiling Floats. *J. Geophys. Res. Biogeosciences* **126**, (2021).
 53. Claustre, H., Johnson, K. S. & Takeshita, Y. Observing the Global Ocean with Biogeochemical-Argo. *Ann. Rev. Mar. Sci.* **12**, 23–48 (2020).
 54. Meinig, C. *et al.* Public–Private Partnerships to Advance Regional Ocean-Observing Capabilities: A Saildrone and NOAA-PMEL Case Study and Future Considerations to Expand to Global Scale Observing. *Front. Mar. Sci.* **6**, (2019).
 55. Trowbridge, J. *et al.* The Ocean Observatories Initiative. *Front. Mar. Sci.* **6**, (2019).
 56. Lombard, F. *et al.* Globally Consistent Quantitative Observations of Planktonic Ecosystems. *Front. Mar. Sci.* **6**, (2019).
 57. Giering, S. L. C. *et al.* Sinking Organic Particles in the Ocean—Flux Estimates From in situ Optical Devices. *Front. Mar. Sci.* **6**, (2020).
 58. Cram, J. A. *et al.* Slow particle remineralization, rather than suppressed disaggregation, drives efficient flux transfer through the Eastern Tropical North Pacific Oxygen Deficient Zone. *Global Biogeochem. Cycles*
doi:10.1002/essoar.10507130.4
 59. Palevsky, H. I. & Doney, S. C. Sensitivity of 21st Century Ocean Carbon

- Export Flux Projections to the Choice of Export Depth Horizon. *Global Biogeochem. Cycles* **35**, (2021).
60. Buesseler, K. O., Boyd, P. W., Black, E. E. & Siegel, D. A. Metrics that matter for assessing the ocean biological carbon pump. *Proc. Natl. Acad. Sci.* **117**, 9679–9687 (2020).
 61. Mayor, D. J., Gentleman, W. C. & Anderson, T. R. Ocean carbon sequestration: Particle fragmentation by copepods as a significant unrecognised factor?: Explicitly representing the role of copepods in biogeochemical models may fundamentally improve understanding of future ocean carbon storage. *BioEssays* **42**, (2020).
 62. Tanioka, T., Matsumoto, K. & Lomas, M. W. Drawdown of Atmospheric pCO₂ via Variable Particle Flux Stoichiometry in the Ocean Twilight Zone. *Geophys. Res. Lett.* (2021). doi:10.1029/2021GL094924
 63. Martin, A. *et al.* The oceans' twilight zone must be studied now, before it is too late. *Nature* **580**, 26–28 (2020).
 64. Eyring, V. *et al.* Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geosci. Model Dev.* **9**, 1937–1958 (2016).
 65. Giering, S. L. C. *et al.* Reconciliation of the carbon budget in the ocean's twilight zone. *Nature* **507**, 480–483 (2014).
 66. Boyd, P. W. Toward quantifying the response of the oceans' biological pump to climate change. *Front. Mar. Sci.* **2**, (2015).
 67. Kriest, I. & Oschlies, A. On the treatment of particulate organic matter sinking in large-scale models of marine biogeochemical cycles. *Biogeosciences* **5**, 55–72 (2008).

68. Weber, T. & Bianchi, D. Efficient Particle Transfer to Depth in Oxygen Minimum Zones of the Pacific and Indian Oceans. *Front. Earth Sci.* **8**, (2020).
69. Wilson, J. D., Barker, S. & Ridgwell, A. Assessment of the spatial variability in particulate organic matter and mineral sinking fluxes in the ocean interior: Implications for the ballast hypothesis. *Global Biogeochem. Cycles* **26**, n/a-n/a (2012).
70. Iversen, M. H. & Robert, M. L. Ballasting effects of smectite on aggregate formation and export from a natural plankton community. *Mar. Chem.* **175**, 18–27 (2015).
71. Resplandy, L., Lévy, M. & McGillicuddy, D. J. Effects of Eddy-Driven Subduction on Ocean Biological Carbon Pump. *Global Biogeochem. Cycles* **33**, 1071–1084 (2019).
72. Riebesell, U. *et al.* Enhanced biological carbon consumption in a high CO₂ ocean. *Nature* **450**, 545–548 (2007).
73. Taucher, J. *et al.* Enhanced carbon overconsumption in response to increasing temperatures during a mesocosm experiment. *Biogeosciences* **9**, 3531–3545 (2012).

Figure Legends



























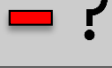

















Figure 1: Uncertain response of export flux to climate change. (a) Percent change and (b) absolute change in globally-averaged export flux in 19 coupled climate models forced with the SSP5-8.5 scenario⁶⁴ taken from the CMIP6 archive (<https://esgf-data.dkrz.de/projects/cmip6-dkrz/>). Percent change is calculated with respect to the mean of years 1850-1900 for each model. Multi-model mean is shown as a thick black line. Data in panels (a) and (b) are available as a Source Data file.





(c) Multi-model mean change in export flux between the averages of 2080-2100 and 1850-1900. 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. POC = particulate organic carbon.

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

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			23,65
Zooplankton vertical migration	 19  0			29–31
Phytoplankton size effect on sinking (*4)	 13  6			5,41,66,67
Temperature dependent remineralization	 8  11			4,20
Oxygen dependent remineralization	 9  10			19,20,68
Viscosity of seawater	 18  1			18
Mineral ballasting	 14  5			13,45,69
Mineral protection	 14  5			48,70
Eddy pump (*5)	 19  0			8,38,71
Fish vertical migration	 19  0			33
Particle stickiness (including transparent exopolymers)	 19  0			15,16,47

Variable stoichiometry in sinking particles	 18  1			46,72,73
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(*1) Summary of the 19 climate models included in the IPCC CMIP6 archive which include a marine biogeochemistry component.

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

(*3) Up (down) arrows indicate that this process is likely to increase (decrease) future export flux, with the size of the symbol indicating the possible influence of the missing process. Question marks indicate that either the global-scale effect, or the size of the effect, is unknown.

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

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