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

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Abstract

The export flux of organic carbon from the upper ocean is the starting point of the transfer and long term storage of photosynthetically-fixed carbon in the deep ocean. This "biological carbon pump" is a significant component of the global carbon cycle, reducing atmospheric CO2 levels by ˜ 50%. Carbon exported out of the upper ocean also fuels the productivity of the mesopelagic zone, including significant fisheries. Despite its importance, export flux is poorly constrained in Earth System Models, with the modelled range in projected future global-mean changes due to climate warming spanning +1.8 to -41%. 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 and future projections of export, as well as identifying the observations and model developments required to achieve more robust characterisation of this important planetary carbon flux. We identify particle fragmentation and zooplankton vertical migration as the mechanisms most likely to substantially influence the magnitude of present-day modelled export flux. Of the processes sufficiently understood to allow implementation in climate models, projections of future export flux and feedbacks to climate are likely to be most sensitive to changes in phytoplankton and particle size spectra, and to temperature-dependent remineralisation. "Known unknown" processes which are not currently represented in models and will have an uncertain impact on future projections include particle stickiness and fish vertical migration. With the advent of new observational technologies, such as biogeochemical-Argo floats and miniaturised camera systems, we will be able to better parameterize models and thus decrease uncertainties in current and future export flux.

Uncertain response of ocean biological carbon export in a changing world

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Abstract

The export flux of organic carbon from the upper ocean is the starting point of the transfer and long term storage of photosynthetically-fixed carbon in the deep ocean. This "biological carbon pump" is a significant component of the global carbon cycle, reducing atmospheric CO_2 levels by ~ 200 ppm. Carbon exported out of the upper ocean also fuels the productivity of the mesopelagic zone, including significant fisheries. Here we show that, despite its importance, export flux is poorly constrained in Earth System Models, with the modelled range in projected future global-mean changes due to climate change spanning +1.8 to -41%. 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 remineralisation) of export. We also identify the observations required to achieve more robust characterisation, and hence improved model parameterization, of export flux, and thus decrease uncertainties in current and future estimates of this important planetary carbon flux.

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 ocean[1]. This 'exported' carbon fuels the biological carbon pump and hence plays a central role in storing carbon in the ocean on climatically-relevant timescales[2]. 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 constrained[3–5].

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 flux[8], 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 remineralise 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 remineralisation, 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 remineralisation[23]. 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% globally[29–31] and potentially even more at specific locations[32]. Although currently poorly constrained by observations, the contribution to carbon flux by vertically migrating fish may contribute up to 16% of global export fluxes[33]. Note that specifics of the plankton community structure are not considered here, e.g. contribution to flux by gelatinous zooplankton[34] or mixotrophs[35], 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 flux[38] (< 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 effect[18] (~ 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 potential[39]. 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 viscosity[18] and changing stoichiometry of sinking particles[46] 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 remineralisation, 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 remineralised 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 remineralisation 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 fragmentation[23]. Additionally, multi-sensor sampling from the biogeochemical-Argo float initiative[53], deployment of uncrewed surface vehicles[54], and time-series programmes which integrate moored platforms and autonomous vehicles[55], 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 Network[63]), 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.

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-node.llnl.gov/projects/cmip6/

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Figure Legends

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.

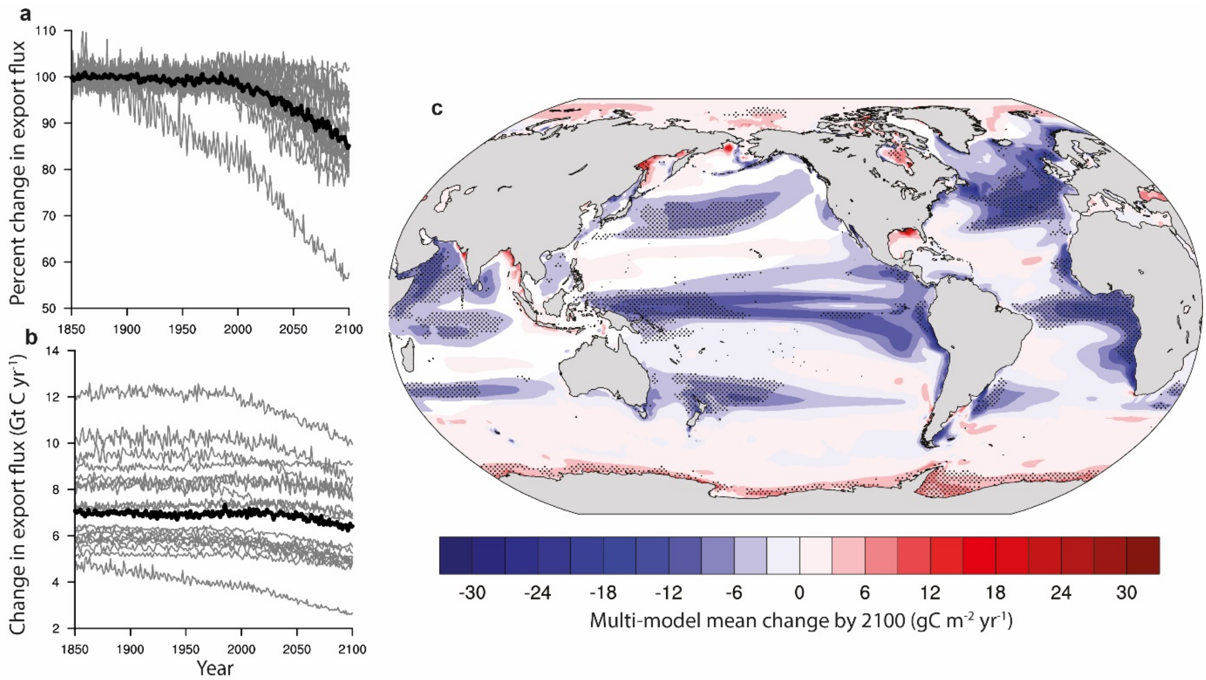
Figure 3: Feedbacks between changing export flux mechanisms and climate. Mechanisms are separated into those which are likely to have a positive, negative or uncertain feedback to climate.

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	+	?	[23,64]
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

(*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 ¼ - 1 degree, and therefore none of the models are eddy-resolving.



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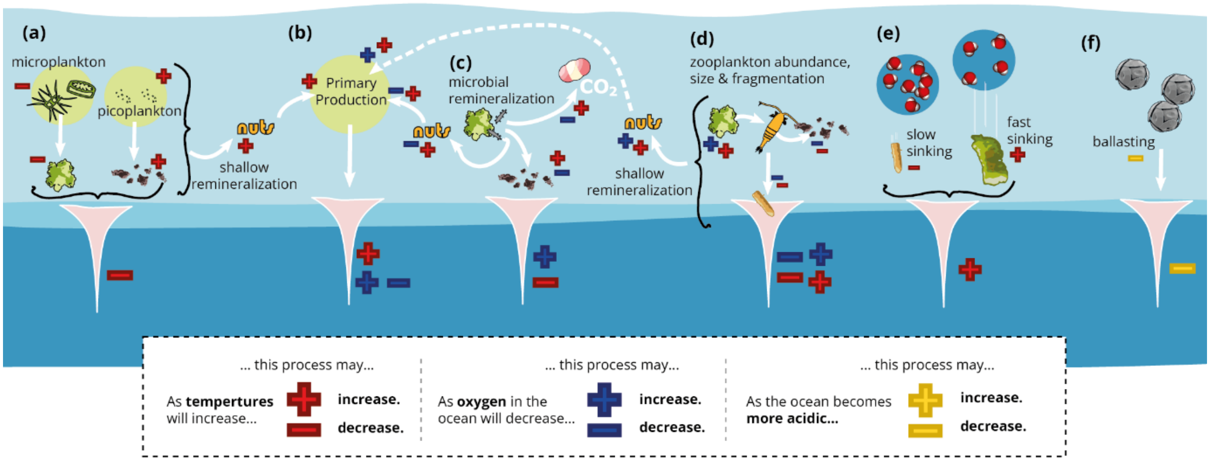

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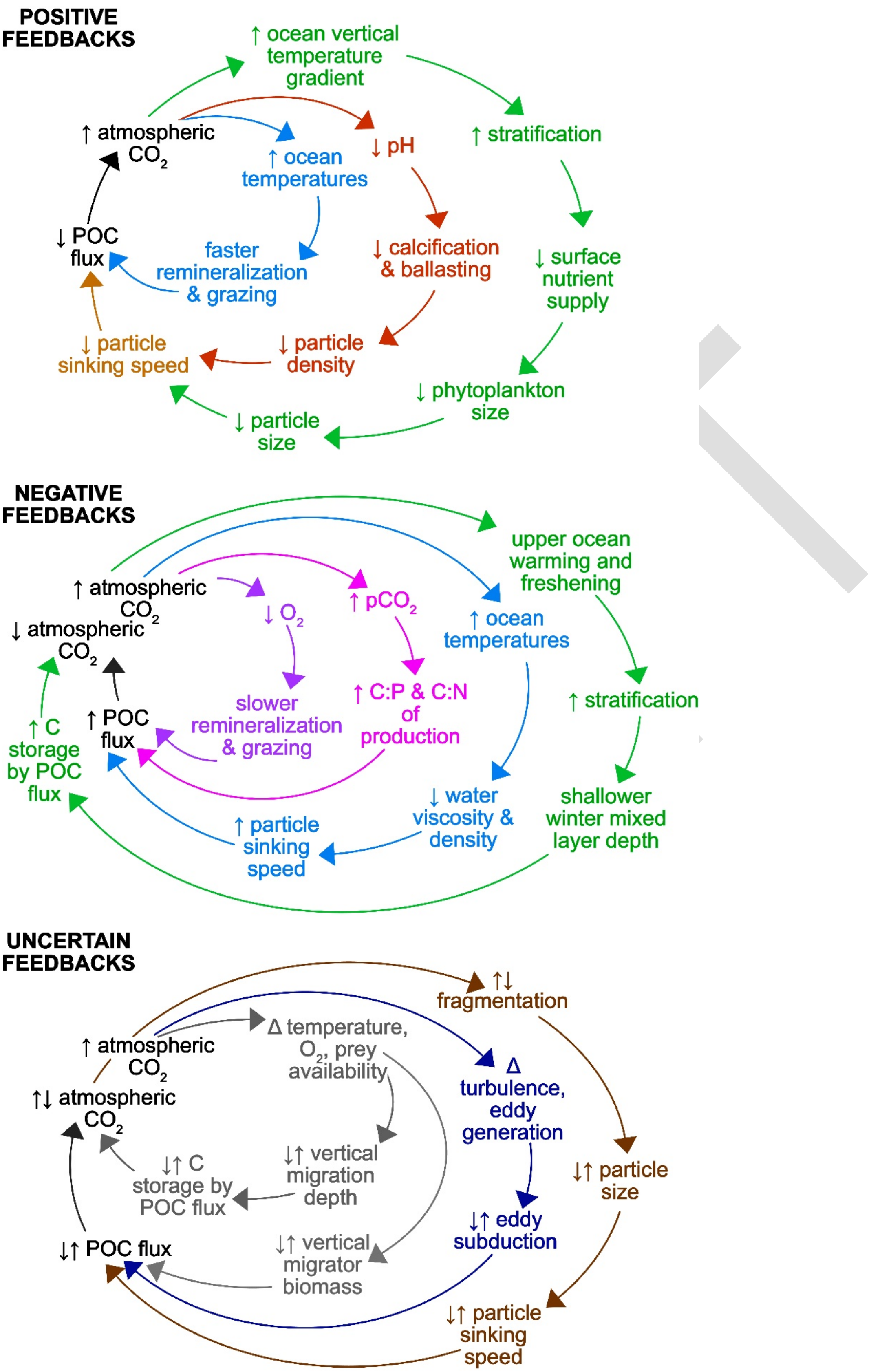

Figure 3: Feedbacks between changing export flux mechanisms and climate. Mechanisms are separated into those which are likely to have a positive, negative or uncertain feedback to climate.

Supplementary Information

Uncertain response of ocean carbon export in a changing world

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Contents:

Supplementary Table 1: Full model analysis of whether export flux processes are excluded/included. 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, and the particle sinking rate and model resolution were also assessed.

Model & *ecosystem module*	Fragmentation	Zooplankton vertical migration	Phytoplankton size effect on sinking (*1)	Temperature dependent remineralization	Oxygen dependent remineralization	Viscosity of seawater	Mineral ballasting	Mineral protection	Fish migration	TEP production /stickiness	Variable stoichiometry (*2)	Sinking rate (small & large POC) (*3)	Model resolution (*4)
Can ESM5	✗	✗	✗	✓	✗	✗	✗	✗	✗	✗	✗	8 m d^{-1}	(*5)
CanESM5-CanOE	✗	✗	✓	✓	✗ (*6)	✗	✗	✗	✗	✗	✗	2 & 30 m d^{-1}	(*5)
CESM & CESM-WACCM *MARBL* (*7)	✗	✗	✗ (*12)	✗	✓	✗	✓	✓	✗	✗	✗	No explicit sinking	1°
CMCC-ESM2 *BFM5.2*	✗	✗	✗	✓	✓	✗	✗	✗	✗	✗	✓	1 m d^{-1}	1°
CNRM, EC-Earth-CC & IPSL *PISCES2* (*7)	✓ (*9)	✗	✓	✓	✓	✗	✗	✗	✗	✗	✗	2 & 30-200 m d^{-1}, depth dependent	1°
CSIRO *WOMBAT*	✗	✗	✗	✗	✗	✗	✓	✗	✗	✗	✗	24 m d^{-1}	1°
GFDL-CM4 *BLING*	✗	✗	✗	✓	✓	✗	✓	✓	✗	✗	✗	50-180 m d^{-1}, depth dependent	¼°
GFDL-ESM4 *COBALT*	✗	✗	✗ (*12)	✓	✓	✗	✓	✓	✗	✗	✗	100 m d^{-1}	½°
MIROC	✗	✗	✗	✓	✓	✗	✗	✗	✗	✗	✗	5 m d^{-1} from 0-200 m	1°
MPI HR & MPI LR *Hamocc6* (*7,*8)	✗	✗	✗	✗	✗ (*6)	✗	✗	✗	✗	✗	✗	3.5-80 m d^{-1}, depth dependent	½°
MRI	✗	✗	✗	✗	✓	✗	✗	✗	✗	✗	✗	2 m d^{-1}	(*10)
NASA-GISS	✗ (*11)	✗	✓	✓	✗	✓	✗	✗	✗	✗	✗	Varies with viscosity	1°
NorESM LM & NorESM MM *Hamocc5.1* (*7)	✗	✗	✗	✗	✗ (*6)	✗	✗	✗	✗	✗	✗	5 m d^{-1}	1°
UK-ESM *Medusa*	✗	✗	✓	✓	✗	✗	✗	✓	✗	✗	✗	2.5 m d^{-1}	1°
Summary (19 models total)	✗ 18 ✓ 1	✗ 19 ✓ 0	✗ 13 ✓ 6	✗ 8 ✓ 11	✗ 9 ✓ 10	✗ 18 ✓ 1	✗ 14 ✓ 5	✗ 14 ✓ 5	✗ 19 ✓ 0	✗ 19 ✓ 0	✗ 18 ✓ 1	1-200 m d^{-1}	¼ - 1°

(*1) We consider whether more than one size of sinking detritus is modelled, i.e. whether large plankton generates large, fast sinking particles and small plankton generate small, slow sinking particles. Sometimes models have different phytoplankton size classes, and large phytoplankton generates a higher fraction of sinking particles than small phytoplankton, so that a change in phytoplankton community composition will result in more/less particles being generated. However, with only one type of sinking particle, the sinking speed will not change with phytoplankton community composition. These models are classed as a “No” for the category of ‘phytoplankton size effect on sinking’.

(*2) A model is classed as “Yes” for variable stoichiometry if C:N:P is allowed to vary in the detritus. A "No" can mean that it does vary in phytoplankton, or that C:Fe varies, or only C:N.
(*3) Small and large POC sinking rates are reported separately for models which include two size classes of particles.
(*4) Model resolution is included as an indication of whether the eddy pump could potentially be simulated.
(*5) ORCA1 tripolar grid, 1° with refinement to 1/3° within 20° of the equator.
(*6) Hamocc6 and CanESM-CanOE switch to denitrification at very low oxygen concentrations, but there is otherwise no oxygen dependence of remineralization.
(*7) ‘Sister’ versions of a model, which are run with different physical models but the same marine biogeochemistry model.
(*8) HAMOCC now includes a more comprehensive aggregation, remineralization, and sinking scheme (Maerz et al., 2020), but not in the CMIP6 archive output used here.
(*9) Large POC decays to small POC, although it is parameterized as a remineralization rate, so the model is classed as a “Yes” for the category of ‘fragmentation’.
(*10) Tripolar grid, primarily 0.5° latitude/1° longitude with meridional refinement down to 0.3° within 10° of the equator.
(*11) POC can decay to DOC, but here we consider fragmentation as the decay from large into small particles so the model is classed as a “No” for the category of ‘fragmentation’.
(*12) CESM-MARBL and COBALT have different phytoplankton types, but only one detritus type, so there is no size effect (i.e. smaller/larger phytoplankton do not result in slow/fast sinking detritus). However, there is a ballasting effect, so via generating ballasting material different phytoplankton do result in slow/fast sinking detritus.

Supplementary Table 2: Detailed rationale for our prioritisation of export flux processes. Details of the evidence in the literature for the baseline and future effects of various processes on export flux are provided. Published studies are classified as baseline (B), future (F), observational (O), experimental (E), model (M) or review (R). Acronyms: OMZ = Oxygen Minimum Zone, POC = particulate organic carbon, DVM = diel vertical migration, IPCC = Intergovernmental Panel on Climate Change, BCP = biological carbon pump.

Process	Baseline effect size and direction	Future effect size and direction	Evidence
Fragmentation	LARGE: Including fragmentation would substantially reduce export.	UNKNOWN: Direction of change unknown. Changes in environmental conditions could lead to changes in zooplankton biomass or distributions, and hence grazing-caused fragmentation, resulting in changes in export. Potentially larger OMZs could result in less zooplankton grazing and fragmentation, and thus increased export.	- Giering et al. (2014) (B, O+M): "Zooplankton fragment and ingest half of the fast-sinking particles, of which more than 30 percent may be released as suspended and slowly sinking matter…" [between 50 - 1000 m]. - Briggs et al. (2020) (B, O): "Fragmentation accounted for 49 ± 22% of the observed flux loss" [between 100 - 1000 m]. - Cavan et al. (2017) (B+F, O): "Here we show in the Eastern Tropical North Pacific OMZ 70% of POC remineralization is due to microbial respiration...Microbial remineralization rates in the OMZ are comparable to those in fully oxic waters but not high enough to offset the decrease in particle disaggregation and consumption by zooplankton, resulting in higher transfer efficiency in the offshore region of the OMZ."
Zooplankton vertical migration	MODERATE-LARGE: Including vertical migration would increase export significantly.	UNKNOWN: No literature on future effect found. Theoretically, changes in environmental conditions lead to changes in zooplankton biomass or migration depth, which changes export. Potentially, expanded OMZs may result in shallower migration and hence reduced export.	- Archibald et al. (2019) (B, M): "The modeled global export flux from the base of the euphotic zone was 6.5 PgC/year, which represents a 14% increase over the export flux in model runs without DVM...The model results were most sensitive to the assumptions for the fraction of individuals participating in DVM, the fraction of fecal pellets produced in the euphotic zone, and the fraction of grazed carbon that is metabolized." - Gorgues et al. (2019) (B, M): "...two relative biomasses of migrating zooplankton (30% and 60%) have been tested. It leads to an active to passive export ratio in agreement with published estimations and to an increase in the carbon export efficiency at 1,000 m between 20% and 40%. However, this effect is partially canceled out by a simulated primary production decrease." - Aumont et al. (2018) (B, M): "About one third of the epipelagic biomass is predicted to perform DVM. The flux of carbon driven by DVM is estimated to be 1.05 ± 0.15 PgC/year, about 18% of the passive flux of carbon due to sinking particles at 150 m." - Hansen & Visser (2016) (B, M): "We estimate that the amount of carbon transported below the mixed layer by migrating zooplankton in the North Atlantic Ocean constitutes 27% (16–30%) of the total export flux associated with the biological pump in that region." - Stukel et al. (2013) (B, O): "We assessed these contributions of mesozooplankton to vertical flux in the California Current Ecosystem. Across

			the range of 9 ecosystem conditions encountered on the cruises, recognizable fecal pellet mass flux varied from 3.5 to 135 mg C m^{-2} d^{-1} (3 to 94% of total passive flux) at the 100 m depth horizon. The active transport of carbon by migratory mesozooplankton taxa contributed an additional 2.4 to 47.1 mg C m^{-2} d^{-1} (1.9 to 40.5% of total passive flux)."
Phytoplankton size effect on sinking	UNKNOWN: Direction of effect is unknown, as it depends on the parameterisation of sinking rate in each model, which then drives whether adding variability would result in a net increase or decrease in export. For example, compared to a model with uniform particle sizes, resolving spatial variability in phytoplankton and particle sizes may result in higher export rates in areas with large phytoplankton and smaller export rates in areas with small phytoplankton; however, it is unknown whether global mean export relative to the uniform case would increase, decrease, or remain the same.	SMALL-LARGE: Decreased phytoplankton and particle size results in slower sinking speeds and hence decreased export. Effect may be modulated by a negative feedback between particle size and remineralisation depth, which boosts surface nutrients as phytoplankton size structure becomes smaller.	- Boyd (2015) (F, M): "Model simulations reveal that in the surface ocean, changes to algal community structure (i.e., a shift toward small cells) has the greatest individual influence (decreased flux) on downward POC flux in the coming decades." - Leung et al. (2021) (F, M): "This negative feedback mechanism (termed the particle-size–remineralization feedback) slows export decline over the next century by ∼14 % globally (from −0.29 to −0.25 GtC yr^{-1}) and by ∼20 % in the tropical and subtropical oceans, where export decreases are currently predicted to be greatest." - Laufkötter et al. (2016) (F, M): "The removal of the sinking particles by remineralisation is simulated to increase in the low and intermediate latitudes in three models, driven by either warming-induced increases in remineralisation or slower particle sinking, and show insignificant changes in the remaining model. Changes in ecosystem structure, particularly the relative role of diatoms matters as well, as diatoms produce larger and denser particles that sink faster and are partly protected from remineralisation. Also this controlling factor is afflicted with high uncertainties, particularly since the models differ already substantially with regard to both the initial (present-day) distribution of diatoms (between 11–94 % in the Southern Ocean) and the diatom contribution to particle formation (0.6–3.8 times higher than their contribution to biomass). As a consequence, changes in diatom concentration are a strong driver for export production changes in some models but of low significance in others." - Bopp et al. (2005) (F, M): "Our global warming simulation shows a large decrease of the export ratio (export production divided by the primary production) with global warming, by as much as 25% at 4xCO_2 (from 10 PgC/yr to 7.5 PgC/yr) whereas primary production decreases by only 15%. This change in the export ratio is explained by the modifications the ecosystem undergoes with global warming: diatoms are replaced by small phytoplankton and recycling of nutrients and carbon in the surface ocean is increased (i.e., the export ratio decreases)."
Temperature dependent remineralisation	UNKNOWN: Including temperature dependent remineralisation rates would change export differently in different regions, but the global mean effect is unclear.	SMALL-LARGE: Warming results in increased remineralisation and hence decreased export. Papers by Cavan et al. suggest the effect is moderate – large (although feedback of changing export not incorporated); those by Laufkötter et al. suggest the	- Marsay et al. (2015) (B, O): "We show that the observed variability in attenuation of vertical POC flux can largely be explained by temperature, with shallower remineralization occurring in warmer waters." - Cael et al. (2017) (B+F, M): "Temperature changes are suggested to have caused a statistically significant decrease in export efficiency of 1.5% ± 0.4% over the past 33 years. Larger changes are suggested in the midlatitudes and Arctic." - Laufkötter et al. (2017) (B+F, M): "The new [temperature] remineralization parameterization results in shallower remineralization in the low latitudes but

		effect is small (feedback of changing export is incorporated).	deeper remineralization in the high latitudes, redistributing POC flux toward the poles. It also decreases the volume of the oxygen minimum zones...While projections of NPP appear to be rather sensitive to assumptions about temperature dependence, all our model projections of POC flux as well as the model studies by Taucher and Oschlies [2011] and Segschneider and Bendtsen [2013] indicate that the POC flux at 100 m depth does not react strongly to increases in temperature, even despite simulated increases in net primary production." - Cavan & Boyd (2018) (F, O): "Our results showed that POC-normalised respiration increased with warming. We estimate that POC export (scaled to primary production) could decrease by 17 ± 7% (SE) by 2100, using projected regional warming (+1.9°C) from the IPCC RCP 8.5 ('business-as-usual' scenario) for our sub-Antarctic site." - Cavan et al. (2019) (F, M): "POC export is projected to decline by 12% by the end of the century according to fundamental metabolic theory and Earth System Models. The inclusion of spatially variable temperature sensitivity terms...resulted in more pronounced projected declines in POC export; applying high sensitivity globally resulted in a decline in export of 30% and applying it just to cold regions resulted in a global decline of up to 23%."
Oxygen dependent remineralisation	UNKNOWN: If models assume homogenous, well-oxygenated remineralisation rates, then including reduced remineralisation rates in OMZs would decrease remineralisation and so increase export, but the magnitude of the effect is unclear.	UNKNOWN: Theoretically, decreased remineralisation occurs in decreased oxygen concentrations, and hence leads to increased export; however, there are no studies examining export changes modulated by oxygen-dependent respiration (or grazing rates) alone.	- Weber & Bianchi (2020) (B, O+M): "...Both OMZs exhibit slow flux attenuation between 100 and 1000 m where suboxic waters reside, and sequester carbon beneath 1000 m more than twice as efficiently...three different mechanisms might explain the shape of the OMZ flux profiles: (i) a significant slow-down of remineralization ...(ii) the exclusion of zooplankton that mediate disaggregation of large particles from suboxic waters, and (iii) the limitation of remineralization by the diffusive supply of oxidants (oxygen and nitrate) into large particles." * - Devol & Hartnett (2001) (B, O): "The generally smaller rain rates off Mexico are probably due to the lower primary production, hence lower initial supply. The lower attenuation rate, however, is hypothesized to result from a decreased oxidation rate of the sinking flux within the oxygen-deficient zone relative to a more typical oxic water column." * * Note that for both of the above studies, the results are not as relevant to export flux, as the upper boundary of OMZs generally are not sufficiently shallow to intercept the export depth.
Viscosity of seawater	SMALL: Including viscosity decreased export by ~3%.	SMALL-MODERATE: Warmer water is less viscous, and thus enables particles to sink more quickly, which increases future export.	- Taucher et al. (2014) (B+F, M): "In our global warming simulation, the viscosity effect accelerates particle sinking by up to 25%..." [But these biggest effects are 2000 years in the future. Export at 130 m in 2000 AD: without viscosity = 6.56, with viscosity = 6.37 GtC yr^{-1}, equivalent to a baseline decrease of <3% with viscosity.]
Mineral ballasting	UNKNOWN: The assumption is that ballasting increases particle sinking speed and thus export, although there is	SMALL-MODERATE: A 50% decrease in calcium carbonate export would equate to only a ~10% decrease in total export from 100 m depth.	- Heinze (2004) (F, M): "For an A1B IPCC emission scenario and constant emission rates after year 2100, the simulation predicts a global decrease of biological $CaCO_3$ export production by about 50% in year 2250." - Hofmann & Schellnhuber (2009) (F, M): [From Fig 1b, $CaCO_3$ export at the bottom of the euphotic zone is reduced by ~0.1 molC m^{-2} yr^{-1} (from a baseline

	weak evidence for this occurring. Including calcite, silicate and lithogenic ballasting could increase export, but the magnitude of change is unclear.		of ~0.2 molC m^{-2} yr^{-1}) by 2200; this ~ 50% reduction in $CaCO_3$ export = ~10% reduction in total export] - Wilson et al. (2012) (B, O): “The absence of a strong globally uniform relationship between $CaCO_3$ and POC in our spatial analysis calls into question whether a simple ballasting mechanism exists...Our findings present a challenge to ocean carbon cycle modelers who to date have applied a single statistical global relationship in their carbon flux parameterizations when considering mineral ballasting...” - Le Moigne et al. (2014) (B, O): “...no globally uniform relationship between export of one type of mineral and POC, contrary to earlier suggestions by Klaas and Archer [2002] and Sanders et al. [2010]...” “Mineral ballasting is of greatest importance in the high-latitude North Atlantic, where 60% of the POC flux is associated with ballast minerals. This fraction drops to around 40% in the Southern Ocean. The remainder of the export flux is not associated with minerals, and this unballasted fraction thus often dominates the export flux. The proportion of mineral-associated POC flux often scales with regional variation in export efficiency (the proportion of primary production that is exported). However, local discrepancies suggest that regional differences in ecology also impact the magnitude of surface export. We propose that POC export will not respond equally across all high-latitude regions to possible future changes in ballast availability.”
Mineral protection	ZERO-SMALL: Scant observational evidence showing effects of mineral protection.	ZERO-SMALL: Scant observational evidence showing effects of mineral protection.	- Iversen & Ploug (2013) (B, E+R): “Our results show that ballasting of aggregates in the upper ocean appears to have a large influence on sinking velocities, while the similar average carbon-specific respiration rates between the treatments indicate no protective mechanisms against remineralization of labile organic matter as also found in copepod fecal pellets (Ploug et al., 2008b).” - Iversen & Robert (2015) (B, E): “This study shows that the inclusion of smectite offers no protection against degradation of organic matter in freshly produced or aged marine snow aggregates.”
Eddy pump	SMALL: Including eddy-driven subduction increases export by 2-5% globally.	SMALL: No studies on future effect; however future eddy characteristics are unlikely to change substantially, and the effect is anyway small. Therefore the eddy pump is not likely to have a large effect on projected global export changes.	- Resplandy et al. (2019) (B, M): “These eddy-driven subduction events are able to transfer carbon below the mixed-layer, down to 500- to 1,000-m depth. However, they contribute <5% to the annual flux at the scale of the basin, due to strong compensation between upward and downward fluxes.” - Harrison et al. (2018) (B, M): “The role of mesoscale circulation in modulating export is evaluated by comparing global ocean simulations conducted at 1° and 0.1° horizontal resolution. Mesoscale resolution produces a small reduction in globally integrated export production (<2%); however, the impact on local export production can be large (±50%), with compensating effects in different ocean basins." - Zhou et al. (2020) (B, O): “Scaling these results to the entire South China Sea basin suggests that cyclonic eddies contribute <4% of the net POC flux but >15% of the opal flux.” - Boyd et al. (2019) (B, R) [contribution of −0.09–2.0 Pg C yr^{-1} from the eddy-subduction pumps]

			- Waite et al. (2016) (B, O): [physical concentration of particles] "Here we show the subsurface distribution of eddy particles funneled into a wineglass shape down to 1000 m, leading to a sevenfold increase of vertical carbon flux in the eddy center versus the eddy flanks"
Fish vertical migration	MODERATE-LARGE: Including fish migration would increase export.	UNKNOWN: No studies on future effect.	- Saba et al. (2021) (B, R): "Based on our synthesis of passive (fecal pellet sinking) and active (migratory) flux of fishes, we estimated that fishes contribute an average (± standard deviation) of about 16.1% (± 13%) to total carbon flux out of the euphotic zone. Using the mean value of model-generated global carbon flux estimates, this equates to an annual flux of 1.5 ± 1.2 PgC yr^{-1}."
Particle stickiness, including transparent exopolymers	UNKNOWN: Effect of TEP unclear as multiple studies suggest it is highly situational and dependent on many factors.	UNKNOWN: No studies on future effect.	- Seebah et al. (2014) (F, E): "...in contrast to expectations based on the established relationship between TEP and aggregation, aggregation rates and sinking velocity of aggregates were depressed in warmer treatments, especially under ocean acidification conditions." - Wohlers et al. (2009) (F, E): "The concentration of transparent exopolymer particles (TEP) increased considerably in the warmest treatment T+6 and to a lesser extent also in the T+4 treatment during the postbloom phase of the experiment, whereas it remained low at T+2 and T+0...The extent to which enhanced TEP formation could affect particle sinking in a warming ocean critically depends on the timing of TEP production and the interplay with other biological processes, e.g., microbial degradation and grazing. In our experiment, particulate matter concentrations had decreased to nearly prebloom levels when TEP concentrations increased, hence limiting the potential for TEP-mediated particle export."
Variable stoichiometry in sinking particles	UNKNOWN: Variable stoichiometry could arise from varying levels of nutrient availability, light, and temperature, along with CO_2 sensitivity for phytoplankton growth. Direction of effect is unknown, as it depends on the parameterisation of stoichiometry in each model, which then drives whether adding variability would result in a net increase or decrease in export. For example, compared to a model with constant Redfield stoichiometry, resolving spatial variability in stoichiometry may result in	SMALL: Predicted increasing C:P and C:N in the future would increase carbon export.	- Tanioka & Matsumoto (2017) (F, M): "P:C plasticity could buffer against a generally expected future reduction in global carbon export production by up to 5% under a future warming scenario compared to a fixed, Redfield P:C." - Riebesell et al. (2007) (F, E): "The stoichiometry of carbon to nitrogen drawdown increased from 6.0 at low CO_2 to 8.0 at high CO_2, thus exceeding the Redfield carbon:nitrogen ratio of 6.6 in today's ocean. This excess carbon consumption was associated with higher loss of organic carbon from the upper layer of the stratified mesocosms." - Taucher et al. (2012) (F, E): "The maximum ratio of POC : PON was significantly enhanced at higher temperatures and reached 15.9 at low, 29.0 at intermediate, and 33.7 at high temperatures." "The maximum ratio of DOC : DON was significantly affected by temperature and reached 25.6 at low, 28.1 at intermediate, and 30.8 at high temperatures." - Moreno et al., 2018 (M, B): "environmentally driven shifts in stoichiometry make the biological pump more influential, and may reverse the expected positive relationship between temperature and $pCO_{2,\,atm}$." "Large-scale gradients in stoichiometry can alter the regional efficiency of the biological pump: P supplied to high C:P regions leads to a larger export of carbon than P supplied to low C:P regions."

	higher carbon export rates in warm, oligotrophic areas with higher C:P ratios and lower carbon export rates in cooler, nutrient-rich areas with lower C:P ratios; however, it is unknown whether global mean carbon export relative to the uniform case would increase, decrease, or remain the same.		

Supplementary Table 3: Information needed to inform process understanding-driven model developments of export flux for our priority processes, and current observational capabilities. In all cases, measurements are ideally needed over large space and time scales to match model scales. Additionally, in all cases, simulating a climate change response also requires the drivers of the processes to be understood, otherwise the model assumption will necessarily be that the process does not change with a changing climate. GOOS EOV = Global Ocean Observing System Essential Ocean Variables.

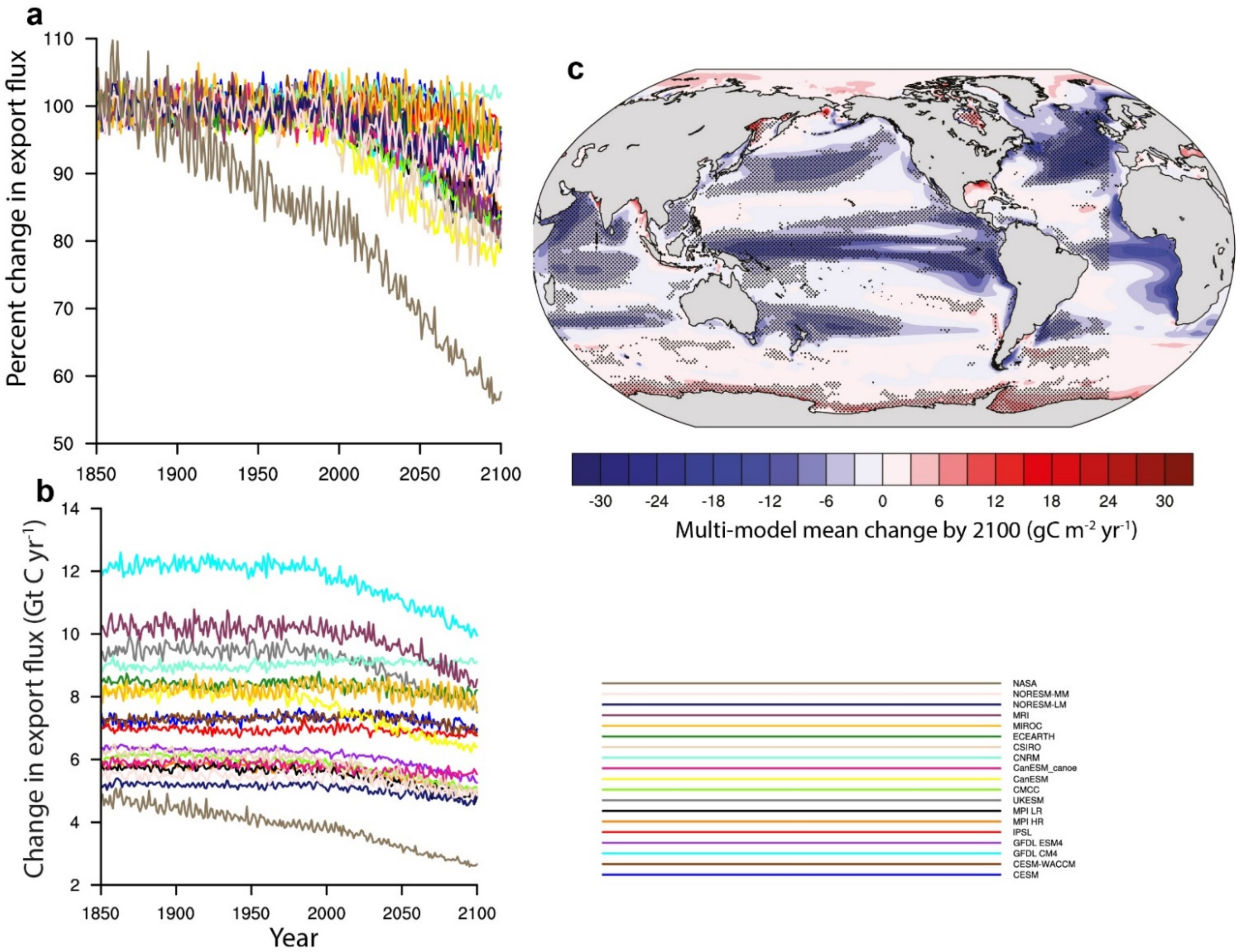
Process	Information needed	Feasibility	GOOS EOV(*1)
Fragmentation	- How does the fragmentation rate vary with depth and in different ocean regions? - What factors drive fragmentation rate? - How does fragmentation rate vary with particle type (e.g. aggregates vs faecal pellets)?	Moderate feasibility. Some knowledge on fragmentation and aggregation rates from lab experiments (O'Brien et al., 2004; Waite et al., 1997), models (Burd & Jackson, 2009; Giering et al., 2014), and indirect observations (Briggs et al., 2020). Most promising methods for large-scale observations are optical measurements on autonomous platforms. For example, bulk rates based on backscatter (Briggs et al., 2020) and *in situ* cameras for particle identification and size spectra (Giering et al., 2020). Rates of detailed driver-specific processes, such as biologically-mediated fragmentation by zooplankton, are difficult to obtain, and there are currently no obvious technological approaches to obtain these data on large scales.	Particulate matter Zooplankton biomass and diversity
Zooplankton vertical migration	- What fraction of zooplankton migrates? - To what depth do they migrate? - What factors drive zooplankton vertical migration and faecal pellet production?	High feasibility. Optical and acoustic measurements allow observations of large-scale patterns (Bianchi & Mislan, 2016). Optical measurements may also provide some taxonomic resolution, although camera avoidance/attraction may cause biases (Hoving et al., 2019; Utne-Palm et al., 2018).	Zooplankton biomass and diversity Oxygen Sea surface temperature/subsurface temperature Phytoplankton biomass and diversity Ocean colour
	- What fraction of faecal pellets are formed above versus below the permanent thermocline/euphotic zone? - How does faecal pellet density and size vary?	Moderate feasibility. Large-scale *in situ* optical data may provide information on particle type, abundance and distribution (and hence particle origin), as well as sinking velocities (Giering et al., 2020).	

	- What are the metabolic rates at depth versus at surface?	Low feasibility. *In situ* metabolic rates are difficult to obtain and require ship-board work. Metabolic markers (e.g. enzyme activity) may prove useful (Yebra et al., 2017), but data are still sparse. Understanding of large-scale, whole population responses to environmental drivers are not yet feasible.	
Phytoplankton size effect on sinking	- What is the size distribution of phytoplankton in the ocean? - How are the size distribution of phytoplankton and the size distribution of particles related?	High feasibility. Information on phytoplankton size and distribution can be obtained from recent developments in satellite-derived products (Mouw et al., 2017), as well as optical devices on autonomous platforms (Lombard et al., 2019).	Phytoplankton biomass and diversity Ocean colour Sea surface temperature/subsurface temperature Nutrients
	- How are particle size and sinking rate related?	Moderate feasibility. Large-scale *in situ* optical data could provide information on particle size and sinking velocities (Giering et al., 2020). Coupled with information on phytoplankton biomass and diversity (e.g. from *in situ* plankton monitoring systems; Lombard et al., 2019), the relationship between particle size and sinking rate could be obtained in the near future.	
Temperature dependent remineralisation	- Does temperature affect different particle types differently? - Does microbial rate temperature sensitivity vary latitudinally?	Moderate to low feasibility. A moderate amount of lab-based data exists (Robinson, 2019), but *in situ* data are still relatively sparse. Large-scale observations of these rates may be obtained indirectly from changes in oxygen and POC concentrations. The acquisition of large-scale information on the sensitivity of these rates remains problematic.	Microbial biomass and diversity (*emerging) Particulate matter Dissolved organic carbon Oxygen Sea surface temperature/subsurface temperature

(*1) To inform process understanding-driven model developments of export flux, we require measurements of key parameters over large space and time scales to match model scales. A useful starting point in assessing feasibility of collating some essential data is through Essential Ocean Variables (EOVs). EOVs have been classified as critical for observing the oceans by the Global Ocean Observing System - an initiative to standardize ocean data collection and promote observing developments (Moltmann et al., 2019). EOVs are assessed for feasibility, capacity and impact, and their maturity rated.

Supplementary Table 4: Table of models assessed and the main marine biogeochemistry module reference.

Climate model & *ecosystem module*	Key references
CanESM5	Swart et al. (2019)
CanESM5-CanOE	Hayashida (2018); Swart et al. (2019)
CESM & CESM-WACCM ***MARBL***	Long et al. (submitted)
CMCC-ESM2 ***BFM5.2***	Vichi et al. (2020)
CNRM, EC-Earth-CC & IPSL ***PISCES2***	Aumont et al. (2015)
CSIRO ***WOMBAT***	Kidston et al. (2011)
GFDL-CM4 ***BLING***	Dunne et al. (2020)
GFDL-ESM4 ***COBALT***	Stock et al. (2020)
MIROC	Hajima et al. (2020)
MPI HR & MPI LR ***Hamocc6***	Ilyina et al. (2013); Mauritsen et al. (2019)
MRI	Nakano et al. (2011); Tsujino et al. (2010)
NASA-GISS	Ito et al. (2020)
NorESM LM & NorESM MM ***Hamocc5.1***	Tjiputra et al. (2020)
UK-ESM ***Medusa***	Sellar et al. (2019); Yool et al. (2021)



Supplementary Figure 1: Uncertain response of export flux to climate change. (a) Percent change 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 to year 2100. Percent change is calculated with respect to the mean of years 1850-1900 for each model. (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 ~ 75% of models (i.e. at least 14 of 19) agree on the sign of the change in export flux.

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