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

Stephanie A. Henson[1]*, Charlotte Laufkötter[2,3], Shirley Leung[4], Sarah L.C. Giering[1], Hilary I. Palevsky[5] and Emma L. Cavan[6]

[1] National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK
[2] Climate and Environmental Physics, Physics Institute, University of Bern, 3012 Bern, Switzerland
[3] Oeschger Centre for Climate Change Research, University of Bern, 3012 Bern, Switzerland
[4] University of Washington, School of Oceanography, Seattle, WA, USA
[5] Department of Earth and Environmental Sciences, Boston College, Chestnut Hill, MA, USA
[6] Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK

*Corresponding author: s.henson@noc.ac.uk

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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 ~ 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.

***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 is the starting point of 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. 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 (Fig. 1a; SSP5-8.5 scenario). Even the direction of change in export flux is uncertain: for 84% of the ocean, the models disagree

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on whether export will increase or decrease by the year 2100 (Fig. 1b). In addition, the differences among models in present-day export flux far exceed the projected changes by 2100 (Supplementary Fig. S1). 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 process understanding of their role in export flux and/or a paucity of suitable observations from which to derive parameterisations, and partly due to computational constraints (Supplementary Tables S1, S2). 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[6], and is represented in all climate models with a marine biogeochemistry module. However, the treatment of sinking particle generation and transformation varies widely (Supplementary Table S1). 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[7–9] and composition, as mineral ballasting[10,11] or association with Transparent Exopolymer Particles (TEP) and other biological ‘glues’ can alter sinking speed[12,13]; b) the temperature-dependent viscosity of the water the particles are sinking through[14,15]; c) the rate at which microbes remineralise the sinking particles, which can be influenced by temperature, oxygen and resource availability[16–18]; and d) the ability of microbes to access carbon within the particles[19,20]. 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).

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[21,22]. Recent observations from the biogeochemical-Argo float array suggest that fragmentation could drive up to 50% of mid-water remineralisation[23]. Fragmentation is not included in any of the current climate models (Table 1) due to a lack of understanding of its drivers and lack of observations to constrain it.

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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[24,25]. 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[26–28] and potentially even more at specific locations[29]. Although currently poorly constrained by observations, the contribution to carbon flux by vertically migrating fish may contribute up to 16% of global export fluxes[30].

Finally, small-scale physical transport of both particulate and dissolved organic matter to depth[6,31] 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[32] (< 2%).

Taking all of the above into account, fragmentation may be the most important currently unaccounted for process for improving modern-day export flux simulations, followed by zooplankton, and potentially fish, vertical migration. Including the effects of seawater viscosity on particle sinking speed, small-scale physical transport, and mineral protection are less likely to significantly improve modern-day export estimates. 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, and TEP production; Table 1) would affect modelled modern-day global export.

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**Uncertainties in response of export flux to future 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 S2). 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[33–35]. 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% [17,36,37]. We thus conclude that 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.

Incorporating the effects of mineral ballasting[38,39], seawater viscosity[15] and changing stoichiometry of sinking particles[40] 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[12,13,41]. 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. For the remaining processes examined here (fragmentation, and zooplankton and fish vertical migration; Table 1), there is great uncertainty as to how much and in which direction these may change with future warming, and therefore the importance of modelling these processes for projections of future export flux is unknown.

**Uncertainties in feedbacks between export flux 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). 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[27,35]. The uncertainties in these climate-export feedbacks 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.

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**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 S3).

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[42,43], primary production and community respiration[44,45], and particle fragmentation[23]. Additionally, multi-sensor sampling from the biogeochemical-Argo float initiative[46], deployment of uncrewed surface vehicles[47], and time-series programmes which integrate moored platforms and autonomous vehicles[48], 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[49,50].

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[51,52], 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.

## 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, 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 data synthesis activities (e.g. JETZON, Joint Exploration of the Twilight Zone Ocean Network[53]), 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.

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**Figure Legends**

**Figure 1: Uncertain response of export flux to climate change.** (Left) Percent change in export flux in 19 coupled climate models in the CMIP6 archive, forced with the SSP5-8.5 scenario. Percent change is calculated with respect to the mean of years 1850-1900 for each model, and ranges from +1.8 to -41%. Multi-model mean is shown as a thick black line. (Right) Multi-model mean change in export flux (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. (a) A shift to smaller phytoplankton species may lead to smaller particles and less export. (b) Higher primary production may allow higher export flux, though complex feedbacks, e.g. via nutrient recycling, lead to high uncertainties for predicted export. (c) The rate of microbial remineralization, which produces smaller particles that are less likely to be exported, should increase due to warming, yet may decrease owing to less oxygen availability. (d) Smaller zooplankton that produce smaller, slower sinking faecal pellets are expected to become more prevalent, hence likely leading to a decrease in export. Alternatively, the expected decrease in zooplankton abundance will lead to less particle fragmentation, which may result in more large particles that are more likely to be exported. (e) Water density is expected to decrease, allowing particles to sink faster, hence leading to higher export rates. (f) Ocean acidification is expected to reduce the abundance of mineral ballast-producing species, such as coccolithophores, which in turn may result in less dense particles that sink more slowly and are less likely to be exported.

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

**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 S4). 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 S1, and the detailed rationale for our prioritisation is in Supplementary Table S2.

| Process | Summary of climate model structure (*1) | Bias in present-day modelled global export without this process (*2) | Direction of change in future global export due to this process (*3) | Key references for this process |
|---|---|---|---|---|
| Fragmentation | ✗ 18 ✓ 1 | + | ? | 23,54 |
| Zooplankton vertical migration | ✗ 19 ✓ 0 | − | ? | 26–28 |
| Phytoplankton size effect on sinking (*4) | ✗ 13 ✓ 6 | ? | ↓? | 34,35,55 |
| Temperature dependent remineralisation | ✗ 8 ✓ 11 | ? | ↓ | 4,17 |
| Oxygen dependent remineralisation | ✗ 9 ✓ 10 | +? | ↑? | 16,17,56 |
| Viscosity of seawater | ✗ 18 ✓ 1 | + | ↑ | 15 |
| Mineral ballasting | ✗ 14 ✓ 5 | −? | ↓ | 11,39,57 |
| Mineral protection | ✗ 14 ✓ 5 | − | ↓ | 58 |
| Eddy pump (*5) | ✗ 19 ✓ 0 | − | = | 6,32,59 |
| Fish vertical migration | ✗ 19 ✓ 0 | − | ? | 30 |
| Particle stickiness (including transparent exopolymers) | ✗ 19 ✓ 0 | ? | ? | 12,13,41 |
| Variable stoichiometry in sinking particles | ✗ 18 ✓ 1 | ? | ↑ | 40,60,61 |

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

(*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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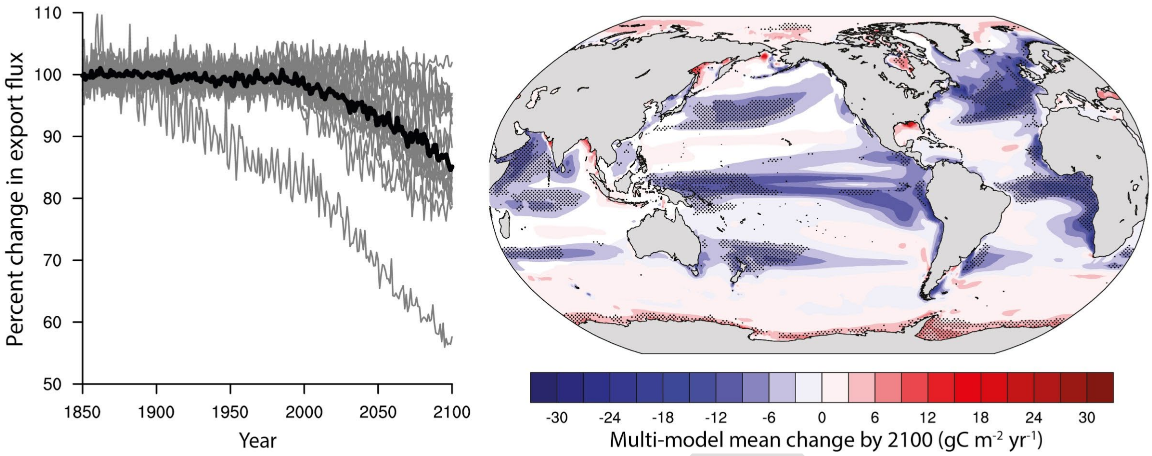


**Figure 1: Uncertain response of export flux to climate change.** (Left) Percent change in export flux in 19 coupled climate models in the CMIP6 archive, forced with the SSP5-8.5 scenario. Percent change is calculated with respect to the mean of years 1850-1900 for each model, and ranges from +1.8 to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

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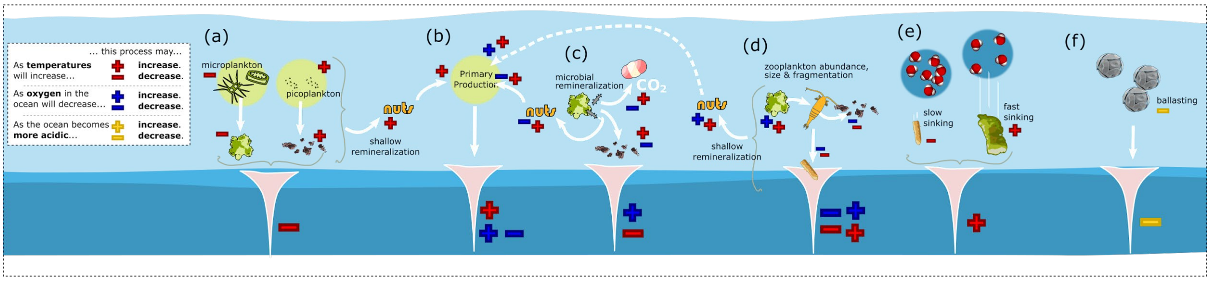


**Figure 2: Potential response of export processes to climate change.** Export will change in response to increasing temperature, decreasing oxygen concentration and ocean acidification. (a) A shift to smaller phytoplankton species may lead to smaller particles and less export. (b) Higher primary production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

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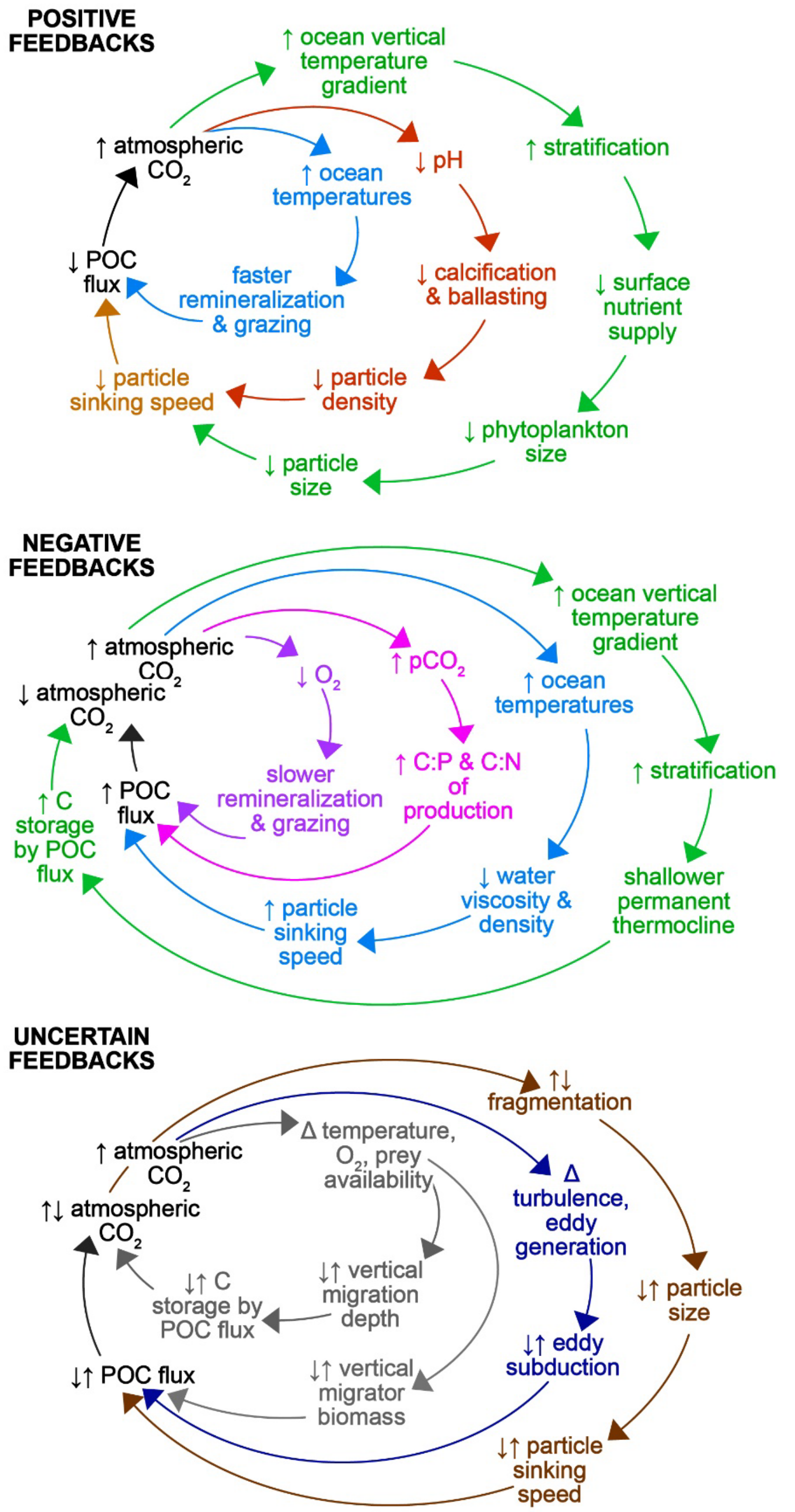


**Figure 3: Feedbacks between changing export flux mechanisms and climate.** Mechanisms are separated into those which are likely to have a positive, negative or uncertain feedback to climate.