Knowledge gaps in quantifying the climate change response of biological storage of carbon in the ocean

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Abstract

The ocean is responsible for taking up approximately 25% of anthropogenic CO2 emissions and stores > 50 times more carbon than the atmosphere. Biological processes in the ocean play a key role, maintaining atmospheric CO2 levels 200 ppm lower than they would otherwise be. The ocean's ability to take up and store CO2 is sensitive to climate change, however the key biological processes that contribute to ocean carbon storage are uncertain, as are their response and feedbacks to climate change. As a result, biogeochemical models vary widely in their representation of relevant processes, driving large uncertainties in the projections of future ocean carbon storage. This review identifies key biological processes that affect how carbon storage may change in the future in three thematic areas: biological contributions to alkalinity, net primary production, and interior respiration. We undertook a review of the existing literature to identify processes with high importance in influencing the future biologically-mediated storage of carbon in the ocean, and prioritised processes on the basis of both an expert assessment and a community survey. Highly ranked processes in both the expert assessment and survey were: for alkalinity – high level understanding of calcium carbonate production; for primary production – resource limitation of growth, zooplankton processes and phytoplankton loss processes; for respiration – microbial solubilisation, particle characteristics and particle type. The analysis presented here is designed to support future field or laboratory experiments targeting new process understanding, and modelling efforts aimed at undertaking biogeochemical model development.

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Key Points:

- Key processes needed to improve projections of the response of ocean carbon storage to climate change identified
- Three themes are addressed: net primary production, interior respiration, and biological contributions to alkalinity
- An expert assessment and community survey used to rank processes according to importance and uncertainty levels

Abstract:

The ocean is responsible for taking up approximately 25% of anthropogenic CO_2 emissions and stores > 50 times more carbon than the atmosphere. Biological processes in the ocean play a key role, maintaining atmospheric CO_2 levels 200 ppm lower than they would otherwise be. The ocean's ability to take up and store CO_2 is sensitive to climate change, however the key biological processes that contribute to ocean carbon storage are uncertain, as are their response and feedbacks to climate change. As a result, biogeochemical models vary widely in their representation of relevant processes, driving large uncertainties in the projections of future ocean carbon storage. This review identifies key biological processes that affect how carbon storage may change in the future in three thematic areas: biological contributions to alkalinity, net primary production, and interior respiration. We undertook a review of the existing literature to identify processes with high importance in influencing the future biologically-mediated storage of carbon in the ocean, and prioritised processes on the basis of both an expert assessment and a community survey. Highly ranked processes in both the expert assessment and survey were: for alkalinity – high level understanding of calcium carbonate production; for primary production – resource limitation of growth, zooplankton processes and phytoplankton loss processes; for respiration – microbial solubilisation, particle characteristics and particle type. The analysis presented here is designed to support future field or laboratory experiments targeting new process understanding, and modelling efforts aimed at undertaking biogeochemical model development.

1. Introduction:

Biological processes contribute significantly to oceanic storage of CO_2 by maintaining a lower concentration of carbon in the surface than in the deep ocean. However, how biological processes will respond to climate change and the subsequent feedbacks to ocean carbon storage are poorly known. As a consequence, the IPCC Assessment Report 6 Working Group I report (Canadell et al., 2021) concluded with high confidence that climate change will result in alterations to the magnitude and efficiency of biological contributions to carbon storage, but that there is low confidence in the magnitude or even sign of these biological feedbacks. This level of uncertainty is reflected in the discrepancies between observation and model based estimates of ocean carbon storage (e.g. Friedlingstein et al., 2022), part of which may be due to poorly represented biological processes. As the contribution of biological processes to ocean CO_2 uptake and storage is expected to gain greater importance with continued climate change (Hauck et al., 2015), improving model representation of these processes (which requires improved observational constraints) is essential. Major knowledge gaps result from the number and complexity of processes involved in biological carbon storage and a lack of observations with which they can be constrained. This lack of data limits both the fundamental understanding of relevant processes, and the development and validation of biogeochemical models as the data are rarely available on the large spatial and long temporal timescales required. The availability of robust model parameterisations is thus limited, resulting in a lack of consensus among climate models on which biological processes should be included (or excluded), and hence significant uncertainty in the magnitude and sign of biological feedbacks to climate change. However, even if sufficient data to build a parsimonious and mechanistic parameterisation of every possible process existed, it is not likely to be feasible to include them all in coupled climate model experiments due to computational constraints. There is therefore a need to prioritise key processes which: a) are significant contributors to biological carbon storage and/or its climate feedback, b) have the potential (with appropriate fieldwork, lab experiments or data synthesis) to generate sufficient data to act as robust model constraints and/or develop new parameterisations suitable for inclusion in Earth System Models (ESMs), c) are computationally tractable (i.e. the process can be incorporated in a model without a prohibitive computational cost), and d) are relevant on the centennial, global scale of IPCC-class climate models.

Here, we identify major knowledge gaps in relation to biological processes that have an influence on determining the future biologically-mediated storage of carbon in the ocean. We focus on 3 ‘Challenges’ (https://bio-carbon.ac.uk/) relevant to better constraining the biological processes that contribute to ocean carbon storage: biological contributions to alkalinity, net primary production and interior respiration.

1.1: Challenge 1 - Biological contributions to alkalinity

Air-sea CO_2 exchange enables seawater CO_2 concentrations to maintain equilibrium with atmospheric CO_2 concentrations. The alkalinity of seawater is a key chemical determinant of the proportion of the dissolved inorganic carbon (DIC) in seawater that exists as CO_2. Alkalinity is therefore the primary control on how much DIC seawater can hold. A mechanistic understanding of all of the biogeochemical processes leading to changes in surface alkalinity is lacking (Middelburg et al., 2020). ESMs therefore simplify and/or ignore potentially relevant processes, resulting in the failure of models to capture observed surface alkalinity in key CO_2 sink regions (Lebehot et al., 2019). This results in a significant overestimation of contemporary surface ocean CO_2 trends in the Atlantic (by 20-40%) and is therefore likely to impact 21st century projections of ocean CO_2 uptake (Lebehot et al., 2019). There is a great diversity in how ESMs represent alkalinity and the main driver of its vertical gradient in the ocean, the carbonate pump (Planchat, Kwiatkowski, et al., 2023). In particular, few ESMs consider aragonite in addition to calcite, and none of them represent benthic calcifiers. The spatial distribution of $CaCO_3$ export at 100 m also varies greatly between ESMs. Finally, there is substantial divergence between models in the way $CaCO_3$ dissolution is influenced by the saturation state, which is projected to decrease over the course of the century (Canadell et al., 2021). More importantly, there are limited representations of the dependency of $CaCO_3$ production on the saturation state, despite evidence suggesting its impact on surface alkalinity projections (Planchat, Bopp, et al., 2023). The surface distribution and mean global profile of alkalinity improved between CMIP5 and CMIP6, predominantly due to an increase in the strength of the carbonate pump, but this is likely to have little effect on the magnitude of the projected ocean carbon sink due to negligible changes in the Revelle factor (Planchat, Kwiatkowski, et al., 2023).

The surface concentration of alkalinity is modified by surface freshwater fluxes or processes that redistribute alkalinity vertically within the water column (Millero, 2007). Alkalinity is removed from and returned to seawater through redox reactions (e.g. nitrification) and formation and dissolution of carbonate minerals. Vertical structure in alkalinity is generated through the formation, sinking and remineralisation of organic matter and particularly biological carbonates (e.g. plankton ‘shells’). The diversity of processes which contribute to the vertical redistribution of alkalinity, and the complexity of the associated ecosystem functions, result in ESMs excluding all but the most well-understood processes. For example, models tend to: a) assume all calcium carbonate is produced with a pure calcite mineralogy (Yool et al., 2013), b) that its production is in a fixed ratio with one or more (typically non-calcifying) phytoplankton types (Collins et al., 2011), or as a function of temperature or latitude, and c) the dissolution of calcite is governed purely by overly simplified seawater thermodynamics (Yool et al., 2013). In practice, open ocean carbonates are produced with a range of chemistries and crystalline structures (e.g. aragonite, calcite and high Mg-calcite, impacting the mineral solubility; Salter et al., 2017), from organisms ranging from pelagic calcifiers (plankton and fish) to benthic calcifiers (e.g. corals, bivalves and gastropods), impacting the $CaCO_3$ distribution, morphology, export pathways and sinking speeds. Carbonates are also dissolved in microenvironments ranging from the guts of grazers to sediment pore-waters (White et al., 2018) and sinking aggregates containing organic matter (Subhas et al., 2022).

1.2: Challenge 2 - Net primary production (NPP)

Current models disagree markedly on the magnitude of contemporary NPP and projections do not agree on even the sign of global NPP changes by the end of the century (Figure 1; CMIP6 models, SSP5-8.5 scenario), with inter-model uncertainty in projections actually increasing since the previous generation of CMIP5 models, especially at regional scales (Kwiatkowski et al., 2020; Tagliabue et al., 2021). Uncertainty in NPP projections across CMIP6 models results from a combination of factors regulating both resource limitation of phytoplankton growth and the loss processes that control phytoplankton standing stocks (Laufkötter et al., 2015). Both components can vary as a function of the different phytoplankton functional types included in models. Moreover, due to the simple parameterisations implemented, it is unlikely that the inter-model uncertainty across CMIP6 models represents the true uncertainty in both contemporary or future NPP (Tagliabue et al., 2021). Despite progress, we lack a critical appraisal of how inter-model differences and missing processes contribute uncertainty to NPP projections.

Key to the rate and efficiency of projected NPP is the way in which models represent the physiology and metabolism of plankton and changes to nutrient supply. Differences in how models parameterise phytoplankton nutrient limitation and resource demands, as well as zooplankton recycling that can amplify or dampen mixing-driven nutrient supply, are a key determinant of inter-model variability (Laufkötter et al., 2015; Tagliabue et al., 2021). For instance, in some regions small changes to nutrient uptake assumptions can modulate the sign of NPP change (Tagliabue et al., 2020). Also important are differences across models in external nutrient input pathways and their sensitivity to change, e.g. aerosols (Yool et al., 2021), ice sheets (Kwiatkowski et al., 2019), land-ocean river fluxes (Terhaar et al., 2019) and whether they include anthropogenic nutrient inputs (Yamamoto et al., 2022). An emerging source of inter-model uncertainty concerns the response of marine N_2 fixers, which can respond to climate changes more rapidly than primary producers and, because they also represent a source of new nitrogen, contribute to NPP trends (Bopp et al., 2021; Wrightson & Tagliabue, 2020). Lastly, we lack sufficient understanding of the role of plankton diversity, acclimation or adaptation, and response to multiple concurrent drivers, to develop parameterisations appropriate for inclusion in ESMs (Boyd et al., 2018; Martiny et al., 2022).

1.3: Challenge 3 - Interior respiration

Climate models vary widely in their parameterisation of processes responsible for particle formation and respiration, resulting in high uncertainty in future projections of particulate organic carbon (POC) flux. Current model projections do not even agree on the sign of change in POC export from the upper ocean by 2100 (Figure 1), with models disagreeing on whether export will increase or decrease over 84% of the ocean (CMIP6, SSP5-8.5; Henson et al., 2022). Uncertainty in model projections of export has actually increased since the previous generation of CMIP5 models (Laufkötter et al., 2016). Preliminary assessment of POC flux to 1000m in CMIP6 models suggests similar inter-model disagreement for deep fluxes and the transfer efficiency (POC flux at 1000m/POC flux at 100m), a measure of the efficiency of the biological carbon pump (Figure 1; Wilson et al., 2022).

Factors altering the efficiency and functioning of interior respiration include those due to altered microbial, phytoplankton and zooplankton community structure (Fu et al., 2016), which alters both the magnitude of POC export from the upper ocean and the type of sinking material produced. A reduction in the viability of calcifying organisms due to ocean acidification may affect biological carbon pump efficiency by reducing the amount of material available to ballast POC (Matear & Lenton, 2014). Other climate effects such as warming and changing nutrient availability could result in alterations to the magnitude and efficiency of the biological carbon pump via changes in phytoplankton community composition (Cabré et al., 2015), which potentially alters particle composition and size, respiration rate and aggregation/fragmentation of sinking particles. Variable organic matter stoichiometry may increase the amount of carbon stored via biological processes relative to the amount of NPP, and so fixed stoichiometry models (as typically used in CMIP6) may underestimate ocean carbon uptake (Kwiatkowski et al., 2018). Additionally, higher water temperatures will tend to increase organismal metabolic rates, more so for respiration than for NPP (Boscolo-Galazzo et al., 2018; Cavan et al., 2019). Resolving uncertainties in future projections of interior respiration is critical, as any increase in respiration would shoal the depth to which organic carbon penetrates into the deep ocean, which would tend to create a positive feedback between respiration and atmospheric CO_2 concentration (Kwon et al., 2009; Segschneider & Bendtsen, 2013), and vice versa.

1.4: Project aims

The aim of this work is to identify major knowledge gaps in relation to biological processes that have an influence on determining the future biologically-mediated storage of carbon in the ocean within 3 ‘Challenges’. We prioritised these knowledge gaps through both an expert assessment of the literature conducted by the project team (which consists of the authors of this paper) and an international community-wide survey. Finally, we compare the results of both methods and speculate how to overcome barriers to inclusion of key processes in ESMs.

2. Methods:

We followed a similar framework as an earlier gap analysis focused on export fluxes (Henson et al., 2022). In this project, we assessed processes in the 3 Challenge themes described above and extended the reach of our assessment by incorporating an international community survey. Our initial task was to undertake a literature review to identify published articles describing (ideally quantitatively) the significance of a particular biological process or processes on ocean carbon storage. We reviewed papers that used observations, experimental work, and/or modelling approaches, and papers that focused both on contemporary conditions and the response to future climate change. In total, we reviewed 193 papers and collated information regarding the importance and uncertainty in each process into extensive evidence tables (Tables S1-S3).

On the basis of the literature review, we sorted the identified processes into groups. This was necessary to reduce the number of possible process categories to ~ 15 per Challenge. Each group may encompass several sub-processes. For example, within the primary production Challenge, we identified a group of processes that we term ‘Resource limitation of growth’. This includes limitation by all the major macronutrients, i.e. nitrate, phosphate and silicate, although we recognise that the supply mechanisms of, and NPP response to, different nutrients may differ. These groupings were necessary to assist both with our expert assessment and the community survey. Greater than 15 categories would have made the survey design and analysis difficult, as well as made the survey so long as to be off-putting to respondents. The process categories within each Challenge, and the short descriptive text used in the survey to clarify what each category encompasses, are given in Tables 1-3.

The expert assessment of the identified processes was undertaken by the authors of this study. We assessed each process for its ‘Importance’ and ‘Uncertainty’ and assigned each a low, medium or high rating. We defined Importance as a process having a substantial/moderate/weak (for high/medium/low rating) influence on determining the future biologically-mediated storage of carbon in the ocean. We defined Uncertainty as a process having minimal/some/strong (for high/medium/low rating) supporting evidence, and additionally contrasting evidence with no consensus reached by the scientific community (high uncertainty), or no clear consensus reached by the scientific community (medium uncertainty), or consensus has been reached by the community (low uncertainty).

For the expert assessment, each member of the project team evaluated the evidence gathered from the literature review and independently assigned an Importance and Uncertainty rating to each process, based on the presented evidence (Tables S1-S3). After the results had been compiled, we met to discuss our individual results and reach consensus on the final ratings, focusing our discussions primarily on those processes for which there was disagreement.

2.1: Community survey development, data collection and analysis

To obtain a broad sample of responses, a questionnaire was developed in English (the full survey is provided in Supplementary Text 1). The survey was distributed in autumn 2022 using social media and through the authors’ professional and personal networks, resulting in 120 complete responses. Quantitative data were analysed in R v4.1.0 using the Tidyverse collection of packages (Wickham et al., 2019). Likert data were analysed using the ‘Likert’ function from the Likert package in R.

Section A of the survey collected demographic information (age, gender identity, education, location). Section B gathered information about respondent’s scientific expertise (area of expertise, career stage, length of time in oceanography). The remainder of the questionnaire captured respondent’s views on the key processes for the 3 Challenges of net primary production, interior respiration and biological contributions to alkalinity. These were defined to participants as “Net Primary Productivity is the net rate at which marine life converts dissolved CO_2 into organic carbon”, “Interior respiration refers to the biological processes controlling the conversion of organic carbon contained in non-living material into inorganic carbon” and “Biological contributions to alkalinity are the inputs and range of natural biological processes that act to alter seawater alkalinity". The aim of the survey was to rank those processes which, if included in global climate models, could potentially decrease uncertainty in projections of future ocean carbon storage. Respondents had the option to skip any questions in any Challenge that they felt were outside their area of expertise. Respondents were asked to choose and rank the top 3 processes they thought had an important influence on determining the future biologically-mediated storage of carbon in the ocean associated with each of the 3 Challenges. The topic of each Challenge was first defined before respondents were asked about their level of expertise (high/moderate/some/little/no expertise) in each Challenge area. Respondents could choose not to complete the process selection for a particular Challenge. They were then asked their opinion on the importance of the Challenge, using a 5-point Likert scale. Respondents were asked to rank, in order of importance, the top three processes associated with the role of that Challenge in ocean carbon storage. Anonymised survey results are available in Data Set S1.

Ethics Statement: All respondents completed the survey themselves and gave their permission to use the results. Individuals were not identifiable from the data provided. The survey described in this paper was reviewed and approved by the University of Plymouth Science and Engineering Research Ethics Committee.

3. Results:

The importance and uncertainty ratings assigned to each process by the expert assessment are given in Tables 1-3, with the evidence supporting these assessments in Tables S1-S3. In the following sections, we briefly discuss the rationale for identifying processes as having high importance. We do not provide details in the main text of the rationale for identifying processes as having medium or low importance, but the supporting evidence is given in Tables S1-S3. Note that 'high' importance in this study indicates that there is strong evidence for a particular process's importance, and that processes or fields of research which have been understudied are therefore likely to present fewer topics rated as high importance.

3.1: Biological contributions to alkalinity - expert assessment

Of the 15 shortlisted processes considered significant for biological contributions to alkalinity, two were ranked as having high importance based on the available evidence: high level understanding of calcium carbonate production and rain ratio.

High level understanding of calcium carbonate production refers to the amount and distribution of biological $CaCO_3$ production and its sensitivity to climate change. A change in calcification induces a surface alkalinity and DIC anomaly in a 2:1 ratio and thus has a direct consequence on the air-sea carbon flux and ocean buffer capacity. However, although projections of this anomaly are generated by ESMs (Planchat, Kwiatkowski, et al., 2023), it is difficult to verify the projected changed over the observational era due to the small amplitude of the alkalinity anomaly (Ilyina et al., 2009), and the overprinting of any biological alkalinity signals by water-cycle change driven changes. Furthermore, the impacts of climate change and ocean acidification on calcifiers are likely to be highly region- and taxa-dependent, due to the spatial heterogeneity in environmental stressors (e.g. with respect to acidification; Orr et al., 2005) and the heterogeneity in sensitivity of calcifiers to these changes (e.g. Leung et al., 2022; Seifert et al., 2020). For example, increased light availability in the polar regions could favour calcification by coccolithophores, while shoaling of the saturation horizons could threaten pteropods or cold-water corals (Leung et al., 2022; Orr et al., 2005). In the tropics, increased temperature could significantly impact corals through bleaching events (Bindoff et al., 2019).

It should be noted that although calcification induces biological carbon storage, via sinking of particulate inorganic carbon to the interior ocean, it also induces outgassing of CO_2 from the ocean surface, due to the imbalance in carbonate chemistry that it causes.

Rain ratio is the ratio between the export of particulate inorganic carbon (PIC) and POC. Assessing changes in this ratio in response to climate change and ocean acidification is central to estimating the overall impact of biology on alkalinity and DIC in the ocean surface layer. The rain ratio anomaly can be used to estimate biologically-mediated changes in surface carbonate chemistry, and hence in air-sea carbon flux (Humphreys et al., 2018), as well as, in the longer term, the ocean's buffer capacity in the face of rising atmospheric CO_2 concentration (Zeebe & Wolf-Gladrow, 2001). Yet, although POC export remains uncertain in ESM projections, most models show a decrease (Henson et al., 2022) while the sign of change in the projected PIC export is more uncertain, driving divergent rain ratio anomalies in projections (Planchat, Bopp, et al., 2023).

3.2: Net primary production - expert assessment

Of the 15 shortlisted processes considered significant for NPP, four were ranked as having high importance for reducing uncertainty in future model projections based on the available evidence. These were resource limitation of growth, phytoplankton loss processes, nitrogen fixation and zooplankton processes.

Resource limitation of growth was the top ranked process due to its central and well understood role as a bottom-up driver of oceanic primary production. Within this process grouping, we identified phytoplankton growth limitation by macronutrients, micronutrients, or light, and more specific forms of co-limitation of growth by nutrients and light, multiple nutrient types and the role of inorganic and organic nutrient limitation as being of particular importance. There is a rich body of observational literature supporting these forms of growth limitation and whilst most ESMs currently represent macronutrient, light and micronutrient (e.g. iron) limitation to varying extents, there are nuances to these relationships that require refinement and development in order to improve confidence in model projections (Laufkötter et al., 2015; Steinacher et al., 2010; Tagliabue et al., 2020).

Phytoplankton loss processes, including mortality and zooplankton grazing, were also considered to be of high importance as they modulate the standing stocks of primary producers, and models tend to derive NPP rates as the product of resource-limited growth and standing stocks (Bindoff et al., 2019). Under the simplest scenario, grazing or mortality rates that are set too high act to depress NPP, whereas when rates are too low NPP may be higher than observational estimates. On more regional scales recent inter-model comparisons demonstrate that correctly representing zooplankton grazing, for example, can significantly alter the balance between production and grazing in low latitude regions, particularly in response to thermal changes (Laufkötter et al., 2015). Viral mortality is also increasingly recognised as a key factor with the potential to control bloom formation and termination, yet viruses remain poorly described in marine ecosystem models and are largely absent in ESMs (Flynn et al., 2021).

Nitrogen fixation is a globally significant source of new nitrogen to the ocean that may compensate stratification-driven declines in nitrate availability (Bindoff et al., 2019), yet its role in aiding the biological storage of carbon in the ocean in the context of a changing climate remains unclear (Bopp et al., 2022). Modelling studies that have demonstrated significant differences in model estimates of NPP when nitrogen fixation is included or excluded indicate a crucial role for this process in centennial-scale projections of ocean productivity (Bopp et al., 2022; Tagliabue et al., 2021; Wrightson & Tagliabue, 2020).

Furthermore, recent observational studies have greatly expanded the geographic range and taxonomic identities of diazotrophic organisms in the ocean (e.g. Sipler et al., 2017). Overall it is clear that N_2 fixation will likely play an important role in future projections of NPP change (Bopp et al., 2022; Paulsen et al., 2017; Wrightson & Tagliabue, 2020), with uncertainty associated with the response of different groups of nitrogen fixers and their physiological feedbacks in a changing climate (Wrightson et al., 2022).

Zooplankton processes were also a highly ranked category, with this grouping including specific processes such as rates of zooplankton growth, respiration and grazing, and also the role zooplankton play in nutrient recycling. Zooplankton are a critical component of the ocean food web and it is already recognised that improved representation of zooplankton in ESMs will likely improve estimates of carbon cycling (Petrik et al., 2022). Furthermore, increased uncertainties in NPP projections may arise due to inter-model differences in the parameterisation of grazing rates, particularly their response to temperature changes (Tagliabue et al., 2021). With regards to nutrient excretion, mesozooplankton nutrient regeneration may provide a significant fraction of the total phytoplankton and bacterial production requirements (Hernández-León et al., 2008) and how their recycling rates respond in a changing climate can vary markedly (Richon & Tagliabue, 2021).

3.3: Interior respiration - expert assessment

For interior respiration we concluded that, of the 15 processes assessed, 6 of them had high importance based on the available evidence: biotic fragmentation, aggregation, preferential remineralisation, microbial solubilisation, particle characteristics and particle type.

Biotic fragmentation refers to the breaking-up of particles into smaller pieces, predominantly via zooplankton flux feeding or swimming. Fragmentation is likely to be highly significant in controlling flux attenuation, with recent estimates finding that, at least during high flux events, fragmentation contributes ~ half of flux loss in the mesopelagic (Briggs et al., 2020), although this study was unable to distinguish between biotic and abiotic (via turbulence or shear) fragmentation. The swimming action of Euphausids readily fragments particles and at typical abundances could interact with 50-100% of particles in the upper 100m of the ocean (Dilling & Alldredge, 2000; Goldthwait et al., 2004). Alternatively (or additionally) fragmentation may occur as a consequence of flux-feeding whereby zooplankton consume marine aggregates or fecal pellets and in the process break off small fragments of the particle, either unintentionally (sloppy feeding; Lampert, 1978) or deliberately to increase the nutritional content of particles for subsequent ingestion (microbial gardening; Mayor et al., 2014). In a modelling study, particle fragmentation by small copepods was predicted to account for ~ 80% of the flux attenuation of fast sinking particles (Mayor et al., 2020).

Aggregation refers to the formation of larger particles from smaller ones which can be mediated by sticky exudates that increase the success rate of collisions. As single cells are rarely sufficiently large or dense to sink independently, aggregation must take place in the upper epipelagic or mesopelagic to account for the presence of phytoplankton material in deep sediment traps (Durkin et al., 2021). Observation and model-based studies have concluded that aggregation is an essential precursor to large flux events (Gehlen et al., 2006; Jackson, 2005; Martin et al., 2011). Aggregation has been shown to occur by the production of transparent exopolymer particles (TEP) by diatoms, possibly in response to nutrient limitation (Martin et al., 2011), or via differential settling whereby faster sinking particles 'catch up' with slower sinking particles and coagulate (Riebesell, 1991). Despite its role as a significant means of particle formation and transformation, the mechanisms underlying how, when and why aggregation occurs remain poorly known.

Preferential remineralisation describes the differences in remineralisation depth of the constituents of particulate organic matter relative to carbon. In sinking organic matter, phosphate and nitrate tend to be preferentially and rapidly remineralised relative to carbon (Anderson & Sarmiento, 1994; Schneider et al., 2003). The drawdown of excess carbon relative to nitrogen or phosphate ('carbon over-consumption') represents a potential negative feedback mechanism, as it results in additional drawdown of atmospheric CO_2 (Riebesell et al., 2007). Modelling work suggests that C:P or C:N variability in the mesopelagic can alter the strength of carbon sequestration by ~ 20% (Tanioka et al., 2021; Tian et al., 2004).

Microbial solubilisation is the respiration of dissolved and particulate organic material by microbial communities, where rates may be impacted by environmental conditions, the microbial community structure, metabolic rates and growth efficiency. The influence of temperature, oxygen concentration and pressure on rates of microbial respiration are reasonably well understood (Amano et al., 2022; Cavan et al., 2019; Weber & Bianchi,

2020) and are implicitly incorporated into some biogeochemical models (Laufkötter et al., 2017). However the relative contributions to respiration by particle-attached or free-living microbial communities is not well-constrained, and neither are the details of how microbial ecology affect respiration, such as the conditions under which colonies may be established on sinking particles, mortality rates, and cell attachment and detachment (Nguyen et al., 2022).

Particle characteristics describes the size, shape, porosity, density and strength of particles. These characteristics can alter particle sinking speeds, and their susceptibility to remineralisation and aggregation/fragmentation. Sinking speed is often considered to be directly linked to particle size via Stokes' Law, however several studies have found no clear correlation (Iversen & Lampitt, 2020; Williams & Giering, 2022), although large data syntheses seem to show some connection (Cael et al., 2021). Instead, the particle's excess density and/or morphology are likely to be critical factors (Prairie et al., 2019; Trudnowska et al., 2021). Most global climate models only distinguish two particle sizes at most (Henson et al., 2022), although size-resolving schemes have been used in uncoupled simulations (Kriest & Oschlies, 2008). There are as yet insufficient observations to establish the links between remineralisation potential and particle shape, porosity or strength.

Particle type refers to whether a particle is, for example, a fecal pellet, aggregate, carcass etc., which will affect the sinking speed, and their susceptibility to remineralisation and aggregation/fragmentation. The phytoplankton and zooplankton community composition will also affect the types of particles generated. The details of the sinking particle type, e.g. whether diatom frustule, zooplankton carcass, diazotrophs, salps etc. plays a strong role in setting the sinking velocity and thus carbon storage (e.g. Bonnet et al., 2023; Durkin et al., 2021; Halfter et al., 2022; Maerz et al., 2020; Steinberg et al., 2023), with sometimes contradictory evidence in the literature for the importance of different particle types (e.g. salp fecal pellets; Iversen et al., 2017; Steinberg et al., 2023). The complexity of the possible particle types, and how they may combine into multi-component aggregates, and the lack of a direct correspondence with remineralisation potential presents a major challenge for robust modelling of the biological carbon pump.

For all of the processes identified above as having high importance to interior biological carbon storage, there are significant remaining uncertainties regarding the mechanisms at play. In addition, observational constraints mean that there is little information on how these processes may vary temporally and spatially. Both of these factors make incorporating the interior respiration processes we identify as 'high importance' into biogeochemical models challenging.

3,4: Community survey results

In total, we received 120 responses to the community survey (Data Set S1). The demographics of the respondents are shown in Figure 2. For those who declared their gender identity, 51% of respondents identified as female, 47% identified as male, and 1.8% identified as non-binary. The majority of respondents had attained a PhD-level qualification (78%), with the most common career stages being lecturer/professor (30%), research scientist (25%) and post-doc researcher (13%). The country in which respondents currently worked showed a wide geographical spread, albeit with a predominance from the global north, with all continents (except South America) having at least one respondent. The majority of respondents currently worked in the UK (54%), as might be expected given that the BIO-Carbon programme is UK-funded. A range of expertise was captured in the survey, with those focusing on modelling (45 respondents) and observations (48 respondents) roughly equally represented, with fewer focusing on experimental work (27 respondents). The majority of respondents identified as biogeochemists (63 respondents) or marine ecologists (49 respondents). Note that respondents could choose more than one answer for these two questions.

In total, 105, 88 and 61 respondents completed the sections on NPP, interior respiration and biological contributions to alkalinity, respectively. Of these, those with high or moderate expertise numbered 57, 40 and 23, respectively. We only present results from those who considered themselves to have high or moderate expertise, noting that this is only approximately half of those completing the ranking for a particular Challenge and in some cases, particularly for alkalinity, represents a rather small sample size. The overall ranking of processes from the community survey is shown in Figure 3.

The self-identified field of expertise of the respondents sometimes changed the ranking of the processes, although generally the top 5 were similar (Figure 4). For NPP, resource limitation of growth, zooplankton processes, phytoplankton loss processes and organic matter cycling were in the top 5, regardless of field of expertise. For those identifying as modellers, food web complexity was additionally in the top 5; for observationalists and experimentalists, phytoplankton adaptation and acclimation made the top 5 processes. For interior respiration, microbial solubilisation, organic matter lability, particle characteristics and zooplankton processes were in the top 5, regardless of expertise. Additionally, particle type made the top 5 for modellers and observationalists, and biotic fragmentation for experimentalists. For alkalinity, there was somewhat more disparity in the top 5 processes between expertise, however note that only 4 respondents identifying as experimentalists with high/moderate expertise in alkalinity participated. All fields of expertise agreed that high level of understanding of calcium carbonate production, riverine supply of alkalinity and biotically mediated dissolution are in the top 5 most important processes, with physiology of calcium carbonate production, sedimentary processes, primary production and remineralisation, rain ratio, and plankton community making the top 5 for different expertise groups. Additional segregation of expertise into field of study (e.g. biogeochemistry, ecology etc.) is reported in Figure S1 but not discussed further due to the small sample size in many categories.

4. Discussion:

We identified some key knowledge gaps associated with the biological storage of carbon, which were prioritised on the basis of their potential to reduce uncertainty in model estimates of the future biologically-mediated storage of carbon in the ocean. In general, the expert assessment and community survey agreed in terms of the most significant processes (Figure 3). For example, resource limitation of growth (for NPP), microbial solubilisation (for interior respiration) and high level understanding of calcium carbonate production (for alkalinity) were within the top ranking processes for both the survey and expert assessment. Some significant differences did emerge however, such as the low ranking of N_2 fixation (for NPP) in the survey, which was ranked as high importance in the expert assessment. These differences may arise from a combination of the pre-existing bias in the literature used for the expert assessment and potentially the inherent limitations of a community survey. Whereas the project team spent considerable time on combing the literature, assessing the papers, assembling the evidence tables, and discussing the results to reach consensus on the rankings, the community survey was designed to be completed in approximately 15 minutes and respondents were not provided with the evidence collated for the expert assessment.

Although processes may have been identified as important here, unless it is tractable to observe them in sufficient detail to develop efficient model parameterisations, incorporating many of these processes into climate models remains challenging. Parameterisations for the ocean biogeochemistry component of climate models can be developed from theory, idealised simulations, laboratory experiments or field observations. In order to develop a robust parameterisation for a process, observations from a single experiment or field programme alone (or even a handful of data points) are rarely sufficient. Instead, data representative of a broad range of environmental conditions are ideally required, which, in the field, demands good spatial and seasonal coverage, and also international cooperation to collate such data. Data synthesis activities are crucial to these efforts, as are attempts to standardise sampling and analysis protocols to generate directly inter-comparable datasets.

Parameterisation of many of the processes identified in this study requires data collection at sea. The growing adoption and use of autonomous technologies has greatly increased the amount of field data available, particularly by providing the opportunity to resolve temporal and vertical variability, and in the case of the BGC-Argo network, spatial variability as well. Although new methods and novel sensors (e.g. Estapa et al., 2019; Giering et al., 2020) to obtain biogeochemically-relevant data (e.g. Briggs et al., 2020; Clements et al., 2022) from autonomous vehicles have emerged, nevertheless many of the processes identified here cannot be observed remotely, or inferred through proxies, for example organism-particle interactions, nutrient recycling rates, microbial activity etc. This presents challenges for model development but also opportunities for observational and experimantal programmes to broaden efforts to capture new information about relevant processes or for focussed process studies.

Even with additional sources of data, challenges remain in incorporating additional processes into the ocean biogeochemistry component of climate models. Developing robust parameterisations requires observations or experiments across a wide dynamic range of conditions, and evaluating model results requires independent data with the appropriate spatial and seasonal coverage. Adding additional parameterisations to models increases the complexity, and so run time and storage requirements which, particularly in the case of global ESMs, may be prohibitive. Therefore, demonstrating that the additional processes have a significant impact on the relevant components of the model, which will depend on the objectives for developing the model (which can be diverse), is important. In the context of our work here, the objective may be to improve representation of ocean carbon fluxes, such as net primary production or the strength of the biological carbon pump, and their climate feedbacks for example. Demonstrating an impact on model performance may be achieved through 1-D 'test bed' versions of climate models which can be simply and quickly run, potentially through sensitivity simulations with multiple permutations to establish the form or parameter values needed to represent an additional process. Alternatively, offline physics from coupled model output can be used to run multiple experiments at global scale that may be highly complex (e.g. Bopp et al., 2022; Tagliabue et al., 2020; Wrightson et al., 2022). Rapid testing of alternate or additional parameterisations in a 3-D framework can also be achieved using the transport matrix method (Khatiwala, 2007).

Our literature review and community survey highlighted several processes that have high importance and high uncertainty which may act as focal areas for future projects. More broadly, maximising the gains from modelling, fieldwork and experimental studies relies on collaboration between communities. Co-design of research projects from the outset can ensure outputs will be useful to both communities, as well as fostering early recognition of emerging research topics and potential limitations. Considering the potential for scaling-up field or experimental data at the project planning stage, for example through empirical or mechanistic relationships with commonly observed (and modelled) environmental variables will ensure the broadest applicability of the project results. This will require data synthesis activities to be embedded in research programmes, as the information obtained from a single project is rarely sufficient to provide data on the large space and time scales necessary for model development and validation. Data synthesis is most effective and impactful when data is shared openly and hence wide collaboration is facilitated. Exploring how model behaviour reflects differences in model parameterizations, functional equations, and parameter values in both the euphotic and mesopelagic zones and conducting sensitivity analyses will assist in ensuring alterations to biogeochemical models are both parsimonious and robust.

Significant challenges lie ahead in modelling the diversity of living organisms' responses to climate forcing and the subsequent feedbacks through the ocean's carbon cycle. Identifying high priority knowledge gaps is a crucial first step in this process and requires synergy across observational, experimental and modelling communities.

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Open Research: Full anonymised results of the community survey are available as part of the Supporting Information (Data Set S1) and from http://dx.doi.org/10.5281/zenodo.10435533

Table 1: Expert assessment of importance and uncertainty in processes related to the biological contribution to alkalinity.

Process	**Definition**	**Importance**	**Uncertainty**
High level understanding of calcium carbonate production	e.g. the amount and distribution of biological $CaCO_3$ production and its sensitivity to future environmental change.	High	Medium
Rain ratio	High-level controls on Particulate Inorganic Carbon to Particulate Organic Carbon (PIC:POC) ratio of export.	High	Medium
Mineralogy of calcium carbonate production	Production of calcium carbonates such as aragonite and high magnesium calcite which have higher solubilities than standard calcite.	Medium	High
Plankton community	Our understanding of and ability to represent calcifiers within the planktonic ecosystem models.	Medium	High
Fish derived carbonates	Carbonates produced in the guts of bony fish.	Medium	High
Biotically mediated dissolution	Dissolution of $CaCO_3$ in zooplankton/fish guts and within fecal pellets and aggregates.	Medium	Medium
Abiotic dissolution	Dissolution of $CaCO_3$ in undersaturated waters.	Medium	Medium
Riverine supply of alkalinity	Alkalinity input to the ocean via rivers.	Medium	Medium
Physiology of $CaCO_3$ production	How $CaCO_3$ is produced by different organisms.	Low	High
Sedimentary processes	Alkalinity fluxes across the sediment-water interface, in response to processes such as anaerobic sulphate reduction.	Low	High
Calcium carbonate within sea ice	Formation and dissolution of carbonates changing the total alkalinity to dissolved inorganic carbon ratio within sea ice.	Low	High
Nutrient cycling	Processes beyond primary production and remineralisation such as nitrification/denitrification.	Low	Medium
Organic alkalinity	Contribution of weakly acidic functional groups present in Dissolved Organic Matter.	Low	Medium
Primary production and remineralisation	Assimilation and release of nutrients that contribute to total alkalinity.	Low	Low

Table 2: Expert assessment of importance and uncertainty in net primary production processes.

Process	Definition	Importance	Uncertainty
Resource limitation of growth	Limitation of phytoplankton growth by both major and micro nutrients and light.	High	Medium
Phytoplankton loss processes	All losses of phytoplankton biomass to grazing or mortality.	High	Medium
N_2 fixation	Conversion of dinitrogen into fixed nitrogen by diazotrophs.	High	Medium
Zooplankton processes	Activity of zooplankton, encompassing grazing, nutrient recycling etc.	High	Medium
Phytoplankton adaptation, acclimation	Ability of phytoplankton to adjust their physiology in response to environmental changes.	Medium	High
Microbial loop	Turnover of organic nutrients and carbon by bacteria.	Medium	High
Response to thermal stress	How plankton are parameterised to respond to temperatures exceeding their thermal optimum.	Medium	High
Phytoplankton physiology	The cellular functioning of phytoplankton, including their photosynthesis, respiration and nutrient acquisition traits.	Medium	Medium
Plankton metabolism	Chemical processes that occur within individual organisms.	Medium	Medium
External nutrient inputs	Supply of nutrients into the ocean from rivers, sediments, atmosphere and hydrothermal venting.	Medium	Medium
Micronutrients	Nutrients typically present at low concentration - including iron, manganese, zinc, cobalt, nickel.	Medium	Medium
Organic matter cycling	Transformation of dissolved and particulate organic matter into inorganic forms, including acquisition of organic nutrients.	Low	High
Food web complexity	The number of groups in a food web (including plankton, bacteria, fish and viruses) and their interactions.	Low	High
Mixotrophy	Plankton that utilise both autotrophy and heterotrophy.	Low	High

Table 3: Expert assessment of importance and uncertainty in interior respiration processes.

Process	Definition	Importance	Uncertainty
Biotic fragmentation	Fragmentation of particles into smaller pieces by the action of zooplankton flux feeding or swimming.	High	Medium
Aggregation	Formation of larger particles by the aggregation of smaller particles. Transparent Exopolymer Particles (TEP) and other sticky exudates may increase the success rate of collisions.	High	Medium
Preferential remineralisation	Preferential remineralisation of elements relative to carbon of dissolved organic matter (DOM) and particulate organic matter (POM)	High	Medium
Microbial solubilisation	Microbial respiration of dissolved and particulate organic material. The rate of solubilisation may be impacted by the microbial community and metabolic rates and growth efficiencies. Pressure, temperature and oxygen concentration, and other factors will impact these rates.	High	Medium
Particle characteristics	The size, morphology, porosity and density of particles which can affect their sinking speed and susceptibility to remineralisation, fragmentation or (dis)aggregation (excluding the role of ballast).	High	Medium
Particle type	The type of particle (e.g. fecal pellet, aggregate, single cell, carcass, mucus web) will affect the sinking speed and susceptibility to remineralisation or fragmentation/aggregation.	High	Medium
Zooplankton vertical migration	Daily vertical migration of zooplankton between euphotic and mesopelagic depths. Also referred to as active flux, with excretion, egestion, respiration and mortality occurring in the mesopelagic.	Medium	High
Fish-mediated processes	Daily vertical migration of fish and their contribution to flux via fecal pellet production.	Medium	High
Ontogenetic migration	Seasonal migration of zooplankton to mesopelagic depths where they remain over winter (also referred to as the lipid pump).	Medium	High
Mineral ballasting	Biomineral (biogenic silica, calcium carbonate) or lithogenic (dust) material which increases the specific density and sinking speed of particles.	Medium	Medium
Organic matter lability	Particulate organic matter and dissolved organic matter is composed of compounds of varying lability, with some more readily remineralised than others.	Medium	Medium
Zooplankton processes	Zooplankton particle interactions (e.g. grazing, fecal pellet production, coprophagy) excluding biotic fragmentation and diel vertical migration.	Medium	Medium
Ectoenzymatic hydrolosis	Microbial excretion of extracellular enzymes to degrade complex organic compounds.	Low	High
Viral infection	Viral infection of cells can lead to cell lysis. This may lead to the viral shuttle, i.e. increased secretion of sticky material promoting aggregation, or to the viral shunt, i.e. increased DOC production and a reduction in transfer of carbon to higher trophic levels.	Low	High
Abiotic fragmentation	Fragmentation of particles into smaller pieces by turbulence or shear.	Low	Medium

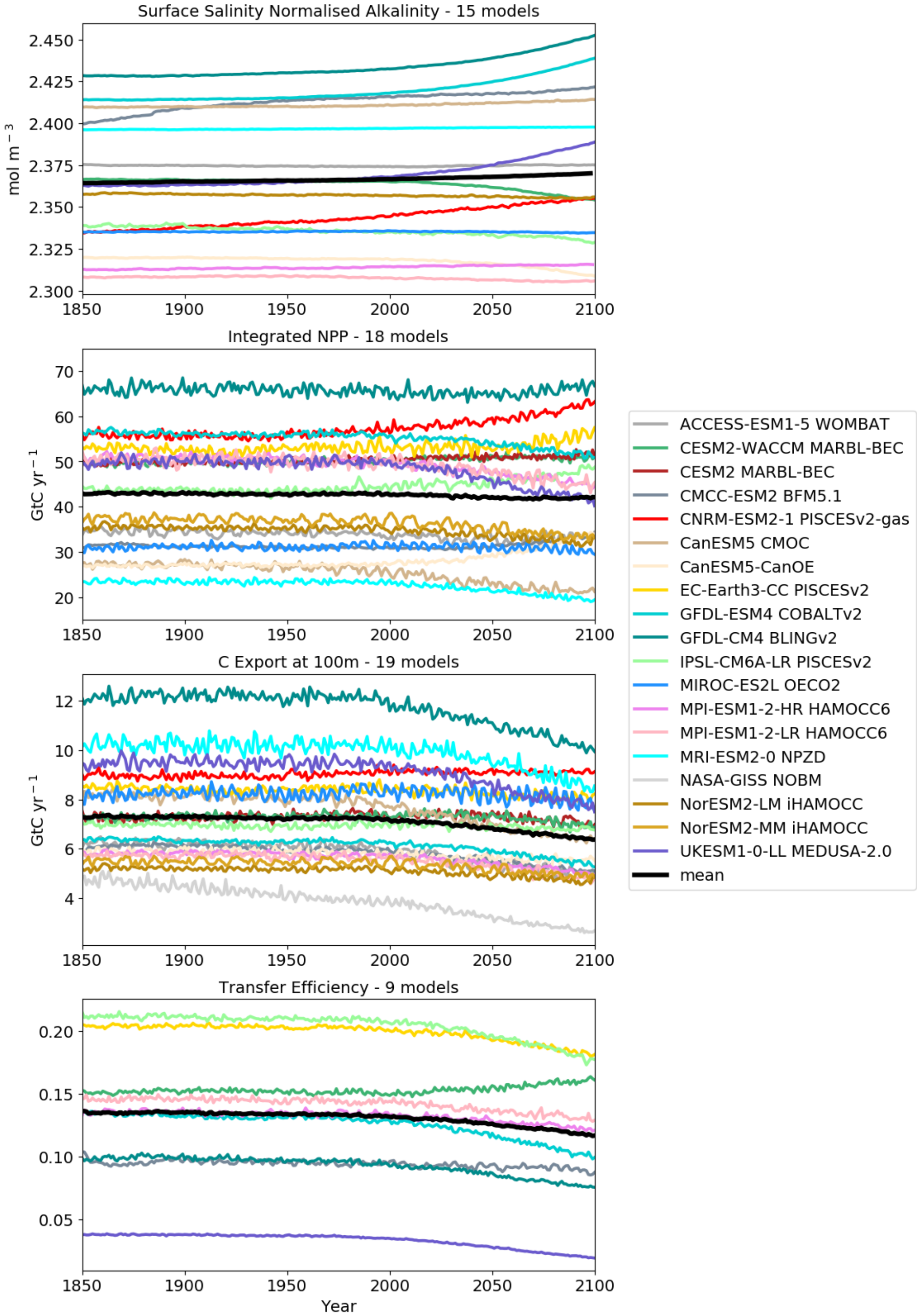

Figure 1: Time series of global mean salinity normalised alkalinity, NPP, POC flux at 100m and transfer efficiency (POC flux at 1000m/POC flux at 100m) for the period 1850-2100 (scenario SSP5.8-5) taken from the CMIP6 model output archive. Thick black line shows the multi-model mean.

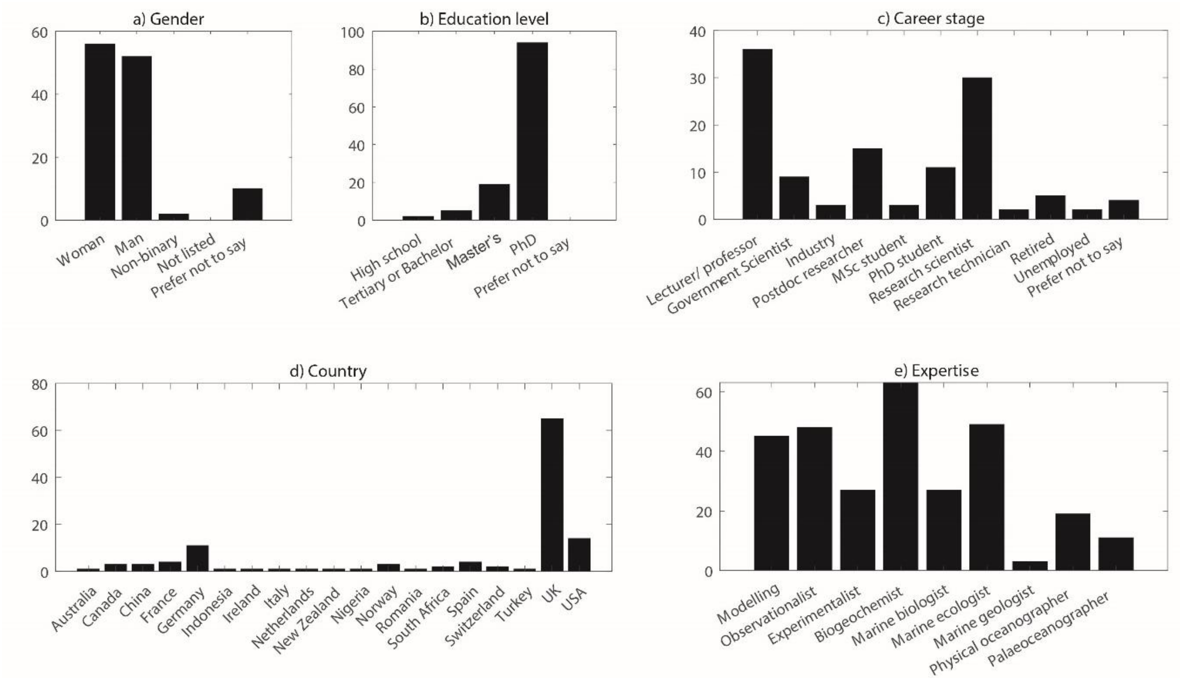

Figure 2: Demographics of survey respondents (n = 120). Note that for 'expertise' respondents could choose more than one category.

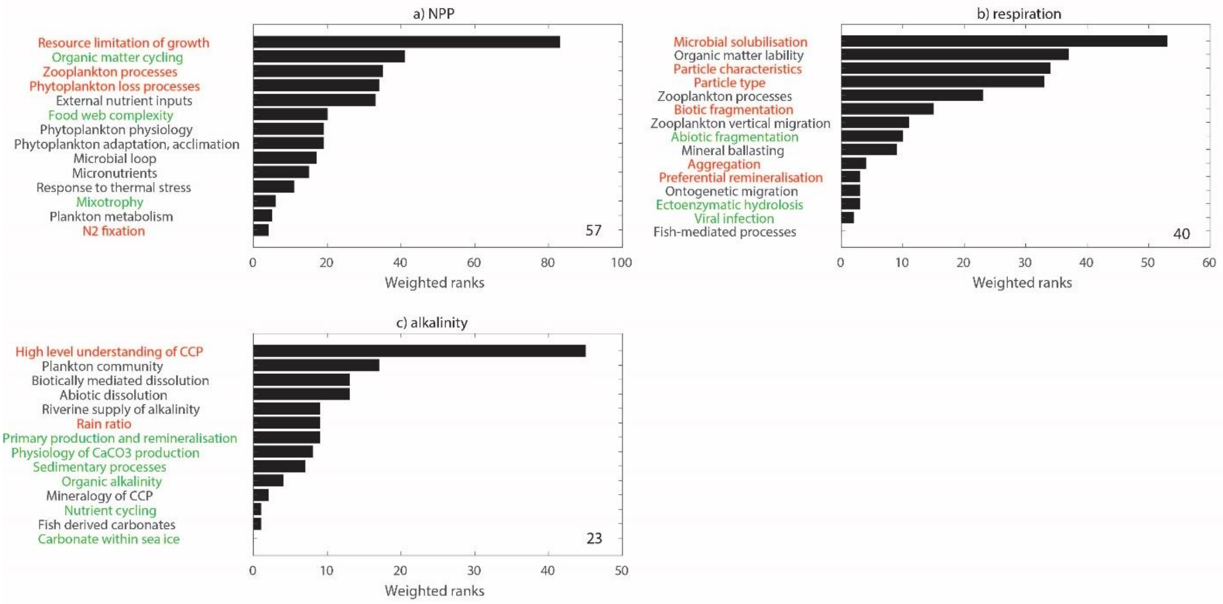

Figure 3: Community survey ranking of processes important to determining the future biologically-mediated storage of carbon in the ocean associated with each of the 3 Challenges. Only those respondents who assessed their expertise as high or moderate for a particular Challenge were included in the analysis. Responses are weighted so that the 1st ranked choice = 3 points, 2nd ranked choice = 2 points, and the 3rd ranked choice = 1 point. Numbers in bottom right corner of plots indicate number of respondents in that category. CCP = calcium carbonate production. Processes marked in red (green) were rated as having high (low) importance in the expert assessment.

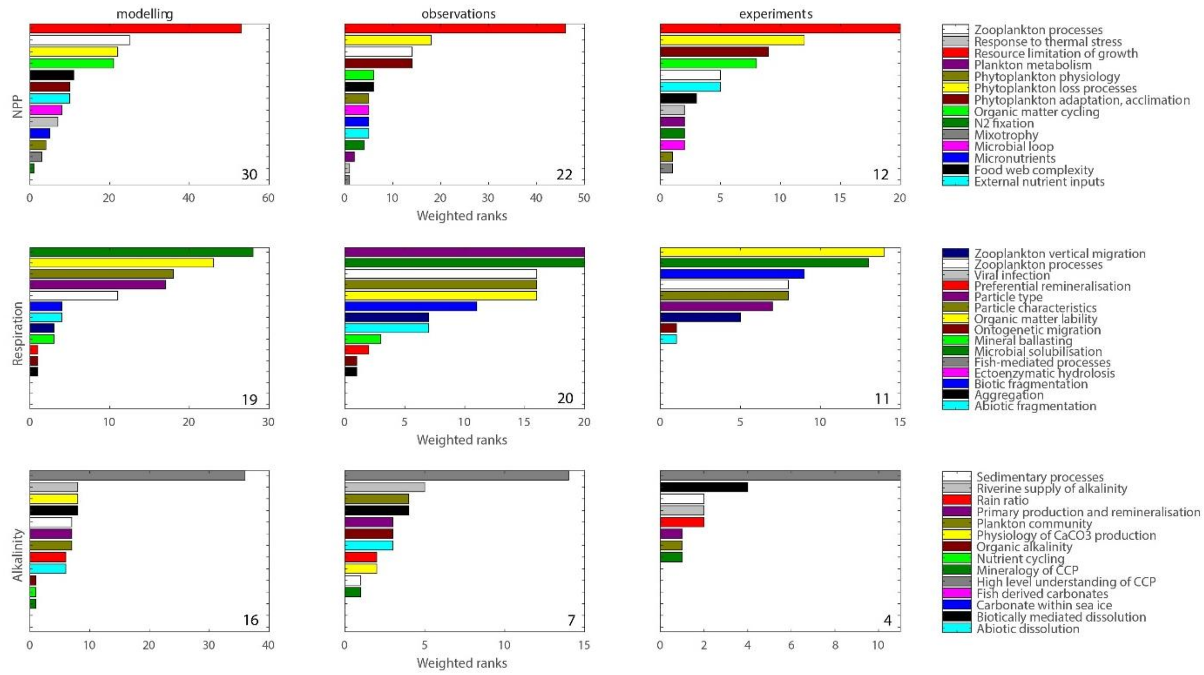

Figure 4: Community survey ranking of processes, plotted according to expertise of the respondent. Only those respondents who assessed their expertise as high or moderate for a particular Challenge were included in the analysis. Note that respondents could choose more than one option for their expertise (or none). Numbers in bottom right corner of plots indicate number of respondents in that category. CCP = calcium carbonate production.

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