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

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13

14 **Key Points:**

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

21

22 **Abstract:**

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

42

43 **1. Introduction:**

44 Biological processes contribute significantly to oceanic storage of CO₂ by maintaining
45 a lower concentration of carbon in the surface than in the deep ocean. However, how biological
46 processes will respond to climate change and the subsequent feedbacks to ocean carbon storage
47 are poorly known. As a consequence, the IPCC Assessment Report 6 Working Group I report
48 (Canadell et al., 2021) concluded with high confidence that climate change will result in
49 alterations to the magnitude and efficiency of biological contributions to carbon storage, but
50 that there is low confidence in the magnitude or even sign of these biological feedbacks. This
51 level of uncertainty is reflected in the discrepancies between observation and model based
52 estimates of ocean carbon storage (e.g. Friedlingstein et al., 2022), part of which may be due
53 to poorly represented biological processes. As the contribution of biological processes to ocean
54 CO₂ uptake and storage is expected to gain greater importance with continued climate change
55 (Hauck et al., 2015), improving model representation of these processes (which requires

56 improved observational constraints) is essential. Major knowledge gaps result from the number
57 and complexity of processes involved in biological carbon storage and a lack of observations
58 with which they can be constrained. This lack of data limits both the fundamental
59 understanding of relevant processes, and the development and validation of biogeochemical
60 models as the data are rarely available on the large spatial and long temporal timescales
61 required. The availability of robust model parameterisations is thus limited, resulting in a lack
62 of consensus among climate models on which biological processes should be included (or
63 excluded), and hence significant uncertainty in the magnitude and sign of biological feedbacks
64 to climate change. However, even if sufficient data to build a parsimonious and mechanistic
65 parameterisation of every possible process existed, it is not likely to be feasible to include them
66 all in coupled climate model experiments due to computational constraints. In the context of
67 climate modelling, there is therefore a need to prioritise key processes which: a) are significant
68 contributors to biological carbon storage and/or its climate feedback, b) have the potential (with
69 appropriate fieldwork, lab experiments or data syntheses) to generate sufficient data to act as
70 robust model constraints and/or develop new parameterisations suitable for inclusion in Earth
71 System Models (ESMs), c) are computationally tractable (i.e. the process can be incorporated
72 in a model without a prohibitive computational cost), and d) are relevant on the centennial,
73 global scale of IPCC-class climate models.

74

75 Here, we identify major knowledge gaps in relation to biological processes that have
76 an influence on determining the future biologically-mediated storage of carbon in the ocean.
77 We focus on 3 ‘Challenges’ that were pre-defined by the BIO-Carbon programme ([https://bio-](https://bio-carbon.ac.uk/)
78 [carbon.ac.uk/](https://bio-carbon.ac.uk/)). Critical areas regarding the role played by biological processes in the ocean
79 carbon cycle include their contributions to alkalinity, their net production of organic carbon
80 pools via primary production and how interior respiration modulates the transfer of organic
81 carbon through the ocean interior. These issues represent areas where there is little to no
82 consensus in existing ESMs and strong potential for emergent feedbacks in a changing climate,
83 linking into strategic priorities of the World Climate Research Programme. Below we expand
84 on the three key challenges in more detail. The framework for assessment detailed here could
85 equally be applied to other aspects of the marine carbon cycle in the future.

86

87 *1.1: Challenge 1 - Biological contributions to alkalinity*

88 Air-sea CO₂ exchange enables seawater CO₂ concentrations to maintain equilibrium
89 with atmospheric CO₂ concentrations. The alkalinity of seawater is a key chemical determinant

90 of the proportion of the dissolved inorganic carbon (DIC) in seawater that exists as CO₂.
91 Alkalinity is therefore the primary control on how much DIC seawater can hold. A mechanistic
92 understanding of all of the biogeochemical processes leading to changes in surface alkalinity
93 is lacking (Middelburg et al., 2020). ESMs therefore simplify and/or ignore potentially relevant
94 processes, resulting in the failure of models to capture observed surface alkalinity in key CO₂
95 sink regions (Lebehot et al., 2019). This results in a significant overestimation of contemporary
96 surface ocean CO₂ trends in the Atlantic (by 20-40%) and is therefore likely to impact 21st
97 century projections of ocean CO₂ uptake (Lebehot et al., 2019). There is a great diversity in
98 how ESMs represent alkalinity and the main driver of its vertical gradient in the ocean, the
99 carbonate pump (Planchat, Kwiatkowski, et al., 2023). In particular, few ESMs consider
100 aragonite in addition to calcite, and none of them represent benthic calcifiers. The spatial
101 distribution of CaCO₃ export at 100 m depth also varies greatly between ESMs. Finally, there
102 is substantial divergence between models in the way CaCO₃ dissolution is influenced by the
103 saturation state, which is projected to decrease over the course of the century (Canadell et al.,
104 2021). Importantly, there are also limited representations of the dependency of CaCO₃
105 production on the saturation state, despite evidence suggesting it has a significant impact on
106 surface alkalinity projections (Planchat, Bopp, et al., 2023). Although the surface distribution
107 and mean global profile of alkalinity improved between CMIP5 and CMIP6 (i.e. over the last
108 ~ 10 years of climate model development), predominantly due to an increase in the strength of
109 the carbonate pump, this is likely to have little effect on the magnitude of the projected ocean
110 carbon sink due to negligible changes in the Revelle factor (Planchat, Kwiatkowski, et al.,
111 2023).

112

113 The surface concentration of alkalinity is modified by surface freshwater fluxes and/or
114 processes that redistribute alkalinity vertically within the water column (Millero, 2007).
115 Alkalinity is removed from and returned to seawater through redox reactions (e.g. nitrification),
116 and formation and dissolution of carbonate minerals. Vertical structure in alkalinity is
117 generated through the formation, sinking and remineralisation of organic matter and
118 particularly biological carbonates (e.g. plankton ‘shells’). The diversity of processes which
119 contribute to the vertical redistribution of alkalinity, and the complexity of the associated
120 ecosystem functions, result in ESMs excluding all but the most well-understood processes. For
121 example, ESMs tend to: a) assume all calcium carbonate is produced with a pure calcite
122 mineralogy (Yool et al., 2013), b) that its production is in a fixed ratio with one or more
123 (typically non-calcifying) phytoplankton types (Collins et al., 2011), or as a function of

124 temperature or latitude, and c) the dissolution of calcite is governed purely by overly simplified
125 seawater thermodynamics (Yool et al., 2013). In practice, open ocean carbonates are produced
126 with a range of chemistries and crystalline structures (e.g. aragonite, calcite and high Mg-
127 calcite; Salter et al., 2017), by organisms ranging from pelagic calcifiers (plankton and fish) to
128 benthic calcifiers (e.g. corals, bivalves and gastropods). The range of carbonate minerals and
129 structures affects the CaCO₃ distribution, morphology, export pathways and sinking speeds.
130 Carbonates are also dissolved in microenvironments ranging from the guts of grazers to
131 sediment pore-waters (White et al., 2018), and are also found in sinking aggregates containing
132 organic matter (Subhas et al., 2022).

133

134 *1.2: Challenge 2 - Net primary production (NPP)*

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

148

149 Projections of future changes in NPP depend strongly on the way in which models
150 represent the physiology and metabolism of plankton and changes to nutrient supply.
151 Differences in how models parameterise phytoplankton nutrient limitation and resource
152 demands, as well as zooplankton recycling that can amplify or dampen mixing-driven nutrient
153 supply, are a key determinant of inter-model variability (Laufkötter et al., 2015; Tagliabue et
154 al., 2021). For instance, in some regions small changes to nutrient uptake assumptions can alter
155 the sign of NPP change (Tagliabue et al., 2020). Also important are differences across models
156 in external nutrient input pathways and their sensitivity to change, e.g. aerosols (Yool et al.,
157 2021), ice sheets (Kwiatkowski et al., 2019), land-ocean river fluxes (Terhaar et al., 2019) and

158 whether anthropogenic nutrient inputs are included (Yamamoto et al., 2022). An emerging
159 source of inter-model uncertainty is the response of marine N₂ fixers, which can respond to
160 climate changes more rapidly than primary producers and, because they also represent a source
161 of new nitrogen, contribute to driving trends in NPP (Bopp et al., 2021; Wrightson &
162 Tagliabue, 2020). Lastly, we lack sufficient understanding of the role of plankton diversity,
163 acclimation or adaptation, and response to multiple concurrent drivers, to develop
164 parameterisations appropriate for inclusion in ESMs (Boyd et al., 2018; Martiny et al., 2022).

165

166 *1.3: Challenge 3 - Interior respiration*

167 Climate models vary widely in their parameterisation of processes responsible for
168 particle formation and respiration, resulting in high uncertainty in future projections of
169 particulate organic carbon (POC) flux. Current model projections do not even agree on the sign
170 of change in POC export from the upper ocean by 2100 (Figure 1), with models disagreeing on
171 whether export will increase or decrease over 84% of the ocean (CMIP6, SSP5-8.5; Henson et
172 al., 2022). Uncertainty in model projections of export has actually increased since the previous
173 generation of CMIP5 models (Laufkötter et al., 2016). Preliminary assessment of POC flux to
174 1000m in CMIP6 models suggests a similar level of inter-model disagreement for both deep
175 fluxes and the transfer efficiency (POC flux at 1000m/POC flux at 100m), a measure of the
176 efficiency of the biological carbon pump (Figure 1; Wilson et al., 2022).

177

178 Factors altering the efficiency and functioning of interior respiration include those due
179 to altered microbial, phytoplankton and zooplankton community structure (Fu et al., 2016),
180 which alters both the magnitude of POC export from the upper ocean and the type of sinking
181 material produced. A reduction in the viability of calcifying organisms due to ocean
182 acidification may affect biological carbon pump efficiency by reducing the amount of material
183 available to ballast POC (Matear & Lenton, 2014). Other climate effects such as warming and
184 changing nutrient availability could result in alterations to the magnitude and efficiency of the
185 biological carbon pump via changes in phytoplankton community composition (Cabré et al.,
186 2015), which potentially alters particle composition and size, respiration rate and
187 aggregation/fragmentation of sinking particles. Variable organic matter stoichiometry may
188 increase the amount of carbon stored via biological processes relative to the amount of NPP,
189 and so fixed stoichiometry models (as typically used in CMIP6) may underestimate ocean
190 carbon uptake (Kwiatkowski et al., 2018). Additionally, higher water temperatures will tend to
191 increase organismal metabolic rates, more so for respiration than for NPP (Boscolo-Galazzo et

192 al., 2018; Cavan et al., 2019). Resolving uncertainties in future projections of interior
193 respiration is critical, as any increase in respiration would shoal the depth to which organic
194 carbon penetrates into the deep ocean, which would tend to create a positive feedback between
195 respiration and atmospheric CO₂ concentration (Kwon et al., 2009; Segschneider & Bendtsen,
196 2013), and vice versa.

197

198 *1.4: Project aims*

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

206

207 **2. Methods:**

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

218

219 On the basis of the literature review, we sorted the identified processes into groups.
220 This was necessary to reduce the number of possible process categories to ~ 15 per Challenge.
221 Each process group may encompass several sub-processes. For example, within the primary
222 production Challenge, we identified a group of processes that we term ‘Resource limitation of
223 growth’. This includes limitation by all the major macronutrients, i.e. nitrate, phosphate and
224 silicate, although we recognise that the supply mechanisms of, and NPP response to, different
225 nutrients may differ. These groupings were necessary to assist both with our expert assessment

226 and the community survey. Greater than 15 categories would have made the survey design and
227 analysis difficult, as well as made the survey so long as to be off-putting to respondents. The
228 process categories within each Challenge, and the short descriptive text used in the survey to
229 clarify what each category encompasses, are given in Tables 1-3.

230

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

240

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

247

248 *2.1: Community survey development, data collection and analysis*

249 To obtain a broad sample of responses, a questionnaire was developed in English (the
250 full survey is provided in Supplementary Text S1). The survey was distributed in autumn 2022
251 using social media and through the authors’ professional and personal networks, resulting in
252 120 complete responses. Quantitative data were analysed in R v4.1.0 using the Tidyverse
253 collection of packages (Wickham et al., 2019). Likert data were analysed using the ‘Likert’
254 function from the Likert package in R; no importance weightings were assigned to questions.

255

256 Section A of the survey collected demographic information (age, gender identity, education,
257 location). Section B gathered information about respondents’ scientific expertise (area of
258 expertise, career stage, length of time in oceanography). The remainder of the questionnaire
259 captured respondents’ views on the key processes for the 3 Challenges of net primary

260 production, interior respiration and biological contributions to alkalinity. These were defined
261 to participants as “Net Primary Productivity is the net rate at which marine life converts
262 dissolved CO₂ into organic carbon”, “Interior respiration refers to the biological processes
263 controlling the conversion of organic carbon contained in non-living material into inorganic
264 carbon” and “Biological contributions to alkalinity are the inputs and range of natural
265 biological processes that act to alter seawater alkalinity”. The aim of the survey was to rank
266 those processes which, if included in global climate models, could potentially decrease
267 uncertainty in projections of future ocean carbon storage. Respondents had the option to skip
268 any questions in any Challenge that they felt were outside their area of expertise. Respondents
269 were asked to choose and rank the top 3 processes they thought had an important influence on
270 determining the future biologically-mediated storage of carbon in the ocean associated with
271 each of the 3 Challenges. The topic of each Challenge was first defined before respondents
272 were asked about their level of expertise (high/moderate/some/little/no expertise) in each
273 Challenge area. Respondents could choose not to complete the process selection for a particular
274 Challenge. They were then asked their opinion on the importance of the Challenge, using a 5-
275 point Likert scale. Respondents were asked to rank, in order of importance, their top three
276 processes. Respondents were informed that “importance” in the context of the survey meant
277 how significant the process was likely to be for determining the future biologically-mediated
278 storage of carbon in the ocean. Respondents were also reminded that the focus for this survey
279 was the global and centennial scales relevant to coupled climate models. Anonymised survey
280 results are available in Data Set S1.

281

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

286

287 **3. Results:**

288 The importance and uncertainty ratings assigned to each process by the expert
289 assessment are given in Tables 1-3, with the evidence supporting these assessments in
290 Supplementary Tables S1-S3. In the following sections, we briefly discuss the rationale for
291 identifying processes as having ‘high’ importance. We do not provide details in the main text
292 of the rationale for identifying processes as having medium or low importance, but the
293 supporting evidence is given in Supplementary Tables S1-S3. Note that ‘high’ importance in

294 this study indicates that there is strong evidence for a particular process's importance in ocean
295 carbon storage. This implies that processes or fields of research which have been understudied
296 are therefore likely to present fewer topics rated as high importance.

297

298 *3.1: Biological contributions to alkalinity - expert assessment*

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

302

303 *High level understanding of calcium carbonate production* refers to the amount and
304 distribution of biological CaCO₃ production and its sensitivity to climate change. A change in
305 calcification induces a surface alkalinity and DIC anomaly in a 2:1 ratio and thus has a direct
306 consequence on the air-sea carbon flux and ocean buffer capacity. However, although
307 projections of this anomaly are generated by ESMs (Planchat, Kwiatkowski, et al., 2023), it is
308 difficult to verify the projected change over the observational era due to the small amplitude
309 of the alkalinity anomaly (Ilyina et al., 2009), and the overprinting of any biological alkalinity
310 signals by changes driven by alterations to the water-cycle. Furthermore, the impacts of climate
311 change and ocean acidification on calcifiers are likely to be highly region- and taxa-dependent,
312 due to the spatial heterogeneity in environmental stressors (e.g. with respect to acidification;
313 Orr et al., 2005) and the heterogeneity in sensitivity of calcifiers to these changes (e.g. Leung
314 et al., 2022; Seifert et al., 2020). For example, increased light availability in the polar regions
315 could favour calcification by coccolithophores, while shoaling of the saturation horizons could
316 threaten pteropods or cold-water corals (Leung et al., 2022; Orr et al., 2005). In the tropics,
317 increased temperature could significantly impact warm-water corals through bleaching events
318 (Bindoff et al., 2019). It should be noted that although calcification induces biological carbon
319 storage, via sinking of particulate inorganic carbon (PIC) to the interior ocean, it also induces
320 outgassing of CO₂ from the ocean surface, due to the imbalance in carbonate chemistry that it
321 causes.

322

323 *Rain ratio* is the ratio between the export of PIC and POC. Assessing changes in this
324 ratio in response to climate change and ocean acidification is central to estimating the overall
325 impact of biology on alkalinity and DIC in the ocean's surface layer. The rain ratio anomaly
326 can be used to estimate biologically-mediated changes in surface carbonate chemistry, and
327 hence in air-sea carbon flux (Humphreys et al., 2018), as well as, in the longer term, the ocean's

328 buffer capacity in the face of rising atmospheric CO₂ concentration (Zeebe & Wolf-Gladrow,
329 2001). Although the future trend in POC export remains uncertain in ESM projections, most
330 models show a decrease (Henson et al., 2022) by 2100; however the sign of change in the
331 projected PIC export is more uncertain, driving divergent rain ratio anomalies in projections
332 (Planchat, Bopp, et al., 2023).

333

334 *3.2: Net primary production - expert assessment*

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

339

340 *Resource limitation of growth* was the top ranked process due to its central and well
341 understood role as a bottom-up driver of oceanic primary production. Within this process
342 grouping, we identified phytoplankton growth limitation by macronutrients, micronutrients, or
343 light, or co-limitation of growth by multiple nutrients and light, and the role of inorganic and
344 organic nutrient limitation as being of particular importance. There is a rich body of
345 observational literature supporting these forms of growth limitation and whilst most ESMs
346 currently represent macronutrient, light and micronutrient (e.g. iron) limitation to varying
347 extents, there are nuances to these relationships that require refinement and development in
348 order to improve confidence in model projections (Laufkötter et al., 2015; Steinacher et al.,
349 2010; Tagliabue et al., 2020).

350

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

362

363 *Nitrogen fixation* is a globally significant source of new nitrogen to the ocean that may
364 compensate for the expected decline in nitrate availability due to increasing stratification in a
365 warmer ocean (Bindoff et al., 2019). However, the role of nitrogen fixation in aiding the
366 biological storage of carbon in the ocean in the context of a changing climate remains unclear
367 (Bopp et al., 2022). Modelling studies that have demonstrated significant differences in model
368 estimates of NPP when nitrogen fixation is included or excluded indicate a crucial role for this
369 process in centennial-scale projections of ocean productivity (Bopp et al., 2022; Tagliabue et
370 al., 2021; Wrightson & Tagliabue, 2020). Furthermore, recent observational studies have
371 greatly expanded the known geographic range and taxonomic identities of diazotrophic
372 organisms in the ocean (e.g. Sipler et al., 2017). Overall it is clear that nitrogen fixation will
373 likely play an important role in future projections of NPP change (Bopp et al., 2022; Paulsen
374 et al., 2017; Wrightson & Tagliabue, 2020), also there remains substantial uncertainty
375 associated with the climate response of different groups of nitrogen fixers and their
376 physiological feedbacks in a changing climate (Wrightson et al., 2022).

377

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

389

390 *3.3: Interior respiration - expert assessment*

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

394

395 *Biotic fragmentation* refers to the breaking-up of particles into smaller pieces,
396 predominantly via zooplankton flux feeding or swimming. Fragmentation is likely to be highly
397 significant in controlling flux attenuation, with recent estimates finding that, at least during
398 high flux events, fragmentation contributes ~ 50% of flux loss in the mesopelagic (Briggs et
399 al., 2020), although this study was unable to distinguish between biotic and abiotic (via
400 turbulence or shear) fragmentation. The swimming action of Euphausiids readily fragments
401 particles and at typical abundances they could interact with 50-100% of particles in the upper
402 100m of the ocean (Dilling & Alldredge, 2000; Goldthwait et al., 2004). Alternatively (or
403 additionally) fragmentation may occur as a consequence of flux-feeding whereby zooplankton
404 consume marine aggregates or fecal pellets and in the process break off small fragments of the
405 particle, either unintentionally (sloppy feeding; Lampert, 1978) or deliberately to increase the
406 nutritional content of particles for subsequent ingestion (microbial gardening; Mayor et al.,
407 2014). In a modelling study, particle fragmentation by small copepods was predicted to account
408 for ~ 80% of the flux attenuation of fast sinking particles (Mayor et al., 2020).

409

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

422

423 *Preferential remineralisation* describes the differences in remineralisation depth of the
424 constituents of particulate organic matter relative to carbon. In sinking organic matter,
425 phosphate and nitrate tend to be preferentially and rapidly remineralised relative to carbon
426 (Anderson & Sarmiento, 1994; Schneider et al., 2003). The drawdown of excess carbon relative
427 to nitrogen or phosphate (‘carbon over-consumption’) represents a potential negative feedback
428 mechanism, as it results in additional drawdown of atmospheric CO₂ (Riebesell et al., 2007).

429 Modelling work suggests that C:P or C:N variability in the mesopelagic can alter the strength
430 of carbon sequestration by ~ 20% (Tanioka et al., 2021; Tian et al., 2004).

431

432 *Microbial solubilisation* is the respiration of dissolved and particulate organic material
433 by microbial communities, where rates may be impacted by environmental conditions, the
434 microbial community structure, metabolic rates and growth efficiency. The influence of
435 temperature, oxygen concentration and pressure on rates of microbial respiration are
436 moderately well understood (Amano et al., 2022; Cavan et al., 2019; Weber & Bianchi, 2020)
437 and are implicitly incorporated into some biogeochemical models (Laufkötter et al., 2017).
438 However the relative contributions to respiration by particle-attached or free-living microbial
439 communities is not well-constrained, and neither are the details of how microbial ecology affect
440 respiration, such as the conditions under which colonies may be established on sinking
441 particles, mortality rates, and cell attachment and detachment (Nguyen et al., 2022).

442

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

454

455 *Particle type* refers to whether a particle is, for example, a fecal pellet, aggregate,
456 carcass etc., which will affect the sinking speed and susceptibility to remineralisation and
457 aggregation/fragmentation. The phytoplankton and zooplankton community composition will
458 also affect the types of particles generated. The details of the sinking particle type, e.g. whether
459 diatom frustule, zooplankton carcass, diazotroph, salps etc. plays a strong role in setting the
460 sinking velocity and thus carbon storage (e.g. Bonnet et al., 2023; Durkin et al., 2021; Halfter
461 et al., 2022; Maerz et al., 2020; Steinberg et al., 2023), with sometimes contradictory evidence
462 in the literature for the importance of different particle types (e.g. salp fecal pellets; Iversen et

463 al., 2017; Steinberg et al., 2023). The complexity of the possible particle types, how they may
464 combine into multi-component aggregates, and the lack of a direct correspondence with
465 remineralisation potential presents a major challenge for robust modelling of the biological
466 carbon pump.

467

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

474

475 *3.4: Community survey results*

476 In total, we received 120 responses to the community survey (Data Set S1). The
477 demographics of the respondents are shown in Figure 2. For those who chose to declare their
478 gender identity, 51% of respondents identified as female, 47% identified as male, and 1.8%
479 identified as non-binary. The majority of respondents had attained a PhD-level qualification
480 (78%), with the most common career stages being lecturer/professor (30%), research scientist
481 (25%) and post-doc researcher (13%). The country in which respondents currently worked
482 showed a wide geographical spread, albeit with a predominance from the global north, with all
483 continents (except South America) having at least one respondent. The majority of respondents
484 currently worked in the UK (54%), as might be expected given that the BIO-Carbon
485 programme is UK-funded. A range of expertise was captured in the survey, with those focusing
486 on modelling (45 respondents) and observations (48 respondents) roughly equally represented,
487 with fewer focusing on experimental work (27 respondents). The majority of respondents
488 identified as biogeochemists (63 respondents) or marine ecologists (49 respondents). Note that
489 respondents could choose more than one answer for these two questions.

490

491 In total, 105, 88 and 61 respondents completed the sections on NPP, interior respiration
492 and biological contributions to alkalinity, respectively. Of these, those with high or moderate
493 expertise numbered 57, 40 and 23, respectively. We only present results from those who
494 considered themselves to have high or moderate expertise, noting that this is only
495 approximately half of those completing the ranking for a particular Challenge and in some

496 cases, particularly for alkalinity, represents a rather small sample size. The overall ranking of
497 processes from the community survey is shown in Figure 3.

498

499 The self-identified field of expertise of the respondents sometimes changed the ranking
500 of the processes, although generally the top 5 were similar (Figure 4). Note that for some sub-
501 groups the number of respondents is rather low (< 10) and so we only give a broad overview
502 of results, rather than a detailed analysis. For NPP, resource limitation of growth, zooplankton
503 processes, phytoplankton loss processes and organic matter cycling were in the top 5,
504 regardless of field of expertise. For those identifying as modellers, food web complexity was
505 additionally in the top 5; for observationalists and experimentalists, phytoplankton adaptation
506 and acclimation made the top 5 processes. For interior respiration, microbial solubilisation,
507 organic matter lability, particle characteristics and zooplankton processes were in the top 5,
508 regardless of expertise. Additionally, particle type made the top 5 for modellers and
509 observationalists, and biotic fragmentation for experimentalists. For alkalinity, there was
510 somewhat more disparity in the top 5 processes between expertise, however note that only 4
511 respondents identifying as experimentalists with high/moderate expertise in alkalinity
512 participated. All fields of expertise agreed that high level of understanding of calcium
513 carbonate production, riverine supply of alkalinity and biotically mediated dissolution are in
514 the top 5 most important processes, with physiology of calcium carbonate production,
515 sedimentary processes, primary production and remineralisation, rain ratio, and plankton
516 community making the top 5 for different expertise groups. Additional segregation of expertise
517 into field of study (e.g. biogeochemistry, ecology etc.) is reported in Supplementary Figure S1
518 but not discussed further due to the very small sample size in many categories.

519

520 **4. Discussion:**

521 We identified several key knowledge gaps associated with the biological storage of
522 carbon, which were prioritised on the basis of their potential to reduce uncertainty in model
523 estimates of the future biologically-mediated storage of carbon in the ocean. We acknowledge
524 that the community survey and expert assessment (as with any equivalent exercise) is
525 necessarily subjective to some degree, and the results may be affected by the pre-existing
526 knowledge and biases of the participants. Although we defined 'Importance' within the survey
527 questions (see Supplementary Text S1), there will inevitably be differences in respondents'
528 application of the definition. We also recognise that a complete and comprehensive assessment
529 of all available literature was not possible and so inevitably some published work will have

530 been overlooked or omitted. Nevertheless, we provide excerpts from the 193 papers included
531 in our analysis that provide the underlying evidence for our assessment (Supplementary Tables
532 S1-S3).

533

534 In general, the expert assessment and community survey agreed in terms of the most
535 significant processes (Figure 3). For example, resource limitation of growth (for NPP),
536 microbial solubilisation (for interior respiration) and high level understanding of calcium
537 carbonate production (for alkalinity) were within the top ranking processes for both the survey
538 and expert assessment. Some significant differences did emerge however, such as the low
539 ranking of nitrogen fixation (for NPP) in the survey, which was ranked as high importance in
540 the expert assessment. These differences may arise from a combination of the pre-existing bias
541 in the literature used for the expert assessment and potentially the inherent limitations of a
542 community survey. Whereas the project team spent considerable time on combing the
543 literature, assessing the papers, assembling the evidence tables, and discussing the results to
544 reach consensus on the rankings, the community survey was designed to be completed in
545 approximately 15 minutes and respondents were not provided with the evidence collated for
546 the expert assessment.

547

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

559

560 Parameterisation of many of the processes identified in this study requires data
561 collection at sea. The growing adoption and use of autonomous technologies has greatly
562 increased the amount of field data available, particularly by providing the opportunity to
563 resolve temporal and vertical variability, and in the case of the BGC-Argo network, spatial

564 variability as well. Although new methods and novel sensors (e.g. Estapa et al., 2019; Giering
565 et al., 2020) to obtain biogeochemically-relevant data (e.g. Briggs et al., 2020; Clements et al.,
566 2022) from autonomous vehicles have emerged, nevertheless many of the processes identified
567 here cannot be observed remotely, or inferred through proxies, for example organism-particle
568 interactions, nutrient recycling rates, microbial activity etc. This presents challenges for model
569 development, but also opportunities for observational and experimental programmes to
570 broaden efforts to capture new information about relevant processes, or for focussed process
571 studies.

572

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

592

593 Our literature review and community survey highlighted several processes that have
594 high importance and high uncertainty which may act as focal areas for future projects. More
595 broadly, maximising the gains from modelling, fieldwork and experimental studies relies on
596 collaboration between communities. Co-design of research projects from the outset can ensure
597 outputs will be useful to both communities, as well as fostering early recognition of emerging

598 research topics and potential limitations. Considering the potential for scaling-up field or
599 experimental data at the project planning stage, for example through empirical or mechanistic
600 relationships with commonly observed (and modelled) environmental variables will ensure the
601 broadest applicability of the project results. This will require data synthesis activities to be
602 embedded in research programmes, as the information obtained from a single project is rarely
603 sufficient to provide data on the large space and time scales necessary for model development
604 and validation. Data synthesis is most effective and impactful when data is shared openly and
605 hence wide collaboration is facilitated. Exploring how model behaviour reflects differences in
606 model parameterizations, functional equations, and parameter values in both the euphotic and
607 mesopelagic zones and conducting sensitivity analyses will assist in ensuring alterations to
608 biogeochemical models are both parsimonious and robust.

609

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

614

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618 survey respondents, and the community networks that helped distribute the survey.

619

620 **Open Research:** Full anonymised results of the community survey are available as part of the
621 Supplementary Information (Data Set S1) and from
622 <https://dx.doi.org/10.5281/zenodo.10435533>.

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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

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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

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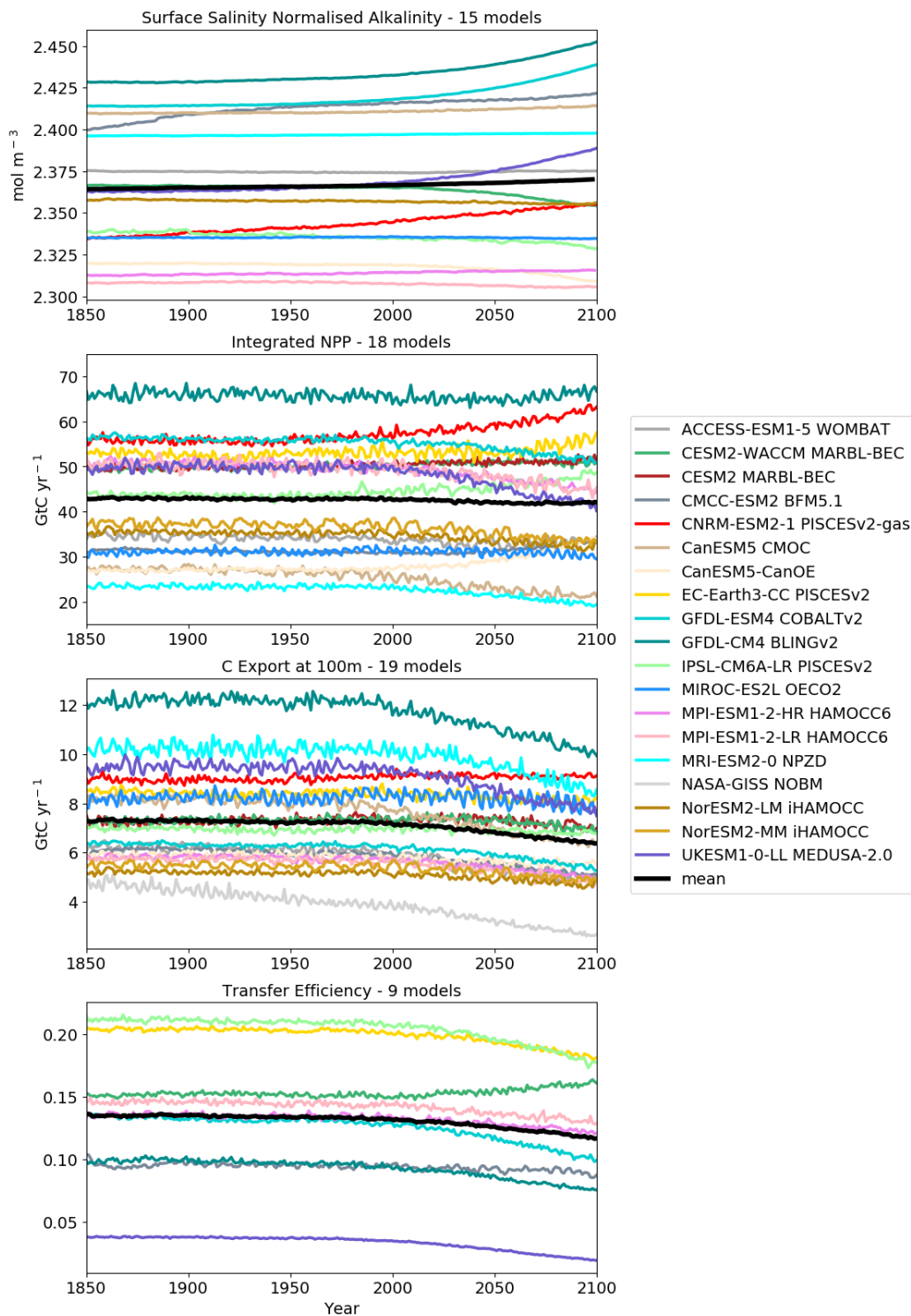
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Table 3: Expert assessment of importance and uncertainty in interior respiration processes.

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	Biom mineral (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
Ecto enzymatic hydrolysis	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

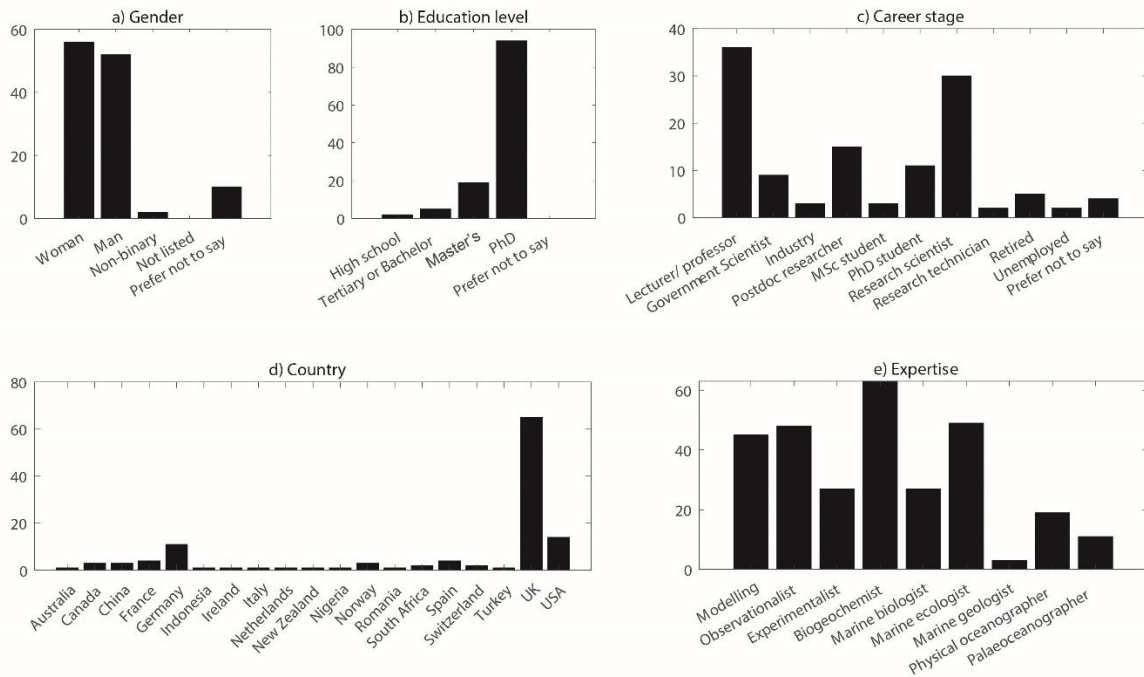
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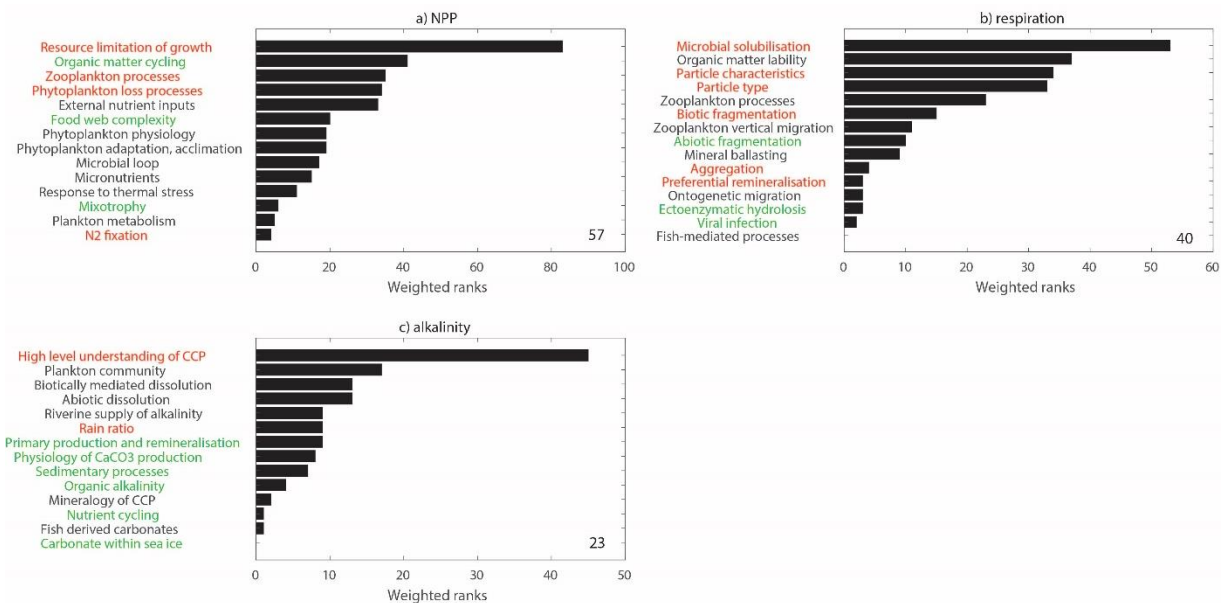
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Figure 1: Time series of global mean salinity normalised alkalinity, net primary production, particulate organic carbon (POC) export at 100m and transfer efficiency (POC flux at 1000m/POC flux at 100m) for the period 1850-2100 (scenario SSP5.8-5) taken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



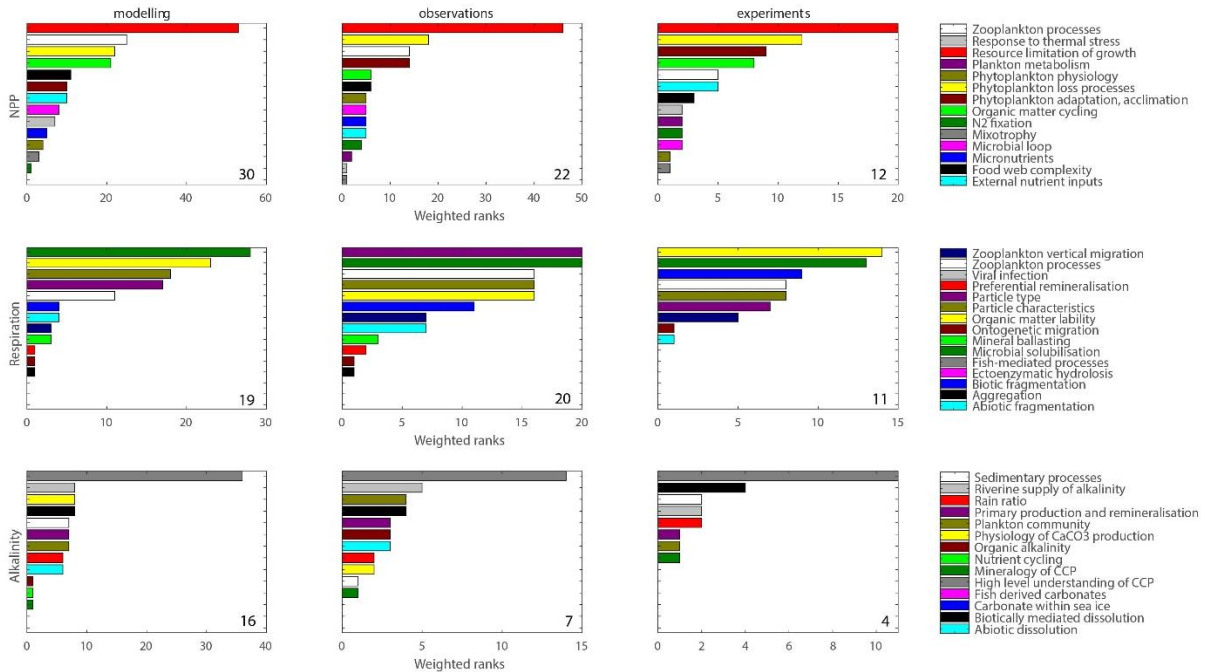
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Figure 2: Demographics of survey respondents (n = 120). Note that for the question on ‘expertise’, respondents could choose more than one category.



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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.



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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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