

Impact of remineralization profile shape on the air-sea carbon balance

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Key Points:

- Six alternative flux profiles fit to a Martin curve yield large differences in atmospheric carbon.
- Structural uncertainty comprises one third of total uncertainty in the ocean's biological pump.

Plain Language Summary

The ocean's "biological pump" regulates atmospheric carbon dioxide levels and climate by transferring organic carbon produced at the surface by phytoplankton to the ocean interior via "marine snow", where the organic carbon is consumed and respired by microbes. This surface to deep transport is usually described by a power-law relationship of sinking particle concentration with depth. Uncertainty in biological pump strength can be related to different variable values ("parametric" uncertainty) or the underlying equations ("structural" uncertainty) that describe organic matter export. We evaluate structural uncertainty using an ocean biogeochemistry model by systematically substituting six alternative remineralization profiles fit to a reference power-law curve. Structural uncertainty makes a substantial contribution, about one third in atmospheric $p\text{CO}_2$ terms, to total uncertainty of the biological pump, highlighting the importance of improving biological pump characterization from observations and its mechanistic inclusion in climate models.

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Abstract

The ocean’s “biological pump” significantly modulates atmospheric carbon dioxide levels. However, the complexity and variability of processes involved introduces uncertainty in interpretation of transient observations and future climate projections. Much work has focused on “parametric uncertainty”, particularly determining the exponent(s) of a power-law relationship of sinking particle flux with depth. Varying this relationship’s functional form introduces additional “structural uncertainty”. We use an ocean biogeochemistry model substituting six alternative remineralization profiles fit to a reference power-law curve, to systematically characterize structural uncertainty, which, in atmospheric $p\text{CO}_2$ terms, is roughly 50% of parametric uncertainty associated with varying the power-law exponent within its plausible global range, and similar to uncertainty associated with regional variation in power-law exponents. The substantial contribution of structural uncertainty to total uncertainty highlights the need to improve characterization of biological pump processes, and compare the performance of different profiles within Earth System Models to obtain better constrained climate projections.

1 Introduction

Carbon and nutrients are consumed by phytoplankton in the surface ocean during primary production, leading to a downward flux of organic matter. This “marine snow” is transformed, respired, and degraded by heterotrophic organisms in deeper waters, ultimately releasing those constituents back into dissolved inorganic form. Oceanic overturning and turbulent mixing returns resource-rich deep waters back to the sunlit surface layer, sustaining global ocean productivity. The “biological pump” maintains this vertical gradient in nutrients through uptake, vertical transport, and remineralization of organic matter, storing carbon in the deep ocean that is isolated from the atmosphere on centennial and millennial timescales, lowering atmospheric CO_2 levels by hundreds of microatmospheres (Volk & Hoffert, 1985; Ito & Follows, 2005). The biological pump resists simple mechanistic characterization due to the complex suite of biological, chemical, and physical processes involved (Boyd et al., 2019), so the fate of exported organic carbon is typically described using a depth-dependent profile to evaluate the degradation of sinking particulate matter.

Various remineralization profiles can be derived from assumptions about particle degradability and sinking speed(s) (Suess, 1980; Martin et al., 1987; Middelburg, 1989;

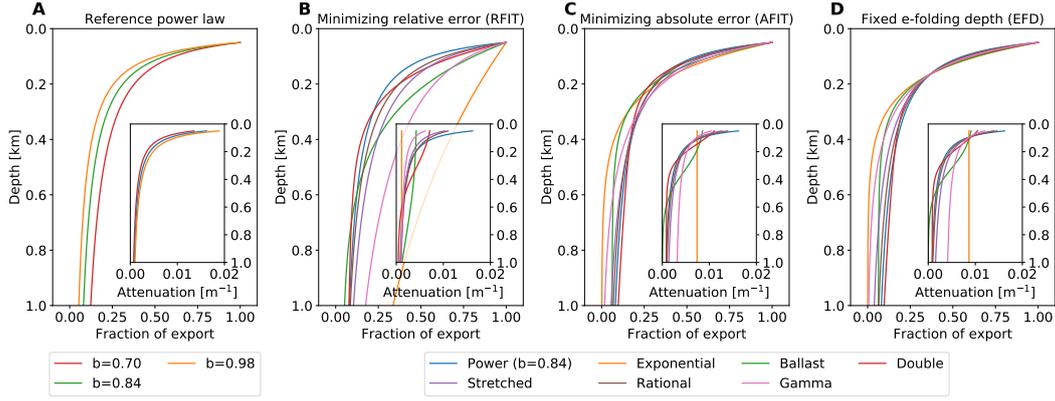


Figure 1. Fraction of sinking particulate organic matter exported from the 50 m surface layer remaining at each depth for (a) the reference power-law (Eq. 1) with exponents 0.84 ± 0.14 , and six alternative functions (Eq. S1–S6) fit to the reference power-law curve ($b=0.84$) by (b) statistically minimizing the relative error (“RFIT”), or (c) the absolute error (“AFIT”), and (d) matching the e-folding depth scale of 164 m (“EFD”). See Materials and Methods, Table S1 for fitting details, coefficients, and fit statistics. Inset plots show the attenuation rate of the export flux with depth $\left[\frac{1}{f} \frac{\partial f}{\partial z}, m^{-1}\right]$.

58 Banse, 1990; Armstrong et al., 2001; Lutz et al., 2002; Rothman & Forney, 2007; Kriest & Oschlies, 2008; Cael & Bisson, 2018). The ubiquitous “Martin Curve” (Martin et al., 1987) is a power-law profile (Eq. 1) that assumes slower-sinking and/or labile organic matter is preferentially depleted near the surface causing increasing sinking speed and/or remineralization timescale with depth (e.g. Kriest & Oschlies, 2011).

$$63 \quad f_p(z) = C_p z^{-b}, \quad (1)$$

64 where $f_p(z)$ is the fraction of the flux of particulate organic matter from a productive layer near the surface (Buesseler et al., 2020) sinking through the depth horizon z [m], 65 C_p [m^b] is a scaling coefficient, and b is a nondimensional exponent controlling how f_p 66 decreases with depth. Eq. 1 is often normalized to a reference depth z_o but this parameter is readily absorbed into C_p . 67 68

69 Considerable effort has been dedicated to determining value(s) for the exponent, 70 b (e.g., Martin et al., 1987, 1993; Berelson, 2001; Primeau, 2006; Kwon & Primeau, 2006; 71 Honjo et al., 2008; Henson et al., 2012; Kriest et al., 2012; Gloege et al., 2017; Wilson 72 et al., 2019). Open ocean particulate flux observations from the North Pacific (Martin

73 et al., 1987) indicate a b value of 0.858. Further analyses of expanded sediment trap datasets
74 suggest a possible range of approximately 0.84 ± 0.14 for the global b value (Martin et
75 al., 1993; Berelson, 2001; Primeau, 2006; Honjo et al., 2008; Gloege et al., 2017), though
76 a much wider range has been observed when including regional variability in b and optically-
77 and geochemically-derived flux estimates (Henson et al., 2012; Guidi et al., 2015; Pavia
78 et al., 2019). This may result from differences in temperature (Matsumoto, 2007), mi-
79 crobial community composition (Boyd & Newton, 1999), particle composition (Armstrong
80 et al., 2001), oxygen concentration (Devol & Hartnett, 2001), particle aggregation (Gehlen
81 et al., 2006; Schwinger et al., 2016; Niemeyer et al., 2019), or mineral ballasting (Gehlen
82 et al., 2006; Pabortsava et al., 2017).

83 Uncertainty in the value of b translates to uncertainty in the biological pump's im-
84 pact on the ocean carbon sink, atmosphere-ocean carbon partitioning, and climate model
85 projections. Thus, constraining b for the modern ocean and how it may differ in the past,
86 or the future, is of much interest from a climate perspective. Varying a global value of
87 b between 0.50–1.4 altered atmospheric $p\text{CO}_2$ by 86–185 μatm after several thousand years
88 of equilibration, in an influential modeling study (Kwon et al., 2009): Higher values of
89 b result in enhanced particle remineralization at shallower depths. Shallow watermasses
90 are more frequently ventilated, allowing remineralized CO_2 to be released back into the
91 atmosphere on shorter timescales. Due to this depth-dependence, a small change of degra-
92 dation depth can appreciably change atmospheric $p\text{CO}_2$ (Yamanaka & Tajika, 1996; Kwon
93 et al., 2009). Varying b over the plausible range in global values between 0.70–0.98 pro-
94 duces a more modest change in atmospheric $p\text{CO}_2$, over the range of $(-16,+12)\mu\text{atm}$ (Gloege
95 et al., 2017), while the modeled uncertainty in atmospheric $p\text{CO}_2$ associated with regional
96 variation in b is estimated between 5–15 μatm (Wilson et al., 2019).

97 Biogeochemical models are subject not only to parametric uncertainty (which value
98 for b and how b varies in space and time), but also structural uncertainty, i.e. which equa-
99 tion(s) to choose for the vertical flux of organic matter. The Martin Curve power-law
100 is an empirical fit to sediment trap data, but several other functional forms have also been
101 put forward (Suess, 1980; Middelburg, 1989; Banse, 1990; Armstrong et al., 2001; Lutz
102 et al., 2002; Dutkiewicz et al., 2005; Rothman & Forney, 2007; Marsay et al., 2015) that
103 fit sediment trap fluxes equivalently well and have equal if not better mechanistic jus-
104 tification (Cael & Bisson, 2018). Atmospheric $p\text{CO}_2$ and many other global biogeochem-
105 ical properties (Kwon & Primeau, 2006; Kriest et al., 2012; Aumont et al., 2017) will be

106 affected by this structural uncertainty, so it is critical to evaluate the impact of choos-
107 ing one remineralization profile “shape” over another.

108 We assess the effect of remineralization profile shape on biological pump strength
109 and evaluate a comprehensive estimate of structural uncertainty in terms of atmosphere-
110 ocean carbon partitioning in a global ocean biogeochemistry model. We substitute the
111 reference power-law curve for six plausible alternative remineralization profiles: expo-
112 nential (Banse, 1990; Dutkiewicz et al., 2005; Marsay et al., 2015; Gloege et al., 2017),
113 ballast (Armstrong et al., 2001; Gloege et al., 2017), double exponential (Lutz et al., 2002),
114 stretched exponential (Middelburg, 1989; Cael & Bisson, 2018), rational (Suess, 1980),
115 and upper incomplete gamma function of order zero (Rothman & Forney, 2007, we use
116 the shorthand “gamma function” for “upper incomplete gamma function of order zero”,
117 although different orders are possible). Each form corresponds to a basic mechanistic de-
118 scription of particle fluxes (Cael & Bisson, 2018), that we tightly constrained to the re-
119 ference profile by statistically minimizing export fraction misfits or by matching degra-
120 dation depth scales (Kwon et al., 2009). See Supporting Information for derivations of
121 these profiles.

122 These simulations indicate that structural uncertainty is an appreciable component,
123 around one third, of total uncertainty for understanding the biological pump (with the
124 remaining two thirds attributed to parametric uncertainty in b). Changing remineral-
125 ization functional form alters atmospheric $p\text{CO}_2$ by $\sim 10\text{-}15 \mu\text{atm}$ depending on how struc-
126 tural uncertainty is quantified, equivalent to ~ 0.08 uncertainty in a global value of the
127 power-law exponent, b , and similar to the uncertainty resulting from regional variation
128 of b .

129 Our results underscore the importance of characterizing basic mechanisms govern-
130 ing the biological pump. Furthermore, our results corroborate that depth-dependence
131 of these mechanisms is particularly important (Gehlen et al., 2006; Kriest & Oschlies,
132 2008): not only is biological pump-driven carbon export and storage an important con-
133 trol on atmospheric $p\text{CO}_2$, we find that rapidly decreasing particle degradation in the
134 upper ocean is equally important for a sufficient quantity of carbon to become isolated
135 in the deep ocean. While a given flux curve may be chosen for historical reasons or math-
136 ematical convenience, its skill should be compared to those of other idealized flux pro-
137 file parameterizations in Earth System Models used for projections of future climate.

2 Materials and Methods

2.1 Fitting the alternative remineralization curves.

We fit the alternative functions for export fluxes and remineralization (Fig. 1, Eq. S1–S6, see Supporting Information) to the reference power-law curve (Eq. 1) with the exponent $b=0.84$ using nonlinear regression on the model vertical grid to minimize the absolute curve mismatch (“ABS” simulations). Subsurface points were weighted equally (1.0), except for a heavily weighted top level (valued 1000, but the overall fit was largely insensitive to the choice of this value) to ensure all the profiles pass through the same value as the control profile, i.e. fraction of export from the productive surface layer is unity. We further matched the e-folding depth of remineralization to the reference (“EFD” simulations) by adding a second heavily weighted point to the reference power-law at 164 m depth ($z_0 e^{(1/b)}$), with an export fraction of e^{-1} . In a third set (“RFIT” simulations), the nonlinear regression is performed on the natural logarithm of the remineralization fraction in order to minimize the relative error of the reference profile match. Goodness of fit is evaluated by the Standard Error of Regression, \mathcal{S} , which is the sum of squared residuals, divided by statistical degrees of freedom (number of points minus number of parameters). Coefficients and \mathcal{S} values for the eighteen curves are given in Table S1.

2.2 Numerical ocean biogeochemistry model.

Alternative remineralization profiles are substituted into global ocean simulations of a coarse resolution (2.8° , 15 vertical level) configuration of the Massachusetts Institute of Technology general circulation model, MITgcm (Marshall et al., 1997), coupled to an idealized marine biogeochemistry model that considers the coupled cycles of dissolved inorganic carbon, alkalinity, phosphate, dissolved organic phosphorus, oxygen, and dissolved iron (Dutkiewicz et al., 2006; Parekh et al., 2005, 2006).

Two-thirds of surface net community production (that depends on light, phosphate, and iron using Michaelis-Menten kinetics) is channelled into dissolved organic matter that is largely remineralized in the surface ocean with a timescale of 6 months (Yamanaka & Tajika, 1997), while one-third is exported to the ocean interior via sinking particulate organic matter subject to depth-dependent remineralization rates. Elemental biological transformations are related using fixed stoichiometric ratios $R_{C:N:P:Fe:O_2} = 117 : 16 : 1 : 4.68 \times 10^{-4} : -170$ (Anderson & Sarmiento, 1994) with a prescribed inorganic to

169 organic rain ratio of 7% (Yamanaka & Tajika, 1996). The total atmosphere-ocean car-
 170 bon inventory is conserved as there is no riverine carbon input or sediment carbon burial,
 171 which may impact the model’s transient behavior and steady state (Roth et al., 2014).
 172 Atmosphere-ocean exchange of CO₂ captures the magnitude and variation of observed
 173 air-sea fluxes (Lauderdale et al., 2016).

174 Our model includes tracers to separate the *in situ* concentrations of carbon into:
 175 (i) a component subducted from the surface layer and transported conservatively by ocean
 176 circulation (the “preformed” carbon concentration, C_{pre}), and (ii) a component that in-
 177 tegrates export and remineralization of sinking particles as a watermass transits the ocean
 178 interior (the “biological” carbon concentration, C_{bio}), which encompasses both soft tis-
 179 sue regeneration and carbonate dissolution, and connects more directly to the biolog-
 180 ical pump (Volk & Hoffert, 1985; Ito & Follows, 2005). We integrate simulations for 10,000
 181 years toward steady state in atmosphere-ocean carbon partitioning.

182 3 Results

183 3.1 Varying the exponent of the reference power-law curve.

184 Global power-law exponent, b , estimates range from 0.70 (Primeau, 2006) based
 185 on sediment traps to ~ 1.00 based on inverse models fit to tracer distributions (Kwon &
 186 Primeau, 2006, 2008; Kwon et al., 2009; Kriest et al., 2012). These values match the global
 187 b interquartile range of 0.70–0.98 in (Gloege et al., 2017). We integrate three simulations
 188 with $b = 0.84 \pm 0.14$ (Fig. 1a) using the standard power-law parameterization (Eq. 1)
 189 to produce a baseline estimate of biological pump parametric uncertainty. The reference
 190 simulation has the exponent $b=0.84$.

191 Higher b values cause the fraction of sinking particulate matter to decrease faster
 192 with depth, that is, attenuation ($1/f_p \cdot \partial f_p / \partial z$) is higher in the upper ocean, whereas
 193 lower exponents have less attenuation and a larger proportion of export reaching the deep
 194 ocean (Figs. 1a and S2a–f). A negative feedback occurs near the surface in our simula-
 195 tions. For example, when b is increased, higher rates of upper ocean attenuation cause
 196 an increase in surface nutrient availability, and therefore more overall biological produc-
 197 tion (see ΔB_C , Table S2). Local biological activity enhancement increases local rates of
 198 particle export, evaluated by integrated fluxes through the deepest mixed layer depth
 199 (ΔE_{mld} , Table S2). However, higher shallow export is compensated by greater upper ocean

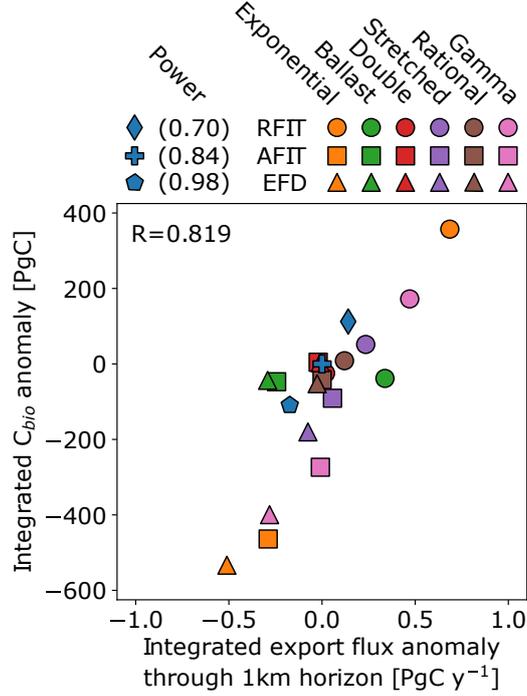


Figure 2. Change in the integrated export flux rate [PgC y^{-1}] passing through the 1 km depth level against integrated biological carbon reservoir anomaly [PgC], both with respect to the power-law curve where $b=0.84$ (Martin et al., 1987). Three power-law simulations ($b=0.84\pm 0.14$) are indicated by the blue symbols (diamond, cross, and pentagon), circle, square, and triangle symbols indicate that profile coefficients (Eq. S1–S6) were derived by minimizing the relative fit error (“RFIT”), minimizing the absolute fit error (“AFIT”), and fixing the e-folding depth of remineralization (“EFD”) to the reference power-law curve. Values are given in Tables S2 and S3.

200 remineralization, due to larger exponent value, resulting instead in reduced export flux
 201 anomalies through 1 km depth (ΔE_{1km} , Table S2), and vice versa when b is decreased
 202 (e.g. global experiments in Kwon et al., 2009; Kriest & Oschlies, 2011). The global ocean
 203 reservoir of biological carbon changes proportionally with ΔE_{1km} (Figs. 2, blue symbols,
 204 S2g–l, and ΔC_{bio} , Table S2) and inversely-proportional to ΔE_{mld} (Fig. S3a).

205 3.2 Impact of alternative remineralization curve shape.

206 Generally speaking, the six alternative remineralization profiles (Eq. S1–S6) ob-
 207 jectively characterized by statistically fitting parameters to match the reference power-
 208 law curve ($b=0.84$) do reproduce similar sinking particle remineralization rates (Fig. 1b–

209 d). This is perhaps not a surprise, since we would not consider these functions to be plau-
 210 sible alternatives to the Martin Curve if they could not describe export fluxes at least
 211 as well as a power-law.

212 Nevertheless, the simple exponential and gamma function curves do not fit the ref-
 213 erence power-law profile as well as the other functions (Fig. 1b–d) because these profiles
 214 cannot capture a strong depth-change in remineralization. The ballast profile has a more
 215 complex distribution of biological carbon anomalies in surface, intermediate, and deep
 216 waters such that the relationship between export flux and ΔC_{bio} is better captured by
 217 considering deeper horizons (e.g. green symbols in Fig. 2 at the 1 km horizon, versus 2 km
 218 in Fig. S3b).

219 Simulations with lower-attenuation profiles result in increased export fluxes (Fig. S4),
 220 and vice versa, as with the simulations varying b (Fig. 2). These particulate flux anoma-
 221 lies translate into changes in the distribution of biological carbon, with positive export
 222 flux anomalies through the 1 km depth horizon (ΔE_{1km}) corresponding to increase in
 223 the biological carbon pool (C_{bio} , Fig. 2), while negative export flux anomalies result in
 224 lower biological carbon concentrations. For instance, in RFIT simulations, the exponen-
 225 tial and gamma function profiles show an increase in 1 km export fluxes and biological
 226 carbon storage, while the reverse occurs for exponential and gamma profiles in AFIT and
 227 EFD simulations.

228 Geographically, stronger ocean interior sinking fluxes tend to redistribute biolog-
 229 ical carbon into the Southern Ocean and deep North Pacific at the expense of the North
 230 Atlantic (Fig. S5–S7), while shallower remineralization tends to increase North Atlantic
 231 biological carbon concentrations whilst decreasing concentrations in the Southern Ocean
 232 and deep North Pacific. This is a reflection of the accumulation of C_{bio} as a water mass
 233 transits the global meridional overturning circulation with the oldest waters upwelling
 234 in the Southern Ocean and North Pacific (Kwon & Primeau, 2006; Kwon et al., 2009;
 235 Kriest & Oschlies, 2011; Kriest et al., 2012; Romanou et al., 2014). These anomalies of
 236 C_{bio} (Fig. S5–S7) account for the direct effects of organic and inorganic particle fluxes.
 237 At the same time, changes in biological activity affect surface alkalinity both through
 238 carbonate export and surface charged nutrient abundance, which reinforces ocean car-
 239 bon uptake or outgassing due to the inverse relationships relating carbon and alkalin-
 240 ity to CO_2 solubility (Kwon et al., 2009). However, atmospheric CO_2 anomalies driven

241 by different remineralization profiles integrate several compensating processes. Indirect
242 carbon changes, including the effect of alkalinity on ocean carbon saturation, regener-
243 ated carbon upwelling, as well as unrealized air-sea exchange due to the finite timescale
244 of atmosphere-ocean CO₂ fluxes (Ito & Follows, 2005; Lauderdale et al., 2013, 2017), that
245 are captured by preformed carbon anomalies actually counteract approximately two-thirds
246 of the direct biological ocean carbon storage.

247 **3.3 Evaluating structural uncertainty of the biological pump.**

248 Altering the strength of the biological pump leads to changes in air-sea carbon bal-
249 ance. The reference simulation has a steady-state atmospheric pCO₂ of 269.3 μ atm. In-
250 creasing b from 0.70 to 0.98 increases pCO₂ by 46.36 μ atm in this model (range: -21.6–
251 24.8 μ atm, wide grey bars in Fig. 3a, Table S2). This is higher than the “nutrient restor-
252 ing” case in Kwon et al. (2009), but lower than their “constant export” case, consistent
253 with our model’s dynamic biological productivity and interactive biogeochemistry response.

254 Alternative profiles with reduced export flux through 1 km and reduced biological
255 carbon storage result in increased atmospheric pCO₂, and vice versa (Fig. 3a, Table S3).
256 The double exponential function has the most free parameters (four) and therefore fits
257 the power-law extremely well, producing small differences in atmospheric pCO₂ (less than
258 2 μ atm). The rational function also agrees well, but could produce larger anomalies if
259 the reference profile’s b -value was further from 1.00, i.e. 0.70. Stretched exponential and
260 ballast curves produce moderate changes in atmospheric pCO₂ but are generally smaller
261 than, or similar to, the 0.14 changes in b for the power-law curves (Fig. 3a). However,
262 the simple exponential and gamma function anomalies clearly deviate from the other sim-
263 ulations, with greater biological carbon concentrations and drawdown of atmospheric CO₂
264 for the RFIT simulations, and the inverse for AFIT and EFD simulations. Export fluxes
265 and remineralization are significantly different in the upper ocean for these parameter-
266 izations, which can be explained by their largely invariant attenuation rates with depth
267 (Fig. 1 insets): simple exponential and gamma parameterizations cannot have both short
268 remineralization lengthscales in the upper ocean and long remineralization lengthscales
269 in the deep ocean.

270 There are multiple ways to compare parametric and structural uncertainty quan-
271 titatively. Parametric uncertainty is found by varying the power-law exponent within

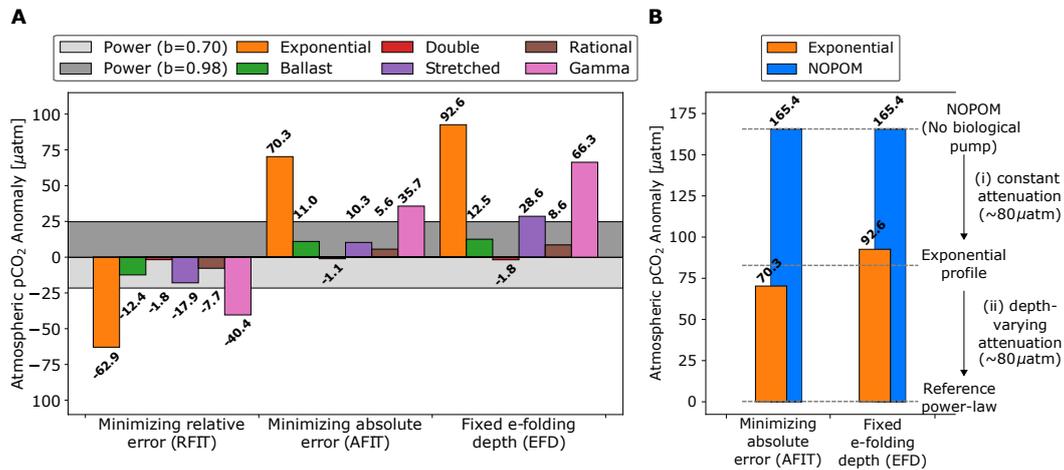


Figure 3. Impact of alternative remineralization curve shape on the air-sea carbon balance (a) atmospheric $p\text{CO}_2$ anomalies (μatm) for remineralization profiles with respect to the reference power-law ($b=0.84$) for power-law exponent values $b=0.70$ and 0.98 , and statistical fits of alternative profiles “RFIT” (left), “AFIT” (middle), and “EFD” (right). Values are given in Tables S2 and S3; (b) comparison of a simulation with no particulate organic matter production (“NOPOM”), i.e. no biological pump, to the simple exponential profile, and reference power law profile for “AFIT” (left), and “EFD” (right) fits. From a “NOPOM” ocean, establishing (i) a biological pump with an exponential remineralization curve and constant attenuation of sinking particles with depth only draws down roughly $80 \mu\text{atm}$ atmospheric CO_2 , while a further $80 \mu\text{atm}$ drawdown can be achieved by establishing (ii) a biological pump with a power-law remineralization profile that has decreasing particle attenuation, or increasing remineralization lengthscale, with depth. Thus, biological pump non-linearity appears to be equally important for air-sea carbon partitioning as export and storage of biological carbon.

272 its plausible global range ($b = 0.84 \pm 0.14$), producing absolute atmospheric $p\text{CO}_2$ anoma-
 273 lies of $21.6\text{--}24.8 \mu\text{atm}$ (Fig. 3a, Table S3). For structural uncertainty, the median change
 274 in absolute atmospheric $p\text{CO}_2$ is $12.47 \pm 10.67 \mu\text{atm}$ (b -anomaly equivalent of 0.07 ± 0.06)
 275 across all simulations with alternate functional forms. We choose the median \pm median
 276 absolute deviation so that our result is robust to large anomalies associated with sim-
 277 ple exponential and gamma functional forms. For RFIT, AFIT, and EFD simulations
 278 separately, the medians are 15.15 ± 10.40 , 10.65 ± 7.30 , and $20.57 \pm 15.37 \mu\text{atm}$, respectively,
 279 giving a $15.15 \pm 4.51 \mu\text{atm}$ grand median (b -anomaly equivalent of 0.09 ± 0.03). Exclud-
 280 ing profiles with largely invariant attenuation rates with depth, i.e. exponential and gamma
 281 function profiles, the overall medians for RFIT, AFIT, and EFD are 10.07 ± 2.32 , 7.96 ± 2.69 ,
 282 and $10.57 \pm 1.98 \mu\text{atm}$, respectively, with a $10.07 \pm 0.50 \mu\text{atm}$ grand median (b -anomaly
 283 equivalent of 0.06 ± 0.00). In summary, our results are largely robust, indicating a struc-
 284 tural uncertainty of $10\text{--}15 \mu\text{atm}$, roughly half of parametric uncertainty for the biolog-
 285 ical pump ($22\text{--}25 \mu\text{atm}$, $b = 0.84 \pm 0.14$), analogous to a ~ 0.08 change in b .

286 **3.4 Role of nonlinearity in the biological pump.**

287 Much emphasis is placed on the biological pump's effect on climate by significantly
 288 lowering atmospheric CO_2 levels, but our exponential and gamma function simulations
 289 indicate that having a biological pump (i.e. uptake, export, and depth-dependent rem-
 290 ineralization) and an associated biological carbon store is not necessarily sufficient to pro-
 291 duce atmospheric carbon drawdown of the expected magnitude, such as a $\sim 200 \mu\text{atm}$ dif-
 292 ference between biotic and abiotic oceans (Volk & Hoffert, 1985). To understand what
 293 aspects of the biological pump are important for significantly lowering atmospheric CO_2 ,
 294 we ran a simulation ("NOPOM") that represents a hypothetical ocean with no partic-
 295 ulate organic matter export. Instead, biological production is channelled into dissolved
 296 organic matter that is remineralized near the surface.

297 Atmospheric $p\text{CO}_2$ in NOPOM increases $165.4 \mu\text{atm}$ (Table S2) with respect to our
 298 reference power-law: slightly less outgassing than Volk and Hoffert (1985), but the NOPOM
 299 ocean does have biological activity and a small biogenic carbon store. This is roughly
 300 twice as large as the outgassing resulting from the use of a simple exponential reminer-
 301 alization profile fit to the reference power-law curve in AFIT and EFD simulations (70.3
 302 and $92.6 \mu\text{atm}$), despite these simulations supporting significant 1 km export fluxes (1.460
 303 and 1.238 PgC y^{-1} , only 20% less than the reference power law) as well as large stores

304 of biological carbon (1830 and 1900 PgC, compared to 176 PgC for NOPOM). Thus, only
305 about half of the biological pump's effect on atmosphere-ocean carbon drawdown ($\sim 80 \mu\text{atm}$)
306 can be attributed to export of particulate organic matter and biological carbon storage
307 (Fig. 3b).

308 The remaining $\sim 80 \mu\text{atm}$ drawdown in atmospheric carbon content is due to the
309 change in shape of remineralization curves between a biological pump represented by AFIT
310 and EFD exponential curves compared to a biological pump represented by the refer-
311 ence power-law profile. Exponential profiles have a constant rate of change of reminer-
312 alization, or attenuation of the sinking particle flux, with depth (Fig. 1c and d, insets),
313 which results in the majority of the sinking particle flux from the surface ocean being
314 remineralized in the upper 2 km. Export fluxes through this horizon are 0.204 and 0.140
315 PgC y^{-1} . Alternatively, attenuation for the power-law curve decreases significantly with
316 depth, leading to a substantial 2 km export flux of 0.802 PgC y^{-1} . Thus, for AFIT and
317 EFD exponential profiles, there is much less abyssal biological carbon storage to act as
318 a long-term reservoir of atmospheric CO_2 , whereas rapidly decreasing attenuation in the
319 reference power-law supports long-term biological carbon storage.

320 In other words, decreasing upper ocean particle attenuation, or increasing reminer-
321 alization lengthscale with depth, appears to be equally important for air-sea carbon par-
322 titioning as export and storage of biological carbon (Fig. 3b).

323 4 Discussion and Conclusions

324 Atmospheric CO_2 levels are intimately tied to the strength of the ocean's biolog-
325 ical pump (Volk & Hoffert, 1985; Ito & Follows, 2005). The challenge of measuring par-
326 ticulate fluxes via sediment traps, optical proxies, or geochemical methods (Martin et
327 al., 1987; Berelson, 2001; Honjo et al., 2008; Henson et al., 2012; Guidi et al., 2015; Pavia
328 et al., 2019), the spatiotemporal variability of fluxes, and the complexity of the govern-
329 ing mechanisms introduce uncertainty into representation of the biological pump in ocean
330 biogeochemistry, ecosystem, and climate models. We explored the impact of structural
331 uncertainty—remineralization profile shape—on atmosphere-ocean carbon partitioning,
332 using seven mechanistically-distinct functional forms of particulate organic matter flux
333 that capture observational spread equivalently well (Cael & Bisson, 2018). In our model,
334 a 0.14 change in the power-law exponent, b , results in a 22–25 μatm change in atmospheric

335 pCO₂, indicating that the structural uncertainty revealed by our simulations of 10–15 μatm
336 is equivalent to ~ 0.08 change in the global b value. Thus structural uncertainty is roughly
337 half the size of parametric uncertainty, making it a substantial one-third contribution
338 to our overall estimate of total uncertainty (the sum of structural and parametric un-
339 certainties) in understanding the biological pump. In addition our result is in the up-
340 per range of the 5–15 μatm uncertainty associated with regional variation in b (Wilson
341 et al., 2019).

342 Historically, the focus been on remineralization *lengthscale* (Kwon et al., 2009), but
343 our results, indicating that vertical gradient in attenuation is a first-order control on cli-
344 mate, imply that multiple *lengthscales* of attenuation are critical to the biological pump’s
345 global impact. Thus, not only is the existence of a biological pump that maintains in-
346 terior ocean biological carbon stores a key factor in the biological pump’s modulation
347 of atmospheric CO₂ levels (Volk & Hoffert, 1985), but also a significant decrease of at-
348 tenuation with depth is necessary to achieve the full amount of drawdown usually at-
349 tributed to the biological pump (Fig. 3b). Even when the exponential profiles’ param-
350 eters are determined by matching the e-folding remineralization depth of the reference
351 power-law curve (Kwon et al., 2009), the result is still large atmospheric pCO₂ anoma-
352 lies caused by largely invariant attenuation rates with depth.

353 Our study evaluates structural uncertainty in the ocean’s biological pump in a sys-
354 tematic way. Although previous studies have compared individual, or a subset, of the
355 alternative remineralization curves used here (e.g., Yamanaka & Tajika, 1996; Gehlen
356 et al., 2006; Kriest & Oschlies, 2008; Schwinger et al., 2016; Gloege et al., 2017; Niemeier
357 et al., 2019; Kriest et al., 2020) with a focus on minimizing model-observational differ-
358 ences, none has attempted to evaluate this structural uncertainty by just changing the
359 shape of the remineralization profile, which we do here by comparing six alternative func-
360 tional forms statistically fit in three different ways to a reference power-law profile. De-
361 spite these profile choices resulting in non-negligible differences in ocean biogeochemi-
362 cal distributions (Kriest et al., 2012; Aumont et al., 2017) and atmospheric CO₂ levels
363 (Kwon et al., 2009), comparison of model output to climatological data (Boyer et al., 2018;
364 Garcia et al., 2018) does not significantly change (Fig. S8), such that all the curves still
365 quantitatively reproduce the observations to a similar degree.

366 As Earth System Models continue to rely on simple biological pump parameter-
367 izations, our estimate of structural uncertainty underscores the importance of research
368 aimed at improving the basic mechanistic characterization of the biological pump (Boyd
369 et al., 2019), and particularly the depth-dependence or evolution of these mechanisms.
370 One such improvement is to consider the spectrum of sinking particle properties, such
371 as size (Schwinger et al., 2016; Niemeier et al., 2019), sinking speeds (Kriest & Oschlies,
372 2008) or material lability (Aumont et al., 2017), and how they effect export fluxes. These
373 studies often derive components that rely on upper and lower incomplete gamma func-
374 tions, as well as gamma distributions, but ultimately do not produce gamma function
375 flux profiles. The Rothman and Forney (2007) profile (Eqn. S6) is a special case of the
376 upper incomplete gamma function (where the order, $a=0$). However, statistical fits of
377 integer orders of the upper incomplete gamma function where $a>0$ to the reference power-
378 law ($b=0.84$) are poor (See Fig. S1, including the simple exponential curve, which is pro-
379 portional to an upper incomplete gamma function of order $a=1$), and as stand-alone rem-
380 ineralization parameterizations may include particle classes whose remineralization pro-
381 files may not exist in the ocean. On the other hand, a more general three-parameter up-
382 per incomplete gamma function parameterization, $C_g\Gamma(a_g, z/\ell_g)$, fits the Martin curve
383 very well with $a_g\approx-0.8$ (Fig. S1), and would correspond to a constant-sinking reactiv-
384 ity continuum model (Aumont et al., 2017) with a power-law reactivity distribution. How-
385 ever, reactivity continuum models do not a describe reactivity using a power law, and
386 instead use lighter-tailed distributions such as the gamma (Boudreau & Ruddick, 1991),
387 beta (Vähätalo et al., 2010), or log-normal distribution (Forney & Rothman, 2012). Thus
388 we did not include these additional profiles in our biological pump structural error en-
389 semble as there is not a justifiable basis for $a>1$, nor a plausible mechanism for $a<0$, un-
390 like the six alternative remineralization curves presented.

391 A better process-based understanding is critical to choosing between these param-
392 eterizations based on their mechanistic underpinnings and thus reducing structural un-
393 certainty, because empirical fits to flux measurements alone cannot currently do so (Gehlen
394 et al., 2006; Cael & Bisson, 2018). Indeed, there are also no guarantees that more ex-
395 tensively sampled ocean nutrient distributions are able to distinguish between the per-
396 formance of idealized and more explicit remineralization schemes either (Niemeier et al.,
397 2019; Schwinger et al., 2016).

398 In our simulations, the parameterizations were forced to be as similar as possible
399 with regard to the three different criteria (minimizing misfit error or matching the ref-
400 erence e-folding depth of remineralization), but functional forms based on different pro-
401 cesses will have different sensitivities to temperature and other phenomena, and there-
402 fore will produce divergent projections and different climate feedbacks. Furthermore, each
403 alternative functional form will be associated with its own parametric uncertainty. Un-
404 fortunately, significantly less is known about the natural range of parameters associated
405 with the alternative remineralization profiles in the real ocean, because they have not
406 been used as widely as the Martin Curve.

407 There are other factors that could affect the distribution, export, and depth de-
408 pendent remineralization of sinking particles, and therefore ocean carbon sink/atmospheric
409 CO₂ sensitivity, that we held the same between simulations. For example, our assump-
410 tion of a closed carbon cycle with no sediment burial or riverine fluxes may underesti-
411 mate the biological pump effect on atmospheric CO₂ for the different remineralization
412 profiles by 4–7 times (Roth et al., 2014) on timescales of 10–100 thousand years. Between
413 different models, the overall strength of the deep ocean carbon store may be more de-
414 pendent on remineralization profile parameters than on different ocean circulations, al-
415 though circulation impact on upper ocean production would modify the overall relation-
416 ships shown here (Romanou et al., 2014; Kriest et al., 2020). Vertical grid resolution and
417 numerical diffusion might also result in changes to the ocean carbon sink (Kriest & Os-
418 chlies, 2011), although again these changes may not manifest in the short timespan that
419 many more complex coupled ocean-ecosystems are integrated for (Kwon et al., 2009; Schwinger
420 et al., 2016). Despite these challenges, it would be valuable to compare these different
421 functional forms within state-of-the-art Earth System Models, either directly or via im-
422 plied remineralization profile shape, to improve confidence in projections involving biosphere-
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438 **-shape** (Lauderdale & Cael, 2021).

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