Article

Century-scale carbon sequestration flux throughout the ocean by the biological pump

In the format provided by the authors and unedited

1. Mechanisms involved in ocean carbon sequestration, including the ocean carbon pumps

2. Sequestration flux and inventory of sequestered carbon

3. Functioning of the biological carbon pump mechanisms

4. Comparisons between our calculations or results for the mixing and migrant pumps and values from the literature

5. Robustness of our results to changes in ocean circulation

6. Obtaining the f_{100} values to implement F_{seq} in models

7. Supplementary Tables S1 and S2

8. Supplementary Methods

9. Additional references

1. Mechanisms involved in ocean carbon sequestration, including the ocean carbon pumps

Marine biogeochemists group carbon sequestration mechanisms into *carbon pumps*. This concept was originally created to explain the observed increasing DIC concentration with depth in the global ocean[45] and consequently did not consider the storage of organic carbon in the sediment. The carbon pumps were later applied to ocean carbon sequestration, in which case their definition included organic carbon transport to the ocean interior and possibly the sediment. Indeed, IPCC[7] definitions of the ocean carbon pumps are as follows: the *solubility pump* is "a physicochemical process that transports dissolved inorganic carbon from the ocean's surface to its interior […] primarily driven by the solubility of carbon dioxide (CO_2) […] and the large-scale, thermohaline patterns of ocean circulation"; the *carbonate pump* consists of "the biological formation of carbonates, primarily by plankton that generate bio-mineral particles that sink to the ocean interior, and possibly the sediment […] accompanied by the release of CO_2 to surrounding water and subsequently to the atmosphere"; and the *biological carbon pump*, which is the focus of this study, transports POC and DOC "to the ocean interior, and possibly the sediment".

Other biologically-driven sequestration mechanisms that are technically not part of the BCPs include: the *microbial carbon pump*, which consists of "microbial processes that transform organic carbon from rapidly-degradable states to biologically-unavailable forms, resulting in long-term carbon storage in the ocean, […] and is the principal mechanism generating and sustaining refractory dissolved organic carbon in the ocean"[16,33,34]; and coastal *blue carbon*, which consists of "rooted vegetation in the coastal zone, such as tidal marshes, mangroves and seagrasses. The latter ecosystems have high carbon burial rates on a per unit area basis and accumulate carbon in their soils and sediments". Coastal blue carbon sequestration is actively debated in the literature[46–49].

2. Sequestration flux and inventory of sequestered carbon by the biological pump

The present work deals with the sequestration flux of biogenic carbon (F_{seq}) in the ocean[2]. but some other studies address the inventory of sequestered DIC_{bio} (C_{seq}[1] or C_{soft}[3]). In the present study, F_{seq} is the flux of biogenic carbon leading to retention of DIC_{bio} in the ocean for ≥ 100 years, whereas C_{seq} is the total inventory of DIC_{bio} below the euphotic zone, assuming instantaneous equilibration of the ocean and atmosphere[1], irrespective of the retention time. The C_{seq} values are generally accompanied by estimates of the corresponding mean sequestration (or residence) times[1,3,5]. The units of F_{seq} are mass per unit time (flux) and that of C_{seq} is mass (inventory), showing that the two quantities are different biogeochemical characteristics of ocean carbon sequestration, used in different types of published studies.

Some recent papers/reviews refer to either metric, i.e., the carbon sequestration flux[2,43] (F_{seq}) or the carbon sequestration inventory (C_{seq}) and timescale[1,3]. Most previous F_{seq} studies have implicitly assumed that DIC_{bio} above a fixed depth or isopycnal surface – generally located between 1,000 and 2,000 – does not remain in the ocean for ≥ 100 years[2,10,13,18], hence null or negligible F_{seq} above this "sequestration depth". On the contrary, our study shows that remineralization is a <u>source of carbon</u> for F_{seq} in the whole water column.

3. Functioning of the biological carbon pump mechanisms

Six BCP mechanisms contribute to global ocean carbon sequestration[11]. In the following bullets, we briefly describe the functioning of the six mechanisms, and Fig. 3a (main text) illustrates the maximum depth to which each of them transports POC and/or DOC. Organic carbon

is progressively remineralized to CO_2 in the water column, and part of the resulting DIC_{bio} is sequestered at different depths (Fig. 3).

The remineralization processes of POC transported by BCPs include ingestion by heterotrophs, which respire part of their food to CO_2, and transformation of POC into DOC by various food-web processes such as solubilization by bacterial exoenzymes and excretion by microbes and animals. Most of the DOC, either remineralized *in situ* or transported downwards by BCP mechanisms, is used and respired to CO_2 by heterotrophic bacteria. Respiratory CO_2 fuels DIC_{bio}.

The different BCP mechanisms are grouped into pumps, which are known under different names proposed by various authors. The settling of organic particles is known as *biological gravitational pump*[11], the three physically-driven mechanisms (mixed layer, eddy subduction, and large scale advection and overturning) as *physical (injection) pumps*[25] or *mixing pump*[28], the diel vertical migrations as *mesopelagic migrant pump*[29]; the seasonal vertical migrations as *seasonal lipid pump*[37], and all mechanisms other than gravitational as *particle injection pumps*[11].

• *Biological gravitational mechanism.* Part of the organic particles produced by photosynthesis and other processes of the pelagic food web in the upper ocean's layer continuously sinks downwards. The sinking POC is progressively remineralized to CO_2 during its downward journey, and the non-remineralized POC may be sequestered in sediment for times reaching millions of years[16].

• *Mixed layer mechanism.* During the seasonal transition from the deepest winter mixed layer to summer stratification at high and mid-latitudes, there are variations in the depth of the mixed layer. These variations cause the downward injection, by deep mixing, of POC and DOC produced in the upper layer, and their isolation at depth when a new shallower mixed layer is formed. The succession of shoaling and deepening of the mixed layer injects POC and DOC to depths between 200 and 1000 m[23].

• *Eddy subduction mechanism.* Frontal circulation with horizontal dimensions ranging from the mesoscale (10–100 km) to the sub-mesoscale (1–10 km) creates "hotspots" of downward vertical transport (i.e. subduction). In these hotspots, POC and DOC are injected down to depths of 150 to 400 and even 500 m[24,25].

• *Large-scale advection and overturning (or Ekman) mechanism.* Large-scale wind-driven circulation causes the injection of POC and DOC from the seasonal mixed layer into the ocean interior, down to depths of 500 to 1000 m[26-28].

• *Diel (nycthemeral) vertical migrations.* During their diel vertical migrations, zooplankton and also fish, jellies and other animals larger than zooplankton[31] ingest organic particles at surface, generally at night time, and release part of the ingested material at depth, a few hours later, under the form of faecal material (POC, mostly zooplankton faecal pellets), excreted DOC and respiratory CO_2. Migrating animals also defecate, excrete and respire during their vertical journeys. The depth of these migrations does not generally exceed 200 m, but can reach a maximum of 600 m in some cases[35,36].

• *Seasonal (ontogenic) vertical migrations.* At high latitudes, some zooplankton taxa spend several months of the year at depths >600 and even 1000 m or more, where they release part of the carbon they had acquired at surface under the form of faecal pellets, excreted DOC, respiratory CO_2 and carcasses of dead organisms. The carbon transported by these organisms is

largely under the form of lipid reserves. This pump transports POC down to depths that can reach 1400 m[37].

4. Comparisons between our calculations or results for the mixing and migrant pumps and values from the literature

Our F_{seq} for the gravitational pump in CONVERSE 1-3 are compared with flux values from the literature Extended Data Table 3, and this comparison is included in the main text. As a complement, our CONVERSE calculations or results for the two other pumps are compared with values from the literature in the following paragraphs.

• *Mixing pump*. We use eq. 13 to estimate the remineralization flux of DOC driven by the mixing pump ($F_{reminDOC}$). In the field, the downward mixing flux of DOC and total export flux below 50 m were estimated to be 15 and 92 mg C m^{-2} d^{-1}, respectively, in the eastern North Atlantic Ocean[50]. Assuming that the two fluxes were entirely remineralized below 50 m, then $F_{reminDOC}$ accounted for ~15% of all F_{remin} ($F_{reminAll}$). This does not necessarily mean that F_{seqDOC} accounted for ~15% of F_{seqAll}, as differential sequestration of $F_{reminDOC}$ and $F_{reminAll}$ may have happened depending on their remineralization depths. Nevertheless, our CONVERSE 1-7 estimates of 11-23% of the biological pump F_{seq} accounted for by the mixing pump F_{seq} (Supplementary Tables S3 and S4) are of the same order as the above field ~15% for F_{remin}, which suggests that our estimates are realistic.

• *Migrant pump: diel vertical migrations*. Our eq. 16 computes F_{remin} for diel vertical migrations by all animals as follows:

$$F_{reminMigrD} = 0.25\ F_{expPOC}, \text{ at } z_{exp} = 100 \text{ m} \tag{16}$$

Hence:

$$F_{reminMigrD} / F_{expPOC} = 0.25 \tag{16a}$$

A synthesis of literature values for zooplankton diel migrations[51] provides the following relationship (parameters of the regression equation derived from the line drawn on Fig. 5b in that review):

$$F_{reminMigrD} / F_{expPOC} \simeq 0.1 + 0.017\ F_{reminMigrD}, \text{ at } z_{exp} = 100\text{-}200 \text{ m} \tag{16b}$$

where the units of $F_{reminMigrD}$ and F_{expPOC} are mg C m^{-2} d^{-1}. According to eq. 16b, our eq. 16 corresponds to $F_{reminMigrD} \simeq 9$ mg C m^{-2} d^{-1}. This $F_{reminMigrD}$ is in the bulk of values used to derive eq. 16b, indicating that our CONVERSE $F_{seqMigrD}$ values (eq. 17) are realistic.

• *Migrant pump: seasonal vertical migrations*. The study[38] from which we derived our eq. 18 was conducted in the northern North Atlantic and concerned the seasonal vertical migrations of the copepod *Calanus finmarchicus*, which were estimated to export 2 to 6 g C m^{-2} y^{-1}. Similar values for other cold waters are[51]: 3.1 g C m^{-2} y^{-1} (Arctic Ocean, mostly large copepods *C. hyperboreus* and *C. glacialis*), 2.0 to 4.3 g C m^{-2} y^{-1} (subarctic North Pacific, *Neocalanus* copepods), and 1.7 to 9.3 g C m^{-2} y^{-1} (subantarctic Southern Ocean, *N. tonsus*). These values are in the same range as those of the study on which we based our CONVERSE calculations, which suggest that our approach could also be used in other cold-water areas than the northern North Atlantic Ocean.

5. Robustness of our results to changes in ocean circulation

In the present study, we are estimating the biological pump mean state in the contemporary ocean, and transient changes in this or future scenarios are an important consideration, although there are outside the scope of this study. Indeed, future changes could affect the sequestration flux of biogenic carbon. For example, the overturning circulation may weaken as predicted by some models (examples[52,53]), which would affect f_{100} and thus F_{seq}. Future changes could also affect carbon export (example[43]), and the change in F_{exp} would affect F_{seq}. Most models predict a slowdown in overturning circulation in the future, while the remineralization of organic carbon in the upper ocean is expected to be enhanced by warming ocean temperatures These effects would increase sequestration times and f_{100} values and thereby increase F_{seq}, particularly above 1000 m.

In addition, the sequestration values above 2,000 and 1,000 m account for ≥50% of the global flux in 63% and 92% of the ocean pixels, respectively, across the seven CONVERSE versions (Supplementary Table S3), and thus cover a wide range of ocean circulation. This indicates that the high fraction of the sequestration flux above 2,000 and 1,000 m is robust to future changes. Our result that the sequestration flux above 2,000 and 1,000 m accounts for a high fraction of the global flux is thus robust to changes in ocean circulation.

6. Obtaining the f_{100} values to implement F_{seq} in models

It is suggested in the main text to compute the 100-year sequestration flux in biogeochemical models. For this purpose, the f_{100} values from a previous model[5] can be used as we have done in the present study, or modellers can calculate f_{100} in their own models using the procedures outlined in a previous publication[5]. In the first case, the f_{100} values may be affected by changes in ocean circulation due to climate change and variability (Supplementary Information 5). In the second case, the f_{100} values could be calculated in a model by implementing a single tracer in the model that tracks carbon from its point of injection to its re-exposure at the surface, i.e., a "resurfacing age" tracer. This has been done for steady circulation models, and also for variable circulation models[42].

7. Supplementary Tables

Table S1. Median F_{TOC} in pixels of the world ocean[44] and number of observations in different depth bins. Pixel depths were obtained via the function getNOAA.bathy using the *marmap* package on Rstudio at https://cran.r-project.org/web/packages/marmap/marmap.pdf

Depth bin	Median F_{TOC} (g C m^{-2} y^{-1})	Number of observations
<2000 m*	0.13	1625
2000 – 3000 m	0.123	3832
3000 – 3500 m	0.0542	3814
3500 – 4000 m	0.044	5570
4000 – 4500 m	0.0397	6228
4500 – 5000 m	0.0305	4788
>5000 m	0.0305	5756

*In the publication[42], there are no F_{TOC} values in pixels <1000 m.

Table S2. Median and lower and upper quartiles of [F_{TOC} / F_{SeqAll}] in pixels, in the seven CONVERSE versions and all versions together.

CONVERSE	F_{seqSed} / F_{seqAll}		
	Median	Lower quartile	Upper quartile
1	0.03	0.01	0.07
2	0.02	0.01	0.04
3	0.03	0.01	0.06
4	0.01	0.01	0.02
5	0.01	0.01	0.02
6	0.02	0.01	0.05
7	0.02	0.07	0.05
All	0.02	0.08	0.04

Table S3. Number of pixels with ≥50% of the sequestration flux above 1,000 and 2,000 m in each of the seven converse versions and in all versions together.

CONVERSE	1	2	3	4	5	6	7	1-7
Total number of pixels where the deepest f_{100} is at								
≥ 1,000 m	9,619	9,619	9,619	9,574	9,574	9,574	8,648	66,227
≥ 2,000 m	8,663	8,663	8,663	8,628	8,628	8,628	7,952	59,825
Fraction (%) of pixels where								
$All_{\leq 1000}$ / All_{ewc}[*] ≥ 50%	60	39	53	73	71	70	78	63
$All_{\leq 2000}$ / All_{ewc}[*] ≥ 50%	98	65	86	100	100	100	99	92

[*] All_{owc}: F_{seq} for all pumps over the entire water column, not including F_{seq} in sediment

8. Supplementary Methods

We described in the main text the calculations for CONVERSE 1. We provide here the differences between CONVERSE 2 to CONVERSE 7 and CONVERSE 1 or other versions.

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 2

There was one difference between CONVERSE 2 and CONVERSE 1, i.e. b values in eqs. 10 and 18 were geographically variable values from a model[14] instead of fixed $b = 0.86$[40].

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 3

There was one difference between CONVERSE 3 and CONVERSE 1, i.e. b values in eqs. 10 and 18 were regionalized estimates in biogeochemical provinces[17] instead of fixed $b = 0.86$[40].

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 4

There were five differences between CONVERSE 4 and CONVERSE 1.

First, we used $z_{exp} = z_{eu}$. Hence, the shallowest Δz considered in each pixel was z_{eu} (eq. 3).

Second, we did not calculate $F_{reminPOC}(\Delta z)$ with eqs. 10 and 11, but instead used the concentrations of POC ($[POC]$; $[M\ L^{-3}]$) and its remineralization rates (k; $[T^{-1}]$) in two POC fractions (slow-sinking and fast-sinking) within each depth interval Δz $[L]$ from SIMPLE-TRIM. With these data, we computed $F_{POC}(\Delta z)$ as follows:

$$F_{reminPOC}(\Delta z) = [([POC]_{slow} \times k_{slow}) + ([POC]_{fast} \times k_{fast})] \times \Delta z \tag{23}$$

We calculated $F_{seqPOC}(\Delta z)$ with eq. 1.

We treated F_{orgPOC} remaining in the deepest Δz as done for CONVERSE 1, i.e. we first computed $F_{reminPOC}(deepest\ \Delta z)$ with eq. (23), and then $F_{seqPOC}(deep)$ with eq. 12 replacing $F_{orgPOC}(deepest\ \Delta z)$ by $F_{reminPOC}(deepest\ \Delta z)$.

Third, for $F_{reminDOC}$, we used directly the values that we had derived from SIMPLE-TRIM (eq. 13), i.e. without multiplying by the export ratio as done in eq. 14.

Fourth, for $F_{reminMigrS}$, we used values in the study cited above[37] whereby the copepod *Calanus finmarchicus* generated a seasonally remineralization flux $F_{reminMigrS} = 1$ to 4 g C m^{-2} y^{-1} at $z_{migrS} = 600$ to $1,400$ m, corresponding to $F_{orgPOC}(z) = 2$ to 8 g C m^{-2} y^{-1}. Hence, $F_{reminMigrS} = 50\%$ $F_{orgPOC}(z)$ at $z_{migrS} = 600$ to $1,400$ m. We computed $F_{reminMigrS}$ as follows:

$$F_{reminMigrS} = 0.5\ F_{orgPOC}(z)\ \text{at}\ z_{migrS} \tag{24}$$

We used $F_{orgPOC}(z)$ from SIMPLE-TRIM at $z_{migrS} = 619$ m, which was the depth closest to 597 m for which values were available in that database.

Fifth, F_{seqPOC} at two fixed depths (z_{fixed}), we linearly interpolated $F_{orgPOC}(z)$ from SIMPLE-TRIM at $z = 919$ and $1,104$ m for the POC flux at $1,000$ m, and at $z = 1,833$ and $2,141$ m for the POC flux at $2,000$ m

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 5

There was one difference between CONVERSE 5 and CONVERSE 4, i.e. $z_{exp} = 100$ m. Hence, the shallowest Δz considered for each pixel in eq. 3 was 100 m.

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 6

CONVERSE 6 was a mix between CONVERSE 1 AND CONVERSE 5, which considered F_{expPOC} = 3.0 Pg C y^{-1} at z_{exp} = 100 m[14] as in CONVERSE 1, but derived the fluxes of the gravitational and mixing pumps from CONVERSE 5.

We used the fluxes from CONVERSE 5 to compute all the pump fluxes of CONVERSE 6 (except one flux, below), and also the fluxes at, below and above 1,000 m and 2,000 m. We multiplied the fluxes from CONVERSE 5 by the export ratio used in eq. 14, i.e. 3.0 Pg C y^{-1} / 7.3 Pg C y^{-1}. This was necessary because the values in CONVERSE 5 were derived from SIMPLE-TRIM where F_{expPOC} = 7.3 Pg C y^{-1} at z_{exp} = 100 m[4] (see also the legend of Supplementary Fig. S2):

$$F_{reminPOC} = F_{reminPOC} \text{ from CONVERSE 5} \times (3.0 \text{ Pg C } y^{-1} / 7.3 \text{ Pg C } y^{-1}) \tag{25}$$

We computed the fluxes of the diel migrant pump as in CONVERSE 1.

Continuous vertical estimation of pixel sequestration fluxes in CONVERSE 7

There were two differences between CONVERSE 7 and CONVERSE 1.

First, for F_{expDOC}, we did not use eqs. 13 and 14, but implemented information from the literature whereby the downward flux of DOC at z_{exp} accounts for ca. 20% of $F_{exp(POC+DOC)}$. Hence:

$$F_{expDOC} = 0.25 \, F_{expPOC} \tag{26}$$

where F_{expPOC} was the value at z_{exp} = 100 m from CONVERSE 1. We assumed that the mixing pump transported DOC rapidly from above z_{exp} to z_{mix}, with the consequence that properties at z_{mix} were the same as those at z_{exp}, hence:

$$F_{mixDOC} = F_{expDOC} \tag{27}$$

In the mixing pump, both $F_{reminDOC}(\Delta z)$ and $f_{100}(\Delta z)$ may be > 0 in some Δz below z_{mix}. Because of the lack of information on the vertical distribution of F_{orgDOC} in the global ocean, we used the following bulk approach to obtain estimates of F_{seqDOC}(pixel) and F_{seqDOC}(global) from z_{mix} downwards.

We assumed that the F_{orgDOC} injected at z_{mix} in a pixel was entirely remineralized at or below z_{mix}:

$$F_{reminDOC} = F_{mixDOC} \tag{28}$$

We also assumed that remineralization occurred above the permanent pycnocline[32], which is traced by isopycnal[17] σ_θ = 1027.6 kg m^{-3}. To be certain of not overestimating $F_{reminDOC}$(pixel), we further assumed that all DOC remineralization occurred within the Δz that included z_{mix} = 500 m, so that the relevant $f_{100}(\Delta z)$ was the value at z' = 530 m (depth for which there were values in the f_{100} database; Fig. 2 and Supplementary Fig. S1). We used eqs. 1 and 26-28 to calculate F_{seqDOC} at and below z_{mix}:

$$F_{seqDOC} = 0.25 \, F_{expPOC} \times f_{100}(531 \text{ m}) \tag{29}$$

Second, for the calculation of pixel F_{seqPOC} ≤ 2,000 m (eq. 21), we considered that F_{seqDOC} = 0 because we assumed above (eq. 28) that all DOC remineralization occurred within the Δz that included z_{mix} = 500 m.

9. Additional references

45. Volk, T. & Hoffert, M. I. Ocean carbon pumps: analysis of relative strengths and efficiencies in ocean-driven atmospheric CO2 changes. in *The carbon cycle and atmospheric CO 2 : natural variations Archean to present. Chapman conference papers, 1984* (eds. Sundquist, E. T. & Broecker, W. S.) 99–110 (American Geophysical Union; Geophysical Monograph 32, 1985).
46. Lovelock, C. E. & Duarte, C. M. Dimensions of Blue Carbon and emerging perspectives. *Biol. Lett.* **15**, 20180781 (2019).
47. Boyd, P. W. *et al.* Potential negative effects of ocean afforestation on offshore ecosystems. *Nat Ecol Evol* **6**, 675–683 (2022).
48. Gallagher, J. B., Shelamoff, V. & Layton, C. Seaweed ecosystems may not mitigate CO2 emissions. *ICES J. Mar. Sci.* **79**, 585–592 (2022).
49. Williamson, P. & Gattuso, J.-P. Carbon Removal Using Coastal Blue Carbon Ecosystems Is Uncertain and Unreliable, With Questionable Climatic Cost-Effectiveness. *Frontiers in Climate* **4**, (2022).
50. Giering, S. L. C. *et al.* Reconciliation of the carbon budget in the ocean's twilight zone. *Nature* **507**, 480–483 (2014).
51. Steinberg, D. K. & Landry, M. R. Zooplankton and the Ocean Carbon Cycle. *Annu. Rev. Mar. Sci.* **9**, 413–444 (2017).
52. Moore, J. K. *et al.* Sustained climate warming drives declining marine biological productivity. *Science* **359**, 1139–1143 (2018).
53. Li, Q., England, M. H., Hogg, A. McC., Rintoul, S. R. & Morrison, A. K. Abyssal ocean overturning slowdown and warming driven by Antarctic meltwater. *Nature* **615**, 841–847 (2023).