



**HAL**  
open science

# Major role of particle fragmentation in regulating biological sequestration of CO<sub>2</sub> by the oceans

Nathan Briggs, Giorgio Dall'olmo, Hervé Claustre

► **To cite this version:**

Nathan Briggs, Giorgio Dall'olmo, Hervé Claustre. Major role of particle fragmentation in regulating biological sequestration of CO<sub>2</sub> by the oceans. *Science*, 2020, 367 (6479), pp.791-793. 10.1126/science.aay1790 . hal-03137759

**HAL Id: hal-03137759**

**<https://hal.science/hal-03137759v1>**

Submitted on 11 Feb 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Title: Major role of particle fragmentation in regulating biological sequestration of CO<sub>2</sub> by the oceans**

**Authors:** Nathan Briggs<sup>1,2\*</sup>, Giorgio Dall’Olmo<sup>3,4</sup>, Hervé Claustre<sup>2</sup>.

**Affiliations:**

<sup>1</sup>National Oceanography Centre, European Way, Southampton, UK.

<sup>2</sup>Sorbonne Université & CNRS, Laboratoire d’Océanographie de Villefranche-sur-mer (LOV), Villefranche-sur-Mer, France.

<sup>3</sup>Plymouth Marine Laboratory, Plymouth, UK.

<sup>4</sup>National Centre for Earth Observations, Plymouth, UK.

\*Correspondence to: natebriggs@gmail.com

**Abstract:** A critical driver of the ocean carbon cycle is the downward flux of sinking organic particles, which acts to lower the atmospheric CO<sub>2</sub> concentration. This downward flux is reduced by over 70% in the mesopelagic zone (100-1000 m), but this loss cannot be fully accounted for by current measurements. For decades, it has been hypothesized that the missing loss could be explained by the fragmentation of large aggregates into small particles, although data to test this hypothesis have been lacking. Here, using robotic observations, we quantified total mesopelagic fragmentation during 34 high-flux events across multiple ocean regions and found that fragmentation accounted for 49±22% of the observed flux loss. Therefore, fragmentation may be the most important process controlling the sequestration of sinking organic carbon.

**One Sentence Summary:** Robotic measurements show that a previously unquantified process – particle fragmentation – exerts a major control on ocean CO<sub>2</sub> storage.

**Main Text:** Large organic particles (>100 μm) sinking through the ocean’s mesopelagic zone (100-1000 m) play a critical role in regulating the global carbon cycle. These particles are part of the “biological carbon pump”, which transfers an estimated 5-12 Pg C per year (1–3) from the sunlit ocean and sequesters 15-30% of this carbon for centuries to millennia in the deep ocean (4–6). The organic carbon that is sequestered directly impacts atmospheric CO<sub>2</sub> concentrations (7). Sinking organic carbon is also a primary source of energy for ocean ecosystems in and below the mesopelagic zone and essential to the ecosystem services they provide (8, 9).

Despite its fundamental importance, we still lack a quantitative, mechanistic understanding of key parts of the biological carbon pump. In particular, we poorly understand the subsurface loss processes that determine the depth at which sinking organic carbon is remineralized to CO<sub>2</sub>. This depth affects, in turn, long-term atmospheric CO<sub>2</sub> sequestration (7). Measurements of sinking particle flux at different depths via underwater sediment traps, radioactive particle tracers, and underwater cameras indicate that on average approximately 70-85% of sinking carbon flux is lost in the mesopelagic (4–6). However, direct consumption of fast-sinking particles, either by attached bacteria (10–12) or by zooplankton (13) appears to explain less than half of this observed flux attenuation. The remaining ≥50% of the observed mesopelagic flux attenuation might be explained by the fragmentation into smaller, slower-sinking particles (12). This would be consistent with the observed seasonal buildup of small particles in the mesopelagic zone (14) and metabolic activities of free-living bacteria that

consume such particles (13). Fragmentation rates have been estimated more directly, in both the laboratory and the upper ocean, from changes in particle size and attributed to several mechanisms. Microbial degradation has been shown to fragment marine particles in the laboratory (15, 16), marine particle fragmentation by zooplankton feeding has been observed both in the laboratory (17) and in the upper ocean (18), and fragmentation due to ocean turbulence has been proposed to explain patterns of particle size in the mixed layer (19, 20). In the mesopelagic zone, however, similar studies have not been practical. As a consequence, the hypothesis that fragmentation can reconcile existing measurements of the mesopelagic carbon budget has not been rigorously tested. To address this gap, we have estimated fragmentation rates at broad scale by simultaneously tracking changes in large (21) and small (14) mesopelagic particle concentrations using optical data collected by Biogeochemical-Argo floats.

We analyzed data from 25 floats deployed across the subpolar North Atlantic and the Atlantic and Indian sectors of the Southern Ocean between 2013 and 2016 (Fig. 1). All floats carried sensors for particulate optical backscattering ( $b_{bp}$ ), a proxy for particulate mass concentration (22), and chlorophyll *a* fluorescence ( $F$ ), a proxy for live phytoplankton biomass (23) (See Table S1 for abbreviations used in this manuscript). Floats profiled to 1000 m with temporal and vertical resolutions of 2-3 days and 1 m, respectively, during spring/summer phytoplankton blooms.  $F$  and  $b_{bp}$  were each divided into three components (Fig. S1) as described in (24): deep sensor blanks, including a background of small refractory particles ( $b_{br}$  and  $F_r$ ); small, labile backscattering ( $b_{bs}$ ) and fluorescing ( $F_s$ ) particles; and large, fast-sinking backscattering ( $b_{bl}$ ) and fluorescing ( $F_l$ ) particles. The division between small and large corresponds roughly to a particle diameter of 100  $\mu\text{m}$  for  $b_{bs}$  vs  $b_{bl}$  and a particle chlorophyll content of 60  $\text{pg}$  for  $F_s$  vs  $F_l$  (24). We attribute  $F_l$  primarily to live phytoplankton aggregates;  $F_l$  represents a subset of  $b_{bl}$ , which additionally includes fecal and detrital matter (21). Between May 2013 and February 2018, we identified 34 pulses of  $b_{bl}$  and/or  $F_l$  in the mesopelagic that were associated with surface phytoplankton blooms and were clearly distinguishable from pre-bloom background concentrations. Bulk large-particle sinking velocity was estimated for each large-particle pulse (e.g. Fig. S2) from the timing of peak concentration vs. depth (24). Mean sinking velocities (and 95% confidence intervals) across all pulses were 74 (58-100)  $\text{m d}^{-1}$  for large backscattering particles and 98 (79-129)  $\text{m d}^{-1}$  for large fluorescing particles.

We observed close coupling between large- and small-particle concentrations during these flux pulses (e.g. Fig. 2). Small-particle concentrations increased rapidly during periods of peak large-particle concentration (Fig. 2; solid black lines) at all depths below 200 m, peaking slightly later (e.g. Fig. 2, left column: peak  $F_s$  lags peak  $F_l$  by  $\sim 2$  d, regardless of depth). This coupling provides strong evidence that large-particle fragmentation drives the observed accumulation of small particles in the mesopelagic, both for large particles in general ( $b_{bl}$ ) and phytoplankton aggregates in particular ( $F_l$ ).

We quantified specific fragmentation rates during each sinking pulse by tracking these changes in the concentrations of large and small particles as a function of depth and time. Full computations, assumptions, and uncertainty budgets (24) are shown in (Figs. S3-S11), along with alternative calculations supporting key methodological assumptions (Figs. S11-S13). Mean fragmentation rate profiles across all pulses varied with depth and particle type from 0.03  $\text{d}^{-1}$  to 0.27  $\text{d}^{-1}$  (Fig. 3). Although wide uncertainty bounds prevent firm conclusions, the patterns in these rates offer preliminary indications of possible fragmentation mechanisms. First, live phytoplankton aggregates ( $F_l$ ) fragmented at higher rates than large sinking particles in general

( $b_{bl}$ ) at all depths in the mesopelagic zone (Fig. 3). Fresh phytoplankton aggregates therefore appear either more fragile than other large sinking particles and/or subject to higher local shear. The latter might result from selective feeding on fresh material by zooplankton. Second, specific fragmentation rates decreased with depth (Fig. 3). This depth dependency could result from passive breakup of more fragile particles closer to the surface. It may also result from higher zooplankton activity closer to the surface, where we expect food to be more abundant and more nutritious. On average, fragmentation accounted for close to 50% of the observed loss rates of large particles in general and 30-60% of large fluorescing particle loss (Fig. 3, lower panels) at all depths between 250 and 950 m.

We also found regional differences in specific fragmentation rates. When calculated using the same parameterizations (24), large-particle ( $b_{bl}$ ) specific fragmentation rates were significantly higher in the Southern Ocean than in the North Atlantic, between 250 m and 600 m (Fig. 4, left panel). On the other hand, fragmentation of fresh phytoplankton aggregates ( $F_l$ ) was not different in the two regions (Fig. 4, right panel). Further differences in  $b_{bl}$  fragmentation were observed between sub-regions of the Southern Ocean (see Table S2). Investigation of these regional differences may help to constrain the drivers of fragmentation.

Our measurements provide geographically-broad and quantitative support for the hypothesis that fragmentation exerts a major control on mesopelagic carbon flux (12), leading to two important implications. First, when added to previous estimates of large-particle consumption by zooplankton and bacteria (13), fragmentation can now fully explain the observed flux attenuation at high latitudes. These results therefore strengthen our mechanistic understanding of the biological carbon pump. Second, our results imply that fragmentation may be the single most important process in determining the depth at which fast-sinking organic carbon is remineralized. By extension, fragmentation appears to be an important regulator of atmospheric CO<sub>2</sub> concentrations (7) and of the delivery of energy to deep-ocean ecosystems vs. its retention in mesopelagic ecosystems (25).

## References and Notes:

1. P. W. Boyd, T. W. Trull, Understanding the export of biogenic particles in oceanic waters: Is there consensus? *Prog. Oceanogr.* **72**, 276–312 (2007).
2. S. A. Henson *et al.*, A reduced estimate of the strength of the ocean's biological carbon pump. *Geophys. Res. Lett.* **38**, 10–14 (2011).
3. D. A. Siegel *et al.*, Global assessment of ocean carbon export by combining satellite observations and food-web models. *Global Biogeochem. Cycles.* **28**, 1–16 (2014).
4. J. H. Martin, G. A. Knauer, D. M. Karl, W. W. Broenkow, VERTEX - carbon cycling in the northeast Pacific. *Deep. Res. Part a-Oceanographic Res. Pap.* **34**, 267–285 (1987).
5. L. Guidi *et al.*, A new look at ocean carbon remineralization for estimating deepwater sequestration. *Global Biogeochem. Cycles.* **29** (2015), doi:10.1002/2014GB005063.
6. S. A. Henson, R. Sanders, E. Madsen, Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles.* **26**, 1–14 (2012).
7. E. Y. Kwon, F. Primeau, J. L. Sarmiento, The impact of remineralization depth on the air-sea carbon balance. *Nat. Geosci.* **2**, 630–635 (2009).

8. X. Irigoien *et al.*, Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* **5**, 3271 (2014).
9. M. A. St. John *et al.*, A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives from the Mesopelagic Community. *Front. Mar. Sci.* **3** (2016), doi:10.3389/fmars.2016.00031.
10. J. R. Collins *et al.*, The multiple fates of sinking particles in the North Atlantic Ocean. *Global Biogeochem. Cycles*, 1471–1494 (2015).
11. A. Belcher *et al.*, Depth-resolved particle-associated microbial respiration in the northeast Atlantic. *Biogeosciences*. **13**, 4927–4943 (2016).
12. D. M. Karl, G. A. Knauer, J. H. Martin, Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. *Nature*. **332**, 438–441 (1988).
13. S. L. C. Giering *et al.*, Reconciliation of the carbon budget in the ocean’s twilight zone. *Nature*. **507**, 480–483 (2014).
14. G. Dall’Olmo, K. A. Mork, Carbon export by small particles in the Norwegian Sea. *Geophys. Res. Lett.* **41**, 2921–2927 (2014).
15. L. R. Pomeroy, D. Deibel, Aggregation of Organic Matter By Pelagic Tunicates. *Limnol. Oceanogr.* **25**, 643–652 (1980).
16. B. A. Biddanda, L. R. Pomeroy, Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. I. Microbial succession. *Mar. Ecol. Prog. Ser.* **42**, 79–88 (1988).
17. S. Goldthwait, J. Yen, J. Brown, A. Alldredge, Quantification of marine snow fragmentation by swimming euphausiids. *Limnol. Oceanogr.* **49**, 940–952 (2004).
18. L. Dilling, A. L. Alldredge, Fragmentation of marine snow by swimming macrozooplankton : A new process impacting carbon cycling in the sea. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **47**, 1227–1245 (2000).
19. G. A. Jackson, Comparing Observed Changes in Particle-Size Spectra with Those Predicted Using Coagulation Theory. *Deep. Res. Part Ii-Topical Stud. Oceanogr.* **42**, 159–184 (1995).
20. J. Ruiz, What generates daily cycles of marine snow? *Deep. Res. Part I Oceanogr. Res. Pap.* **44**, 1105–1126 (1997).
21. N. Briggs *et al.*, High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **58**, 1031–1039 (2011).
22. R. A. Reynolds, D. Stramski, G. Neukermans, Optical backscattering by particles in Arctic seawater and relationships to particle mass concentration, size distribution, and bulk composition. *Limnol. Oceanogr.* **61**, 1869–1890 (2016).
23. C. Roesler *et al.*, Recommendations for obtaining unbiased chlorophyll estimates from in situ chlorophyll fluorometers: A global analysis of WET Labs ECO sensors. *Limnol. Oceanogr. Methods*. **15** (2017), doi:10.1002/lom3.10185.
24. See supplementary materials.

25. D. J. Mayor, R. Sanders, S. L. C. Giering, T. R. Anderson, Microbial gardening in the ocean's twilight zone: Detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus. *BioEssays*. **36**, 1132–7 (2014).
26. N. Briggs, G. Dall'Olmo, H. Claustre, Size-fractionated optical backscattering and chlorophyll fluorescence from 34 high-latitude phytoplankton blooms. (2019), , doi:10.17882/70484.
27. X. D. Zhang, L. B. Hu, M. X. He, Scattering by pure seawater: Effect of salinity. *Opt. Express*. **17**, 5698–5710 (2009).
28. J. M. Sullivan, M. Twardowski, J. R. Zaneveld, C. Moore, in *Light Scattering Reviews 7*, A. A. Kokhanovsky, Ed. (Springer Berlin Heidelberg, 2013), pp. 189–224.
29. N. T. Briggs, W. H. Slade, E. Boss, M. J. Perry, Method for estimating mean particle size from high-frequency fluctuations in beam attenuation or scattering measurements. *Appl. Opt.* **52**, 6710–25 (2013).
30. W. M. Berelson, The Flux of Particulate Organic Carbon Into the Ocean Interior: A Comparison of Four U.S. JGOFS Regional Studies. *Oceanography*. **14**, 59–67 (2001).
31. A. Waite, A. Fisher, P. A. Thompson, P. J. Harrison, Sinking rate versus cell volume relationships illuminate sinking rate control mechanisms in marine diatoms. *Mar. Ecol. Prog. Ser.* **157**, 97–108 (1997).
32. X. Y. Li, B. E. Logan, Size distributions and fractal properties of particles during a simulated phytoplankton bloom in a mesocosm. *Deep. Res. Part I-Topical Stud. Oceanogr.* **42**, 125–138 (1995).
33. A. Hatcher, P. Hill, J. Grant, Optical backscatter of marine flocs. *J. Sea Res.* **46**, 1–12 (2001).
34. E. N. Flory, P. S. Hill, T. G. Milligan, J. Grant, The relationship between floc area and backscatter during a spring phytoplankton bloom. *Deep. Res. Part I-Oceanographic Res. Pap.* **51**, 213–223 (2004).

**Acknowledgments:** We would like to thank the entire international Argo community for its work over decades to create a reliable global profiling float network and its recent work to integrate biogeochemical sensors into this network. We especially thank Antoine Poteau for his development and continuous support of float control and visualization tools used to adapt float vertical and temporal sampling resolutions to the present study requirements. We would also like to thank two anonymous reviewers for their thorough and insightful comments, which led to substantial improvements to this manuscript. **Funding:** The collection of the data used in this manuscript was funded by a European Research Council Advanced grant (remOcean, agreement number 246577) as well as the climate initiative of the BNP Paribas foundation (SOCLIM project), French LEFE- GMMC, and UK BioArgo projects. Analysis was funded by U.S. National Science Foundation Postdoctoral Research Fellowship OCE1420929. Final writing was funded by a European Research Council Consolidator grant (GOCART, agreement number 724416) and a European Research Council Advanced grant (REFINE, agreement number 834177). **Author contributions:** N.B. and G.D. conceptualized the study. N.B. developed the methods, and H.C. managed the data collection to optimize for these methods. N.B. carried out all data analysis, including software development, with periodic feedback from G.D. and H.C. N.B. wrote the original draft and generated all figures. N.B., G.D., and H.C. reviewed and edited the final manuscript. **Competing Interests:** The authors declare no competing interests. **Data and materials availability:** All data used in this study are available from the Argo Global Data Assembly Centers in Brest France (<ftp://ftp.ifremer.fr/ifremer/argo/dac/coriolis>) and Monterey, California



(<ftp://usgodae.org/pub/outgoing/argo/dac/coriolis>) in subfolders named corresponding to the WMO numbers of individual floats given in Table S2 of the supplemental methods. Intermediate (binned) data products used in this study are available at [seanoe.org](http://seanoe.org) (doi:10.17882/70484), along with data processing visualizations for all 34 plumes.

5

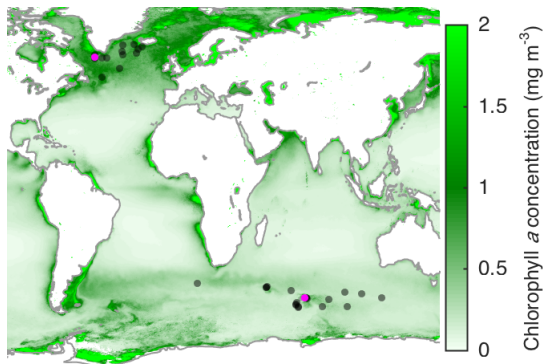
**Supplementary Materials:**

Materials and Methods

Figures S1-S13

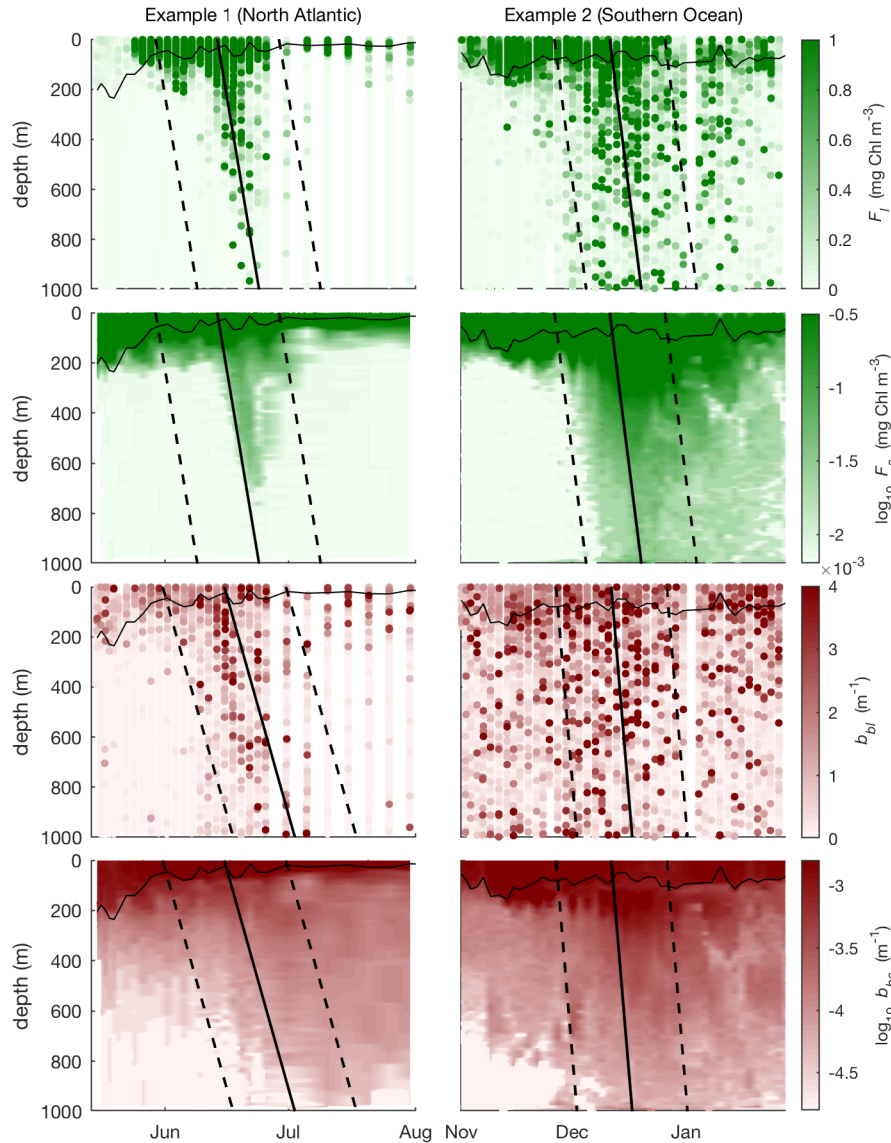
Tables S1-S2

10 References (26-34)

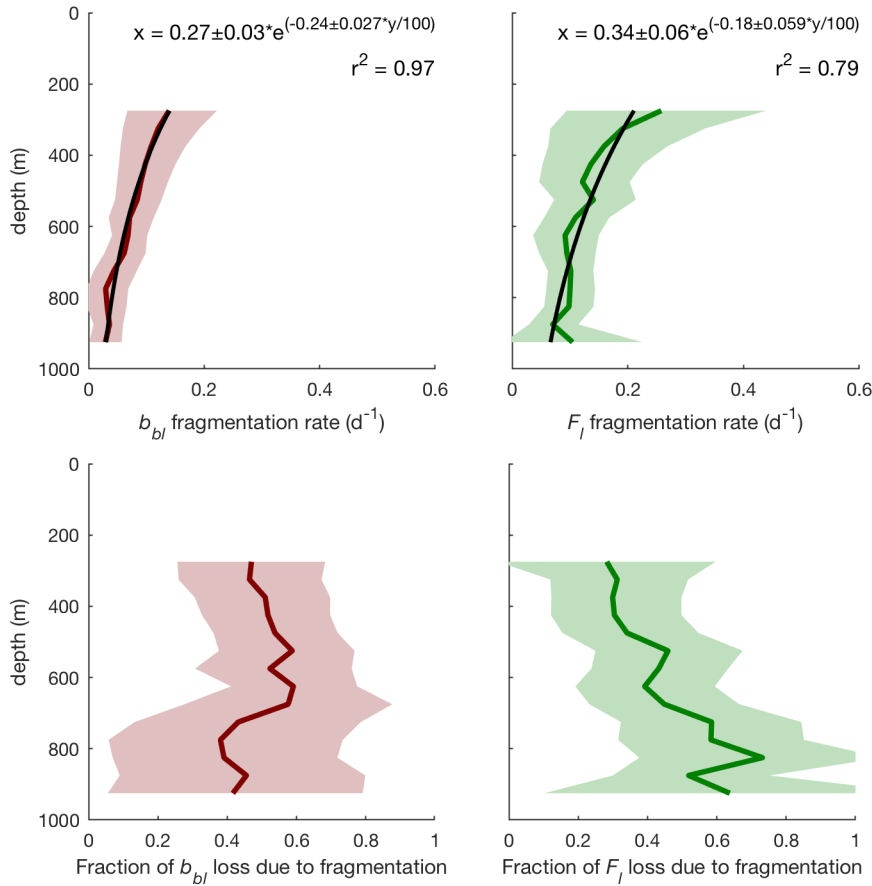


5 **Fig. 1. Location of particle-flux pulses.** Gray circles represent the 34 pulses analyzed in this study. Darker grays indicate overlapping circles. Magenta circles indicate example pulses shown in Fig. 2. The background is a global satellite climatology of surface chlorophyll concentration from MODIS-Aqua (2002-2017).



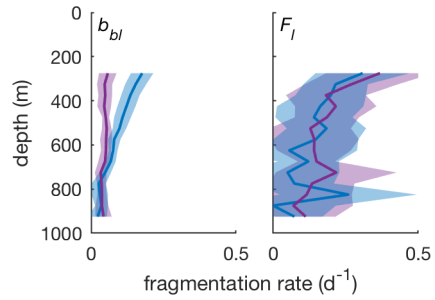


**Fig. 2. Fragmentation of large particles generates small particles at depth.** Large- and small-particle measurements from example large-particle pulses from the North Atlantic (left panels) and Southern Ocean (right panels). Large particle fluorescence  $F_l$  (green circles) and large particle backscattering  $b_{bl}$  (red circles), are shown above corresponding  $\log_{10}$  small-particle fluorescence  $F_s$  (green) and backscattering  $b_{bs}$  (red). Large particle measurements are plotted individually with higher values (darker colors) covering lower values. Thin black lines show mixed-layer depth, thick solid lines show linear least-squares fits of maximum large-particle concentration with depth, and dashed lines show  $\pm 15$  d window used for fragmentation calculations. Similar visualizations for all 34 plumes in this study can be found at [seanoec.org](http://seanoec.org) (doi:10.17882/70484).



5

**Fig. 3. Fragmentation contributes 50% of the observed flux attenuation.** Upper panels show mean specific fragmentation rates of large particles  $b_{bl}$  (red) and of large fluorescing particles  $F_l$  (green) across all large-particle pulses. Lower panels show the mean fraction of  $b_{bl}$  flux attenuation (red) and  $F_l$  flux attenuation (green) explained by this fragmentation. Pale shaded areas show 95% confidence intervals. Black curves and equations in upper panels show least-squared exponential fits of specific fragmentation rates vs. depth.



**Fig. 4. Regional differences in fragmentation.** Comparison between mean specific fragmentation rates of large particles  $b_{bl}$  (left) and of large fluorescing particles  $F_l$  (right) during North Atlantic (purple) and Southern Ocean (blue) phytoplankton blooms. Bold lines show means and shaded areas show two standard errors around the mean.

5



## Supplementary Materials for

Major role of particle fragmentation in regulating biological sequestration of CO<sub>2</sub>  
by the oceans

Nathan Briggs, Giorgio Dall'Olmo, Hervé Claustre.

Correspondence to: [natebriggs@gmail.com](mailto:natebriggs@gmail.com)

**This PDF file includes:**

Materials and Methods

Figs. S1 to S13

Tables S1 to S2

References (26-34)

## Materials and Methods

### Float dataset

All data presented in this study were collected by autonomous profiling floats carrying sensors for chlorophyll *a* fluorescence ( $F$ ) and particulate optical backscattering ( $b_{bp}$ ). All data are publicly available in near-real-time as part of the Biogeochemical Argo program. However, the data used here represent a small fraction of the total Biogeochemical Argo dataset, due to the particular requirements of our analyses. The calculations presented below of large-particle concentration, depth attenuation, and especially bulk sinking velocity require measurements of a pulse of large sinking particles that are statistically distinguishable from the background particle concentration at multiple depths in the mesopelagic. In practice, these large particles are rare relative to the volume sampled by the sensor, and high vertical resolution ( $\sim 1$  m or higher) measurements are required in order to obtain useful, depth-resolved concentrations from a single profile. In addition, typical sinking velocities ( $50$ - $100$  m  $d^{-1}$ ) require temporal frequencies of  $< 5$  d in order to sample a sinking pulse multiple times in the upper mesopelagic, where concentrations are more likely to be high enough to constrain sinking velocity measurements. Most Biogeochemical-Argo floats deployed to date profile at  $5$ - $10$  d intervals and with  $\geq 10$  m resolution in the mesopelagic. For this reason, we limited our analysis to data from PROVOR floats whose sampling resolution we modified specifically for resolving pulses of large, sinking particles. These floats permit dynamic control of key sampling parameters. For the purpose of this study, we actively monitored all PROVOR floats deployed in the North Atlantic subpolar gyre and Southern Ocean between 2013 and 2018 and, during each spring/summer phytoplankton bloom we increased their vertical resolution from  $10$  m to  $1$  m and temporal resolution from  $5$ - $10$  d to  $2$ - $3$  d. High resolution was maintained until we visually confirmed that any associated sinking particle pulse had reached  $1000$  m. Starting in 2014 we extended high-resolution data at least one month after each pulse in order to better constrain sinking velocities. Excluding obvious sensor failures and/or biofouling, we obtained  $110$  spring/summer seasons of data from  $48$  PROVOR floats in the North Atlantic and Southern Ocean during the study period. From these, we visually identified  $34$  clear, brief pulses of large particles (see signal partitioning in next section) that reached the lower mesopelagic ( $> 500$  m). These  $34$  pulses were used for the fragmentation estimates in this study. These pulses (see Fig. 1 of main text and Table S2) cover primarily the subpolar North Atlantic and the Indian sector of the Southern Ocean north of  $52^\circ$  S during the years 2013-2017. Our quantitative fragmentation results therefore apply primarily to these regions, although we might expect to find similar results in other high-latitude open-ocean blooms. The raw data for these floats can be obtained from the Argo Global Data Assembly Centers in Brest France (<ftp://ftp.ifremer.fr/ifremer/argo/dac/coriolis>) and Monterey, California (<ftp://usgodae.org/pub/outgoing/argo/dac/coriolis>) in subfolders named corresponding to the WMO numbers of individual floats given in Table S2. We have also separately published the intermediate (binned) data products from the  $34$  pulses used in this study along with many of the data processing visualizations presented below, but repeated for all  $34$  plumes (26).

### Partitioning of $b_{bp}$ and $F$

We measured Chlorophyll *a* fluorescence  $F$  and the volume scattering function (at  $\sim 124^\circ$  and  $700$  nm wavelength) using factory-calibrated WET Labs ECO sensors. These sensors also measured dissolved organic matter fluorescence (FDOM), used here only to aid data quality control (see below). The volume scattering function was converted to the particulate

backscattering coefficient  $b_{bp}$  by subtracting an estimate of the scattering due to seawater (27) and multiplying by  $2\pi\chi$ , where  $\chi=1.077$  (28).

We partitioned  $b_{bp}$  into three components (see Fig. S1):

$$b_{bp} = b_{bl} + b_{bs} + b_{br}, \quad (1)$$

where  $b_{bl}$  is the optical backscattering coefficient due to “large” particles,  $b_{bs}$  is the optical backscattering coefficient due to small, labile particles, and  $b_{br}$  is a deep blank that includes small refractory particles (see Table S1 for a list of abbreviations). The fraction  $b_{bl}$  was separated from  $b_{bsr}$  (the sum of  $b_{bs}$  and  $b_{br}$ ; see Fig. S1, red line) by applying an 11-point running minimum filter followed by an 11-point running maximum filter (21) to vertical  $b_{bp}$  profiles (see Fig. S1 insets, yellow lines). This filter removes positive spikes due to large individual particles that are rare relative to the sample volume of  $\sim 10$  ml (taking into account  $\sim 10$  cm of movement during the sensors’ 1 s integration time). The residual “spikes” (difference between unfiltered and filtered data) represent  $b_{bl}$  plus a background of instrument noise. We quantified this instrument noise component for each sensor by averaging all residual spikes below 300 m from each profile into 50 m vertical bins, pooling all bins from each float and, removing all bins higher than twice the median, and then calculating the median a second time. This instrument noise component can be thought of as a “blank” for our spike signal, and should not be included in our  $b_{bl}$  estimate. We therefore added this median blank to the filtered profiles to estimate  $b_{bsr}$  (Fig. S1; red line). We then calculated  $b_{bl}$  as the difference between total  $b_{bp}$  (Fig. S1; black line) and  $b_{bsr}$ . The minimum, mean, and maximum  $b_{bp}$  “spike blanks” across all sensors were 0.023, 0.039, and 0.062  $\text{km}^{-1}$  (note the different units), implying that spikes smaller than this level cannot be distinguished from instrument noise and therefore do not contribute to  $b_{bl}$  (but instead contribute to  $b_{bs}$ ). Assuming a backscattering efficiency of 0.024 and a motion-corrected sample volume of 10 ml, these thresholds correspond very roughly to diameters of 98, 128, and 160  $\mu\text{m}$  (29). Then, for each period of interest ( $\sim 1$  month surrounding a large-particle pulse), we estimated  $b_{br}$  as the 25<sup>th</sup> percentile of  $b_{bsr}$  from 850-900 m (Fig. S1; blue line). Assuming that  $b_{br}$  is constant in both depth and time over our period of interest, we subtracted  $b_{br}$  from  $b_{bsr}$  to obtain  $b_{bs}$ , the backscattering due to small, labile particles (Fig. S1; pink shaded region). The same method was used to partition  $F$  into  $F_l$ ,  $F_s$ , and  $F_r$  (Fig. S1, right panel).  $F_l$  spike blanks ranged from 0.006 to 0.012  $\text{mg Chl m}^{-3}$ , roughly equivalent to particle chlorophyll contents of 55-124  $\text{pg Chl}$ , given the 10 ml sample volume. Thus, our  $b_{bl}$  and  $F_l$  signals, although uncalibrated, are estimated for reference to roughly correspond to particles with diameter  $>100 \mu\text{m}$  and chlorophyll content  $>60 \text{pg}$ , respectively, while our  $b_{bs}$  and  $F_s$  signals correspond to scattering or fluorescence by particles  $<100 \mu\text{m}$  in diameter or containing  $<60 \text{pg Chl}$ . Note that both  $b_{br}$  and  $F_r$  include any error in factory dark calibration as well as any signal from refractory material. These refractory pools are treated as blanks and not used further in this study, but for reference mean  $b_{br}$  and  $F_r$  ( $\pm$  standard deviation) for the spring/summer bloom periods analyzed were  $(1.9\pm 0.6)\times 10^{-4} \text{ m}^{-1}$  and  $0.02\pm 0.02 \text{ mg m}^{-3}$ , respectively.

Occasionally, we observed very large spikes in  $b_{bp}$  ( $b_{bl} > 0.008 \text{ m}^{-1}$ ) and/or spikes in FDOM measured by the same ECO sensor. Again, assuming backscattering efficiency of 0.024 (29),  $b_{bl} > 0.008 \text{ m}^{-1}$  corresponds approximately to a diameter of  $>2 \text{ mm}$ . These spikes occurred primarily in discrete layers near 300 m at noon and near the surface at midnight, strongly suggesting that they are caused by live zooplankton or small nekton that are capable of diel vertical migration. We therefore removed all  $b_{bp}$  data from within 25 m of such spikes from the analysis. FDOM

spikes were identified by subtracting an 11-point median filter to isolate the high-frequency signal. These spikes were identified as high-frequency values exceeding twice the difference between the 10<sup>th</sup> and 90<sup>th</sup> percentile for each float. Note that the removal of the largest  $b_{bl}$  spikes could potentially cause an under-estimate of sinking particle concentration (and flux) by excluding the very largest (and potentially fastest) sinking particles. If some of these particles fragment into  $b_{bl}$  or  $b_{bs}$ , they could introduce bias in our fragmentation calculations. We therefore test the impact of removing very large  $b_{bp}$  spikes on our results in the sections below and find negligible impact for this dataset.

### Processing of large-particle signals

We refer to the method for estimating the fragmentation rates presented in the main text as Method 1A. Unless stated otherwise, all methods described in this and the following sections refer to Method 1A. To estimate large-particle concentrations as well as large-particle loss and fragmentation rates,  $b_{bl}$  and  $F_l$  were processed via a series of steps detailed in this subsection. We first used large-particle signals  $b_{bl}$  and  $F_l$  to identify pulses of sinking matter and calculate the associated bulk sinking speeds,  $w_{bbl}$  and  $w_{Fl}$ . We then binned and smoothed  $b_{bl}$  and  $F_l$  and calculated their loss rates with respect to depth and time.

We identified 34 pulses of backscattering spikes ( $b_{bl}$ ) and/or  $F$  spikes ( $F_l$ ) associated with spring or summer blooms in the North Atlantic and Southern Ocean (e.g. Fig. S2, or Fig. 2 of the main text; full list in Table 2). To determine when particle flux peaked at each depth, we visually defined the rough temporal boundaries of each event (e.g. Fig. S2; vertical gray lines) and fit a Gaussian function (at 50 m intervals above 250 m, and 100 m intervals below 250 m due to lower particle concentration) to each large-particle timeseries within these boundaries and below the mixed layer (Fig. S2, black circles and horizontal lines). The width (standard deviation) of the Gaussian function was constrained between 3.5 and 14 days for  $F_l$  fits and between 7 and 14 days for  $b_{bl}$  fits, and the least-squared fit was optimized using the trust-region method. The center of the sinking pulse within the mesopelagic was then determined using a linear regression (Fig. S2, diagonal black line) between the midpoint depths (independent variable) and the timing of the maximum of each Gaussian fit (dependent variable; see Fig. S2, black circles), weighted by the inverse square of its 95% confidence interval (see Fig. S2, horizontal black lines). Overall, slopes (inverse sinking velocities) ranged from -2 to 3.7 d m<sup>-1</sup>. Note that negative slopes are not physically meaningful, but can result from uncertainty in the fit. Removing only negative fits could introduce a bias in our calculation of mean slope. To reduce error from poor fits without introducing such bias, we only retained slopes with 95% confidence intervals narrower than  $\pm 0.015$  d m<sup>-1</sup>. This filtering reduced the initial 34 pulses to 18 high-precision fits of  $b_{bl}$  and 25 of  $F_l$ , each spanning multiple regions of both the North Atlantic and Southern Oceans. See Table S2 for individual inverse velocity estimates and regions. The mean slopes ( $\pm 2$  standard errors) of these high-precision linear regressions across all large-particle pulses are  $0.0136 \pm 0.0036$  d m<sup>-1</sup> for  $b_{bl}$  and  $0.0102 \pm 0.0025$  d m<sup>-1</sup> for  $F_l$ , corresponding to mean sinking velocities (and 95% confidence intervals) of  $\bar{w}_{bbl} = 74$  (58-100) m d<sup>-1</sup> and  $\bar{w}_{Fl} = 98$  (79-129) m d<sup>-1</sup>. Given the broad and overlapping confidence intervals, the difference between  $\bar{w}_{bbl}$  and  $\bar{w}_{Fl}$  is not statistically significant, so it could simply be a result of uncertainty inherent in our calculations. On the other hand, our results may indicate that  $b_{bl}$  contains a substantial fraction of detrital aggregates that sink slightly slower than fresh phytoplankton aggregates. Note also that our decision to remove very large  $b_{bp}$  spikes ( $b_{bl} > 0.008$  m<sup>-1</sup>) might remove not only zooplankton (see previous subsection), but also very large, fast-sinking particles, potentially biasing our calculation of  $\bar{w}_{bbl}$ .



We repeated the above calculations without the very large spike removal step and the difference was minimal:  $\bar{w}_{bbl} = 78$  (59-113) m d<sup>-1</sup>, indicating that this quality control (QC) step did not substantially bias these results. Separately, we repeated our mean sinking velocity calculations including all 34 plumes for both  $\bar{w}_{bbl}$  and  $\bar{w}_{Fl}$  and obtained estimates of 74 (57-104) m d<sup>-1</sup> and 125 (90-206) m d<sup>-1</sup>, respectively. Again, the impact of this QC step on  $\bar{w}_{bbl}$  was minimal. The 28% increase in  $\bar{w}_{Fl}$  when the poorest fits are included could indicate moderate low bias in our  $\bar{w}_{Fl}$  estimate, but we think it is more likely that the low-quality fits are biased high, since a type-I linear regression on random “noise” should yield a slope of zero (equivalent to infinite sinking speed). In any case, neither of these tests yielded estimates that fell outside of the confidence intervals of our fully QCed estimates. The potential effects of this sinking speed uncertainty on our fragmentation estimates is traced in the error propagation exercise below.

Our calculations of fragmentation rate require estimates of both large-particle concentrations ( $b_{bl}$  and  $F_l$ ) and the net changes in the concentrations of these particles ( $db_{bl}/dt$  and  $dF_l/dt$ ) as they sink (see Eq. 5). To reliably calculate these derivatives from the noisy large-particle measurements, we binned and smoothed the large-particle data as described below. Large-particle concentrations were first averaged into 6-day, 50-m bins, with so-called Lagrangian, “pulse-following” temporal boundaries centered around each pulse’s linear sinking velocity fit (see Fig. S3 for bin edge visualization). The Lagrangian bin boundaries simplify calculation of the net loss rate of large particles. For each pulse, we calculated five temporal bins spanning  $\pm 15$  days from the maximum of the large-particle pulse and 14 vertical bins spanning from 250 to 950 m. Although floats profiled to 1000 m, the bottom (beginning) 50 meters of each profile were excluded from further analysis because they often contained unrealistically high spikes, which we attribute to material that had accumulated on the top of the float during drift mode. The top 250 m were not used due to higher concentrations of large particles, which can prevent our large/small-particle filter from establishing a baseline free of large particles (21). The profiling interval during blooms was usually 2-3 days and occasionally 5 days, so temporal bins of 6 days ensured at least one, usually 2-3 profiles were available per bin. The vertical resolution during surface phytoplankton blooms was 1 m, so at least 50 and usually 100-150 measurements were available per 50 m, 6 d bin, equivalent to 0.5 – 1.5 L, given the 10 ml sample volume. Again, the exclusion of very large  $b_{bp}$  spikes could potentially cause a low bias in our  $b_{bl}$  estimates, impacting further calculations, so we repeated the bin averaging process with and without the removal of ( $b_{bl} > 0.008$  m<sup>-1</sup>). Inclusion of these data only increased our  $b_{bl}$  signals by an average of 1.6%, so the overall impact was negligible. Nevertheless, these occasional spikes did introduce “noise” in a few individual plume calculations, so we still chose to remove them.

To further reduce noise, for Method 1A we smoothed the large-particle data using a so-called “Martin curve” power law (4) of the form

$$b_{bl}(z) = b_{bl\_100} * \left(\frac{z}{100}\right)^{-b}, \quad (2)$$

where  $b$  represents the strength of the particle attenuation with depth,  $b_{bl\_100}$  represents  $b_{bl}$  at 100 m and the depth  $z$  is in meters. An analogous equation was used to smooth  $F_l$  as well. Vertical profiles of sinking particle flux below 100 m depth have been repeatedly found to approximate power laws throughout the ocean (30), suggesting that this smoothing method can reduce noise in our  $b_{bl}$  (and  $F_l$ ) profiles without introducing substantial biases at any given depth. We verified the appropriateness of the power-law fit for our dataset by averaging binned  $b_{bl}$  (and  $F_l$ ) profiles from all pulses into a single profile and fitting Eq. 2 between 250 and 950 m. These equations fit

the mean values within two standard errors at every depth (See Fig. S4), supporting this method of vertical smoothing within the depth bounds of the study. The influence of this smoothing step on our mean fragmentation profile is further explored below alongside other uncertainties (see Method 1B).

To avoid over-fitting Eq. 2, we calculated a single value of  $b$  (attenuation of particles with depth) for each 30-day pulse but allowed  $b_{bl\_100}$  (particle concentration) to vary among the five 6-day temporal bins. The power law exponent  $b$  was obtained by averaging all five temporal bins into a single profile (e.g. Fig. S5, colored circles) and optimizing a non-linear least-squares fit of Eq. 2 to the mean  $b_{bl}$  (or  $F_l$ ) profile for the entire 30-day pulse (Fig. S5, black curves). The precision of the fit depends strongly on large-particle concentrations in the shallowest bins. Five of the 34  $b_{bl}(z)$  fits and 11 of the 34  $F_l(z)$  fits yielded very low values at 275 m ( $b_{bl} < 4 \cdot 10^{-5} \text{ m}^{-1}$  or  $F_l < 0.005 \text{ mg m}^{-3}$ ) and were excluded from further analysis for Method 1A. Method 1B (see below) included neither the power law smoothing nor this exclusion step. After this step, Method 1A retained fits of both  $b_{bl}(z)$  and  $F_l(z)$  (e.g. Fig. S5) for 18 pulses, fits of  $b_{bl}(z)$  only for 11 pulses, and fits of  $F_l(z)$  only for five pulses (see Table S2). For the retained large-particle pulses,  $b_{bl\_100m}$  and  $F_{l\_100m}$  were calculated at each temporal bin as the slope of a type-I linear regression, forced through the origin, of dependent variable  $b_{bl}$  (or  $F_l$ ) vs. independent variable  $(z/100)^{-b}$  using the fixed value of  $b$  determined above. Resultant smoothed profiles for each individual temporal bin (black) are shown together with unsmoothed binned profiles (colors) in Fig. S6.

Depth-resolved estimates of the loss of large-particle concentration with depth ( $db_{bl}/dz$  and  $dF_l/dz$ ) were obtained from the derivative of the ‘‘Martin curve’’ power law with respect to depth. Because the ‘‘Lagrangian’’ temporal bin boundaries were chosen to follow the large-particle population as it sinks, the net loss of large particles with depth can be converted to the net loss rate with respect to time via Eq. 3, where  $\bar{w}_{bbl}$  is the mean large-particle sinking speed:

$$\frac{db_{bl}}{dt} = \bar{w}_{bbl} * \frac{db_{bl}}{dz}. \quad (3)$$

Note that due to the Lagrangian frame of reference we adopted, Eq. 3 does not require sink/source terms to account for particles sinking in and out the water parcel under examination. Due to uncertainties in the individual estimates of  $w_{bbl}$ , we calculated  $db_{bl}/dt$  (and similarly  $dF_l/dt$ ) for each temporal bin of each bloom using the single mean estimates of  $\bar{w}_{bbl} = 74 \text{ m d}^{-1}$  and  $\bar{w}_{F_l} = 98 \text{ m d}^{-1}$  calculated earlier in this subsection. Error in mean sinking velocities would lead to systematic bias in  $db_{bl}/dt$  and  $dF_l/dt$  for all plumes, so sinking velocity was propagated to uncertainty bounds for  $db_{bl}/dt$  and  $dF_l/dt$  by recalculating Eq. 3 using upper and lower uncertainty bounds of  $\bar{w}_{bbl}$  and  $\bar{w}_{F_l}$  as input to Eq. 3 (See Table 1). Other sources of uncertainty in  $db_{bl}/dt$  and  $dF_l/dt$  (e.g. uncertainty in power law fits) were assumed to be random and were not propagated, but contribute to inter-plume variability quantified below. Finally, the smoothed estimates of  $b_{bl}$ ,  $db_{bl}/dt$ ,  $F_l$ , and  $dF_l/dt$  were again averaged into 50 m vertical bins to yield smoothed, binned estimates (Fig. S7).

### Processing of small-particle signals

Similar to the large-particle signals, we calculated the net change in small-particle concentration ( $db_{bs}/dt$  and  $dF_s/dt$ ) in a Lagrangian (particle-following) frame of reference, and we calculated mean concentrations and rates of change in the same 6 d, 50 m bins. However, the details of this part of the processing differed for two reasons. First, small-particle concentrations are inherently less noisy than large-particle concentrations (see Fig. S1), so it was not necessary

to smooth the data using a power law. Second, small particles sink more slowly, if at all, so their rates of change were calculated between profiles rather than between vertical bins. Small-particle signals were processed as follows.

To define the Lagrangian frame of reference for small particles, we used a range of small-particle sinking speeds  $\bar{w}_s$  of 0, 5, and 10 m d<sup>-1</sup>. Because  $b_{bs}$  and  $F_s$  include single cells, which are expected to sink at  $\sim 1$  m d<sup>-1</sup> or slower (31), the upper limit of 10 m d<sup>-1</sup> provides a conservative bound, allowing for a substantial fraction of small particles that sink 10-20 times faster than single cells. Each  $b_{bs}$  and  $F_s$  profile was first interpolated to a 1 m grid in order to facilitate calculation of the rate of change. Then, for each pair of consecutive float profiles, a profile of  $db_{bs}/dt$  was calculated at time  $t$  (the midpoint between the two float profiles) as follows

$$\frac{db_{bs}}{dt}(t, z) = \frac{1}{\Delta t} \left( b_{bs} \left( t + \frac{\Delta t}{2}, z + \bar{w}_s \frac{\Delta t}{2} \right) - b_{bs} \left( t - \frac{\Delta t}{2}, z - \bar{w}_s \frac{\Delta t}{2} \right) \right), \quad (4)$$

where  $\Delta t$  is the separation in time between two profiles. We calculated  $dF_s/dt$  in the same way (replacing  $b_{bs}$  with  $F_s$  in Eq. 4). In the simplest case of  $\bar{w}_s = 0$ , Eq. 4 is the difference between two consecutive  $b_{bs}$  profiles, divided by  $\Delta t$ . For  $\bar{w}_s > 0$ ,  $db_{bs}/dt$  at depth  $z$  is calculated using  $b_{bs}$  from the previous profile at a shallower “starting” depth than  $z$  ( $z - \bar{w}_s * \Delta t / 2$ ) and  $b_{bs}$  at a deeper “ending” depth than  $z$  ( $z + \bar{w}_s * \Delta t / 2$ ) from the following profile. Because particle concentrations typically decrease with depth, higher estimates of  $\bar{w}_s$  lead to lower (or more negative) estimates of  $db_{bs}/dt$ . This difference is most important at the top of the mesopelagic, where vertical gradients are the strongest. At each depth, we calculated a central estimate of  $db_{bs}/dt$  and  $dF_s/dt$  based on  $\bar{w}_s = 5$  m d<sup>-1</sup> and upper and lower bounds based on  $\bar{w}_s$  of 10 and 0 m d<sup>-1</sup>, respectively, for uncertainty propagation. See Fig. S8 for example calculations of  $db_{bs}/dt$  and  $dF_s/dt$ . Gridded profiles of both small-particle concentrations ( $b_{bs}$  and  $F_s$ ) and their rates of change ( $db_{bs}/dt$  and  $dF_s/dt$ ) were averaged in the same 6 d, 50 m bins as the large particles for further processing (see Fig. S9).

### Calculation of specific loss rates

This subsection describes the calculation of specific loss rates of optical backscattering fractions  $b_{bl}$  and  $b_{bs}$ , but applies equally to fluorescence fractions  $F_l$  and  $F_s$ , substituting  $b_b$  with  $F$  in all terms and equations below. Assuming no net production of particles in the mesopelagic, we can express  $db_{bl}/dt$  as a function of  $b_{bl}$  and two specific loss-rate parameters: (1) the large-particle specific consumption rate  $m_{bbl}$  that includes ingestion by larger organisms (less egestion) plus remineralization/dissolution by attached organisms, and (2) the specific fragmentation rate  $D_{bbl}$  that represents any physical (e.g., shear stress) or biological (e.g., sloppy feeding) processes that break large particles ( $b_{bl}$ ) into smaller ones ( $b_{bs}$ ):

$$\frac{db_{bl}}{dt}(z, t) = -(m_{bbl}(z, t) + D_{bbl}(z, t))b_{bl}(z, t). \quad (5)$$

Note that  $D_{bbl}$  can in principle be negative, indicating net aggregation, for example if small particles stick to a large sinking particle, or if zooplankton consume small particles and produce large fecal pellets. Note also that zooplankton feeding in the surface and producing fecal pellets in the mesopelagic would violate our assumption of no net mesopelagic particle production and introduce a negative bias in our estimate of  $db_{bl}/dt$ . We further assumed that optical backscattering is conserved when a large particle fragments, so we could express changes in

small-particle backscattering  $db_{bs}/dt$  as a function of  $b_{bs}$ , the small-particle specific consumption rate  $m_{bbs}$ , and a source term due to net fragmentation of large particles,  $D_{bbl}b_{bl}$ :

$$\frac{db_{bs}}{dt}(z, t) = -m_{bbs}(z, t)b_{bs}(z, t) + D_{bbl}(z, t)b_{bl}(z, t). \quad (6)$$

The assumption that fragmentation has minimal effects on bulk optical properties is supported by measurements from both inorganic aggregates in the lab (29) and organic aggregates in situ (21), showing that  $F$  remains unchanged and  $b_{bp}$  is either unchanged or slightly reduced by fragmentation. These findings are likely due to the low fractal dimension of natural marine aggregates, often below two (32–34), which implies that the total particle cross-sectional area concentration (the first-order driver of particulate optical properties) remains constant or even increases with fragmentation. Eqs. 5-6 contain three unknown parameters:  $m_{bbl}$ ,  $D_{bbl}$  and  $m_{bbs}$ . In order to estimate all three parameters for each spatiotemporal bin, we introduced an additional term  $K$ , the ratio of  $m_{bbl}$  to  $m_{bbs}$ :

$$m_{bbl}(z, t) = m_{bbs}(z, t)K. \quad (7)$$

We assumed that the specific rates of consumption of large particles are greater than or equal to the specific rate of consumption of small particles, because we expect  $b_{bs}$  to be either similarly labile to  $b_{bl}$  (if freshly produced in the mesopelagic via fragmentation) or perhaps up to 4 times more refractory as “older”  $b_{bs}$  may accumulate over the time period of the bloom. Therefore, we bounded  $K$  between 1 and 4, with a central estimate of 2. The last subsection provides independent estimates of  $m_{bbs}$  that independently support the choice of this range.

For each 6 d, 50 m bin, we calculated the three specific loss rates  $m_{bbs}$ ,  $m_{bbl}$ , and  $D_{bbl}$  from the five quantities  $b_{bl}$ ,  $b_{bs}$ ,  $db_{bl}/dt$ ,  $db_{bs}/dt$ , and  $K$  by solving Eqs. 5-7. In addition, we calculated the fraction of large-particle loss that is explained by fragmentation as  $D^*_{bbl} = D_{bbl}/(D_{bbl} + m_{bbl})$ . Fig. S10 shows central estimates of all loss parameters (excluding  $m_{bbl}$  and  $m_{Fl}$ , which are simply twice  $m_{bbs}$  and  $m_{Fs}$ , respectively) for all spatiotemporal bins of the example large-particle pulse.

For the uncertainty propagation explained in the next subsection, these calculations were repeated seven times: once using the central estimates of all five quantities, and then six additional times using the upper and lower bounds of  $db_{bl}/dt$ ,  $db_{bs}/dt$ , or  $K$  along with the central estimates of the other two quantities. These bounds represent potential systematic biases stemming from uncertainty in our estimates of the mean values of  $\bar{w}_{bbl}$ ,  $\bar{w}_s$ , and  $K$  (see Table S1).

### Mean fragmentation profiles and their uncertainties

Below 500 m and before and after the central particle pulse,  $F_l$  was often negligible (see Fig. S7), leading to highly uncertain  $D_{Fl}$  fragmentation rates (see Fig. S10). We therefore excluded individual estimates of  $F_l$  and  $F_s$  loss rates where  $F_l < 0.005 \text{ mg m}^{-3}$  (e.g. Fig. S10, black x's) from further analysis (Method 1B, below, did not include this exclusion step). We then computed the median profile of each specific loss rate estimate ( $D_{bbl}$ ,  $m_{bbl}$ ,  $m_{bbs}$ , and  $D^*_{bbl}$ , and corresponding  $F$  loss parameters) across the five temporal bins to obtain a single profile of each specific loss rate for each sinking pulse that reduced the influence of single outliers. Each of these median profiles still contains uncertainty due to several bloom-specific factors, including error in Lagrangian rates of change due to horizontal advection and uncertainty in the power law fits to large-particle concentrations. To obtain a single, more robust estimate across all blooms in

all regions of the study, we calculated the mean of all pulse-specific profiles of specific loss rates (see Fig. 3 of main text), and we used two standard errors of this mean as an estimate of its 95% uncertainty bounds due to pulse-specific errors and variability (see Fig. S11, black dashed lines). We re-calculated these median and mean steps using each of the upper and lower bound fragmentation rates due to uncertainty in  $\bar{w}_{bbl}$ ,  $\bar{w}_s$ , and  $K$ . Upper and lower bounds estimates of  $D$  and  $D^*$  from each individual source of uncertainty are shown in Fig. S11. All uncertainty intervals were added quadratically to calculate combined uncertainty intervals for each estimate (Fig. S11, thin black lines). The largest source of uncertainty in the relative role of fragmentation  $D^*_{bbl}$  in the upper mesopelagic was  $K$ , the ratio of large- to small-particle specific consumption rate (Fig. S11; red lines). In the lower mesopelagic,  $\bar{w}_s$  (Fig. S11; blue lines) and inter-pulse variability (Fig. S11, black dashed lines) dominated  $D^*_{bbl}$  uncertainty. Inter-pulse variability was the dominant source of  $D^*_{Fl}$  uncertainty at nearly all depths. The large-particle sinking velocity  $\bar{w}_l$  was a major source of uncertainty in specific fragmentation rates  $D_{bbl}$  and  $D_{Fl}$ , but not in the relative role of fragmentation in attenuating flux, because  $\bar{w}_l$  affected our estimates of total large-particle flux attenuation and fragmentation in roughly the same proportion.

We also computed regional mean fragmentation profiles for the North Atlantic and Southern Ocean (See Fig. 4 of main text). In this case, we do not present complete uncertainty budgets, but show only two standard errors around the mean (inter-pulse variability), fixing  $K$  and  $w$  at our global central estimates of  $K=2$ ,  $\bar{w}_{bbl} = 74 \text{ m d}^{-1}$ ,  $\bar{w}_{Fl} = 98 \text{ m d}^{-1}$ , and  $\bar{w}_s = 5 \text{ m d}^{-1}$ . This presentation highlights the statistically significant difference between North Atlantic and Southern Ocean mesopelagic particle dynamics. As long as  $K$  and  $w$  parameters are indeed constant between hemispheres, this result implies a significant difference in fragmentation rates.

Method 1A (the primary method described above) includes several steps designed to reduce and quantify “noise” in our final mean fragmentation estimates. To address the possibility that these steps introduce bias in our mean profiles of  $D$  and  $D^*$ , we recalculated  $D$  and  $D^*$  profiles using a second, simpler methodology: “Method 1B” (Fig. S11, green symbols). We started Method 1B with the same bin-averaged estimates of  $b_{bl}$  and  $F_l$  as Method 1A, but three processing steps were omitted. First, for Method 1B,  $b_{bl}$  and  $F_l$  were not smoothed using a power-law fit. Second, blooms with low  $b_{bl}$  and  $F_l$  in the shallowest bin were not excluded, so that all 34 blooms were included in both  $D_{bbl}$  and  $D_{Fl}$  calculations. Third, no bins with low values of  $F_l$  ( $F_l < 0.005 \text{ mg m}^{-3}$ ) were excluded. Instead, taking  $b_b$  for example, all six-day 50 m bin-averaged estimates of  $b_{bl}$  from each depth ( $n=170$ , including five temporal bins for each plume) were averaged to obtain a single mean profile of  $b_{bl}$ . A single mean  $db_{bl}(z)/dz$  profile was estimated as  $db_{bl}(z)/dz = (b_{bl}(z+50) - b_{bl}(z-50))/100[\text{m}]$  and converted to  $db_{bl}(z)/dt$  via Eq. 3, using our central estimate of  $w_{bbl}$ . Individual six-day 50 m bin-averaged estimates of  $b_{bs}$  and  $db_{bs}/dz$  were similarly averaged into single mean profiles for all 34 plumes. Mean  $D_{bbl}$  and  $m_{bbl}$  profiles were then calculated as in Method 1A by solving Eqs. 5-7, using the same central estimates of  $K$  and  $w_{bbs}$  (see Table S1).  $D^*_{bbl}$  was again calculated as  $D_{bbl}/(D_{bbl} + m_{bbl})$ . The same Method-1B steps were repeated for  $F$  to calculate  $D_{Fl}$  and  $D^*_{Fl}$ . The resulting Method-1B mean  $D_{bbl}$ ,  $D^*_{bbl}$ ,  $D_{Fl}$  and  $D^*_{Fl}$  profiles (Fig. S11, green symbols) were more variable with depth but did not show clear, systematic differences from the central Method-1A estimates (thick black lines). This result suggests that our first-order Method-1A findings that high, depth-dependent fragmentation rates explain roughly half of mesopelagic flux attenuation are not artifacts of the smoothing or data removal steps designed to improve precision of our final estimates. Our Method 1A and Method-1B mean  $D^*_{Fl}$  results did show opposite trends with depth (Fig. S11, lower right panel), suggesting, along with the wide Method-1A confidence intervals, that the apparent increase in

$D_{FI}^*$  with depth is not a robust result, but the overall importance of  $D_{FI}^*$  in the mesopelagic was unchanged. In addition, Method-1A  $D_{bb1}$  estimates exceeded Method-1B estimates (Fig. S11, upper left) at all depths below 700 m, suggesting that the power-law fit in Method 1A might have caused an over-estimate of all large-particle loss processes in the lower mesopelagic (see Fig. S4 showing that mean large-particle attenuation with depth below 700 m may be over-estimated by a power law). However, the uncertainty in both methods prevent any strong conclusions on this subject.

#### Alternative estimates of specific loss rates $m_{bbs}$ and $m_{Fs}$

In order to check the assumptions of Method 1, including the likely range of  $K$  and our estimates of  $w_l$ , we compared our Method 1 estimates of small-particle specific loss rates  $m_{bbs}$  and  $m_{Fs}$  (derived from Eqs. 5-7) with estimates from two alternative methods not involving assumptions about either  $K$  or  $w_l$ : Method 2, using early spring data, and Method 3, again using data from the sinking particle pulses. Mean values for all three results agree within uncertainty bounds (Fig. S12), supporting the validity of our methods and assumptions.

For Method 2, we identified 12 events of early spring mixed-layer shoaling from three floats in the North Atlantic. In each event, rapid mixed-layer shoaling caused a mesopelagic particle population with elevated  $F_s$  to become isolated from surface production for  $\geq 2$  d. For a depth range that did not appear to be influenced by vertical mixing (i.e. low  $db_{bs}/dz$ ), we calculated  $b_{bs}(t)$  as described above and estimated  $m_{bbs}$  by least squares fit of  $b_{bs}(t)$  to Eq. 8, where  $t_0$  is the time of the first profile following stratification:

$$b_{bs}(t) = b_{bs}(t_0) \exp(-m_{bbs}(t - t_0)). \quad (8)$$

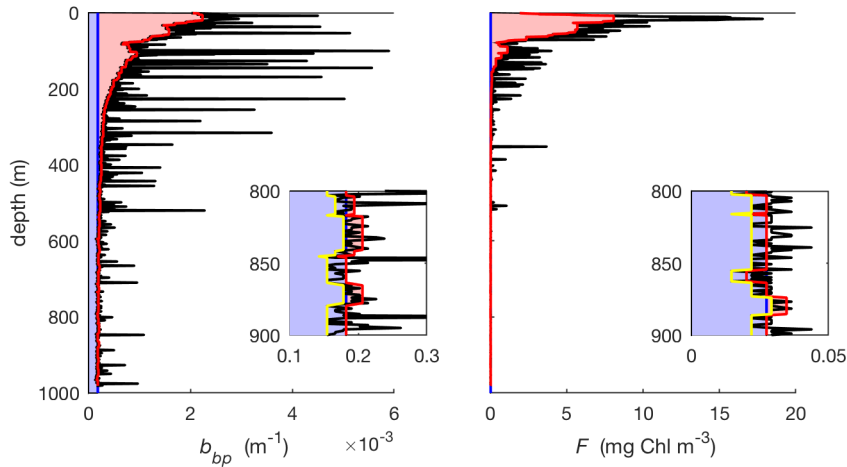
Eq. 8 is a transformation of Eq. 6, with the fragmentation term removed due to negligible large-particle concentrations in the early spring (confirmed by  $b_{bl}$  and  $F_l$  measurements). Depth ranges were between 150 and 300 m. An example calculation is shown in Fig. S13. The same process was repeated for small-particle chlorophyll fluorescence ( $F_s$ ) to estimate its specific loss rate  $m_{Fs}$ . Two of the 12 fits of  $m_{bbs}$  were rejected because  $b_{bs}$  was not significantly  $> 0$ . The remaining 10  $m_{bbs}$  estimates and all 12  $m_{Fs}$  estimates were significantly  $> 0$ . The mean  $m_{bbs}$  and  $m_{Fs}$  of all events, plus or minus two standard errors were  $0.102 \pm 0.028 \text{ d}^{-1}$  and  $0.180 \pm 0.048 \text{ d}^{-1}$ , respectively (Fig. S12; thick black lines). While these estimates correspond to a slightly earlier time period than our bloom calculations and contain no Southern Ocean data, they are valuable because they are simpler, involving no assumptions about large particles or fragmentation, so the approximate agreement with our Method 1  $m_{bbs}$  estimates (Fig. S12) at 275 m is reassuring.

For Method 3, we used the same binned estimates of  $b_{bl}$  and  $b_{bs}$ , and  $db_{bs}/dt$  as Method 1 (e.g. Figs. S7 and S9). However, we further assumed that  $m_{bbs}$  and  $D_{bb1}$  were constant over a 30-day time period (all five temporal bins) and 100 m depth range (two vertical bins). This assumption allowed us to simultaneously solve for  $m_{bbs}$  and  $D_{bb1}$  using only Eq. 6 and multiple measurements of  $b_{bl}$  and  $b_{bs}$ , and  $db_{bs}/dt$ . Estimates of  $db_{bl}/dt$  (which in turn relies on  $\bar{w}_{bb1}$ ) and  $K$  were not needed, so that Method 3 provides a check on Method 1 parameterizations of  $\bar{w}_{bb1}$  and  $K$ . However, the ability to simultaneously constrain  $m_{bbs}$  and  $D_{bb1}$  via Eq. 6 (without Eq. 5 or Eq. 7) relies on the dynamic range of the time-varying measurements of  $b_{bs}$ ,  $b_{bl}$ , and  $db_{bs}/dt$ , so we chose only the six large-particle pulses accompanied by the highest maximum  $F_s$  observed between 500-550 m. Pulses that occurred  $< 1$  month after deep mixing events ( $MLD > 200$  m) were excluded from this analysis to ensure that mesopelagic  $b_{bs}$  (and  $F_s$ ) originated from recent

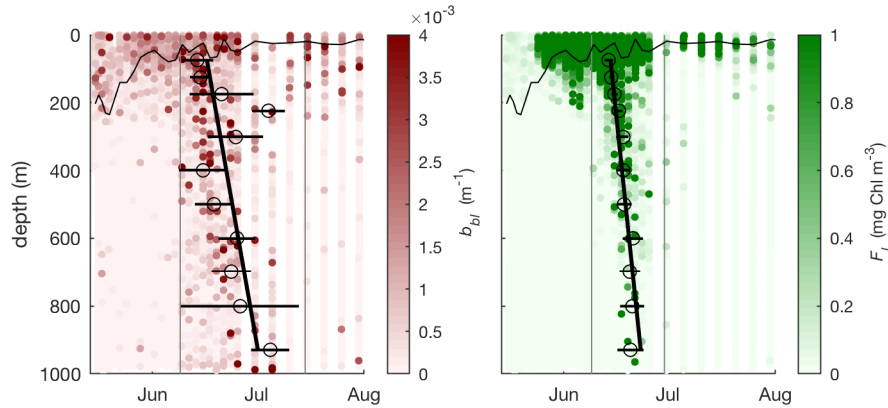
sinking and/or fragmentation, rather than vertical mixing (as in Method 2), in case the specific loss rates of these two particle populations differed.

At 100 m intervals, centered at 200-800 m, Method 3 estimates of  $m_{bbs}$  and  $D_{bbl}$  were obtained by multiple linear regression, forced through the origin, of  $db_{bs}/dt$  as a function of  $D_{bbl}b_{bl}$  and  $-m_{bbs}b_{bs}$  (see Eq. 6), calculated using our central estimate of small-particle sinking velocity  $\bar{w}_s = 5 \text{ m d}^{-1}$ . Each regression contained ten data points (five temporal bins by two depth bins). The mean  $m_{bbs}$  profiles  $\pm 2$  standard errors from all six blooms are shown as gray lines in Fig. S12 (left panel). Method 3 was repeated with fluorescence measurements to obtain  $m_{Fs}$  as well (Fig. S12, right panel). Method 1 estimates (Fig. S12, bold colored lines) fell within the bounds of Method 3 estimates of  $m_{bbs}$  and  $m_{Fs}$  (gray lines) at all depths (Fig. S12). While uncertainty bounds are large, these results provide further confidence in Method 1, including our estimates of  $w_l$  and our choice of  $K$ .

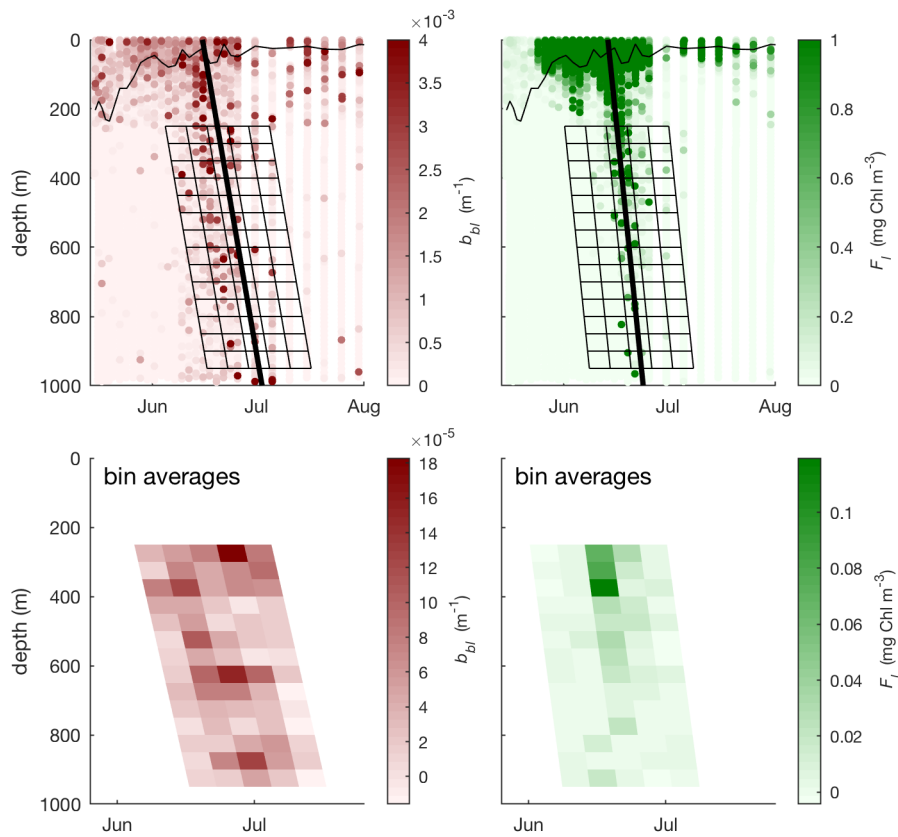




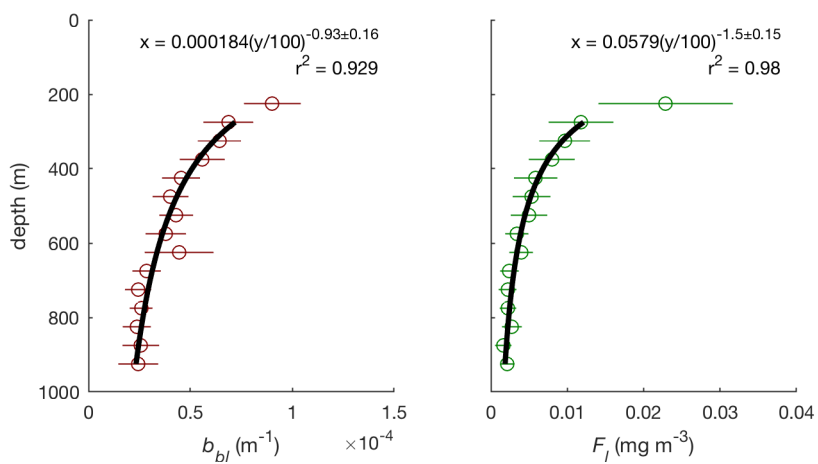
**Fig. S1. Example partitioning of  $b_{bp}$  and  $F$  profiles.** Black lines show total  $b_{bp}$  (left) or  $F$  (right) at native resolution. Yellow lines (insets) show low-pass “spike removal” filters. Red lines show  $b_{brs}$  (left) and  $F_{rs}$  (right) the sum of refractory and small labile particle signals. The difference between red and yellow lines (insets) represents the deep “spike blank” for this bloom period, or the contribution of sensor noise to the high frequency “spike” signal. The difference between black and red lines is the large-particle signal  $b_{bl}$  (left), or  $F_l$  (right). Blue lines show deep blanks  $b_{br}$  (left; well above zero presumably due to refractory material) and  $F_r$  (right; near zero, as refractory pool does not contain chlorophyll) for the bloom period. The difference between red and blue lines (shaded pink) is  $b_{bs}$  (left) or  $F_s$  (right), the contribution of small, labile particles. Data are from float WMO6901523, June 2013 (Example pulse 1 in main text).



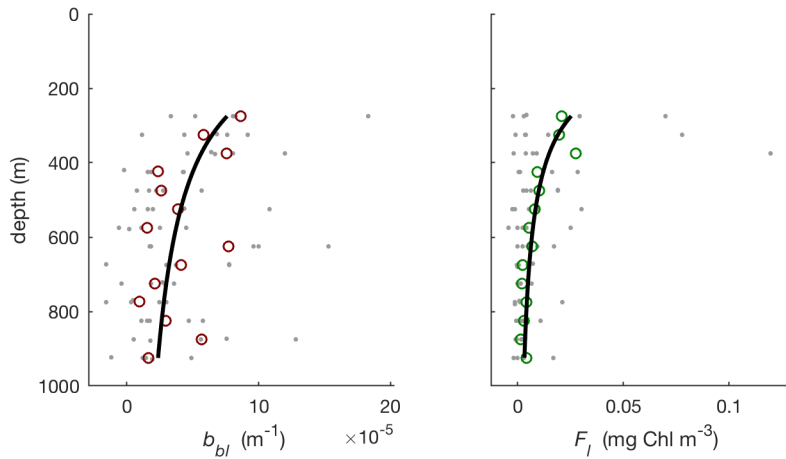
**Fig. S2. Example calculation of bulk large-particle sinking velocities.** Colored circles show raw large-particle (spike) signals  $b_{bl}$  (red) and  $F_l$  (green), with higher values (larger spikes) plotted on top of lower values. Single dark circles against lighter background show the optical signals of single particles. The thin black line shows the mixed-layer depth. Vertical gray lines show initial, visual temporal boundaries of large-particle pulse. Open black circles show timing of the maximum of Gaussian fits to large-particle timeseries, and bold horizontal black lines show the 95% confidence interval of this timing. The diagonal bold black lines show the weighted linear fit to these maxima with respect to depth, used to calculate sinking velocities. Data are from float WMO6901523, 2013 (Example pulse 1 in main text).



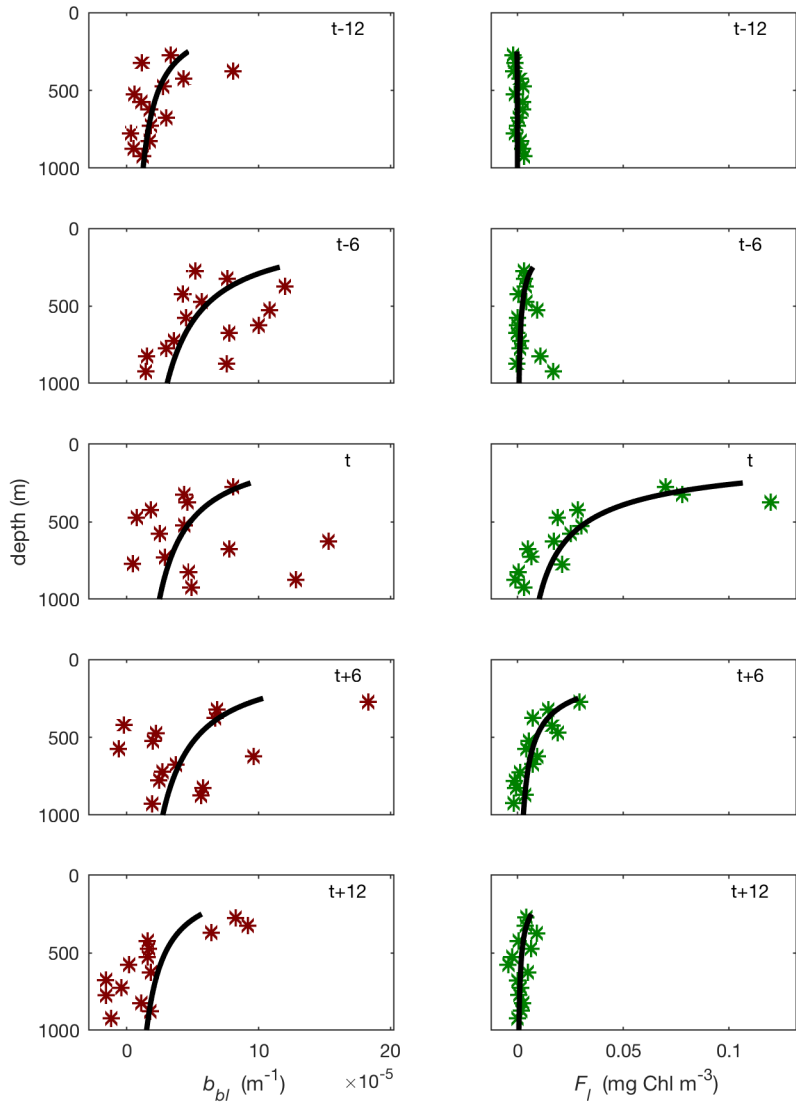
**Fig. S3. Bin averaging of large-particle signals.** Upper panels show  $b_{bl}$  and  $F_l$ , as in Fig. S2, but with bin boundaries overlaid (black grid). Lower panels show bin-averaged  $b_{bl}$  and  $F_l$ . Data are from float WMO6901523, 2013 (Example pulse 1 in main text). A document containing similar plots for all 34 plumes can be found at [seanoe.org](http://seanoe.org) (doi:10.17882/70484).



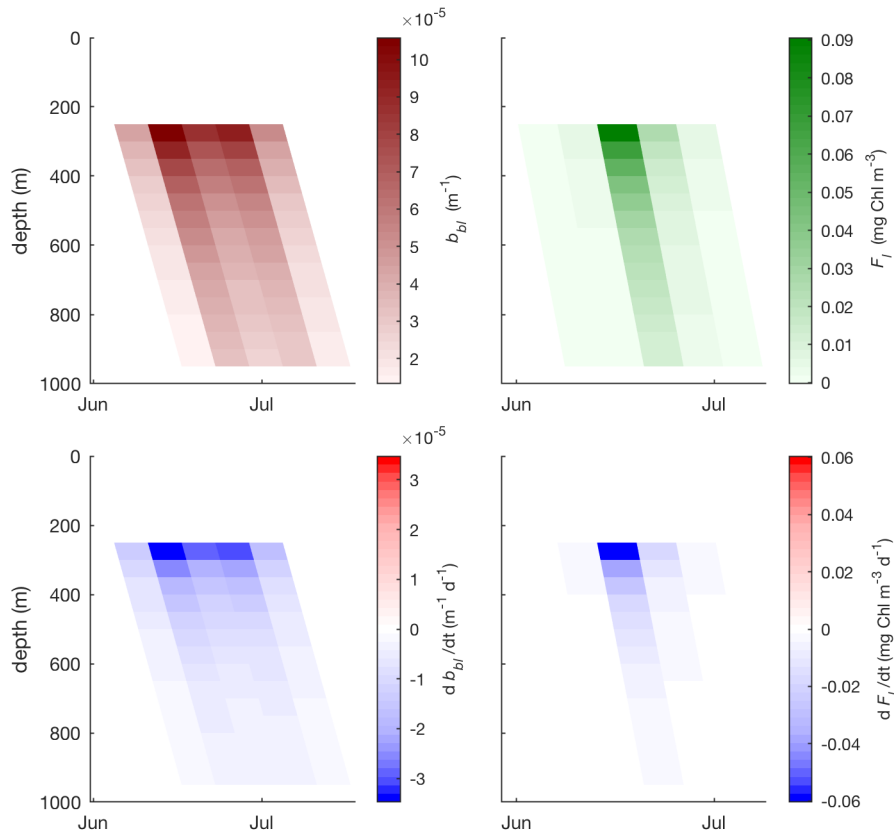
**Fig. S4. Mean binned large-particle profiles from all particle plumes.** Circles show means of all temporal bins from all 34 pulses, horizontal lines show two standard errors around the mean, and black curves and equations show least-squared power-law fits to the mean profiles.



**Fig. S5. Example fits of “Martin curve” power laws to smooth large-particle profiles.** Gray points show individual 6-day, 50 m bin averages of  $b_{bl}$  (left) and  $F_l$  (right). Red and green circles show averages of the five temporal bins, and black curves show least-squared power law fits to these average profiles:  $b_{bl} = 0.000201[\text{m}^{-1}](z/100)^{-0.96}$  and  $F_l = 0.14[\text{mg m}^{-3}](z/100)^{-1.7}$ . Data are from float WMO6901523, 2013 (Example pulse 1 in main text).

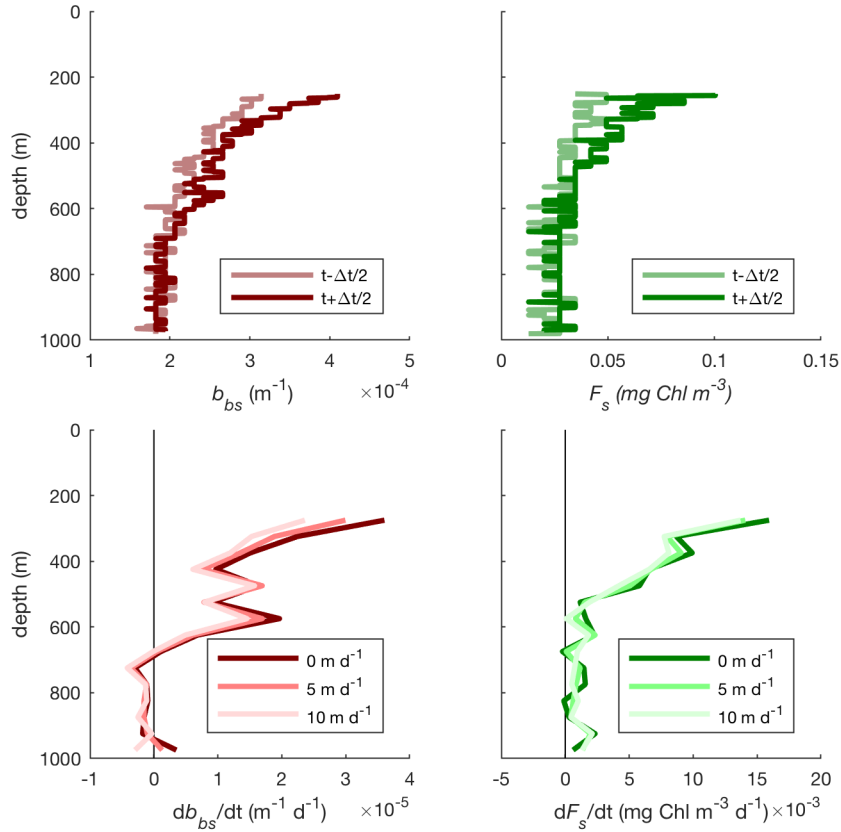


**Fig. S6. Smoothing of large-particle signals for each temporal bin.** The timing of the temporal bin center, relative to time of pulse maximum ( $t$ ), given above each panel, ranges from  $t-12$  (top panels) to  $t+12$  (bottom panels). Red and green stars show unsmoothed 6-day, 50 m binned  $b_{bl}$  and  $F_l$ , respectively. Black curves power-laws (with exponent held constant) fit to each temporal bin. Data are from float WMO6901523, 2013 (Example pulse 1 in main text).

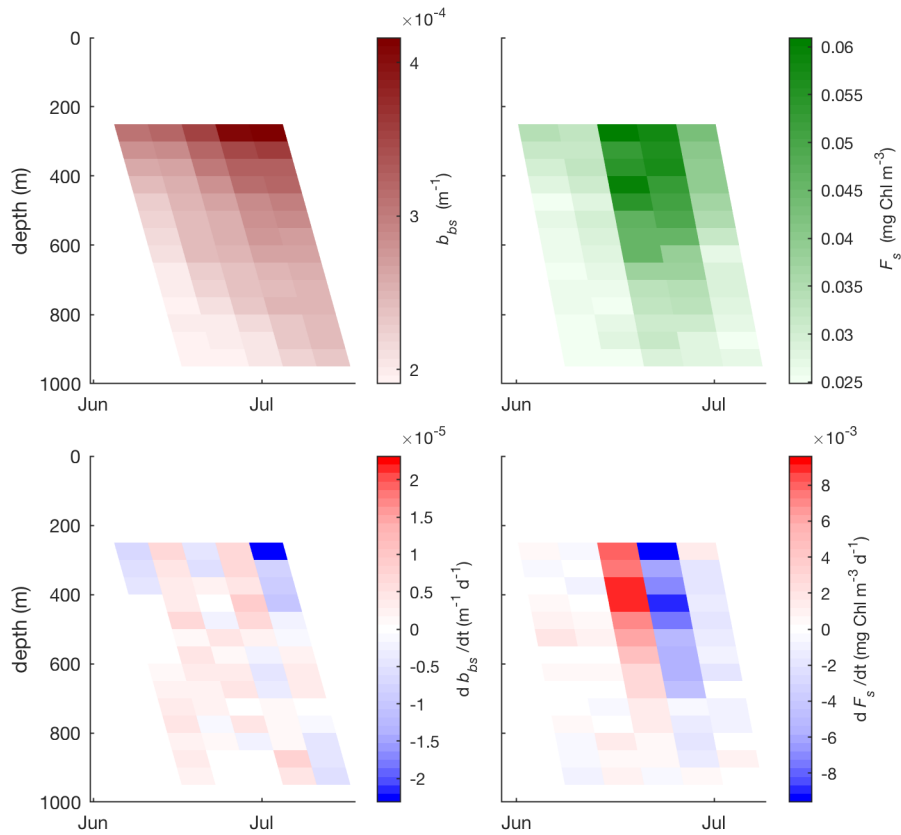


**Fig. S7. Smoothed, binned estimates of large-particle concentrations and their specific net loss rates.** Data are from float WMO6901523, 2013 (Example pulse 1 in main text). A document containing similar plots for all 34 plumes can be found at [seanoec.org](http://seanoec.org) (doi:10.17882/70484).

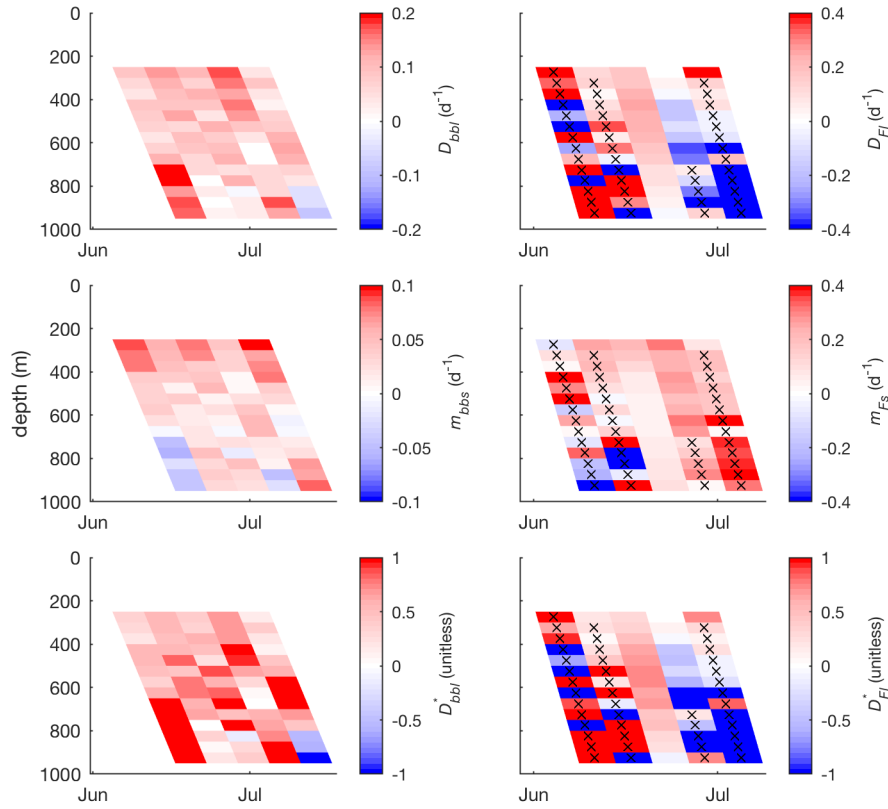




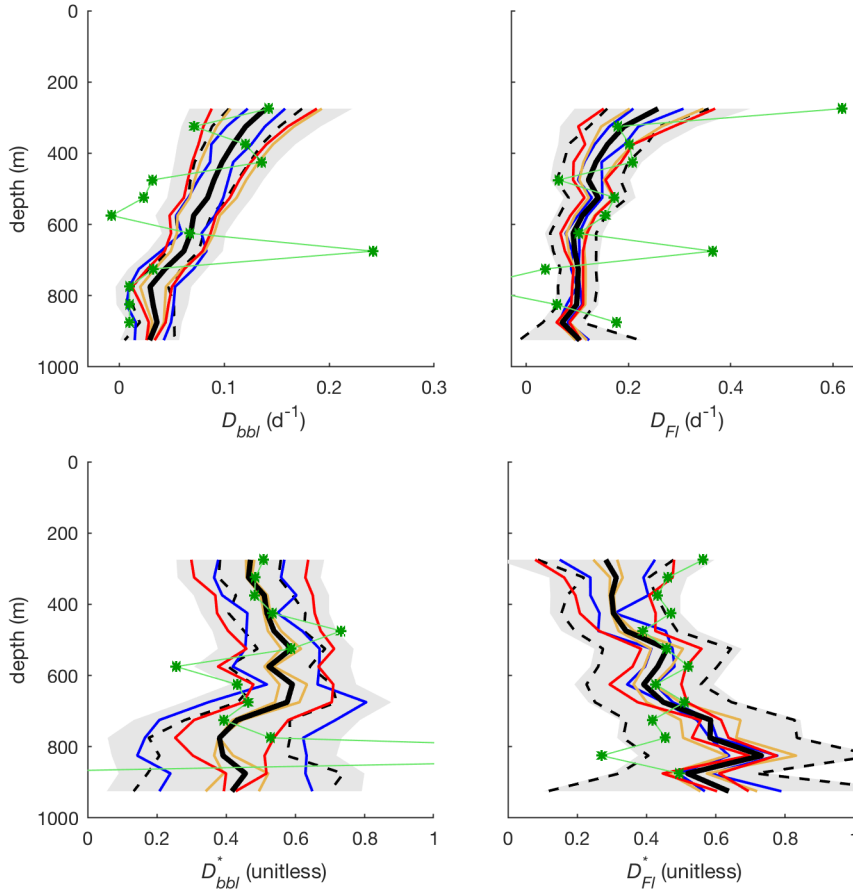
**Fig. S8. Calculation of  $db_{bs}/dt$  and  $dF_s/dt$ .** Top panels show small particle concentrations from two consecutive profiles, with paler colors indicating the earlier profiles. Bottom panels show derived estimates of  $db_{bs}/dt$  (left) and  $dF_s/dt$  (right), bin averaged at 50 m intervals, with colors in lower panels indicating different assumed small-particle sinking velocities ( $\bar{w}_s$ ): 0, 5, and 10  $\text{m d}^{-1}$  in order of dark to light. Data are from float WMO6901523, June 2013 (Example pulse 1 in main text).



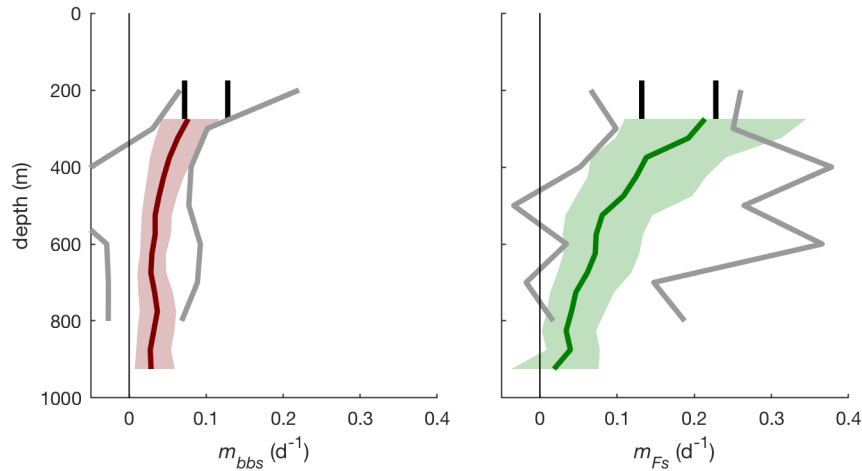
**Fig. S9. Bin-averaged small-particle concentrations and their net rates of change.** Net rates of change are calculated in a Lagrangian (particle-following) frame of reference, shown here assuming a central estimate of small-particle sinking speed,  $\bar{w}_s = 5 \text{ m d}^{-1}$ . Data are from float WMO6901523, 2013 (Example pulse 1 in main text). A document containing similar plots for all 34 plumes can be found at [seanoe.org](http://seanoe.org) (doi:10.17882/70484).



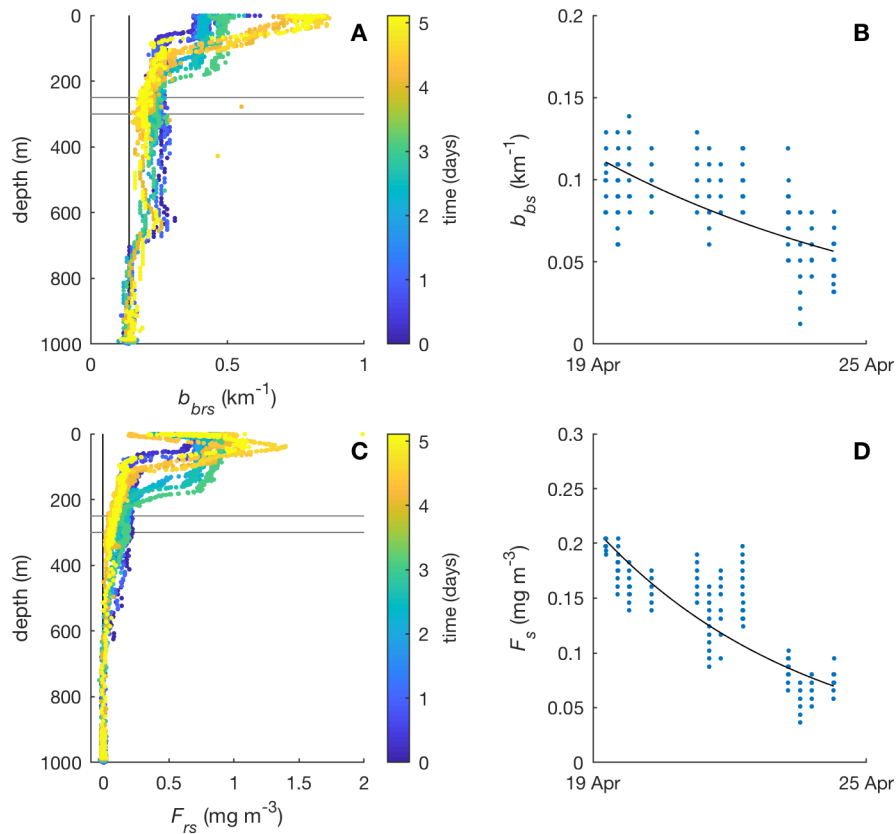
**Fig. S10. Central estimates of mesopelagic particle loss terms in 6 d, 50 m bins for example bloom.** Black x's show bins that are excluded from analysis due to low  $F_l$ . Data are from float WMO6901523, 2013 (Example pulse 1 in main text). A document containing similar plots for all 34 plumes can be found at [seanoe.org](http://seanoe.org) (doi:10.17882/70484).



**Fig. S11. Uncertainty budgets for mean fragmentation terms.** Each panel shows central estimates of mean fragmentation terms across all pulses (thick black lines), along with uncertainty bounds due to pulse-specific error and variability (dashed black lines), mean small-particle sinking velocity  $\bar{w}_s$  (blue), mean large-particle sinking velocity  $\bar{w}_l$  (orange), and the ratio of large- to small-particle specific consumption rate  $K$  (red). The total uncertainty bounds (from the root sum of squares of all individual uncertainty intervals) is shaded in gray. Alternative “Method 1B” central mean fragmentation profiles, calculated without the vertical smoothing step and without removal of low  $b_{bl}$  or  $F_l$ , are shown in green.



**Fig. S12. Alternative calculations of small-particle specific loss rates.** Colored lines show the primary estimates (Method 1A), including mean (dark lines) and confidence intervals (light shaded areas). Thick black lines show depth range and confidence intervals of the mean of early-spring estimates (Method 2). Gray lines show confidence intervals of the mean of the alternative bloom-period estimates (Method 3).



**Fig. S13. Example Method-2 calculation of  $m_{bbs}$  and  $m_{F_s}$ .** (A) Vertical profiles of  $b_{brs}$  showing progressive loss of a stranded small-particle population between 250 m and 600 m over five days following mixed-layer shoaling. Colors show time in days since the day of the first profile. Vertical black lines show estimates of deep “blank”  $b_{br}$ , and horizontal gray lines show depth window of  $m_{bbs}$  calculations. (B) Timeseries of  $b_{bs}$  in the 250-300 m window (blue) and least-squared fit of exponential Eq. S8 (black curve). (C) Vertical profiles of  $F_{rs}$  (colors and lines following panel A). (D) Timeseries of  $F_s$  in the 250-300 m window (blue) and least-squared fit of exponential Eq. S8 (black curve). Data in all panels are from float WMO6901647, 2015.

**Table S1. Abbreviations used in this manuscript.**

Symbol	Central Value (confidence range)†	Units	Description
$b_{bl}$		$m^{-1}$	$b_{bp}$ due to large particles
$b_{bp}$		$m^{-1}$	particulate optical backscattering coefficient
$b_{br}$		$m^{-1}$	$b_{bp}$ due to refractory particles (includes sensor blank)
$b_{bs}$		$m^{-1}$	$b_{bp}$ due to small, labile particles
$b_{brs}$		$m^{-1}$	$b_{br} + b_{bs}$
$D_{bbl}$		$d^{-1}$	specific loss rate of $b_{bl}$ due to fragmentation
$D_{bbl}^*$		–	Fraction of total $b_{bl}$ loss due to fragmentation
$D_{Fl}$		$d^{-1}$	specific loss rate of $F_l$ due to fragmentation
$D_{Fl}^*$		–	Fraction of total $F_l$ loss due to fragmentation
$F$		mg Chl $m^{-3}$	Chlorophyll <i>a</i> fluorescence (factory calibrated)
$F_l$		mg Chl $m^{-3}$	$F$ due to large particles
$F_r$		mg Chl $m^{-3}$	$F$ due to refractory particles (interpreted as sensor blank)
$F_s$		mg Chl $m^{-3}$	$F$ due to small particles
$F_{rs}$		mg Chl $m^{-3}$	$F_r + F_s$
$K$	2 (1-4)	–	Ratio of $m_{bbl}/m_{bbs}$ or $m_{Fl}/m_{Fs}$
$m_{bbs}$		$d^{-1}$	specific loss rate of $b_{bs}$
$m_{bbl}$		$d^{-1}$	specific loss rate of $b_{bl}$ due to direct consumption
$m_{Fs}$		$d^{-1}$	specific loss rate of $F_s$
$m_{Fl}$		$d^{-1}$	specific loss rate of $F_l$ due to direct consumption
$\bar{w}_{bbl}$	74 (58-100)	$m d^{-1}$	mean sinking velocity of large “marine snow” particles
$\bar{w}_{bbs}$	5 (0-10)	$m d^{-1}$	mean sinking velocity of small, labile particles
$\bar{w}_{Fl}$	98 (79-129)	$m d^{-1}$	mean sinking velocity of chlorophyll within large particles
$\bar{w}_{Fs}$	5 (0-10)	$m d^{-1}$	mean sinking velocity of chlorophyll within small particles

†Central Values only given for constant parameters used in fragmentation calculations



**Table S2. Overview of large-particle pulses analyzed.**

See Table 1 for definition of terms in the column headings. Region abbreviations are for the Iceland Basin (ICB), Irminger Sea (IRS), Labrador Sea (LAS), other North Atlantic (NAT), Crozet Islands (CRO), East of Kerguelen Islands (KER\_E), West of Kerguelen Islands (KER\_W), and other Southern Ocean (SO). Example pulses (Fig. 2 of main text) are shown in bold font.

Float WMO Number	$b_{bl}$ pulse date	region	LAT (°N)	LON (°E)	$w_{bbI}^{-1}$ (d m <sup>-1</sup> )	$w_{FI}^{-1}$ (d m <sup>-1</sup> )	$b_{bl}$ power- law exponent	$F_I$ power- law exponent	$b_{bl}$ 275 m (m <sup>-1</sup> )	$F_I$ 275 m (mg m <sup>-3</sup> )	$D_{bbI}$ 275 m (d <sup>-1</sup> )	$D_{FI}$ 275 m (d <sup>-1</sup> )	$D_{bbI}^*$ 275 m	$D_{FI}^*$ 275 m
6901516	6-Jun-13	ICB	62.27	-21.96	0.019±0.012	0.012±0.003	-0.69±0.55	-2±1.3	9.10E-05	0.012	0.03	0.28	-0.15	0.33
6901520	30-May-13	ICB	61.54	-24.41	-	0.021±0.013	-0.94±0.6	-	0.00013	0.0037	0.04	-	0.22	-
6901647	3-Jun-15	ICB	59.14	-24.77	0.018±0.013	0.011±0.004	-	-0.33±0.99	3.80E-05	0.0077	-	-0.09	-	-0.30
6901647	8-Jun-17	ICB	63.44	-26.54	0.021±0.012	0.015±0.004	-0.74±0.82	-2.8±0.81	0.00018	0.027	0.06	0.54	0.23	0.52
6901523	1-Jul-14	IRS	60.50	-33.66	0.008±0.01	-	-0.47±0.52	-	0.0001	2.10E-07	0.08	-	0.58	-
6901482	30-Jun-14	IRS	63.29	-33.31	0.008±0.01	-	-0.31±0.67	-	8.70E-05	0.00097	0.06	-	0.47	-
6901519	30-Jun-14	IRS	59.01	-33.19	0.012±0.009	-	-0.24±0.56	-1.8±4.4	8.30E-05	0.0054	0.07	0.37	1.26	0.64
<b>6901523</b>	<b>15-Jun-13</b>	<b>LAS</b>	<b>57.44</b>	<b>-49.96</b>	-	<b>0.01±0.003</b>	<b>-0.96±0.77</b>	<b>-1.7±0.72</b>	<b>7.60E-05</b>	<b>0.025</b>	<b>0.11</b>	<b>0.30</b>	<b>0.41</b>	<b>0.28</b>
6901527	25-May-15	LAS	58.02	-49.24	0.009±0.006	0.009±0.002	-	-2.2±0.85	2.60E-05	0.028	-	0.53	-	0.67
6901486	22-May-15	LAS	58.47	-50.99	0.021±0.007	0.007±0.004	-	-2.4±0.88	2.10E-05	0.037	-	0.60	-	0.69
6901524	28-May-15	LAS	57.06	-43.18	-	0.01±0.011	-	-3.7±0.52	2.70E-05	0.022	-	0.85	-	0.69
6901527	3-Jul-16	LAS	57.33	-45.00	-	0.006±0.007	-	-1.2±1.4	3.10E-05	0.0092	-	0.19	-	0.37
6901525	14-May-14	NA	48.65	-43.71	0.006±0.008	0.006±0.007	-0.77±0.53	-1±0.51	6.10E-05	0.023	0.14	0.23	0.58	0.29
6901516	16-Jun-14	NA	52.86	-34.83	0.006±0.005	0.005±0.003	-0.27±0.54	-	4.10E-05	0.0022	0.01	-	0.28	-
6901575	10-Nov-15	CRO	-44.06	49.68	-	0.019±0.008	-0.8±0.54	-1.5±0.87	5.30E-05	0.017	0.06	0.12	0.30	0.21
6901493	10-Nov-15	CRO	-44.06	49.65	0.026±0.015	0.016±0.01	-0.99±0.74	-2.1±0.67	6.20E-05	0.017	0.08	0.14	0.33	0.07
6901583	27-Nov-15	CRO	-44.14	53.20	0.017±0.009	0.002±0.003	-0.5±0.52	-0.72±0.84	5.50E-05	0.015	0.07	-0.13	0.33	-0.16
6901578	14-Nov-16	CRO	-45.61	63.61	-	-	-1.2±0.44	-	5.80E-05	0.0049	0.11	-	0.41	-
6901490	5-Feb-15	KER_E	-48.68	72.85	0.004±0.011	0.005±0.003	-1.9±0.69	-1.1±0.67	9.00E-05	0.011	0.34	0.36	0.60	0.64
6901004	5-Feb-15	KER_E	-48.71	72.77	-0.002±0.012	0.005±0.006	-1.7±1.5	-0.9±0.56	9.70E-05	0.0085	0.31	0.24	0.63	0.70
6901583	2-Dec-16	KER_E	-48.98	83.68	0.019±0.012	0.009±0.01	-0.73±0.5	-1.1±1.2	5.90E-05	0.0077	0.08	0.05	0.47	-0.06
6902734	13-Dec-16	KER_E	-49.12	73.39	-	-	-1.3±0.58	-1.6±0.4	8.80E-05	0.033	0.23	0.45	0.57	0.66
<b>6902738</b>	<b>11-Dec-16</b>	<b>KER_E</b>	<b>-48.50</b>	<b>72.04</b>	-	<b>0.009±0.007</b>	<b>-1.2±0.58</b>	<b>-1.3±0.33</b>	<b>0.00011</b>	<b>0.056</b>	<b>0.23</b>	<b>0.32</b>	<b>0.69</b>	<b>0.84</b>
6902735	8-Dec-16	KER_W	-52.67	68.28	-	0.003±0.009	-0.72±0.71	-	4.60E-05	0.0041	0.11	-	0.55	-
6902739	10-Dec-16	KER_W	-52.75	68.19	-	0.001±0.005	-1.3±0.42	-2.3±0.86	5.80E-05	0.0056	0.20	0.89	0.58	0.40
6901574	11-Jan-16	KER_W	-50.66	67.25	-	0.002±0.011	-2.2±1	-	7.20E-05	0.0031	0.34	-	0.54	-
6901579	13-Feb-15	KER_W	-51.78	67.49	-	-	-1.4±0.91	-	5.60E-05	0.0016	0.27	-	0.72	-
6901574	9-Feb-15	KER_W	-51.80	67.52	-	-	-1.2±0.54	-	6.20E-05	0.0017	0.21	-	0.69	-
6901575	14-Dec-17	SO	-46.64	108.43	-	0.019±0.006	-1.5±0.4	-2±1	9.40E-05	0.0065	0.18	1.55	0.40	0.66
6901583	1-Jan-18	SO	-48.87	116.81	-	0.014±0.014	-1.1±0.82	-	5.10E-05	0.0012	0.14	-	0.41	-
6901578	24-Dec-17	SO	-46.27	95.03	0.019±0.009	0.018±0.007	-1.2±0.53	-4.1±2.2	7.10E-05	0.0076	0.10	0.45	0.33	0.43
6902737	20-Dec-17	SO	-52.17	82.00	0.02±0.015	-	-1.7±0.59	-1.4±0.38	0.00012	0.0065	0.15	0.19	0.31	0.43
6902736	31-Dec-17	SO	-52.46	96.61	-	-	-2.1±1.2	-4.6±1.9	0.00011	0.0055	0.26	0.98	0.47	0.64
6901492	20-Dec-13	SO	-41.96	10.34	0.014±0.014	0.019±0.007	-0.98±0.66	-1.2±1.2	4.80E-05	0.0087	0.12	0.03	0.38	0.40

## References and Notes:

1. P. W. Boyd, T. W. Trull, Understanding the export of biogenic particles in oceanic waters: Is there consensus? *Prog. Oceanogr.* **72**, 276–312 (2007).
2. S. A. Henson *et al.*, A reduced estimate of the strength of the ocean's biological carbon pump. *Geophys. Res. Lett.* **38**, 10–14 (2011).
3. D. A. Siegel *et al.*, Global assessment of ocean carbon export by combining satellite observations and food-web models. *Global Biogeochem. Cycles.* **28**, 1–16 (2014).
4. J. H. Martin, G. A. Knauer, D. M. Karl, W. W. Broenkow, VERTEX - carbon cycling in the northeast Pacific. *Deep. Res. Part a-Oceanographic Res. Pap.* **34**, 267–285 (1987).
5. L. Guidi *et al.*, A new look at ocean carbon remineralization for estimating deepwater sequestration. *Global Biogeochem. Cycles.* **29** (2015), doi:10.1002/2014GB005063.
6. S. A. Henson, R. Sanders, E. Madsen, Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles.* **26**, 1–14 (2012).
7. E. Y. Kwon, F. Primeau, J. L. Sarmiento, The impact of remineralization depth on the air-sea carbon balance. *Nat. Geosci.* **2**, 630–635 (2009).
8. X. Irigoien *et al.*, Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* **5**, 3271 (2014).
9. M. A. St. John *et al.*, A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives from the Mesopelagic Community. *Front. Mar. Sci.* **3** (2016), doi:10.3389/fmars.2016.00031.
10. J. R. Collins *et al.*, The multiple fates of sinking particles in the North Atlantic Ocean. *Global Biogeochem. Cycles*, 1471–1494 (2015).
11. A. Belcher *et al.*, Depth-resolved particle-associated microbial respiration in the northeast Atlantic. *Biogeosciences.* **13**, 4927–4943 (2016).
12. D. M. Karl, G. A. Knauer, J. H. Martin, Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. *Nature.* **332**, 438–441 (1988).
13. S. L. C. Giering *et al.*, Reconciliation of the carbon budget in the ocean's twilight zone. *Nature.* **507**, 480–483 (2014).
14. G. Dall'Olmo, K. A. Mork, Carbon export by small particles in the Norwegian Sea. *Geophys. Res. Lett.* **41**, 2921–2927 (2014).
15. L. R. Pomeroy, D. Deibel, Aggregation of Organic Matter By Pelagic Tunicates. *Limnol. Oceanogr.* **25**, 643–652 (1980).
16. B. A. Biddanda, L. R. Pomeroy, Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. I. Microbial succession. *Mar. Ecol. Prog. Ser.* **42**, 79–88 (1988).
17. S. Goldthwait, J. Yen, J. Brown, A. Alldredge, Quantification of marine snow fragmentation by swimming euphausiids. *Limnol. Oceanogr.* **49**, 940–952 (2004).
18. L. Dilling, A. L. Alldredge, Fragmentation of marine snow by swimming

- macrozooplankton : A new process impacting carbon cycling in the sea. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **47**, 1227–1245 (2000).
19. G. A. Jackson, Comparing Observed Changes in Particle-Size Spectra with Those Predicted Using Coagulation Theory. *Deep. Res. Part Ii-Topical Stud. Oceanogr.* **42**, 159–184 (1995).
  20. J. Ruiz, What generates daily cycles of marine snow? *Deep. Res. Part I Oceanogr. Res. Pap.* **44**, 1105–1126 (1997).
  21. N. Briggs *et al.*, High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **58**, 1031–1039 (2011).
  22. R. A. Reynolds, D. Stramski, G. Neukermans, Optical backscattering by particles in Arctic seawater and relationships to particle mass concentration, size distribution, and bulk composition. *Limnol. Oceanogr.* **61**, 1869–1890 (2016).
  23. C. Roesler *et al.*, Recommendations for obtaining unbiased chlorophyll estimates from in situ chlorophyll fluorometers: A global analysis of WET Labs ECO sensors. *Limnol. Oceanogr. Methods.* **15** (2017), doi:10.1002/lom3.10185.
  24. See supplementary materials.
  25. D. J. Mayor, R. Sanders, S. L. C. Giering, T. R. Anderson, Microbial gardening in the ocean’s twilight zone: Detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus. *BioEssays.* **36**, 1132–7 (2014).
  26. N. Briggs, G. Dall’Olmo, H. Claustre, Size-fractionated optical backscattering and chlorophyll fluorescence from 34 high-latitude phytoplankton blooms. (2019), , doi:10.17882/70484.
  27. X. D. Zhang, L. B. Hu, M. X. He, Scattering by pure seawater: Effect of salinity. *Opt. Express.* **17**, 5698–5710 (2009).
  28. J. M. Sullivan, M. Twardowski, J. R. Zaneveld, C. Moore, in *Light Scattering Reviews 7*, A. A. Kokhanovsky, Ed. (Springer Berlin Heidelberg, 2013), pp. 189–224.
  29. N. T. Briggs, W. H. Slade, E. Boss, M. J. Perry, Method for estimating mean particle size from high-frequency fluctuations in beam attenuation or scattering measurements. *Appl. Opt.* **52**, 6710–25 (2013).
  30. W. M. Berelson, The Flux of Particulate Organic Carbon Into the Ocean Interior: A Comparison of Four U.S. JGOFS Regional Studies. *Oceanography.* **14**, 59–67 (2001).
  31. A. Waite, A. Fisher, P. A. Thompson, P. J. Harrison, Sinking rate versus cell volume relationships illuminate sinking rate control mechanisms in marine diatoms. *Mar. Ecol. Prog. Ser.* **157**, 97–108 (1997).
  32. X. Y. Li, B. E. Logan, Size distributions and fractal properties of particles during a simulated phytoplankton bloom in a mesocosm. *Deep. Res. Part Ii-Topical Stud. Oceanogr.* **42**, 125–138 (1995).
  33. A. Hatcher, P. Hill, J. Grant, Optical backscatter of marine flocs. *J. Sea Res.* **46**, 1–12 (2001).
  34. E. N. Flory, P. S. Hill, T. G. Milligan, J. Grant, The relationship between floc area and

backscatter during a spring phytoplankton bloom. *Deep. Res. Part I-Oceanographic Res. Pap.* **51**, 213–223 (2004).