

Viral infection switches the balance between bacterial and eukaryotic recyclers of organic matter during algal blooms

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2 **Viral infection switches the balance between bacterial and eukaryotic recyclers**
3 **of organic matter during algal blooms**

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27

28 ***Abstract.***

29 Algal blooms are hotspots of marine primary production and play central roles in microbial
30 ecology and global nutrient cycling. When blooms collapse, organic carbon is transferred to higher
31 trophic levels, microbial respiration or sinking in proportions that depend on the dominant
32 mortality agent. Viral infection can lead to bloom termination, but its impact on the fate of carbon
33 remains an open question. Here, we characterized the consequences of viral infection on the
34 microbiome composition and biogeochemical landscape of marine ecosystems by conducting a
35 large-scale mesocosm experiment. Monitoring of seven induced coccolithophore blooms, which
36 showed different degrees of viral infection, revealed that only high levels of viral infection caused
37 significant shifts in the composition of free-living bacterial and eukaryotic assemblages.
38 Intriguingly, viral infection favored the growth of eukaryotic heterotrophs (thraustochytrids) over
39 bacteria as potential recyclers of organic matter. By combining modeling and quantification of

40 active viral infection at a single-cell resolution, we estimate that viral infection can increase per-
41 cell rates of extracellular carbon release by 2-4.5 fold. This happened via production of acidic
42 polysaccharides and particulate inorganic carbon, two major contributors to carbon sinking into
43 the deep ocean. These results reveal the impact of viral infection on the fate of carbon through
44 microbial recyclers of organic matter in large-scale coccolithophore blooms.

45

46 ***Introduction.***

47 Marine algae are responsible for half of Earth's primary production and form the basis of the
48 oceanic food chain¹. Algal blooms² are ephemeral events of phytoplankton proliferation that occur
49 annually across the globe³ covering thousands of square kilometers. Upon demise, a small fraction
50 of algal biomass is sequestered into the deep sea; the rest is transferred to higher trophic levels via
51 predation, or recycled by heterotrophic bacteria and their predators, a process called the "microbial
52 loop"^{4,5}. It has long been hypothesized that the cause of bloom termination affects the surrounding
53 microbiome and fate of carbon. Viral infection enhances lysis of host cells and release of dissolved
54 organic matter (DOM), leading to bacterial growth at the expense of organic carbon sinking, in a
55 process coined the "viral shunt"⁶. It has also been suggested that viral infection increases particle
56 formation and thus biomass sinking. This accelerates the biologically driven sequestration of
57 carbon into the deep sea in the so-called "viral shuttle" process^{7,8}. However, we still lack
58 quantitative assessment of how viruses alter microbial composition and influence the fate of carbon
59 during algal blooms.

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61 In order to provide a holistic and quantitative view of viral infection and its effect on carbon flow
62 in the ocean, we investigated the dynamics of seven replicate mesocosm blooms of the
63 cosmopolitan calcifying microalga *Emiliania huxleyi*. The blooms were induced by nutrient
64 addition to a natural microbial community from the Norwegian fjord of Raunefjorden and the
65 different enclosures spontaneously showed absent, moderate, or high levels of viral infection of
66 the dominant alga. Combining daily monitoring of a variety of biological and biogeochemical
67 parameters, we quantified the impact of viral infection on the associate eukaryotic and bacterial
68 communities and on carbon cycling from the cellular to the biogeochemical level. Our results
69 demonstrate how viruses impact microbial communities in coccolithophore blooms and their
70 biogeochemical consequence on the fate of carbon.

71

72 ***Succession of prominent community members during algal bloom dynamics***

73 Our mesocosm experiment consisted of four uncovered enclosures (bag 1-bag 4) and three air-
74 tight sealed enclosures to collect aerosols (bag 5-bag 7). The enclosures were immersed in a fjord
75 near Bergen, Norway, filled with 11m³ of fjord water containing natural planktonic communities
76 (**Fig. 1a**) and nutrients were added on series of consecutive days (**Fig. 1b**). During 24 days, we
77 monitored phytoplankton and bacterial cell counts using flow cytometry, determined microbiome
78 composition using amplicon sequencing (bacterial and eukaryotic), measured various
79 biogeochemical parameters (see Methods), and determined infection states of single cells using
80 single molecule fluorescent *in situ* hybridization⁹. These biological and chemical features were
81 compared to the surrounding fjord waters.

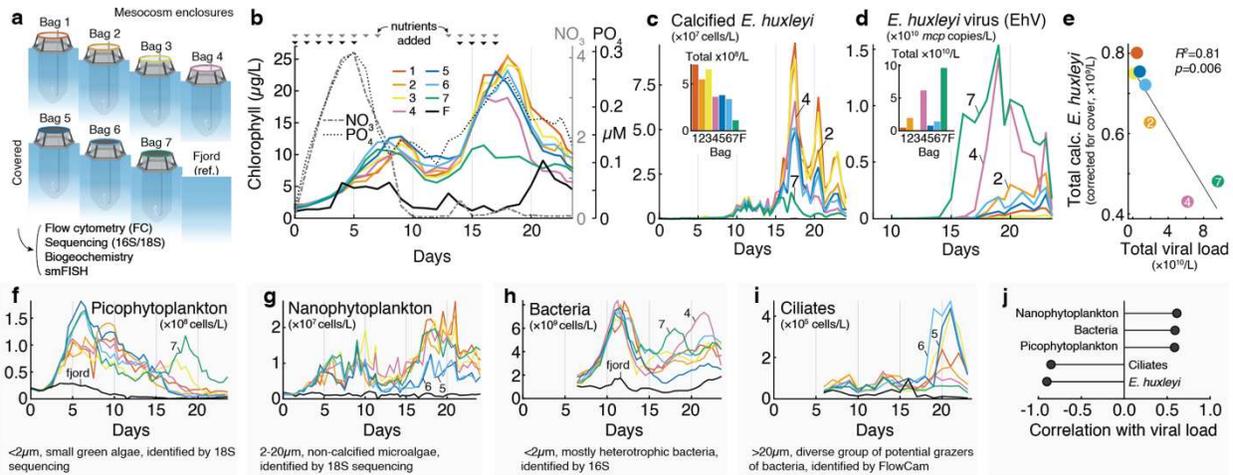
82 In the initial phase (Day 0-10), the enclosures were nitrate and phosphate replete following
83 nutrient addition; at later stages (Day 10-23), the enclosures were nitrate, but not phosphate,
84 limited (**Fig. 1b**). Bulk chlorophyll measurements displayed two peaks in all enclosures, with a
85 first smaller phytoplankton bloom (Day 0-10) followed by a second bloom reaching 25 µg/L of

86 chlorophyll (Day 10-23). Calcified *E. huxleyi* cells, quantified by flow cytometry, dominated the
87 second bloom (**Fig. 1c**). *E. huxleyi* is a cosmopolitan bloom-forming alga and one of the planet's
88 major calcite producers, causing the transport of large amounts of carbon into sediments¹⁰. In
89 addition to slight differences in average *E. huxleyi* cell abundance between covered and uncovered
90 enclosures, we also observed stark differences in *E. huxleyi* demise dynamics across bags (Day
91 18-24), with up to 90% lower algae abundances in bags 4 and 7 compared to the highest
92 concentration within each day. Previous studies attribute the demise of natural blooms of *E. huxleyi*
93 to virus-induced mortality caused by the *E. huxleyi*-specific giant coccolithovirus (EhV)¹¹⁻¹³. To
94 assess the impact of EhV, we estimated its abundance in the 2-20 μm size fraction (to focus on
95 infected *E. huxleyi* cells and viral particles associated with its biomass) by qPCR of the major
96 capsid protein (*mcp*) gene (**Fig. 1d**). Viral abundance varied considerably between replicate
97 mesocosms: bag 7 (covered) and bag 4 (uncovered) showed high concentrations of biomass-
98 associated EhV with up to 1.54×10^{10} *mcp* copies/L and 1.42×10^{10} *mcp* copies/L, respectively, while
99 bag 5 (covered) and bag 3 (uncovered) showed low to no detectable viral load. Virus-induced
100 mortality had a direct impact on algal abundance: viral abundance explained 81% of the variance
101 in *E. huxleyi* concentration across enclosures, suggesting that viral concentration controls the
102 magnitude of an *E. huxleyi* bloom (**Fig. 1e**). For this estimate, we controlled for the different *E.*
103 *huxleyi* abundances due to bag cover (bags 5-7) by adding the difference between covered and
104 uncovered bag averages to the uncovered bags. Nonetheless, the fact that bloom demise was
105 observed even with low or no viral infection suggested that other mortality agents may also
106 dominate in *E. huxleyi* blooms. In enclosures with low viral load (bags 1, 3, 5, and 6), we observed
107 up to a six-fold increase in ciliates that could potentially graze on *E. huxleyi*¹⁴ (measured by
108 imaging flow microscopy, **Fig. 1i**).

109 The first phytoplankton bloom (Day 0-10) which we termed the mixed bloom, preceding
110 the *E. huxleyi* bloom, was dominated by the pico-phytoplankton *Bathycoccus* and *Micromonas*,
111 representing over 40% of the community in the 0.2-2 μm size-fraction (**Supplementary Fig. 1**).
112 This bloom reached 1.81×10^8 cell/L in bag 5 (**Fig. 1f**). Nano-phytoplankton (**Fig. 1g**) were also
113 important players in this mixed bloom and sequencing of the 2-20 μm size fraction 18S rDNA
114 revealed that dinoflagellates (Group-I Clade-I) were especially abundant (see further information
115 below).

116 Phytoplankton cells fix inorganic carbon into organic biomass, and secrete part of it in the
117 form of metabolites that heterotrophic bacteria can use for growth¹⁵⁻¹⁸. Interestingly, the dissolved
118 organic carbon (DOC) concentration increased only moderately after each of the blooms
119 (**Supplementary Fig. 2**). This could be explained by a fast-bacterial assimilation as we observed
120 a more than tenfold exponential increase in bacterial abundance between days 5-13 (**Fig. 1h**),
121 doubling every 24-36 hours. By contrast, bacteria were less abundant during the *E. huxleyi* bloom
122 and demise compared to the mixed bloom, showing an average of less than twofold increase after
123 day 20 (**Fig. 1h**). In the two most infected bags, bag 4 and bag 7, the increase in bacterial abundance
124 was 2-3-fold during the demise phase. Overall, total viral load in the different enclosures was
125 significantly negatively correlated with the abundance of host (*E. huxleyi*) and grazer (ciliates)
126 concentrations but not with pico-nano-phytoplankton or bacteria abundances (**Fig. 1j**). The
127 negative correlation between grazing and viral lysis was confirmed via grazing dilution assays
128 across the whole mesocosm (**Supplementary Fig. 3**), suggesting that the two top-down mortality
129 agents compete during algal blooms.

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 134 **Figure 1: An overview of the mesocosm setup and dynamics of prominent community**
 135 **members.** **a**, Schematic view of the seven mesocosm enclosures during the mesocosm experiment.
 136 The fjord water was used as the microbial inoculum seeding the enclosures and was sampled as a
 137 reference for microbial dynamics under natural conditions. **b**, Fluorometric chlorophyll
 138 measurements (left axis), where each color corresponds to a different bag. Nitrate and phosphate
 139 concentrations over time averaged across enclosures (right axes). Arrows on the top indicate
 140 nutrient addition. **c**, Calcified *E. huxleyi* abundance measured by flow cytometry, based on high
 141 side scatter and high chlorophyll signals. The small bar chart shows the integrated abundance of
 142 *E. huxleyi* over time (see Methods). **d**, Concentration of EhV based on qPCR of *mcp* (major capsid
 143 protein) gene in 2-20 μm pore filters. The small bar chart shows the integrated abundance of EhV
 144 over time. **e**, Scatter plot of total calcified *E. huxleyi* abundance (corrected for bag cover) as a
 145 function of total viral abundance, with a linear model fit. **f-i**, Absolute abundances of key players
 146 in the microbial succession, sorted by peak abundance time: **f**, picophytoplankton abundance
 147 measured by flow cytometry, based on low side scatter and low chlorophyll signals; **g**, non-
 148 calcifying *E. huxleyi* and other nanophytoplankton abundance measured by flow cytometry, based
 149 on low side scatter and high chlorophyll signals; **h**, absolute abundance of bacteria measured by
 150 flow cytometry after SYBR green staining; **i**, ciliate abundance measured by imaging flow
 151 microscopy and annotated using EcoTaxa. **j**, Correlation between EhV viral load and average
 152 planktonic abundances across bags.

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 155 **Effects of viral infection on the composition of microbial assemblages**

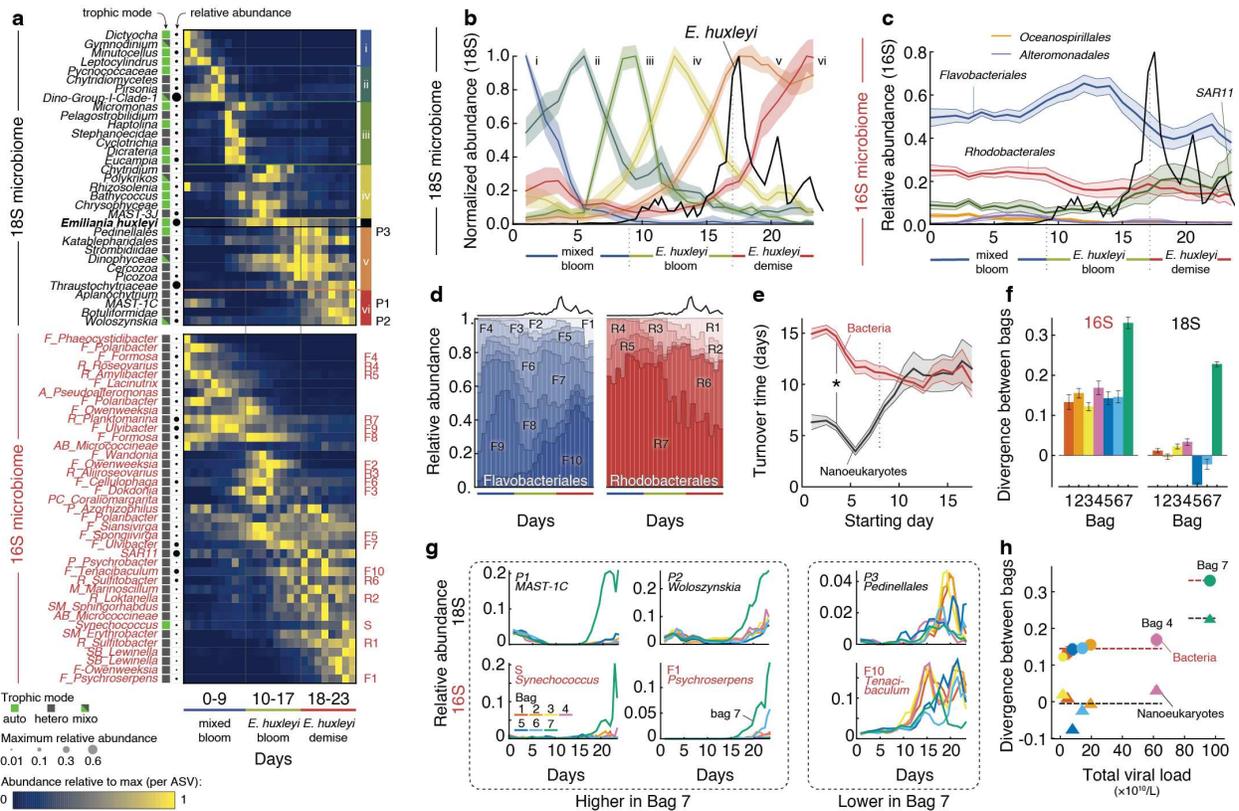
156 To understand how viral infection can alter the composition of planktonic communities, we
 157 conducted microbiome profiling of all the mesocosm enclosures. We opted for a detailed time
 158 series based on samples collected daily of both the bacterial (0.2-2 μm size fraction, 16S
 159 amplicons) and nanoeukaryotic (2-20 μm size fraction, 18S amplicons) communities. Throughout
 160 the two blooms, we observed a repeatable pattern of eukaryotic and bacterial taxa successions (**Fig.**
 161 **2a**). The relative abundance of *E. huxleyi* defines three major phases: the mixed bloom, (days 0-
 162 8), the exponential growth phase of *E. huxleyi* (days 8-17), and its demise (days 18-23).
 163 Nanoeukaryotes, clustered according to the relative abundance patterns at the genus level, showed
 164 a rapid succession of boom-and-bust cycles, each about 5-10 days long (**Fig. 2b, Supplementary**
 165 **Fig. 4.5**). Unique clusters of nanoeukaryote species bloom upon *E. huxleyi* growth (Cluster 5) and

166 demise (Cluster 6) thus defining a bloom associated protist microbiome. By comparison, bacterial
167 succession was much less dynamic: the composition at the order level was relatively stable (**Fig.**
168 **2c**). The mixed bloom was associated with bacterial groups known to be involved in algal biomass
169 remineralization, such as Flavobacteriales^{19,20} and Rhodobacterales. We also observed a slow,
170 more than ten-fold increase in relative abundance of SAR11, usually found in oligotrophic
171 environments²¹, throughout the *E. huxleyi* bloom. This facilitation of SAR11 growth by *E. huxleyi*
172 is in line with previous observations of their co-occurrence²² and could be mediated by the
173 organosulfur compound dimethylsulfoniopropionate (DMSP), which *E. huxleyi* produces and
174 excretes^{23,24} and that SAR11 can utilize as a reduced source of sulfur²⁵. In contrast to the relative
175 stability of the bacterial composition at the order level, there were clear successions at the genus
176 level within the two dominant bacterial orders, *Flavobacteriales* and *Rhodobacterales* (**Fig. 2d**,
177 **Supplementary Fig. 6**). The *E. huxleyi* bloom and demise coincided with the relative increase of
178 two genera: *Tenacibaculum*, a potential fish parasite frequently associated with algal blooms²⁰,
179 and *Sulfitobacter*, a genus containing DMSP degrading species that are pathogenic to *E. huxleyi*
180 cells²⁴. Gammaproteobacteria such as *Vibrionales*, *Pseudomonadales*, or *Alteromonadales*, often
181 reported as dominant members in bloom-associated communities²⁶, were absent in the planktonic
182 populations, but may thrive in the particle-associated niche (in the >20 μm size fraction).

183 To further compare bacterial and eukaryotic dynamics, we computed their turnover time
184 as defined by the exponential rate at which the Bray-Curtis similarity declined over time (see
185 Methods). Given their small size and known fast growth rates, we expected heterotrophic bacteria
186 to respond much faster to our nutrient additions (N and P) than eukaryotes. To our surprise,
187 eukaryotes were the first responders to nutrient addition, and their assemblage turned over much
188 faster (every five days initially) than bacteria which only showed significant growth towards the
189 end of the first bloom (turnover every 10 days) (**Fig. 2e**). The sequence of response to the nutrient
190 addition can be explained by the direction of nutrient flow in phytoplankton blooms when nutrients
191 increase: eukaryotes, especially phytoplankton, were likely nitrogen and/or phosphorous-limited
192 at the start of the experiment, whereas bacteria appeared to be carbon-limited and required organic
193 carbon released upon demise of the first mixed bloom in order to grow.

194 Despite strong compositional similarities amongst the seven enclosures, the bacterial and
195 nanoeukaryotic assemblages gradually diverged between enclosures after the mixed bloom.
196 During the *E. huxleyi* bloom demise, bag 7 (the most virally infected) diverged in microbiome
197 composition from the other enclosures (**Fig. 2f**, **Supplementary Fig. 7**). Eukaryotes such as
198 MAST-1C (a heterotrophic flagellate), *Woloszynskia* (a mixotrophic dinoflagellate), as well as the
199 cyanobacterium *Synechococcus* and the bacterium *Psychroserpens* (family *Flavobacteriaceae*)
200 were overrepresented in bag 7 (**Fig. 2g**, **Supplementary Fig. 8,9**). The growth of *Synechococcus*
201 during high viral infection suggests that the resulting flux of DOM benefit not only heterotrophic
202 but also autotrophic bacterial growth^{27,28}. Recent ecosystem modeling suggests this may be due to
203 efficient recycling of growth-limiting nutrients in the photic zone during viral infection²⁹. The
204 eukaryotes *Pedinellale* (autotroph) and the bacterium *Tenacibaculum* (family *Flavobacteriaceae*)
205 grew less in bag 7 than in the rest of the enclosures. In contrast to observation in the highly infected
206 bag 7, the moderately infected bag 4 showed a 16S and 18S-based composition that did not differ
207 significantly from the less infected enclosures (**Fig 2h**). These findings suggest that substantial
208 change in microbial assemblages during viral induced *E. huxleyi* demise is conditional on high
209 viral infection levels.

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Figure 2: Microbial succession during the growth and demise of algal blooms with different viral loads. **a**, Bacterial and eukaryotic microbial succession throughout the experiment duration, averaged across enclosures. Each row is an amplicon sequencing variant (ASV) with bacteria in red and eukaryotes in black. The trophic modes of each ASV are detailed in the box color with autotrophs in green, heterotrophs in grey, and mixotrophs in green/grey. Days are shown in columns. 18S species are grouped by clusters of different colors, indicated on the right of the heatmap. 16S abbreviations: F: Flavobacteriales; R: Rhodobacteriales; A: Alteromonadales AB: Actinobacteridae; M: Methylophilales; P: Pseudomonadales; PC: Puniceicoccales; SM: Sphingomonadales; SB: Sphingobacteriales. **b**, Succession of 18S-based ASVs in the 2-20 μ m fraction, clustered by similarity of their relative abundance dynamics averaged across bags. The shaded area represents the standard deviation within each cluster. The absolute abundance of *E. huxleyi* enumerated with flow cytometry is overlaid as a guide (black line, not to scale). Each cluster is normalized to its own maximum abundance and their species composition is detailed in panel **a**. **c**, Relative abundance of major bacterial orders throughout the bloom, averaged for all enclosures using 16S amplicon sequencing of the 0.2-2 μ m fraction. The absolute abundance of *E. huxleyi* enumerated with flow cytometry is overlaid as a guide (black line, not to scale). **d**, Relative abundance of different Flavobacteria and Rhodobacteria genera within each order averaged across all enclosures. The dark line on the top represents *E. huxleyi* abundance trends as a guide. **e**, Rate at which bacteria and nanoeukaryotic community similarities change over time. Nanoeukaryotic communities initially turnover much faster than the bacterial ones (until day 8, $p < 0.001$ by Kolmogorov-Smirnov test). **f**, Compositional divergence within one bag, compared across several days, for 16S and 18S. The divergence of a bag is defined as the change in pairwise Bray-Curtis

237 distance between the focal bag and all other bags from the start of the *E. huxleyi* bloom to its
238 demise. **g**, Eukaryotic and bacterial ASVs that are overrepresented or underrepresented in bag 7.
239 **h**, Correlation, per bag and per 16S or 18S ASV, between total viral load and percentage
240 dissimilarity in microbial composition from one day to another.

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242 ***Viral infection impacts the composition of organic matter recyclers***

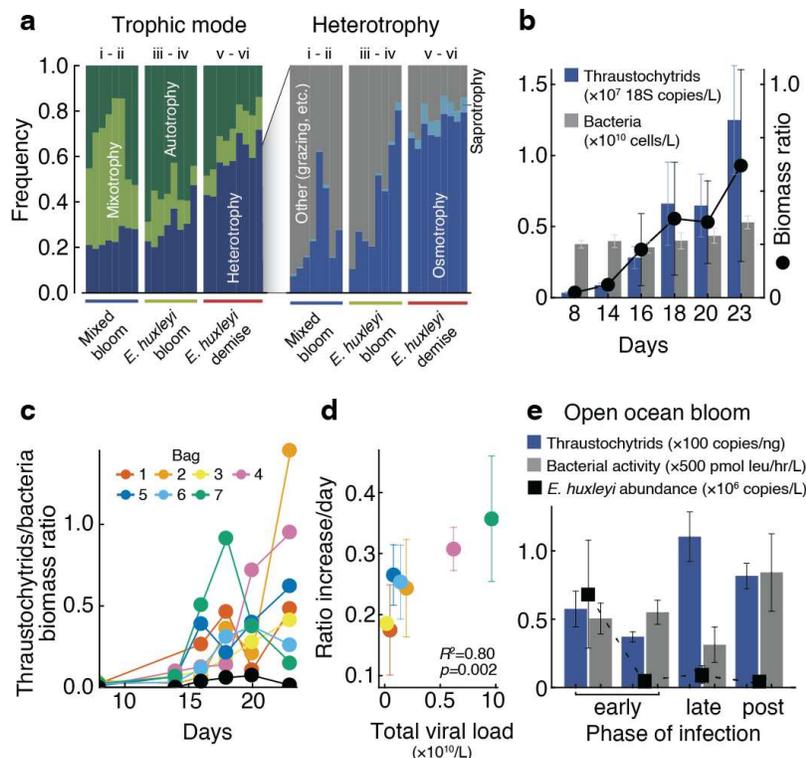
243 During *E. huxleyi* demise, a large flux of organic carbon derived from lysed phytoplankton
244 biomass became available for bacterial recycling, with estimates of about 270 $\mu\text{g C/L/day}$ from *E.*
245 *huxleyi* alone (see Methods). Yet bacterial growth was moderate. This could be explained by
246 several factors, including enrichment of particle-attached (e.g., biofilm-like) bacterial growth that
247 did not influence the free-living abundances, removal of bacteria by aggregation and sinking, or
248 increased bacterial cell death by phages or bacterivores³⁰. However, the abundance of typical
249 bacterivores like dinoflagellates remained low and ciliate abundance only increased late into the
250 demise of the *E. huxleyi* bloom (day 20-23) (**Fig. 1i**). The low number of predators, combined with
251 the observation that dissolved organic carbon concentration stabilized during bloom demise, led
252 us to hypothesize that bacteria competed for nutrients with another group of heterotrophs.

253 To identify other heterotrophs, we re-examined the eukaryotic microbiome in search for
254 organic matter recyclers. Functional annotation of the nano-eukaryotes (see Methods) revealed that
255 while eukaryotic assemblages were composed of autotrophs and mixotrophs during the first mixed
256 bloom, heterotrophs, and specifically osmotrophs, became highly abundant through the *E. huxleyi*
257 bloom and demise (**Fig. 3a**). These heterotrophs were dominated by thraustochytrids
258 (*Thraustochytriaceae* and *Aplanochytrium* in **Fig. 2a**), part of a diverse lineage of eukaryotic
259 osmotrophs³¹, which contributed over 50% of all 18S rDNA reads in the 2-20 μm size fraction
260 during bloom demise, across all bags. Thraustochytrids are known to possess an arsenal of
261 extracellular digestive enzymes, making them important decomposers of organic matter in coastal
262 sediments³² and deep-sea particles³³. With their large intracellular lipid reserves, they also serve
263 as an important food source for higher trophic levels³⁴. However, the importance of
264 thraustochytrids in microbial food webs has yet to be explored. During algal blooms, they could
265 potentially play a significant role as decomposers³⁵, bacterivores, or even parasites³⁶. Some
266 members of the group are also known to produce ectoplasmic nets, through which they can extract
267 intracellular nutrients of preyed cells^{37,38} such as senescent diatoms^{39,40}.

268 In order to quantify the absolute abundance of thraustochytrids, we performed digital
269 droplet PCR (ddPCR) targeting thraustochytrid 18S rDNA across all mesocosm enclosures. While
270 undetected during the mixed bloom, thraustochytrids total biomass, estimated based on values of
271 64 18S rDNA copies/cell (see Methods) and 1.65×10^{-10} g of carbon/cell⁴¹ increased steadily after
272 day 16 and was comparable to that of bacteria during the *E. huxleyi* bloom demise (**Fig. 3b**,
273 **Supplementary Table 1**). Though we cannot elucidate the mechanism of competition between
274 thraustochytrids and heterotrophic bacteria, possibilities include direct inhibition of bacterial
275 growth by antimicrobial lipids⁴², niche separation in the degradation of different components of
276 the organic matter, or efficient capture of organic matter by ectoplasmic nets directly from
277 senescent *E. huxleyi* cells. Thraustochytrids are most likely not intracellular parasites of *E. huxleyi*,
278 since we did not detect any 18S amplicon reads of this group within *E. huxleyi* cells that were
279 sorted and sequenced.

280 While the *E. huxleyi* demise reproducibly triggered the growth of eukaryotic degraders in
281 all bags, thraustochytrids growth was further enhanced in bags with strong viral infection of *E.*
282 *huxleyi* (**Fig. 3c**). Specifically, total viral load was well correlated with the exponential rate at

283 which the ratio of thraustochytrid to bacterial biomass increased (**Fig. 3d**). We further examined
 284 the ecological importance of this phenomena by using samples collected from an open-ocean *E.*
 285 *huxleyi* bloom in the North Atlantic⁴³ where different phases of viral infection were observed. We
 286 quantified the absolute abundances of thraustochytrid using ddPCR and compared it with bacterial
 287 production rates measured with leucine incorporation⁴⁴. We detected higher thraustochytrid
 288 abundance and lower bacterial production during late viral infection phase relative to the early
 289 phase of bloom infection (**Fig. 3e**), suggesting that thraustochytrids are major beneficiaries from viral
 290 induced *E. huxleyi* bloom demise. Sequencing of larger 18S rDNA fragments from the mesocosm
 291 and open ocean samples revealed a single dominant species across these ecosystems, whose closest
 292 relative is an uncultivated clone (94% identity), potentially indicating that this thraustochytrid
 293 species specializes on exudates from *E. huxleyi* demise and has not been reported before
 294 (**Supplementary Fig. 10**).
 295
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 298 **Figure 3: Viral induced bloom demise changes the composition of organic matter recyclers.**
 299 **a**, Analysis of predicted eukaryotic traits plotted per phase of the *E. huxleyi* bloom. Relative
 300 abundance of autotrophy, mixotrophy, and heterotrophy, defined through literature search (left).
 301 Trophic modes within heterotrophy, as defined by⁴⁵ (right). **b**, Thraustochytrid to bacteria ratios
 302 throughout the experiment duration. The blue bars represent thraustochytrid concentrations
 303 obtained by digital droplet PCR and the grey bars represent bacterial concentrations measured by
 304 flow cytometry, averaged across all bags. Circles represent ratios of thraustochytrids to bacterial
 305 biomass in the averaged mesocosm enclosures, using a conservative conversion factor of
 306 thraustochytrid copies/L to cell/L (see Methods and **Supplementary Table 1**). **c**, Converting
 307 thraustochytrid and bacteria abundances to biomass to obtain biomass ratios shows increasing ratio
 308 during *E. huxleyi* bloom (days 10-17) and demise (days 17-24) in all bags. **d**, Exponential rate of

309 change of the biomass ratio of thraustochytrids to bacteria plotted as a function of total viral load,
310 per bag (see Methods). e, Concentration of thraustochytrids measured by ddPCR, *E. huxleyi* cells
311 measured by qPCR, and bacterial production using leucine incorporation⁴⁴, in three phases of an
312 open ocean *E. huxleyi* bloom infection.

313

314 ***Viral infection enhances population-level and per-cell rates of carbon release***

315 During *E. huxleyi* blooms, which can cover over 100,000 square kilometers in the ocean⁴⁶, cell
316 concentrations can account for 75% or more of the total number of photosynthetic plankton in the
317 area⁴⁶. The algal biomass and coccoliths that form the *E. huxleyi*'s calcified shell have profound
318 impact on the carbon cycle and global CaCO₃ export flux⁴⁷. We therefore investigated the
319 biogeochemical consequences of viral infection of *E. huxleyi* blooms by quantifying different
320 components of the carbon cycle, focusing on organic carbon in the form of transparent exopolymer
321 particles (TEP) and particulate inorganic carbon (PIC).

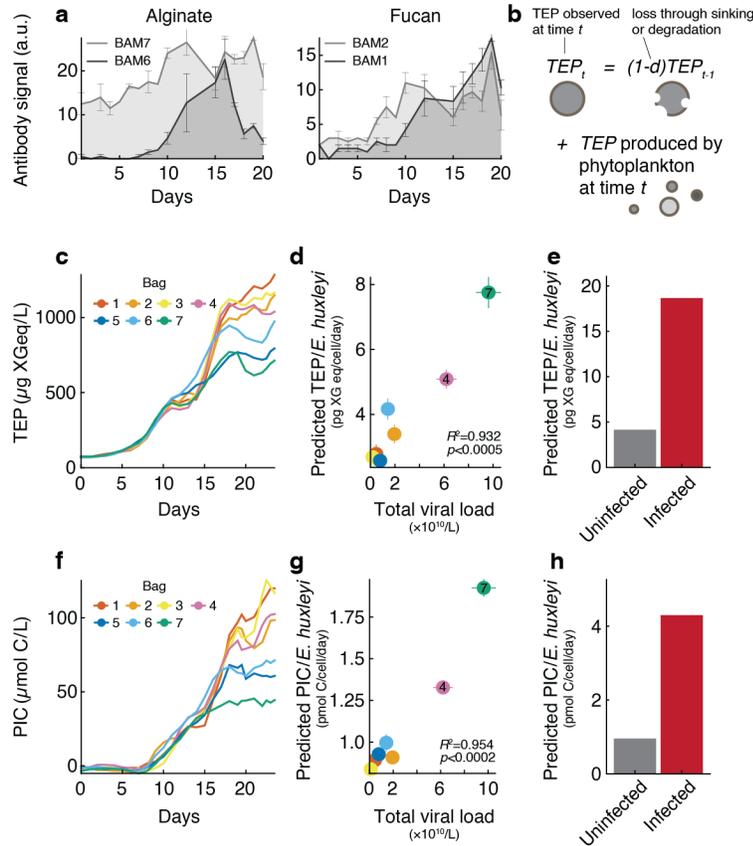
322 TEP are made of acidic polysaccharides that form due to abiotic coagulation of dissolved
323 carbohydrates secreted by phytoplankton and are an important component of the marine particulate
324 organic carbon. TEP represent a potential source of food for bacteria or other heterotrophs^{48,49},
325 although recent work suggests that certain polysaccharides within TEP can be recalcitrant for
326 microbes, challenging its degradation⁵⁰. TEP are an essential vector for carbon export by triggering
327 aggregation and sinking but their chemical composition has only recently been elucidated. To
328 better identify the polysaccharides in TEP during *E. huxleyi* blooms, we used carbohydrate
329 microarray analysis on the particulate fraction⁵¹. Out of the alginate and sulfated fucans epitopes,
330 the ones recognized by the monoclonal antibodies BAM6⁵² and BAM1⁵³ respectively,
331 accumulated during the *E. huxleyi* bloom and are thus likely *E. huxleyi*-related (**Fig. 4a**). BAM6
332 signal decreased during the demise phase, suggesting potential degradation of its recognized
333 epitope by the demise associated microbiome. In contrast, the accumulation of the epitope detected
334 with BAM1 suggests that this sulfated fucan did not serve as a substrate for thraustochytrids or
335 bacteria⁵⁴, but may be part of TEP and thus relevant for carbon export via sinking particles⁵⁰.

336 To decipher the effects of viral infection on TEP production, we modeled TEP
337 concentration as a function of its producers' abundances (*E. huxleyi*, non-calcified
338 nanophytoplankton and picophytoplankton) and a TEP loss rate through sinking or degradation
339 (**Fig. 4b**) that we fitted to *in situ* TEP measurements (**Fig. 4c**) (see Methods). The model described
340 the TEP abundance well, achieving an average R^2 of 98.8%. Using the model, we estimated that
341 the amount of TEP produced per *E. huxleyi* cell per day was 60-75% of the total TEP pool at the
342 onset of bloom demise (**Supplementary Fig. 11**). There was a strong dependence of estimated
343 TEP per cell on viral infection: TEP production per *E. huxleyi* cell was more than twice as high in
344 the infected bag 7 than in non-infected bags. Across all bags, there was a strong correlation to total
345 viral load ($R^2 = 0.932, p < 0.0005$, **Fig. 4d**), consistent with previous results suggesting higher
346 export during viral-associated *E. huxleyi* blooms in open ocean and mesocosm experiments^{43,55}.
347 This suggests that, at the population level, *E. huxleyi* cells secreted twice the amount of carbon in
348 presence of high viral load. To validate this correlation, we applied the same model for particulate
349 organic carbon (POC) production. The model gave an excellent fit ($R^2 > 0.98$ across all bags) but
350 the estimate for the amount of organic carbon per *E. huxleyi* cell (4-6 pg C/cell, in line with other
351 estimates⁵⁶ (**Supplementary Fig. 12**)) was uncorrelated with the total viral load ($p > 0.05$).

352 Since viral infection remodels the algal host metabolism^{57,58}, we hypothesized that infected
353 and non-infected cells in the same bloom may differ in their actual TEP production, and sought to
354 quantify this process as opposed to simply averaging TEP over the entire bulk population. To

355 differentiate infected from non-infected cells, we probed viral mRNA in single *E. huxleyi* cells⁹
356 and obtained a time-course of the fraction of actively infected cells in two different enclosures
357 (**Supplementary Fig. 13**). At most 10% and 25% of all *E. huxleyi* cells were infected in bags 2
358 and 4 respectively, reflecting the heterogeneity of cell fates within each bloom succession and
359 demise. By assuming that non-infected cells produced the same amount of TEP regardless of the
360 bag's viral load, we estimated that an infected *E. huxleyi* cell produced ~19 pg xanthan gum (XG)
361 equivalent/day (see Methods), or 4.5 times more TEP than its non-infected bystander cell (**Fig.**
362 **4e**). Notably, viral infection did not increase secretion of proteinaceous material: the measurement
363 and modeling of protein-rich particles (Coomassie Stained Particles) (**Supplementary Fig. 14**)
364 showed no correlation with viral load, indicating that the cellular response to infection is specific
365 to certain metabolic products.

366 Particulate inorganic carbon (PIC) in the form of calcium carbonate is the basis of one of
367 the main processes making up the marine carbon cycle, the carbonate pump, by which inorganic
368 carbon is exported along with organic matter to the deep ocean. A major part of PIC in the ocean
369 is comprised of coccolithophore shells, particularly *E. huxleyi*'s coccoliths⁵⁹. PIC accumulated
370 over time in our study (**Fig. 4f**). We fitted the PIC curves to a model accounting for *E. huxleyi*
371 coccolith production, a degradation rate, and a term allowing for shedding and re-calcification (see
372 Methods). Like TEP, predicted PIC per *E. huxleyi* cell at the population level was significantly
373 correlated to total viral load from about 1 to 2 pmol PIC/cell/day ($R^2 = 0.954, p < 0.0002$, **Fig.**
374 **4g**) which is consistent with lab-based measurements⁶⁰. Using the measured fraction of active
375 single-cell infection, we estimated that infected single cells produced 4.5 times more PIC per cell
376 than their non-infected bystander cells (**Fig. 4h**). Overall these data suggest that active viral
377 infection can have remarkable consequences on exportable carbon (TEP and PIC) release both on
378 the population-level (2-fold increase) and per infected cell (4.5-fold increase).



379
 380 **Figure 4: Viral infection promotes release of PIC and TEP production from a**
 381 **coccolithophore bloom.** **a**, Alginate and fucan abundance in particulate organic matter (POM)
 382 over time, based on mixed water from bags 1-4, measured by carbohydrate microarray analysis.
 383 BAM1, 2, 6 and 7 correspond to glycan-specific monoclonal antibodies, used to measure the
 384 relative abundance of their recognized polysaccharide epitopes in POM water extracts. **b**, Scheme
 385 of TEP modeling, as a function of phytoplankton concentrations and degradation rate which
 386 enables prediction of the *E. huxleyi* contribution to the TEP pool. **c**, TEP concentration measured
 387 by Alcian blue staining over time, per bag. **d**, Predicted TEP/cell as a function of total viral load
 388 for each bag, for *E. huxleyi* cells. **e**, Predicted TEP/cell secretion in infected versus non-infected
 389 *E. huxleyi* cells using intracellular measurements of actively infected single cells. **f**, PIC production
 390 during algal bloom succession. **g**, Predicted PIC/cell as a function of total viral load for each bag,
 391 for *E. huxleyi* cells. **h**, Predicted PIC/cell production in infected versus non-infected *E. huxleyi*
 392 cells using intracellular measurements of actively infected single cells.

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 395 **Conclusion**

396 Here we provide in depth characterization of the microbial and biogeochemical dynamics of two
 397 successive algal blooms in replicate mesocosm enclosures, which provides a unique experimental
 398 platform to quantify the impact of viral infection at the ecosystem level. Starting from the same
 399 microbial inoculum, our mesocosm enclosures underwent ordered microbial successions that
 400 culminated in massive blooms of the coccolithophore *E. huxleyi*. Viral infection of *E. huxleyi* took
 401 drastically different courses in the enclosures, with little to high levels of viral infection leading to
 402 a bloom demise. Our study made three critical observations regarding the microbial ecology and

403 the biogeochemical effects of algal blooms and their viral infection (**Fig. 5**), generating novel
404 hypotheses for future lab-based mechanistic studies.

405 First, we showed that viral-induced changes in the microbiome, as in bag 7, are only
406 observed when there is a high level of viral infection (**Fig. 5 (1)**). Given that only one in seven
407 enclosures experienced such high levels of viral production, its occurrence in natural ecosystems
408 may be rare but can profoundly impact microbial diversity and community composition. It is also
409 possible that the microbiome response takes longer than the duration of our experiment or may be
410 localized to particle-attached communities. Indeed, as viral infection enhanced TEP production,
411 this could promote the formation of marine snow and a specific particle-associated microbiome.

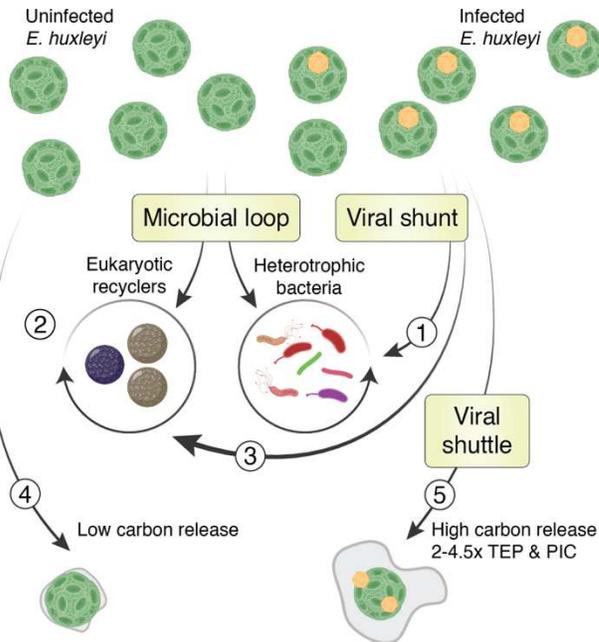
412 Second, we estimated that the biomass of eukaryotic osmotrophs can be comparable to that
413 of heterotrophic bacteria during *E. huxleyi* blooms and demise (**Fig. 5 (2)**) and that viral infection
414 may enhance their growth (**Fig. 5 (3)**), including in open ocean blooms. This abundance of large,
415 underappreciated eukaryotic osmotrophs, may shape the carbon flux through the marine trophic
416 network. Since they are larger than the average bacterium, eukaryotic osmotrophs can escape
417 grazing by many micrograzers and shorten the carbon transfer to larger predators as zooplankton.
418 Thus, the competition between prokaryotic and eukaryotic degraders can reshape higher trophic
419 levels. More generally, our findings highlight that a complete understanding of the carbon flux in
420 phytoplankton blooms requires deeper understanding of both the associated prokaryotic and
421 eukaryotic microbial communities and the interactions between them⁶¹. Currently, only a few
422 studies explore the competition between thraustochytrids and bacteria for DOM⁶². More work is
423 needed to fully establish the role of eukaryotic osmotrophs in the microbial loop, especially in the
424 context of viral infections and the associated metabolome⁶³.

425 Third, by relating ecosystem changes and biogeochemical processes to the varying degrees
426 of active viral infection and lysis, we have shown that even mild viral infection can significantly
427 affect the production and release of extracellular carbon, both organic and inorganic. In particular,
428 our experimental setup enabled the parameterization of TEP and PIC production in the absence
429 (**Fig. 5 (4)**) or presence (**Fig. 5 (5)**) of viral infection^{43,55,64}. We estimated that *E. huxleyi* carbon
430 secretion in the presence of viruses increases between 2 to 4.5-fold per cell, either through a
431 population level response, or a specific metabolic remodeling of infected cells. Taken together, the
432 increase in TEP and PIC production per cell could lead to elevated vertical carbon transport
433 through aggregation and increase of the cellular ballast. Overproduction of TEP by infected cells
434 increases the formation of sinking aggregates, and may protect non-infected cells by trapping
435 newly produced virions in sticky particles or can mask receptors needed for viral entry⁹.
436 Alternatively, TEP could be involved in the transport of virions to neighboring cells, in analogy to
437 the human T-cells leukemia virus which encases itself in a host-derived carbohydrate-rich adhesive
438 extracellular cocoon that enables its efficient and protected transfer between cells^{65,66}. The
439 increased production of PIC per cell is surprising since viral infection is thought to promote
440 decalcification⁶⁷. Nevertheless, higher turnover of coccolith shedding and recalcification, or
441 thicker coccoliths could be potential defense mechanisms, enabling lower viral adsorption and
442 efficient removal of attached viral particles.

443 Taken together, our results provide a strong evidence that viral infection does not only play
444 an important ecological role as a principal cause of phytoplankton mortality, but also has profound
445 consequences for the fate of carbon, both by diverting carbon from bacteria towards larger
446 eukaryotes and by potentially enhancing vertical export (**Fig. 5**). This refined assessment of viral
447 impacts on the fate of carbon in the ocean helps bridge the scales between dynamic processes at
448 the single cell, population, and biogeochemical levels, and will thus enable us to anticipate better

449 the consequences of a changing ocean on fundamental ecosystem processes, services and
450 feedbacks.

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456 **Figure 5: Consequences of viral infection on microbial community composition and carbon**
457 **cycling.** Arrows represent the direction of carbon flow. (1) The bacterial and eukaryotic
458 microbiomes are remodeled in response to viral infection only when level of infection is high. (2)
459 Thraustochytrid rival bacteria as significant recyclers of organic matter during *E. huxleyi* demise.
460 (3) Thraustochytrids benefit from viral infection of *E. huxleyi*. (4) When the demise is not virus-
461 associated, *E. huxleyi* populations release a small amount of organic and inorganic carbon. (5)
462 Viral infection increases *E. huxleyi* population carbon release between 2-4.5 fold under the form
463 of TEP and PIC as compared to (4).

464
465

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