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# What happens to biomass burning-emitted particles in the ocean? A laboratory experimental approach based on their tracers

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## Highlights

- (a) Dynamics assessment of anhydrosugars in seawater
- (b) Assimilation and mineralization of anhydrosugars by marine bacteria
- (c) Levoglucosan is a substrate that can be used for cell maintenance
- (d) Anhydrosugars showed the selection of Roseobacter clade in seawater
- (e) Anhydrosugars are semilabile compounds compared to glucose

1 **What happens to biomass burning-emitted particles in the ocean?**  
2 **A laboratory experimental approach based on their tracers**

3 **Juan Miguel González-Sánchez<sup>1</sup>, Christos Panagiotopoulos<sup>1,2\*</sup>, Candice Antich<sup>1</sup>, Laure Papillon<sup>1</sup>, Nicole**  
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## 38 ABSTRACT

39 Wildfires, controlled burns, and biofuel combustion (biomass burning or BB) are major contributors to particulate matter in the  
40 atmosphere and thus have an impact on climate, human health, and ecosystems. Once emitted, the particulate matter derived from BB  
41 can be taken up by the oceans. However, the fate and impact of BB in the marine biological carbon pump, and carbon cycle are largely  
42 unknown. This work presents the first attempt to investigate the bioavailability of two BB tracers, levoglucosan and galactosan, in seawater  
43 inoculated with marine prokaryotes. Levoglucosan and galactosan were incubated with a marine bacterial inoculum and monitored for six  
44 weeks under controlled laboratory conditions. Along with the anhydrosugar concentrations, multiple chemical and biological parameters  
45 were monitored over time. The results indicate that levoglucosan and galactosan can be assimilated by marine prokaryotes as their  
46 concentrations decreased by  $97 \pm 4\%$  and  $36 \pm 21\%$  ( $n = 3$ ) of their initial values. However, this decrease occurred only after a 9 and 15  
47 days from the beginning of the experiment, respectively. The decrease in the levoglucosan and galactosan concentrations was  
48 accompanied by an increase in both heterotrophic prokaryotic production, and abundance. These results demonstrate that these  
49 anhydrosugars have the potential to be assimilated by heterotrophic prokaryotes and thus contribute to the microbial food web  
50 functioning. Under our experimental conditions, levoglucosan exhibited a bacterial growth efficiency of  $17 \pm 5\%$  ( $n = 3$ ), suggesting that  
51 most of the levoglucosan is mineralized into  $\text{CO}_2$ . Prokaryotic diversity analyses revealed the predominance of a few bacterial genera from  
52 the Roseobacter clade that were selected after the addition of the anhydrosugars. The presence of this widespread marine bacterial clade  
53 reflects its ability to process semilabile compounds (here levoglucosan and galactosan) originating from BB and contribute to the dissolved  
54 organic matter pool in surface seawaters.

55 *keywords:* biomass burning, anhydrosugars, marine biological carbon pump, carbon cycle, semilabile dissolver organic matter,  
56 Roseobacter clade

## 57 **1. Introduction**

58 Wildfires, controlled burns, and biofuel combustion (biomass burning, BB) are major contributors to the emission of  
59 particulate matter in the atmosphere (up to 90% of primary organic aerosol (Bond et al., 2004) and thus have an impact on  
60 climate, human health, and ecosystems. Furthermore, the importance of BB emissions can potentially increase in the future  
61 due to the climate change-driven rise in wildfire occurrence in several regions of the world (Dennison et al., 2014; Ponomarev  
62 et al., 2021; Sierra-Hernández et al., 2022), including the Mediterranean Basin (Durrieu de Madron et al., 2011), and the  
63 parallel increase in fire severity in high biomass-containing woody vegetation (Daniau et al., 2012; Nolde et al., 2021; van  
64 Wees et al., 2021; Walker et al., 2020).

65 Once emitted, BB particulate matter can be deposited in the terrestrial ecosystem or eventually transported to the ocean.  
66 Although previous investigations showed the presence of BB tracers (PAHs and anhydrosugars) in several compartments of  
67 aquatic ecosystems including sinking particles (Castro-Jiménez et al., 2012; Schreuder et al., 2018; Simoneit and Elias, 2000;  
68 Theodosi et al., 2013), concentrated dissolved organic matter (Panagiotopoulos et al., 2013), and sediments (Froehner et al.,  
69 2010; Guigue et al., 2017; Hopmans et al., 2013; Schreuder et al., 2018; Theodosi et al., 2013) the fate of BB particulate  
70 matter in the marine environment is currently unknown, particularly its link with the microbial food web and the biological  
71 carbon pump (BCP). Recent investigations have demonstrated that wildfires can potentially trigger phytoplankton blooms  
72 (Tang et al., 2021) and modify the composition of their communities (Kramer et al., 2020) pointing to a possible utilization of  
73 such substrates by marine planktonic microorganisms. Conversely, the survival and the persistence of these substrates in  
74 sediments (Froehner et al., 2010; Hopmans et al., 2013) may imply a slow degradation mechanism in the marine environment  
75 which may be compound dependent. The above contrasting results clearly demonstrate that there is a gap in knowledge on  
76 the dynamics of BB particulate matter in seawater.

77 Several studies have highlighted the importance of atmospheric nutrient input in oligotrophic regions (Letelier et al.,  
78 2019; Van Wambeke et al., 2021) whereas incubation experiments comprising organophosphate compounds (Vila-Costa et  
79 al., 2019) atmospheric particulate matter (i.e., Saharan dust and anthropogenic aerosols; Djaoudi et al., 2020) and fossil fuel  
80 particles (i.e diesel, ship soot; Martinot et al., 2023) have shown an active response by marine heterotrophic prokaryotes.  
81 Interestingly, the former study on organophosphate compounds showed that in seawater bacteria (particularly  
82 Flavobacteria) exist with a high potential to utilize such organophosphate substrates, while the latter study on atmospheric  
83 aerosols highlighted significant differences in the metabolic response of heterotrophic prokaryotes between Saharan dust  
84 and anthropogenic aerosol substrates.

85 This work presents the first attempt to investigate the bioavailability of two BB-produced molecules (i.e., levoglucosan  
86 and galactosan) in seawater inoculated with marine microorganisms. These anhydrosugars are produced during wildfires  
87 and/or BB events and are due to the pyrolysis of cellulose and hemicellulose occurring at temperatures > 300 °C (levoglucosan  
88 represents > 90% of the anhydrosugars). Since cellulose and hemicellulose account for 60 – 80% of the dry weight of wood,  
89 levoglucosan is very abundant in BB emitted particles and thus is an unequivocal tracer of these processes (Bhattarai et al.,  
90 2019).

91 To investigate the bioavailability of these two molecules, a novel method was developed to extract these anhydrosugars  
92 from their salty matrix and monitor their evolution for 44 days under controlled laboratory conditions. Along with the  
93 anhydrosugar concentration, multiple parameters (dissolved organic carbon or DOC, inorganic nutrient concentrations,  
94 heterotrophic prokaryotic production, abundances of heterotrophic prokaryotes, and heterotrophic prokaryotic diversity)  
95 were monitored to achieve a complete picture of their fate in seawater in relation to the physiological responses and changes  
96 in the taxonomic composition of the prokaryotic communities. Furthermore, two experiments (one with a reference labile  
97 substrate, glucose; and one control, a nonamended substrate with an organic molecule) were run in parallel for comparison  
98 purposes.

## 99 **2. Materials and methods**

### 100 *2.1. Experimental outset*

#### 101 *2.1.1. Seawater sampling*

102 Seawater was pumped at 30 m depth at the SOLEMIO station (26 March 2021) in the Bay of Marseille (43.24°N; 5.29°E),  
103 filtered online through GF/F glass-fiber filters and then transferred to two 20 L Nalgene Carboys (previously washed with 5  
104 % HCl, Milli-Q water and seawater). Seawater was allowed to stand in the dark at 5 °C for approximately two months to allow  
105 labile organic matter to be degraded (DOC concentrations dropped from 70±1 to 65±1 µM C) and then filtered through a

106 Whatman Polycap cartridge (0.2 µm) to remove any particles or microorganisms. This 'prokaryotic free' seawater was used  
107 as background for the biodegradation experiments, and hence, it can be considered as 'recalcitrant' marine DOC.

### 108 2.1.2. Preparation of bacterioplankton inoculum

109 The bacterioplankton inoculum was prepared with seawater collected at the same site one day before the experiments  
110 were run. First, 10 L of seawater was filtered at 0.8 µm using polycarbonate filters (precleaned with 10% HCl solution and  
111 Milli-Q water) to remove bacterioplankton predators, phytoplanktonic organisms, and detrital particles. Then, this 0.8 µm  
112 filtrate was further concentrated to reach high bacterial abundances by filtration through 0.2 µm polycarbonate filters until  
113 a final volume of 0.9 L, in which we resuspended the 0.2 µm filters. The bacterioplankton inoculum contained  $3.95 \times 10^6$   
114 heterotrophic prokaryotes as indicated by flow cytometry. The DOC concentration of the inoculum was  $100 \pm 6 \mu\text{M C}$  ( $n = 2$ ).

### 115 2.1.3. Batch preparation

116 Biodegradation experiments were performed in 2 L precombusted Schott bottles (450 °C, 6 h) containing 1.95 L of  
117 'prokaryotic free' seawater and the natural prokaryotic community (i.e., 0.05 L of bacterioplankton inoculum). Anhydrosugars  
118 and glucose standards were added to each incubation bottle at a final concentration of 10 µM C resulting in initial DOC  
119 concentrations of ~ 70 µM C in the bottles, typical carbon concentrations of surface water at this sampling site. Control  
120 experiments were run in triplicate without the addition of any organic substrate. To avoid nutrient limitation throughout the  
121 experiments and maintain a C/N/P ratio of approximately 106/16/1, nitrate ( $\text{NaNO}_3$ ), and phosphate ( $\text{NaH}_2\text{PO}_4$ ) were added  
122 to each bottle, including the triplicate controls, to achieve final concentrations of  $3.32 \pm 0.04 \mu\text{M N}$  and  $0.20 \pm 0.01 \mu\text{M P}$ .  
123 Incubations were run for 44 days in the dark at 21 °C to ensure the degradation of substrates. To prevent oxygen depletion,  
124 the bottles were opened for a few seconds every 2-3 days and stirred quickly by hand. Several parameters were monitored  
125 at selected time points for a duration of approximately 6 weeks (Table S1). These parameters included the anhydrosugar  
126 concentrations, dissolved organic carbon concentration ([DOC]), inorganic nutrient (nitrate, nitrite, phosphate and silicate)  
127 concentrations, heterotrophic prokaryotic production (HPP), heterotrophic prokaryote abundance (HPA), and heterotrophic  
128 prokaryotic diversity (HPD).

## 129 2.2. Sample analyses

### 130 2.2.1. Anhydrosugars

131 Anhydrosugars were sampled from bottles after filtration on precombusted (450 °C, 6 h) Whatman GF/F (retention size,  
132 0.7 µm) and stored at -20 °C until analysis. Anhydrosugars were extracted from their salty matrix using a mixed anion-cation  
133 exchange resin (Amberlite® IRN-150). First, a 2.5 g bed of resin was packed in a 20 mL glass syringe. Prior to use, the resin  
134 was conditioned using successively of acetonitrile, methanol, and water (3×15 mL each). A 2 mL volume of sample was loaded  
135 and allowed to stand for 20 min, and the anhydrosugars were then eluted with 30 mL of Milli-Q water. The sample was  
136 freeze-dried and redissolved in 1 mL of an acetonitrile/water mixture (90/10, v/v) containing 0.01% TEA, and 2 µM  
137 deuterated levoglucosan (internal standard for MS).

138 Analyses were performed by an Agilent LC-ESI-Q-TOF/MS system equipped with an LC system (Agilent 1290 Infinity)  
139 coupled to a Q-TOF (Agilent 6530 Accurate-Mass). Separation was performed with a Luna® 3 µm  $\text{NH}_2$  100 Å (150 x 2 mm,  
140 Phenomenex) at 25 °C. Both solvents, acetonitrile (A) and water (B) contained 0.01% TEA. The flow rate was set at 200 µL  
141  $\text{min}^{-1}$  and the gradient elution was as follows: 97% of A for 7 min; it gradually goes to 80% of A for 6 min; held for 2 min;  
142 returns to initial conditions in 1 min and is held until the end of the analysis (20 min since injection). The injection volume  
143 was 10 µL. Detection was performed in negative mode under the following conditions: drying gas flow 5 L  $\text{min}^{-1}$  at 275 °C,  
144 sheath gas flow 11 L  $\text{min}^{-1}$  at 250 °C, nebulizer pressure 60 psig, capillary voltage 5000 V, nozzle voltage 2000 V, fragmentor  
145 voltage 100 V, skimmer voltage 65 V, and octopole RF 750 V. MS data were recorded at full scan in the range of 50 to 350  
146 m/z at a rate of 1 spectrum  $\text{min}^{-1}$ .

### 147 2.2.2. Quality assurance/quality control

148 The extraction efficiencies of levoglucosan and galactosan were  $89 \pm 8$  and  $71 \pm 6\%$  ( $n = 14$ ), respectively, at a  
149 concentration of 2 µM. To correct for extraction variability, 2 µM galactosan (surrogate) was added to the levoglucosan  
150 subsamples before extraction, and vice versa. Then, the anhydrosugar concentration was calculated as follows:

$$151 \quad [\text{anhyd.}]_{inc} = \frac{[\text{anhyd.}]_{sample}}{i \cdot j [\text{surrogate}]_{sample}} \quad (1)$$

152 where  $[\text{anhyd.}]_{inc}$  is the concentration of the anhydrosugar in the incubation batch,  $[\text{anhyd.}]_{sample}$  is the  
153 concentration provided by the LC-Q-TOF,  $[\text{surrogate}]_{sample}$  is the concentration of surrogate,  $i$  is the preconcentration  
154 factor of 2,  $j$  is extraction efficiency ratio between the two anhydrosugars (which was necessary since levoglucosan  
155 systematically present higher extraction efficiencies than galactosan). The latter factor was fairly constant in each extraction.  
156 The detection limits of levoglucosan and galactosan in the LC-Q-TOF were 100 and 60 nM, respectively.

157 2.2.3. *Dissolved organic carbon*

158 DOC subsamples were filtered through a 25 mm precombusted (450 °C, 6 h) Whatman GF/F filter (nominal retention size,  
159 0.7 µm) and 15 mL of filtrate was acidified with 21 µL of pure H<sub>2</sub>SO<sub>4</sub> (95-98%) and stored at 5 °C until analyses. DOC  
160 concentration was measured by high-temperature combustion on a Total Carbon Analyzer (Shimadzu TOC 5000) (Para et al.,  
161 2013; Sohrin and Sempéré, 2005). To avoid random errors associated with day-to-day instrument variability, all samples from  
162 a given biodegradation experiment were analyzed in a single day. The procedural blanks (i.e., Milli-Q water) ranged from 1  
163 to 2 µM C and were subtracted from the values presented here. Deep seawater reference samples (provided by D. Hansell,  
164 Univ. of Miami) were run daily (43.5 µM C, *n* = 4) to check the accuracy of the DOC analyses. The concentrations represent  
165 the average of two replicates, ensuring a coefficient of variance (CV) below 2%.

166 2.2.4. *Inorganic nutrients*

167 Inorganic nutrient subsamples were filtered with a precombusted GF/F filter (450 °C, 6 h) and stored at -20 °C until  
168 analyses. Concentrations of nitrite, nitrate, phosphate and silicate were measured by colorimetry using a gas-segmented  
169 continuous flow analyzer (Aminot and Kérouel, 2007). The detection limits of nitrite, nitrate, phosphate, and silicate were  
170 0.03, 0.05, 0.02, and 0.05 µM, respectively. In-house standards, which were regularly compared to commercially available  
171 products, were analyzed to ensure the reproducibility of the analyses. The standard deviation of triplicate measurements  
172 was generally better than 5% at the 0.5 µM level for all nutrients.

173 2.2.5. *Heterotrophic prokaryotic production*

174 Heterotrophic prokaryotic production (HPP) was immediately estimated after sampling by <sup>3</sup>H-leucine incorporation using  
175 the centrifugation method (Smith and Azam, 1992). The detailed protocol has been described elsewhere (Djaoudi et al.,  
176 2020). Briefly, 1.5 mL samples were incubated in the dark for 1–2 h after the addition of <sup>3</sup>H-leucine at a final concentration  
177 of 20 nM, with the standard deviation of the triplicate measurements being on average 9%. Isotopic dilution was checked  
178 and was close to 1 (Van Wambeke et al., 2018); and thus, a conversion factor of 1.5 kg C mol leucine<sup>-1</sup> was applied to convert  
179 leucine incorporation to carbon equivalents (Kirchman, 1993).

180 2.2.6. *Heterotrophic prokaryote abundance*

181 Subsamples (1782 µl) for heterotrophic prokaryote abundances (HPA) were immediately fixed with 18 µL of mix of  
182 glutaraldehyde and pluronic acid (0.25% and 0.01%, respectively of final volume) and then stored at -80 °C upon analyses.  
183 Analyses were performed using an Accuri C6 (BD Biosciences) flow cytometer with an error measurement < 5%, as described  
184 elsewhere (Layglon et al., 2020).

185 2.2.7. *Heterotrophic prokaryotic diversity*

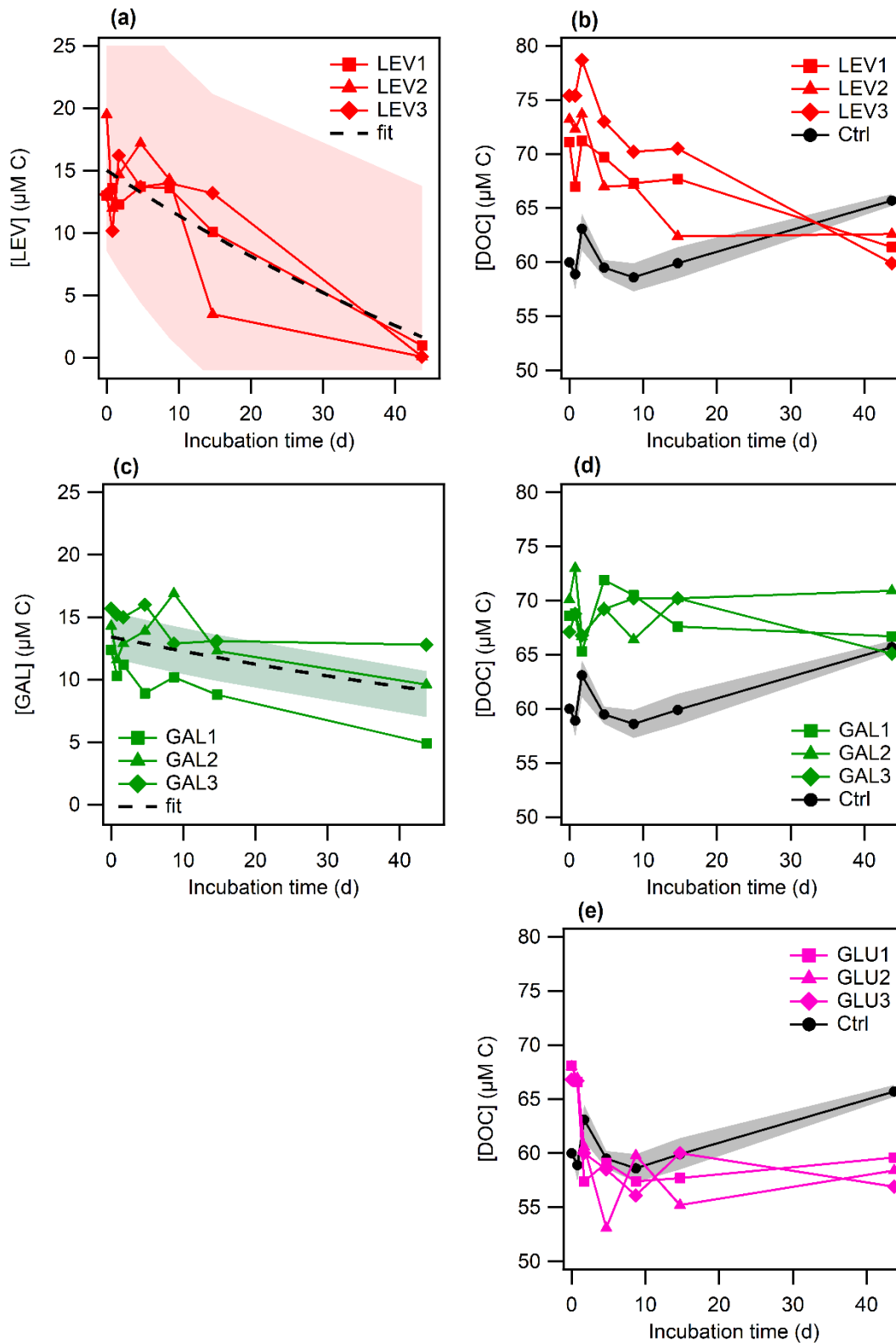
186 Polycarbonate filters (0.2 µm) were used to collect prokaryotes from 300 mL of sample. The filters were stored at -80 °C.  
187 After thawing, they were cut with sterile scissors into small pieces, immersed in 750 µL of sterile saline TSE buffer (50 mM  
188 Tris-HCl, 750 mM sucrose, 20 mM EDTA, 40 mM NaCl, pH = 9.0) and vortexed horizontally for 5 min at ambient temperature.  
189 Cell lysis was performed with lysozyme, SDS and proteinase K as reported elsewhere (Boström et al., 2004). DNA was  
190 precipitated in 70% ethanol, 0.1 M sodium acetate (pH = 5.2) and linear polyacrylamide (Genelute-LPA, Sigma-Aldrich)  
191 (Gaillard et al., 1990). After 2 rinsing steps with 70% ethanol, DNA pellets were air-dried, resuspended in Milli-Q water, and  
192 stored at -20 °C. Amplification of the V4-V5 region of 16S rRNA gene was performed with primers 515F-Y/926R (Parada et  
193 al., 2016) as described previously (Misson et al., 2021). Extraction and amplification negative controls did not yield any  
194 amplification product. After purification (Nucleospin Gel and PCR clean-up, Macherey-Nagel), PCR products were paired-end  
195 sequenced (2×300 bp) with an Illumina MiSeq sequencer by Eurofins (Germany). Sequencing reads were deposited in the  
196 National Center for Biotechnology Information Sequence Read Archive (NCBI SRA) under the accession number  
197 PRJNA908786. MiSeq raw reads were analyzed with DADA2 (Callahan et al., 2016) in RStudio (R Team, 2021) as described  
198 previously (Misson et al., 2021). Taxonomic information was assigned to amplicon sequence variants (ASV) with the SILVA  
199 database v.138.1 (Quast et al., 2013). Sequences classified as mitochondria or chloroplasts were removed from the dataset.  
200 Alpha and beta diversity analyses were performed with RStudio using the *phyloseq* (McMurdie and Holmes, 2013) package  
201 and represented using *ggplot2* (Wickham, 2016) and *metacoder* (Foster et al., 2017) packages. Differences in alpha and beta  
202 diversity metrics were tested for significance (P value < 0.05) using ANOVA with Tukey post hoc tests and PERMANOVA with  
203 *stats* and *microbial* (Guo K. and Gao P, 2021) packages, respectively.

## 204 **3. Results & Discussion**

### 205 *3.1. General observations*

206 The results of this study showed that levoglucosan concentrations decreased from  $15 \pm 4$  to  $0.4 \pm 0.5 \mu\text{M C}$  ( $n = 3$ )  
207 throughout the experiment (Fig. 1a). This decrease was also mirrored by the corresponding decrease in DOC concentrations,  
208 which dropped from  $73 \pm 2$  to  $61 \pm 1 \mu\text{M C}$  (Fig. 1b). In contrast, the decrease in galactosan concentrations was less  
209 pronounced and dropped from  $14 \pm 2$  to  $9 \pm 4 \mu\text{M C}$  (Fig. 1c), while DOC concentrations remained relatively unchanged  
210 (initial:  $69 \pm 2$  and final:  $68 \pm 3 \mu\text{M C}$ ; Fig. 1d). In a parallel biodegradation experiment run with glucose, the results showed  
211 that DOC concentrations rapidly decreased during the first two days of incubation, dropping from  $67.6 \mu\text{M C}$  to  $59.4 \mu\text{M C}$  ( $n$   
212 = 3) and then remained stable until the end of the experiment (Fig. 1e). Overall, DOC concentrations in the glucose  
213 experiment dropped by  $10 \pm 3 \mu\text{M C}$  indicating a complete depletion of the molecule as  $10 \mu\text{M C}$  was initially added to the  
214 batch as a glucose substrate. These results agree with laboratory incubation experiments (Djaoudi et al., 2020) and field  
215 studies indicating the rapid utilization of glucose by marine heterotrophic prokaryotes (Kirchman et al., 2001). Finally, in the  
216 control experiments (no added organic substrate), DOC concentrations remained fairly constant at  $\sim 60 \mu\text{M C}$  throughout  
217 the experiment (Fig. 1b, d, and e) indicating that changes in DOC concentrations for the other experiments were associated  
218 with heterotrophic bacterial activities that were ignited from the addition of a degradable substrate (anhydrosugar/glucose).

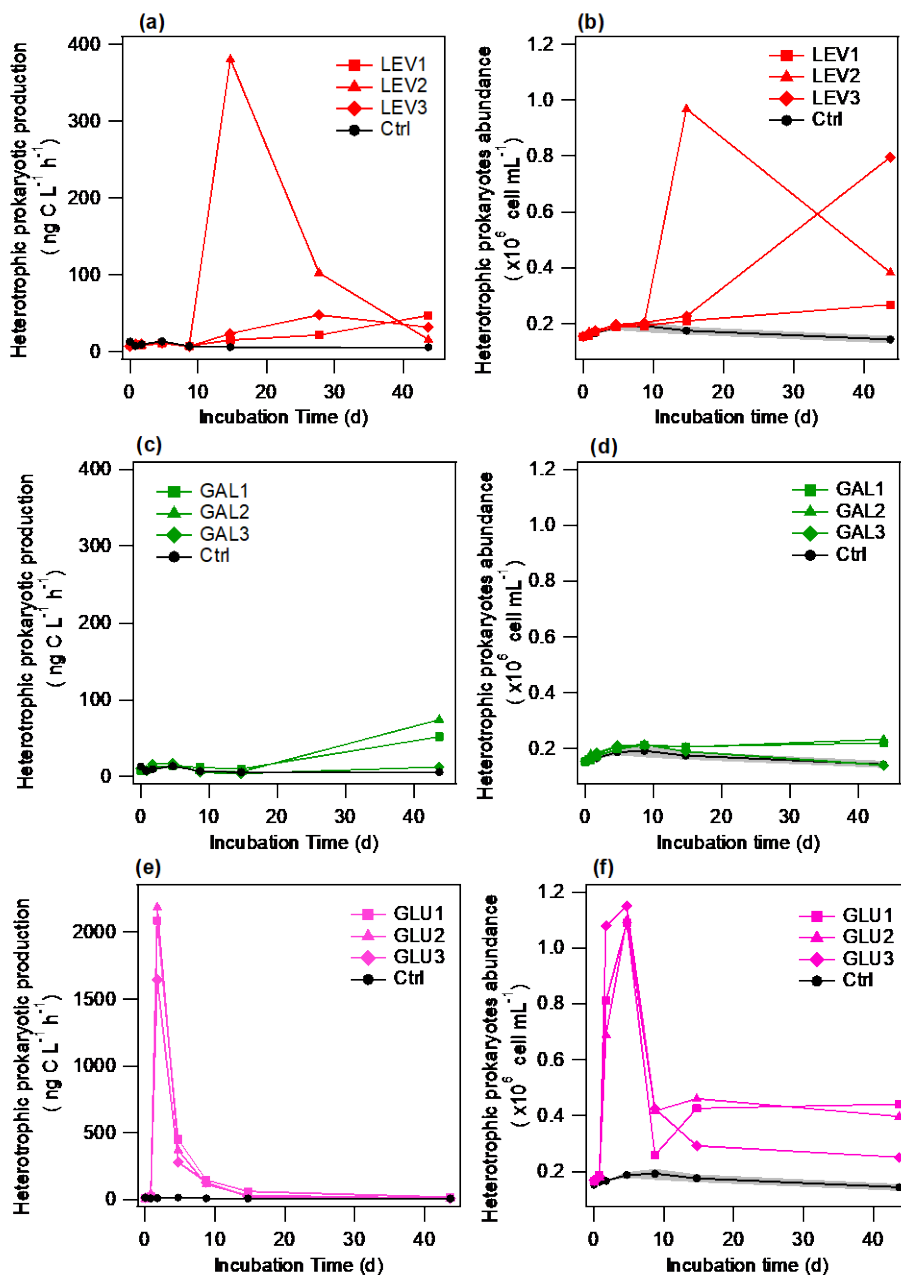




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**Fig. 1.** Time course responses of anhydrosugars (levoglucosan: a and galactosan: c) and DOC concentrations (b, d, e) for all biodegradation experiments. The exponential fit of the average anhydrosugar concentrations is also presented with a dashed line with a 95% confidence interval shaded with a red/green surface (a, c). The time response of the mean DOC concentrations in the control experiments is shown in black (b, d, e), with the maximum and minimum observed values shaded in black. Abbreviations: LEV, levoglucosan; GAL, galactosan; GLU, glucose; Ctrl, control.

225 In line with the above observations, the decrease in the concentration of anhydrosugars and glucose was accompanied  
 226 by an increase in heterotrophic prokaryotic production (HPP) and abundance (HPA) (Fig. 2). In the levoglucosan experiments  
 227 (Fig. 2a and b), both HPP and HPA reached maximum values after at least ~15 d, whereas for the galactosan experiment,  
 228 significant increases in both parameters (Fig. 2c and d) were observed only at the end of the incubation period (44 days),  
 229 consistent with the slight decrease in galactosan concentration and DOC. In the glucose experiments (Fig. 2e and f), a rapid  
 230 increase in both HPP and HPA was observed after ~ 1 d of incubation, with maximum values of  $2000 \pm 300 \text{ ng C L}^{-1} \text{ h}^{-1}$  and  
 231  $(1.11 \pm 0.03) \times 10^6 \text{ cell mL}^{-1}$ , respectively, representing an increase of at least one order of magnitude from the initial values.  
 232 As expected, control experiments showed little variation in HPP and HPA, with values relatively stable at  $\sim 10 \text{ ng C L}^{-1} \text{ h}^{-1}$   
 233 and  $\sim 1.7 \times 10^5 \text{ cell mL}^{-1}$ , indicating low prokaryotic activity in the absence of added organic substrate.



234  
 235 **Fig. 2.** Time course responses of heterotrophic prokaryotic production (HPP: a, c, e) and abundances (HPA: b,d,f) in  
 236 anhydrosugars (levoglucosan and galactosan) and glucose biodegradation experiments. The time response of the mean of HPP and HPA values in the control experiments are shown in black dots, with the maximum and minimum  
 237 observed values shaded in black. Abbreviations: LEV, levoglucosan; GAL, galactosan; GLU, glucose; Ctrl, control.  
 238

239 For the levoglucosan experiment, the measurements of HPP and HPA showed a degree of variability among replicates,  
240 which was not a measurement artifact since all investigated parameters were consistent within replicates. Indeed, HPP and  
241 HPA increases were observed first in the second replicate of the levoglucosan experiment (LEV2 in Fig. 2a and b), which  
242 displayed simultaneous decreases in DOC and levoglucosan concentrations (Fig. 1a and b). This variability may be related to  
243 differences in the ignition time at which some species of heterotrophic prokaryotes start to degrade the substrate added  
244 within the replicates, the low frequency of sampling during the most intense period of prokaryotic activity (which may miss  
245 the real time of peaks in this case) and finally the biological heterogeneity and complexity of biotic interactions within the  
246 bottles. Such variability among the replicates has already been reported in similar biodegradation experiments carried out  
247 with atmospheric aerosols (Djaoudi et al., 2020), phytoplankton culture (Suroy et al., 2015) or fast sinking particles  
248 (Panagiotopoulos et al., 2002).

249 Inorganic nutrient concentrations showed similar patterns with the above observations (Fig. S1). For levoglucosan, nitrate  
250 and phosphate concentrations decreased after ~44 d of incubation (initial concentrations:  $3.3 \pm 0.1$  and  $0.20 \pm 0.1$   $\mu\text{M}$ ,  
251 respectively; final concentrations:  $2.6 \pm 0.3$ , and  $0.16 \pm 0.01$   $\mu\text{M}$ , respectively) indicating that the utilization of these nutrients  
252 provides the N and P sources necessary to degrade levoglucosan by marine heterotrophic prokaryotes. In contrast, for the  
253 galactosan experiment, nitrate and phosphate concentrations remained constant and similar to those of the control  
254 experiment. Finally, nitrite and silicate concentrations for all the experiments were similar to the control experiment  
255 indicating, low utilization compared to the initial concentration of these nutrients during the experiments and/or equilibrium  
256 between uptake and mineralization processes. In contrast, in the glucose experiment, a significant increase in nitrite and  
257 phosphate concentrations was observed at the end of the incubation, showing a decoupling between nutrient uptake and  
258 regeneration with time.

### 259 3.2. Are anhydrosugars labile substrates assimilated by marine prokaryotes?

260 The results of this study demonstrated that anhydrosugars exhibited different dynamics compared to a labile substrate  
261 such as glucose with regard to their utilization by marine heterotrophic prokaryotes. Specifically, levoglucosan and galactosan  
262 exhibited a distinct lag time during which their concentration remained unchanged (Fig. 1a and c), in contrast to the  
263 immediate degradation of glucose which occurred 1 d after the beginning of the experiment (Fig. 1e). In fact, levoglucosan  
264 assimilation started between 9 and 15 d, while for galactosan, it was after 15 d. Although the decrease in both anhydrosugars  
265 was much slower than that of glucose, galactosan showed a much longer persistence in seawater than levoglucosan. The  
266 average half-life times (calculated assuming first-order kinetics (Castro-Jiménez et al., 2022)) were  $78 \pm 12$  and  $8 \pm 1$  d ( $n =$   
267 3) for galactosan and levoglucosan, respectively. Previous field studies in marine and aquatic environments showed a rapid  
268 utilization of glucose by bacterioplankton with glucose always exhibiting the shortest turnover time (5-12 h) over other  
269 monosaccharides including galactose (Bunte and Simon, 1999; Skoog et al., 1999). Considering that levoglucosan and  
270 galactosan are dehydrated forms of glucose and galactose, respectively the differences in assimilation between these two  
271 anhydrosugars observed in this experiment may be possibly to the different utilization rates between glucose and galactose  
272 as demonstrated for the marine environment.

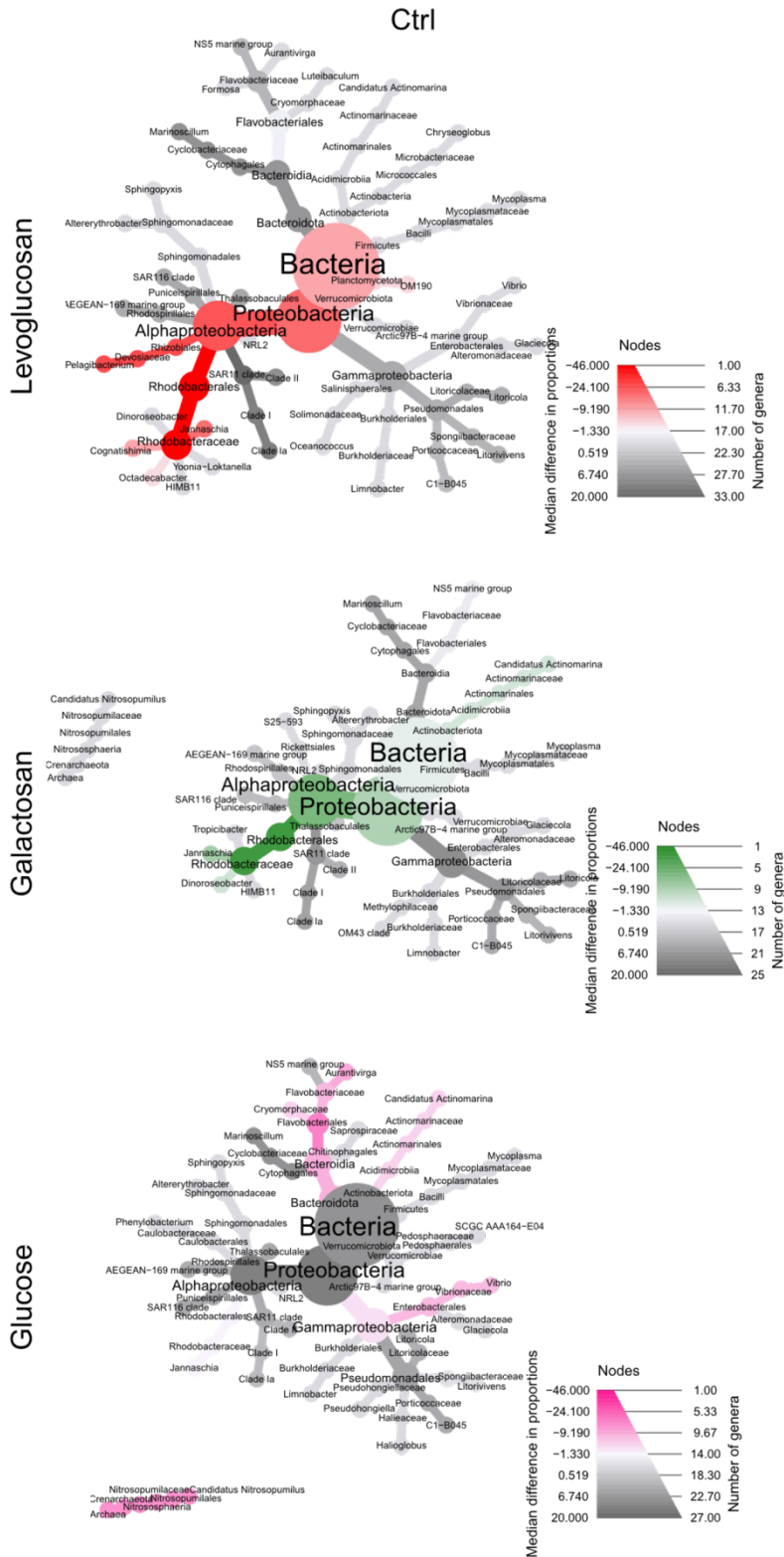
273 The time responses of HPP and HPA (Fig. 2) confirmed that both levoglucosan and galactosan are bioavailable substrates,  
274 although they do not appear to be the first choice for marine heterotrophic prokaryotes compared to a model of labile  
275 substrates such as glucose. They can be partially taken up at the scale of a few weeks, suggesting that they may be considered  
276 semilabile compounds based on their reactivity (Carlson and Hansell, 2015; Nelson and Wear, 2014). The semilabile nature  
277 of these substrates also concurs with the radiocarbon measurements made on levoglucosan ( $\Delta = 48.5\%$ ) and galactosan  
278 ( $\Delta = 35.4\%$ ) standards used for this biodegradation experiment highlighting the modern age of these compounds which  
279 further points to recent photosynthetic molecules (Nouara et al., 2019).

280 The low uptake of anhydrosugars by marine heterotrophic prokaryotes, as revealed by biodegradation experiments, is  
281 consistent with their detection at low concentrations in marine sediments (Hopmans et al., 2013; Schreuder et al., 2018) or  
282 other aquatic ecosystems (Elias et al., 2001). Nevertheless, as the compounds are semilabile, they might potentially be  
283 biodegraded and thus reintegrated into the carbon cycle. To better understand the biological fate of C for anhydrosugars,  
284 the bacterial growth efficiency (BGE) of levoglucosan was calculated (see details in Supplementary Section S1). Under our  
285 experimental conditions, levoglucosan had a BGE of  $17 \pm 5\%$  ( $n=3$ ). Compared to the BGE calculated for glucose ( $70 \pm 10\%$ ;  
286  $n=3$ ), and assuming conservative leucine-carbon conversion factors through the 4 experiments and time, this suggests that  
287 levoglucosan is primarily used by bacteria for cell maintenance and energetic needs rather than growth, resulting in its  
288 mineralization into  $\text{CO}_2$ . The BGE of galactosan was not calculated due to its very low degradation during the incubation  
289 period and possible interference with the biological simultaneous use of bulk marine DOC. However, the fate of this  
290 compound will likely be the same as levoglucosan due to the low HPP and HPA observed.

### 291 3.3. Which bacteria can process anhydrosugars?

292 To further explore the prokaryotic populations involved in anhydrosugar degradation we analyzed community structure  
293 through 16S rRNA gene sequencing at three different incubation times (0, 4.7 and 43.7 days). The results showed that the  
294 initial (T0) prokaryotic community was mostly composed of Alphaproteobacteria (50-68%), with a strong predominance of  
295 the SAR11 clade, along with diverse Gammaproteobacteria. Such dominance of SAR11 is common in oligotrophic NW  
296 Mediterranean surface waters (Coclet et al., 2019; Navarro et al., 2023; Salter et al., 2014). This pattern remained highly  
297 similar throughout the experiment in the control condition (Fig. 3 and S1). Similarly, no significant changes were observed in  
298 community richness between the initial community and the control condition during the 43.7 days of incubation (Fig. 3 and  
299 4). In contrast, the prokaryotic community richness significantly decreased after 4.7 days in glucose-amended incubation ( $P$   
300  $< 0.002$ ). The presence of glucose also prompted a significant shift in community structure ( $P < 0.01$ ) linked to the fast  
301 development of Gammaproteobacteria from the Vibrionaceae family, representing 68-76% of the entire community after  
302 4.7 days of incubation (Fig. S1). Such opportunistic growth of Gammaproteobacteria, especially Vibrionaceae is consistent  
303 with previous work (Eilers et al., 2000; Haider et al., 2023). Depletion of glucose triggered a succession by members of  
304 Bacteroidota from the Cryomorphaceae and Flavobacteriaceae families, together with Crenarchaea from the Nitrosopumilus  
305 genera. Given the ability of *Nitrosopumilus* to perform ammonium oxidation (Walker et al., 2010) and the copiotrophic  
306 character of Cryomorphaceae or Flavobacteriaceae known to contribute to heterotrophic blooms after phytoplanktonic blooms  
307 (Ho et al., 2017; Teeling et al., 2016), we propose that the succession of dominant prokaryotes observed with glucose addition  
308 reflects niche partitioning between opportunists (Vibrionaceae) and recyclers using organic matter from dead organisms  
309 (Bacteroidota) and regenerating nutrients (*Nitrosopumilus*). This hypothesis is consistent with the nutrient dynamics  
310 described above.

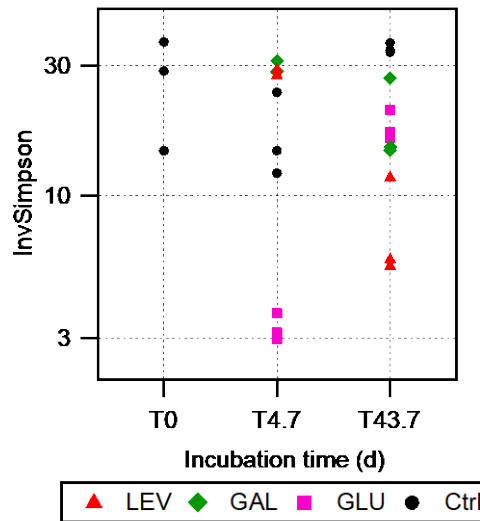
311 For levoglucosan and galactosan, the prokaryotic richness did not significantly vary in the short term ( $P > 0.05$ , Fig. 4), in  
312 coherence with the observed delay ( $> 8.7$  days) of the decay of these anhydrosugars. A significant decrease in the prokaryotic  
313 diversity was observed at the end of the incubation (43.7 days) for levoglucosan ( $P < 0.01$ ). The observed decrease was less  
314 pronounced than that observed for glucose after 4.7 days. Similarly, distance analysis did not reveal any significant change  
315 in community structure after 4.7 days of incubation, but it significantly shifted after 43.7 days of incubation with levoglucosan  
316 and galactosan compared to the initial community and the previous sampling time ( $P < 0.01$ ). This significant shift  
317 corresponded to the development of Alphaproteobacteria from the family Rhodobacteraceae, with a notable development  
318 of genera *Dinoroseobacter*, *Jannaschia* and *HIMB11*, with less consistency among replicates for the latter. For two replicates  
319 exposed to levoglucosan, Alphaproteobacteria from the Rhizobiales order were particularly enriched (Fig. 3). The SAR11 clade  
320 exhibited an important decrease in its proportion with the addition of levoglucosan. The three genera of Rhodobacteraceae  
321 selected with anhydrosugars are known to belong to the Roseobacter group (Durham et al., 2014; Wagner-Döbler et al.,  
322 2009, 2003). Their delayed selection in our experiments is consistent with the delayed growth and slow growth efficiency  
323 mentioned above. This suggests a specific enzymatic capacity of these genera for processing anhydrosugars. Very few studies  
324 have reported the bacterial mechanisms and/or metabolic pathways for levoglucosan degradation (Iwasaki et al., 2018;  
325 Kuritani et al., 2020), although it appears to be a common function/process distributed across different bacterial phyla (Kaur  
326 et al., 2023). However, the demonstration of such potential for marine bacteria including the bacterial degradation of  
327 galactosan, remains to our knowledge unknown and warrants further investigation. Nevertheless, our study suggests for the  
328 first time the association of widespread marine bacterial genera with the biodegradation of biomass burning tracers. The  
329 Roseobacter group is known for its abundance and tremendous diversity in the global ocean (Daniel et al., 2018; Luo and  
330 Moran, 2014). By suggesting the importance of specific enzymatic capacities to process semilabile compounds, this work  
331 paves the way for further research linking the molecular composition of semilabile organic compounds accumulating in  
332 epipelagic/mesopelagic waters and the diversity of the Roseobacter group.  
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**Fig. 3.** Heat trees comparing the relative variations in the most abundant (> 2%) prokaryotic taxa between the control condition and different amendments after 43.7 days. Taxa more represented in the control condition appear in dark colors while taxa enriched in levoglucosan, galactosan or glucose-amended conditions appear in red, green, or pink, respectively. Node size is related to the number of genera representing the taxa. The color intensity of edges and nodes is proportional to the enrichment of the taxa in the corresponding condition (median difference based on triplicate experiments). Light gray taxa show similar representation in the compared conditions.

341 The noteworthy heterogeneity of genera from the Roseobacter group selected among replicates with anhydrosugars  
 342 addition suggests a functional redundancy that deserves further investigation, the functional ability to process these  
 343 semilabile compounds appears to be held at the Roseobacter group scale. The demonstrated ability to exchange plasmids  
 344 between phylogenetically distant members of this group (Petersen and Wagner-Döbler, 2017) could largely contribute to  
 345 their functional redundancy. Such functional redundancy could even be extended to Rhizobiales, since the possibility of  
 346 genetic exchange between roseobacters and rhizobia has been demonstrated (Bartling et al., 2017). This could explain the  
 347 selection of some Rhizobiales in two replicates of the levoglucosan condition observed in our work.  
 348



349 **Fig. 4. Inverse Simpson index for prokaryotic richness at three incubation times.**  
 350

351

#### 352 **4. Conclusions**

353 Our findings have shown that BB tracers (levoglucosan and galactosan) can be assimilated by marine heterotrophic  
 354 prokaryotes on a time scale of a few weeks and thus may be considered as semilabile substrates. Although these two  
 355 anhydrosugars cannot entirely represent the complex biomass burning particles the present study suggests that marine  
 356 prokaryotes mostly use these substrates for cell maintenance and energetic needs (and thus carbon is mostly mineralized  
 357 into CO<sub>2</sub>). Prokaryotic diversity analyses revealed the predominance of a few bacterial genera from the Roseobacter clade  
 358 that were specifically selected by the addition of the anhydrosugars. These results suggest that the tremendous diversity of  
 359 this widespread marine bacterial clade could reflect its ability to process a large diversity of semilabile compounds (here  
 360 represented by levoglucosan and galactosan) constituting dissolved organic matter pools in surface ocean waters.

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 365

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 369

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584

585 **Competing interests**

586 The authors declare that they have no known competing financial interests or personal relationships that could have  
587 appeared to influence the work reported in this paper.

588

589 **Author contributions**

590 CP conceived and designed the study. LP collected the seawater. JMGS and CP collected all samples. JMGS and CA  
591 developed the method to determine anhydrosugars in seawater and performed the analyses. NG, FVW and BM performed  
592 the nutrient, bacterial production and bacterial diversity analyses, respectively. JMGS, CP, FVW and BM synthesized the data  
593 and write the manuscript with inputs from all authors.