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1 **Impact of dust addition on the microbial food web under present and future**
2 **conditions of pH and temperature**

3

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20 **Keywords:** bacteria, microeukaryotes, virus, community composition, top-down



21 **Abstract**

22 In the oligotrophic waters of the Mediterranean Sea, during the stratification period, the
23 microbial loop relies on pulsed inputs of nutrients through atmospheric deposition of aerosols
24 from both natural (Saharan dust) and anthropogenic origins. While the influence of dust
25 deposition on microbial processes and community composition is still not fully constrained, the
26 extent to which future environmental conditions will affect dust inputs and the microbial
27 response is not known. The impact of atmospheric wet dust deposition was studied both under
28 present and future (warming and acidification) environmental conditions through experiments in
29 300 L climate reactors. Three dust addition experiments were performed with surface seawater
30 collected from the Tyrrhenian Sea, Ionian Sea and Algerian basin in the Western Mediterranean
31 Sea during the PEACETIME cruise in May-June 2017. Top-down controls on bacteria, viral
32 processes and community, as well as microbial community structure (16S and 18S rDNA
33 amplicon sequencing) were followed over the 3-4 days experiments. Different microbial and
34 viral responses to dust were observed rapidly after addition and were most of the time higher
35 when combined to future environmental conditions. The input of nutrients and trace metals
36 changed the microbial ecosystem from bottom-up limited to a top-down controlled bacterial
37 community, likely from grazing and induced lysogeny. The composition of mixotrophic
38 microeukaryotes and phototrophic prokaryotes was also altered. Overall, these results suggest
39 that the effect of dust deposition on the microbial loop is dependent on the initial microbial
40 assemblage and metabolic state of the tested water, and that predicted warming, and acidification
41 will intensify these responses, affecting food web processes and biogeochemical cycles.



42 **1. Introduction**

43 Input of essential nutrients and trace metals through aerosol deposition is crucial to the ocean
44 surface water biogeochemistry and productivity (at the global scale: *e.g.*, Mahowald et al., 2017;
45 in the Mediterranean Sea: *e.g.*, Guieu and Ridame, 2020) with episodic fertilization events
46 driving microbial processes in oligotrophic regions such as the Pacific Ocean, the Southern
47 Ocean and the Mediterranean Sea.

48 The summer Mediterranean food web is characterized by low primary production (PP) and
49 heterotrophic prokaryotic production (more classically abbreviated as BP for bacterial
50 production) constrained by nutrient availability further limiting dissolved organic matter (DOM)
51 utilization and export, resulting in DOM accumulation. Therefore, inputs of bioavailable
52 nutrients through deposition of atmospheric particles are essential to this microbial ecosystem.
53 Indeed, these nutrient pulses have been shown to support microbial processes but the degree to
54 which the microbial food web is affected might be dependent on the degree of oligotrophy of the
55 water (Marín-Beltrán et al., 2019; Marañon et al., 2010).

56 In the Mediterranean Sea, dust deposition stimulates PP and N₂ fixation (Guieu et al., 2014;
57 Ridame et al., 2011) but also BP, bacterial respiration, virus production, grazing activities, and
58 can alter the composition of the microbial community (*e.g.*, Pulido-Villena et al., 2014; Tsiola et
59 al., 2017; Guo et al., 2016; Pitta et al., 2017; Marín-Beltrán et al., 2019). Overall, in such
60 oligotrophic system, dust deposition appears to predominantly promote heterotrophic activity
61 which will increase respiration rates and CO₂ release.

62 Anthropogenic CO₂ emissions are projected to induce an increase in seawater temperature
63 and an accumulation of CO₂ in the ocean, leading to its acidification and an alteration of ocean
64 carbonate chemistry (IPCC, 2014). In response to ocean warming and increased stratification,



65 low nutrient low chlorophyll (LNLC) regions such as the Mediterranean Sea, are projected to
66 expand in the future (Durrieu de Madron et al., 2011). Moreover, dust deposition is also expected
67 to increase due to desertification (Moulin and Chiapello, 2006). Hence, in the future ocean, the
68 microbial food web might become even more dependent on atmospheric deposition of nutrients.
69 Expected increased temperature and acidification might have complex effects on the microbial
70 loop by modifying microbial and viral and community (*e.g.*, Highfield et al., 2017; Krause et al.,
71 2012; Hu et al., 2021; Allen et al., 2020; Malits et al., 2021). While increasing temperature in
72 combination with nutrient input might enhance heterotrophic bacterial growth (Degerman et al.,
73 2012; Morán et al., 2020) more than PP (Marañón et al., 2018), future environmental conditions
74 could push even further this microbial community towards heterotrophy. But so far, the role of
75 dust on the microbial food web in future climate scenarios is unknown.

76 Here, we studied the response of Mediterranean microbial and viral communities (*i.e.*, viral
77 strategies, microbial growth, and controls, as well as community composition) to simulated wet
78 Saharan dust deposition during onboard minicosm experiments conducted in three different
79 basins of the Western and Central Mediterranean Sea under present and future projected
80 conditions of temperature and pH. To our knowledge, this is the first study assessing the effect of
81 atmospheric deposition on the microbial food web under future environmental conditions.



82 2. Material & Method

83 *2.1 Experimental set-up*

84 During the ProcEss studies at the Air-sEa Interface after dust deposition in the
85 Mediterranean sea project cruise (PEACETIME), onboard the R/V “Pourquoi Pas ?” in
86 May/June 2017, three experiments were conducted in 300 L climate reactors (minicosms) filled
87 with surface seawater collected at three different stations (Table 1), in the Tyrrhenian Sea (TYR),
88 Ionian Sea (ION) and in the Algerian basin (FAST). The experimental set-up is described in
89 details in Gazeau et al. (2020). Briefly, the experiments were conducted for 3 days (TYR and
90 ION) and 4 days (FAST) in trace metal free conditions, under light, temperature and pH-
91 controlled conditions following ambient or future projected conditions of temperature and pH.
92 For each experiment, the biogeochemical evolution of the water, after dust deposition, under
93 present and future environmental conditions was followed in three duplicate treatments: i)
94 CONTROL (C1, C2) with no dust addition and under present pH and temperature conditions, ii)
95 DUST (D1, D2) with dust addition under present environmental conditions and iii)
96 GREENHOUSE (G1, G2) with dust addition under projected temperature and pH for 2100
97 (IPCC, 2014; ca. +3 °C and -0.3 pH units). The same dust analog was used as during the DUNE
98 2009 experiments described in Desboeufs et al. (2014) and the same dust wet flux of 10 g m⁻²
99 was simulated. Such deposition event represents a high but realistic scenario, as several studies
100 reported even higher short deposition events in this area of the Mediterranean Sea (Ternon et al.,
101 2010; Bonnet and Guieu, 2006; Loÿe-Pilot and Martin, 1996). After mixing the dust analog (3.6
102 g) in 2 L of ultrahigh-purity water, this solution was sprayed at the surface of the dust amended
103 treatments (D1, D2 and G1, G2; Gazeau et al., 2020).



104 Samples were taken at t-12h (while filling the tanks), t0 (just before dust addition), t1h,
105 t6h, t12h, t24h, t48h, t72h and t96h (after dust addition, and t96h only for FAST).

106 2.2. Growth rates, mortality, and top down controls

107 BP was estimated at all sampling points from rates of ^3H -Leucine incorporation
108 (Kirchman et al., 1985; Smith and Azam, 1992) as described in Gazeau et al. (2021). Briefly,
109 triplicate 1.5 mL samples and one blank were incubated in the dark for 1-2 h in two temperature-
110 controlled incubators maintained respectively at ambient temperature for C1, C2, D1 and D2 and
111 at ambient temperature +3 °C for G1 and G2. HB, *Synechococcus*, picoeukaryotes and
112 heterotrophic nanoflagellates (HNF) abundances were measured by flow cytometry as described
113 in Gazeau et al. (2020). Bacterial cell specific growth rates were estimated assuming exponential
114 growth and a carbon to cell ration of 20 fg C cell⁻¹ (Lee and Fuhrman, 1987). Net growth rates
115 (h⁻¹) were calculated from the exponential phase of growth of BP, abundances of *Synechococcus*
116 and picoeukaryotes cells, observable from at least three successive sampling points. Mortality
117 was estimated as the difference between HB present between two successive sampling points and
118 those produced during that time.

119 2.3. Viral abundance, production and life strategy

120 Virus abundances were determined on glutaraldehyde fixed samples (0.5% final
121 concentration, Grade II, Sigma Aldrich, St Louis, MO, USA) stored at -80 °C until analysis. Flow
122 cytometry analysis was performed as described by Brussaard (2004). Briefly, samples were
123 thawed at 37 °C, diluted in 0.2 µm filtered autoclaved TE buffer (10:1 Tris-EDTA, pH 8) and
124 stained with SYBR-Green I (0.5 × 10⁻⁴ of the commercial stock, Life Technologies, Saint-Aubin,
125 France) for 10 min at 80 °C. Virus particles were discriminated based on their green fluorescence



126 and SSC during 1 min analyses (Fig. S1). All cytogram analyses were performed with the Flowing
127 Software freeware (Turku Center of Biotechnology, Finland).

128 Viral production and bacterial losses due to phages were assessed by the virus reduction approach
129 (Weinbauer et al., 2010) at t₀, t₂₄ h and t₄₈h in all six minicosms. Briefly, 3 L of seawater were-
130 filtered through 1.2- μ m-pore-size polycarbonate filter (Whatman[©]), and heterotrophic
131 prokaryotes (HB, filtrate) were concentrated by ultrafiltration (0.22 μ m pore size, Vivaflow 200[©]
132 polyethersulfone, PES) down to a volume of 50 mL. Virus-free water was obtained by filtering 1
133 L of seawater through a 30 kDa pore-size cartridge (Vivaflow 200[©], PES). Six mixtures of HB
134 concentrate (2 mL) diluted in virus-free water (23 mL) were prepared and distributed into 50 mL
135 Falcon tubes. Three of the tubes were incubated as controls, while the other three were inoculated
136 with mitomycin C (Sigma-Aldrich, 1 μ g mL⁻¹ final concentration) as inducing agent of the lytic
137 cycle in lysogenic bacteria. All tubes were incubated in darkness in two temperature-controlled
138 incubators maintained respectively at ambient temperature for C1, C2, D1 and D2 and at ambient
139 temperature +3 °C for G1 and G2. Samples for HB and viral abundances were collected every 6 h
140 for a total incubation period of 18 h.

141 The estimation of virus-mediated mortality of HB was performed according to Weinbauer et al.
142 (2002) and Winter et al. (2004). Briefly, increase in virus abundance in the control tubes represents
143 lytic viral production (VPL), and an increase in mitomycin C treatments represents total (VPT),
144 *i.e.*, lytic plus lysogenic, viral production. The difference between VPT and VPL represents
145 lysogenic production (VPLG). The frequency of lytically infected cells (FLIC) and the frequency
146 of lysogenic cells (FLC) were calculated as:

$$147 \text{ FLIC} = 100 \times \text{VPL} / \text{BS} \times \text{HB}_i \quad (1)$$

$$148 \text{ FLC} = 100 \times \text{VPLG} / \text{BS} \times \text{HB}_i \quad (2)$$



149 where HB_i is the initial HB abundance in the viral production experiment and BS is a theoretical
150 burst size of 20 viruses per infected cell (averaged BS in marine oligotrophic waters, Parada et al.,
151 2006).

152

153 2.4 DNA sampling, sequencing and sequence analysis

154 To study the temporal dynamics of the microbial diversity, water samples (3 L) were
155 collected in acid-washed containers from each minicosm at t_0 , t_{24h} , and at the end of the
156 experiments (t_{72h} at TYR and ION and t_{96h} at FAST). Samples were filtered onto 0.2 μm PES
157 filters (Sterivex©) and stored at -80°C until DNA extraction. Nucleic acids were extracted from
158 the filters using a phenol-chloroform method and DNA was then purified using filter columns from
159 NucleoSpin® PlantII kit (Macherey-Nagel©) following a modified protocol. DNA extracts were
160 quantified and normalized at $5\text{ng } \mu\text{L}^{-1}$ and used as templates for PCR amplification of the V4
161 region of the 18S rRNA (~ 380 bp) using the primers TAREuk454FWD1 and TAREukREV3
162 (Stoeck et al., 2010) and the V4-V5 region of the 16S rRNA (~ 411 bp) using the primers 515F-Y
163 ($5'$ -GTGYCAGCMGCCGCGGTAA) and 926R-R ($5'$ -CCGYCAATTYMTTTRAGTTT) (Parada
164 et al., 2016). Following polymerase chain reactions, DNA amplicons were purified, quantified and
165 sent to Genotoul (<https://www.genotoul.fr/>, Toulouse, France) for high throughput sequencing
166 using paired-end 2x250bp Illumina MiSeq. Note that although we used universal primer, Archaea
167 were mostly not detected and the prokaryotic heterotrophic communities corresponded essentially
168 to Eubacteria, therefore the taxonomic description referred to the general term 'bacterial
169 communities'

170 All reads were processed using the Quantitative Insight Into Microbial Ecology 2 pipeline
171 (QIIME2 v2020.2, Bolyen et al., 2019). Reads were truncated 350bp based on sequencing



172 quality, denoised, merged and chimera-checked using DADA2 (Callahan et al., 2016). A total of
173 714 and 3070 amplicon sequence variants (ASVs) were obtained for 16S and 18S respectively.
174 Taxonomy assignments were made against the database SILVA 132 (Quast et al., 2013) for 16S
175 and PR2 (Guillou et al., 2013) for 18S. All sequences associated with this study have been
176 deposited under the BioProject ID: PRJNA693966.

177 2.5 Statistics

178 Alpha and beta-diversity indices for community composition were estimated after
179 randomized subsampling to 26000 reads for 16S rDNA and 19000 reads for 18S rDNA. Analysis
180 were run in QIIME 2 and in Primer v.6 software package (Clarke and Warwick, 2001).
181 Differences between the samples richness and diversity were assessed using Kruskal-Wallis
182 pairwise test. Beta diversity were run on Bray Curtis dissimilarity. Differences between samples'
183 beta diversity were tested using PERMANOVA (Permutational Multivariate Analysis of
184 Variance) with pairwise test and 999 permutations. The sequences contributing most to the
185 dissimilarity between clusters were identified using SIMPER (similarity percentage). A linear
186 mixed model was performed using the R software (R Core Team, 2020) using the nlme package
187 (Pinheiro et al., 2014) to test if the amended treatments differed from the controls at t24h and
188 t72h or t96h.



189 3. Results

190 3.1. Microbial growth, mortality and top-down controls

191 Significant increases in heterotrophic bacterial cell specific growth rates were observed in
192 all experiments with dust under D and G (Fig. 1, $p \leq 0.016$ after 24 h and 72 h) relative to C, the
193 highest growth rates relative to C were observed already 24 h after dust seeding. Bacterial net
194 growth rates were also higher in D and especially in G relative to C (Table 2). *Synechococcus*
195 and picoeukaryotes net growth rates showed a similar trend (Table 2). Heterotrophic bacterial
196 mortality was also higher than in C especially at TYR and in G at ION and FAST (Fig. 1). Over
197 the course of the three experiments, the slope of the linear regression between bacterial biomass
198 and bacterial production was below 0.4 in the three treatments suggesting a weak bottom up
199 control (Fig. 2A; Ducklow, 1992). The slope decreased in D and G relative to C. Overall, the top
200 down index, as described by Morán et al. (2017), was higher in G (0.92) relative to C and D
201 (0.80). The relationship between log transformed HNF and bacterial abundance (Fig. 3B), plotted
202 according to the model in Gasol (1994), showed that HNF were below the MRA (Mean realized
203 HNF abundance) in all treatments, suggesting a top down control of HNF abundance. HNF and
204 bacteria were weakly coupled in all treatments. The relationship between total viruses and
205 bacterial abundance was weaker in D and G relative to C (Fig. S2).

206

207 3.2. Viral dynamics and processes

208 The abundance and production of virus-like particles (VLP) increased following an east
209 to west gradient (Table 1). Viral strategy (lysogenic vs. lytic replication) was also different
210 between stations, with a higher frequency of lysogenic cells (FLC) at TYR and ION (23 and



211 19%, respectively Table 1) and a higher frequency of lytically infected cells (FLIC) at FAST
212 (43%, Table 1).

213 During TYR and ION experiments, the relative contribution of VLP populations was similar
214 and stable over time with Low DNA viruses representing over 80% of the community (Figs. 3
215 and S3). The Low DNA VLP abundance was however slightly higher in D and G relative to C
216 after 24 h at TYR and significantly higher at ION after 48h ($p = 0.037$; Fig. S3). In contrast to
217 the other two stations, at FAST, Giruses were also present and increased in all treatments but
218 especially in G where they made up to 9% of the viral community at the end of the experiment
219 (Figs. 3 and S3). The abundance of high DNA viruses at FAST also increased independent of
220 treatments and accounted for 16 – 18% of the community at the end of the experiment (Figs. 3
221 and S3).

222 The sampling strategy for production and life strategies of HB viruses allowed to
223 discriminate independently the effect of i) greenhouse conditions (sampling at T0 before dust
224 addition), ii) dust addition (sampling at T24) and the combined effects of dust addition and
225 greenhouse. Lytic viral production (VPL) increased significantly at T0 in G at TYR and ION
226 compared to C ($p \leq 0.036$). The addition of dust induced higher VPL in D at TYR compared to C
227 (Fig.1). No significant impact of dust on VPL was observed in G compared to D after 24h for
228 any of the experiments. Changes in viral infection strategy were observed with G conditions at
229 T0 where, FLC decreased relative to the non-G treatments at TYR and ION, and especially at
230 FAST ($p = 0.047$). FLIC increased slightly in G at TYR and ION already at T0. Dust addition
231 had no detectable significant effect on this parameter for any experiments. Looking at the
232 relative share between lytic and lysogenic infection, dust addition favored lytic infection at TYR
233 (no lysogenic bacteria were observed after 24h) but the contribution of both infection strategies



234 remained unchanged compared to C at ION and FAST. Greenhouse conditions also favored
235 replication through lytic cycle already at T0 for all three experiments and this trend was not
236 impacted by dust addition.

237 3.3. Microbial community composition

238 Microbial community structure, bacteria and micro-eukaryotes from 16S rDNA and 18S
239 rDNA sequencing respectively, responded to dust addition in all three experiments relative to C
240 (Figs. 4 and 5). After quality controls, reads were assigned to 714 and 1443 ASVs for 16S and
241 18S respectively.

242 3.3.1. Bacterial community composition

243 The initial community composition (t-12h) was significantly different at the three stations
244 (PERMANOVA; $p = 0.001$, Fig. S4a, S5). Rapid and significant changes in the bacterial
245 community composition were observed already 24 h after dust addition (Fig. 4). Despite the
246 initial different communities, the three stations appeared to converge towards a closer
247 community composition in response to dust addition (Fig. S5). At TYR, communities in D and G
248 significantly changed 24 h after dust addition (PERMANOVA; $p = 0.001$). This cluster presented
249 no significant differences between treatments (D and G) or time (24 and 72 h). The differences
250 between C and D/G were attributed to a relative increase of ASVs related to different
251 *Alteromonas* sp., OM60 and *Pseudophaeobacter* sp. and *Erythrobacter* sp.; contribution of
252 ASVs related to SAR11 and Verrucomicrobia and *Synechococcus* decreased (Table S1a). At
253 ION, the bacterial community composition significantly changed 24 h after dust addition
254 (PERMANOVA; $p = 0.001$) and was significantly different between D and G (PERMANOVA; p
255 $= 0.032$). As observed at TYR, no further change occurred between 24 h and the end of the



256 experiment (72 h; Fig. 4). The difference between the controls and dust amended minicosms
257 were assigned to an increase of ASVs related to different *Alteromonas* sp., *Erythrobacter* sp.,
258 *Dokdonia* sp. and OM60, and a decrease of ASVs related to SAR11, *Synechococcus*,
259 Verrucomicrobia, Rhodospirillales and some Flavobacteria (Table S1b). Several ASVs related to
260 *Alteromonas* sp., *Synechococcus* sp. and *Erythrobacter* sp. were further enriched in G compared
261 D while *Dokdonia* sp. was mainly present in D. At FAST, the bacterial community after 24 h
262 only significantly changed in G (PERMANOVA; $p = 0.011$; Fig. 4). However, after 96 h, the
263 community in D and G were similar and appeared to transition back to the initial state at 96 h
264 (PERMANOVA; $p = 0.077$). The higher relative abundance in *Erythrobacter* sp., *Synechococcus*
265 sp., different ASVs related to *Alteromonas* sp. and Flavobacteria appeared to contribute mainly
266 to the difference between C and D/G (Table S1) while ASVs related to SAR11,
267 Verrucomicrobia, *Celeribacter* sp. *Thalassobius* sp. and Rhodospirillales were mainly present in
268 C (Table S1c).

269 3.3.2 Nano- and micro-eukaryotes community composition

270 The diversity of initial community was large (Fig. S5) and significantly different at the three
271 stations (PERMANOVA; $p = 0.001$; Fig. S4b). At TYR, the nano- and micro-eukaryotes
272 community responded rapidly (24 h) to dust addition (PERMANOVA; $p = 0.003$). This initial
273 high diversity disappeared after 72 h, with similar communities in all minicosms (Fig. S5). They
274 were significantly different from initial and t24h communities ($p = 0.002$ and 0.03 respectively;
275 Fig 5) in D/G. The variations at t24h were attributed to changes in the dinoflagellate
276 communities in particular to an increase in ASVs related to *Heterocapsa rotundata*,
277 Gymnodiniales and Gonyaulacales as well as to an increase in Chlorophyta (Table S2a). At ION,
278 no significant changes were observed between C and D/G after 24 h. However, after 72 h, the



279 communities were significantly different in D ($p = 0.018$) and G ($p = 0.05$) compared to the
280 communities at t24h in these treatments (Table S2B). In D, diversity was significantly higher at
281 t72h compared to t24h and to C at the same sampling time ($p = 0.036$). In contrast, diversity in G
282 at t72h was lower than at t24h and lower to the one observed in C at the same sampling time ($p =$
283 0.066 ; Fig S6). These differences were mainly attributed to changes in ASVs related to
284 dinoflagellates and to the increase at t72h of *Emiliana huxleyi* and Chlorophyta in D and G,
285 respectively (Table S2b). At FAST, significant differences were observed between the controls
286 and initial communities compared to the dust amended (D and G) treatments at t24h ($p = 0.036$).
287 No major differences were observed between D/G at t24h and t96h ($p = 0.06$). The differences
288 were mainly attributed to changes in dinoflagellates ASVs and to an increase in Acantharea and
289 *Emiliana huxleyi* in D and G treatments at t96h (Table S2c).



290 **4. Discussion**

291 Pulsed inputs of essential nutrients and trace metals through aerosol deposition are crucial to
292 surface microbial communities in LNLC regions such as the Mediterranean Sea (reviewed in
293 Guieu and Ridame, 2020). Here we assessed the impact of dust deposition on the late spring
294 microbial loop under present and future environmental conditions on the surface water of three
295 different Mediterranean basins (Tyrrhenian, TYR; Ionian, ION; and Algerian, FAST). The initial
296 conditions at the three sampled stations for the onboard experiments are described in more
297 details in Gazeau et al. (2020). Briefly, very low levels of dissolved inorganic nutrients were
298 measured at all three stations, highlighting the oligotrophic status of the waters, typical of the
299 stratified conditions observed in the Mediterranean Sea in late spring/early summer (*e.g.*, Bosc et
300 al., 2004; D'Ortenzio et al., 2005). Despite similar total chl. *a* concentrations at the three stations
301 (Gazeau et al., 2020), PP was higher at FAST (Table 1, Gazeau et al., 2021; Marañón et al.,
302 2021). The initial microbial communities differed substantially between the three stations as
303 shown by pigments (Gazeau et al., 2020), 18S and 16S rDNA sequencing (this study). DOC
304 concentrations were slightly higher at TYR where PP was the lowest (Gazeau et al., 2021). HB,
305 HNF abundances (Gazeau et al., 2020), as well as viral abundance and production increased
306 following the east to west gradient of the initial water conditions.

307 The dust addition induced similar nitrate + nitrite (NO_x) and dissolved inorganic phosphate
308 (DIP) release during all three experiments. Rapid changes were observed on plankton stocks and
309 metabolisms, suggesting that the impact of dust deposition is constrained by the initial
310 composition and metabolic state of the investigated community (Gazeau et al., 2020; 2021).
311 While no direct effect of warming and acidification was observed on the amount of nutrient
312 released from dust, Gazeau et al., (2020, 2021) showed that biological processes were generally



313 enhanced by these conditions and suggested that deposition may weaken the biological pump in
314 future climate conditions. Here we are further investigating how dust addition in present and
315 future conditions affected, on a short-term scale (≤ 4 days), the microbial trophic interactions and
316 community composition.

317 4.1. Trophic interactions after dust addition under present and future conditions

318 Parallel nutrient enrichment incubations conducted in darkness showed that *in situ*
319 heterotrophic bacterioplankton communities, were N, P co-limited at TYR, mainly P limited at
320 ION and N limited at FAST (Van Wambeke et al., 2020). However, the HB appeared to be
321 weakly bottom up controlled (Ducklow, 1992) in our experiment especially in D and G (Fig 2a).
322 Such top-down control on the bacterioplankton has been previously observed in the
323 Mediterranean Sea (Siokou-Frangou et al., 2010) and might increase under future conditions as
324 suggested by the higher top-down index in G ($G = 0.92$ vs. $C/D = 0.80$, Morán et al., 2017).

325 Bacterial mortality increased relative to controls in D and G at TYR, and only in G at ION
326 and FAST. The weak coupling between bacteria and viruses, as well as the increased virus
327 production and relative abundance of lytic cells (see below), only explained a small fraction of
328 the estimated bacterial mortality (max. 17%), suggesting an additional grazing pressure on
329 bacteria. HNF abundances increased in D at TYR and at all stations in G (Gazeau et al., 2020),
330 which could explain the increased bacterial mortality. Increased grazing rate by HNF on bacteria
331 with dust addition has been previously reported in the Eastern Mediterranean Sea (Tsiola et al.,
332 2017). While our results suggest a strong grazing pressure on bacteria, HNF appeared to be top-
333 down controlled as well (Gasol, 1994, Fig 3b), potentially by the increasing populations of
334 mixotrophic dinoflagellates or Giruses (see below). It is also possible that HB were grazed by



335 mixotrophic nanoflagellates or by larger protozoans, or that the HNF abundance was
336 underestimated by flow cytometry.

337 Considering the seasonal impact of grazing and viral mortality in the Mediterranean Sea,
338 where higher grazing pressure and lysogeny were observed in the stratified nutrient-limited
339 waters in summer (Sánchez et al., 2020), it will be important to further study the seasonal impact
340 of dust deposition on trophic interactions and indirect cascading impact on microbial dynamics
341 and community composition.

342

343 *4.2. Viral processes and community during dust enrichment in present and future conditions*

344 Viruses represent pivotal components of the marine food web, influencing genome evolution,
345 community dynamics, and ecosystem biogeochemistry (Suttle, 2007). The environmental and
346 evolutionary implications of viral infection differ depending on whether viruses establish lytic or
347 lysogenic infections. Lytic infections produce virion progeny and result in cell destruction while
348 viruses undergoing lysogenic infections can replicate as “dormant” prophages without producing
349 virions or can switch to a lytic productive cycle upon an induction event. Understanding how
350 viral processes are impacted by changes in environmental conditions, is thus crucial to better
351 constrain microbial mortality and cascading impacts on marine ecosystems. Aerosol deposition
352 was already identified as a factor that stimulates virus production and viral induced mortality of
353 bacteria in the Mediterranean Sea (Pulido-Villena et al., 2014; Tsiola et al., 2017) while the
354 impact of future environmental conditions remains more controversial (Larsen et al., 2008;
355 Brussaard et al., 2013; Maat et al., 2014; Vaqué et al., 2019; Malits et al., 2021). The combined



356 effect of aerosol deposition and future conditions of temperature and pH on the viral
357 compartment has, to our knowledge, never been investigated.

358 The rapid changes in viral production and lifestyle observed in all three experiments support the
359 idea that the viral component is sensitive to the environmental variability even on short (hourly)-
360 time scales. The dynamics in viral activities was however impacted differently depending on the
361 treatments and the experiments. Viral production increased in D and G at TYR and only in G at
362 ION and FAST. Regarding the G treatments, increase in viral production was detected before
363 dust addition for all three experiments and remained mostly unchanged for the remaining of the
364 incubation. This suggests that water warming, and acidification were responsible for most
365 changes in viral activities while dusts had no detectable impact in such conditions regardless of
366 the studied station. Based on our results, the most likely explanation for observed changes in
367 viral production is an activation of a lysogenic to lytic switch. The factors that result in prophage
368 induction are still not well constrained, but nutrients pulses and elevated temperatures have been
369 identified as potential stressors (Danovaro et al., 2011 and references therein). Consistent with
370 the observation of N, P co-limited bacterial community at TYR, it is likely that nutrients released
371 from dust upon deposition to surface water activate the productive cycle of temperate viruses at
372 this station. Such mechanism was also speculated during another dust addition study (Pulido-
373 Villena et al., 2014). Under future conditions (G), the low proportion of lysogens was associated
374 to higher frequency of lytically infected cells relative to C and D at TYR and ION. These trends
375 probably reflect an indirect effect of enhanced bacterial growth with increased temperature not
376 only on prophage induction (Danovaro et al., 2011; Vaqué et al., 2019; Mojica and Brussaard,
377 2014) but also on the kinetics of lytic infections. Intriguingly, the enhanced viral production did
378 not translate into marked changes in viral abundance. The abundance of Low DNA virus



379 population, which typically comprises virus of bacteria, actually decreased between t0 and t48h
380 pointing to possible viral decay, potentially related to an adsorption onto dust particles
381 (Weinbauer et al., 2009; Yamada et al., 2020) and the potential export of viral particle to deeper
382 water layers (Van Wambeke et al. 2020). While recurrent patterns emerged from this study, the
383 amplitude of viral responses varied between the experiments. At TYR, where heterotrophic
384 metabolism was higher, the dust addition induced higher viral production relative to controls
385 than at the two other sites, which suggests that viral processes, as other microbial processes, are
386 dependent on the initial metabolic status of the water.

387 Overall, no marked changes were observed for viral communities and abundances after dust
388 addition, both under present and future conditions relative to controls, except at FAST where the
389 abundance of Girus population increased significantly in G from t24h until the end of the
390 experiment. Giruses typically comprise large double stranded DNA viruses that infect
391 nanoeukaryotes including photosynthetic (microalgae) and heterotrophic (HNF, amoeba,
392 choanoflagellate) organisms (Brussaard and Martinez, 2008; Needham et al., 2019; Fischer et al.,
393 2010; Martínez et al., 2014). The presence of Giruses at FAST in this treatment might be
394 explained by the increase in nano-eukaryote abundances at t72h and their decline after 96 h of
395 incubation (Gazeau et al., 2020). The coccolithophore *Emiliana huxleyi* appears as one of the
396 potential host candidates for these Giruses. The abundance of *E. huxleyi* increased in D and G at
397 this station and this phytoplankter is known to be infected by such giant viruses (Jacquet et al.,
398 2002; Schroeder et al., 2002; Pagarete et al., 2011). It is not clear from our results whether
399 increased Girus abundance is due to the greenhouse effect only (as discussed above for viruses of
400 HB) or the combination of dust addition and greenhouse effects. While temperature warming
401 was shown to accelerate viral production in several virus – phytoplankton systems (Mojica and



402 Brussaard 2014, Demory et al. 2017), a temperature-induced resistance to viral infection was
403 specifically observed in *E. huxleyi* (Kendrick et al., 2014). Previous experiments have also
404 reported a negative impact of acidification on *E. huxleyi* virus dynamics (Larsen et al., 2008). By
405 contrast, nutrient release following dust seeding could indirectly stimulate *E. huxleyi* virus
406 production (Bratbak et al., 1993) or induced switching between non-lethal temperate to lethal
407 lytic stage (Knowles et al., 2020) under future conditions. Targeted analyses are of course
408 required to identify the viral populations selected in G and the outcomes of their infection.
409 Nonetheless, this is the first time, to our knowledge, that dust deposition and enhanced
410 temperature and acidification have been shown to induce the proliferation of G viruses. The impact
411 of dust deposition under future environmental conditions on the viral infections processes could
412 have significant consequences for microbial evolution, food web processes, biogeochemical
413 cycles, and carbon sequestration.

414

415 4.3 Microbial community dynamic after dust addition under present and future conditions

416 While changes in bacterial community composition during various type of dust addition
417 experiments have shown only minor transient responses (e.g., Marañón et al., 2010; Hill et al.,
418 2010; Laghdass et al., 2011; Pulido-Villena et al., 2014; Marín-Beltrán et al., 2019), here
419 microbial community structure showed quick, significant and sustained changes in response to
420 dust addition in all three experiments. Similar to other parameters observed during these
421 experiments (discussed above and in Gazeau et al., 2020; Gazeau et al., 2021), the degree of
422 response in terms of community composition was specific to the tested waters.



423 At TYR, where primary production was low, only transient changes after 24 h of incubation
424 were observed, before the micro-eukaryotes community converged back close to initial
425 conditions. In contrast, the bacterial community significantly and rapidly changed after 24 h and
426 remained different after 72 h. At FAST, where the addition of dust appeared to promote
427 autotrophic processes, the micro-eukaryotes community responded quickly 24 h after dust
428 addition, while minor and delayed changes, probably related to the lower BP growth rates
429 compared to the other tested waters, were observed in the bacterial community. At ION both
430 eukaryotes and bacterial community responded to dust addition. The delayed response of micro-
431 eukaryotes after 72 h compared to the quick bacterial response at 24 h suggests that HB were
432 better at competing for nutrient inputs at this station and that autotrophic processes may be
433 responding to bacterial nutrient regeneration after a lag phase, further suggesting the tight
434 coupling between heterotrophic bacteria and phytoplankton at this station. The combined effect
435 of decreased pH and elevated temperature on marine microbes is not yet well understood
436 (reviewed in O'Brien et al., 2016). The absence of significant community changes at TYR and
437 FAST while changes were observed at ION, suggests that the response might be dependent on
438 other environmental factors, which need to be further studied.

439 Dust addition likely favors certain group of micro-organisms, suggesting a quicker response
440 of fast growing/copiotrophic groups as well as the increase of specialized functional groups (Guo
441 et al., 2016; Westrich et al., 2016; Maki et al., 2016). Potential toxicity effects of metals released
442 from dust/aerosols on certain micro-organisms have also been reported (Paytan et al., 2009;
443 Rahav et al., 2020). Here, the micro-eukaryotic community was dominated by a diverse group of
444 dinoflagellates which were responsible for the main variations between treatments at all stations.
445 The overwhelming abundance of dinoflagellates sequences over other micro-eukaryotes could be



446 biased by the large genomes and multiple ribosomal gene copies per genome found in
447 dinoflagellates (Zhu et al., 2005) or due to their preferential amplification. However, the
448 dominance of dinoflagellates in surface water at this time of the year in the Mediterranean Sea is
449 not uncommon (García-Gómez et al., 2020) and was also observed in surface waters of the three
450 sampled stations by Imaging Flow Cytobot (Marañón et al., 2021). While pigment data suggest
451 an increase of haptophytes and pelagophytes in D (Gazeau et al., 2020), the sequencing data only
452 show the presence of *Emiliana huxleyi* as responsible for some of the community changes after
453 dust addition at ION and FAST. These pigments could also indicate the presence of
454 dinoflagellates through tertiary endosymbiosis, in particular *Karlodinium* sp. (Yoon et al., 2002;
455 Zapata et al., 2012), which is an important mixotrophic dinoflagellate (Calbet et al., 2011)
456 observed in D and G at ION and FAST. The variations in dinoflagellate groups might have
457 important trophic impacts due to their diverse mixotrophic states (Stoecker et al., 2017) and the
458 effect of dust addition on mixotrophic interactions should be further studied to better understand
459 the cascading impact of dust on food webs and the biological pump.

460 Positive to toxic impacts on cyanobacteria have been reported from atmospheric deposition
461 experiments (e.g., Paytan et al., 2009; Zhou et al., 2021). Here, *Synechococcus* appeared to be
462 inhibited at TYR while it was enhanced at ION and FAST, especially under future conditions
463 (this study, Gazeau et al., 2020). The same ASVs appeared to be inhibited at TYR and ION
464 while promoted at FAST and a different ASVs increased at ION. *Synechococcus* has recently
465 been shown to be stimulated by wet aerosol addition in P-limited conditions but inhibited in N-
466 limited conditions, in the South China Sea (Zhou et al., 2021). It was also shown to be repressed
467 by dust addition in nutrient limited tropical Atlantic (Marañón et al., 2010). This suggests that



468 different *Synechococcus* ecotypes (Sohm et al., 2016) might respond differently to dust addition
469 depending on the initial biogeochemical conditions of the water.

470 In the three experiments, the main bacterial ASVs responsible for the differences between
471 the control and treatments were closely related to different *Alteromonas* strains. *Alteromonas* are
472 ubiquitous in marine environment and can respond rapidly to nutrient pulses (López-Pérez and
473 Rodríguez-Valera, 2014). Some *Alteromonas* are capable to grow on a wide range of carbon
474 compounds (Pedler et al., 2014). They can produce iron binding ligands (Hogle et al., 2016) to
475 rapidly assimilate Fe released from dust. Thus, they could have significant consequences for the
476 marine carbon and Fe cycles during dust deposition events. Other copiotrophic γ -Proteobacteria,
477 such as *Vibrio*, have been observed to bloom after dust deposition in the Atlantic Ocean
478 (Westrich et al., 2016). Guo et al. (2016) using RNA sequencing, also show that γ -Proteobacteria
479 quickly outcompete α -Proteobacteria (mainly SAR11 and Rhodobacterales) that were initially
480 more active. Here, while SAR11 relative abundance decreased in all experiments after 24h, other
481 α -Proteobacteria related to the aerobic anoxygenic phototroph (AAP) *Erythrobacter* sp.,
482 increased in response to dust, in particular under future conditions. Other AAP, such as OM60,
483 also responded to dust addition in our experiment and in the Eastern Mediterranean Sea (Guo et
484 al., 2016). Fast growing AAP might quickly outcompete other HB by supplementing their
485 growth with light derived energy (e.g., Koblížek, 2015). They have also been shown to be
486 stimulated by higher temperature (Sato-Takabe et al., 2019). AAP response to dust and future
487 conditions could have a significant role in marine biogeochemical cycles.

488 5. Conclusion

489 The microbial food web response to dust addition was dependent on the initial state of the
490 microbial community in the tested waters. A different response in trophic interactions and



491 community composition of the microbial food web, to the wet dust addition, was observed at
492 each station. Generally greater changes were observed in future conditions. Pulsed input of
493 nutrients and trace metals changed the microbial ecosystem from bottom-up limited to a top-
494 down controlled bacterial community, likely from grazing and induced lysogeny. The
495 composition of mixotrophic microeukaryotes and phototrophic prokaryotes was also altered.

496 Overall, the impact of such simulated pulsed nutrient deposition will depend on the initial
497 biogeochemical conditions of the ecosystem, with likely possible large impact on microbial
498 trophic interactions and community structure. All effects might be generally enhanced in future
499 climate scenarios. The impact of dust deposition on metabolic processes and consequences for
500 the carbon and nitrogen cycles and the biological pump based on these minicosm experiments
501 are further discussed in Gazeau et al. (2021), and the *in situ* effect of a wet dust deposition event
502 is explored in Van Wambeke et al. (2020), in this special issue.

503 **6. Data availability**

504 Guieu et al., Biogeochemical dataset collected during the PEACETIME cruise. SEANOE.
505 <https://doi.org/10.17882/75747> (2020). All sequences associated with this study have been
506 deposited under the BioProject ID: PRJNA693966.

507 508 **7. Author contributions**

509 FG and CG designed the experiment. All authors participated in sampling or sample
510 processes. JD analyzed the data and wrote the paper with contributions from all authors.

511 **8. Competing interests**

512 The authors declare that they have no conflict of interest.



513 **9. Special issue statement**

514 This article is part of the special issue ‘Atmospheric deposition in the low-nutrient–low-
515 chlorophyll (LNLC) ocean: effects on marine life today and in the future (ACP/BG inter-
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522

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533

534 **12. References**



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858 Tables and Figures

859 **Table1:** Initial conditions (t-12h) at the three stations sampled for the dust addition experiments. Other
 860 parameters are presented in more details in Gazeau et al. (2020; 2021)

Variables	TYR	ION	FAST
Location	Tyrrhenian Basin	Ionian Basin	Algerian Basin
Coordinates	39.34N, 12.60E	35.49N, 19.78E	37.95N, 2.90E
Temperatures (°C)	20.6	21.2	21.5
DOC (μM) ²	72.2	70.2	69.6
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$) ¹	0.063	0.066	0.072
BP ($\text{ng C L}^{-1} \text{h}^{-1}$) ²	11.6	15.1	34.6
Bacterial abundance ($\times 10^5 \text{ cells mL}^{-1}$) ¹	4.79	2.14	6.15
Viral abundance ($\times 10^6 \text{ VLP mL}^{-1}$)	3.01	1.44	2.79
% Lysogenic bacteria FLC	22.7	19.4	7.8
% Lytic bacteria FLIC	17.5	37.2	42.7
Viral production ($\times 10^4 \text{ VLP mL}^{-1} \text{h}^{-1}$)	2.05	1.36	7.99
HNF abundance (cells mL^{-1}) ¹	110	53	126
Diatoms (cells L^{-1}) ¹	340	900	1460
Dinoflagellates (cells L^{-1}) ¹	2770	3000	3410
Ciliates (cells L^{-1}) ¹	270	380	770

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862 DOC: dissolved organic carbon, * BP: heterotrophic prokaryotic production, HNF: Heterotrophic
 863 nanoflagellates

864 ¹Results presented in Gazeau et al. 2020

865 ²Results presented in Gazeau et al. 2021

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868 **Table 2.** Net growth rates (h^{-1}) calculated from the exponential phase of growth of BP,
 869 abundances of *Synechococcus* and picoeukaryotes cells, observable from at least three
 870 successive sampling points. Values \pm standard error are shown, as well as the period of
 871 exponential phase (period, in days). nd: no significant exponential phase noted.

			C1	C2	D1	D2	G1	G2
TYR	μ_{BP}^{app}	mean \pm sd	0.076 \pm 0.025	0.066 \pm 0.018	0.116 \pm 0.008	0.194 \pm 0.02	0.164 \pm 0.019	0.1503 \pm 0.003
		period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
TYR	μ_{syn}^{app}	mean \pm sd	nd	nd	nd	nd	0.014 \pm 0.05	0.033 \pm 0.003
		Period					2 - 3	2 - 3
TYR	$\mu_{picoeuk}^{app}$	mean \pm sd	nd	nd	nd	nd	0.024 \pm 0.004	nd
		period					2 - 3	
ION	μ_{BP}^{app}	mean \pm sd	0.042 \pm 0.007	0.041 \pm 0.005	0.09 \pm 0.02	0.14 \pm 0.006	0.13 \pm 0.01	0.14 \pm 0.03
		Period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
ION	μ_{syn}^{app}	mean \pm sd	nd	nd	0.011 \pm 0.001	0.015 \pm 0.001	0.038 \pm 0.002	0.045 \pm 0.008
		Period			0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
ION	$\mu_{picoeuk}^{app}$	mean \pm sd	0.018 \pm 0.001	0.012 \pm 0.007	0.043 \pm 0.014	0.034 \pm 0.014	0.057 \pm 0.012	0.053 \pm 0.008
		Period	0.5 - 3	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
FAST	μ_{BP}^{app}	mean \pm sd	0.020 \pm 0.002	0.026 \pm 0.003	0.089 \pm 0.014	0.090 \pm 0.007	0.12 \pm 0.005	0.16 \pm 0.014
		Period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
FAST	μ_{syn}^{app}	mean \pm sd	0.022 \pm 0.002	0.024 \pm 0.002	0.039 \pm 0.001	0.045 \pm 0.003	0.064 \pm 0.001	0.063 \pm 0.001
		Period	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
FST	$\mu_{picoeuk}^{app}$	mean \pm sd	0.020 \pm 0.002	0.012 \pm 0.001	0.023 \pm 0.004	0.026 \pm 0.001	0.040 \pm 0.002	0.034 \pm 0.005
		Period	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2

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881 **Figure legends:**

882 **Figure 1.** Bacterial and viral parameters in the three experiments (TYR, ION and FAST) in each minicosm
883 (D1, D2, G1 and G2). The values are normalized to the controls: the data are presented as the difference
884 between the treatments and the mean value of the duplicate controls. The first row represents the
885 bacterial cell specific growth rates and relative mortality rates at t24h after dust addition. The second
886 row represents the relative viral productions at t24h and at T0 for the G treatments. The last row
887 represents the viral strategies: the percentages of lytic (FLIC) or lysogenic (FLC) cells at t24h and at T0 for
888 the G treatments.

889 **Figure 2.** (A) Log-log linear regression between bacterial biomass and bacterial production, dotted lines
890 represent linear regressions for each treatment. (B) Relationships between log HNF abundance and log
891 bacterial prey abundance. Solid black and dotted black lines corresponds to the Mean Realized HNF
892 Abundance (MRA) and theoretical Maximum Attainable HNF Abundance line (MAA) respectively. The
893 samples are grouped per treatments.

894 **Figure 3.** Relative abundance of viral populations at the initial (*in situ*: at t-12h before dust addition) and
895 final time points in all minicosms (C1, C2, D1, D2, G1 and G2) during the three experiments (TYR, ION
896 and FAST).

897 **Figure 4.** nMDS plot of bacterial community composition over the course of the three experiments
898 based on Bray-Curtis dissimilarities of 16S rDNA sequences. Samples clustering at different level of
899 similarity are circled together. All circles represent clusters which are significantly different from each
900 other ($p < 0.05$) based on a PERMANOVA test.

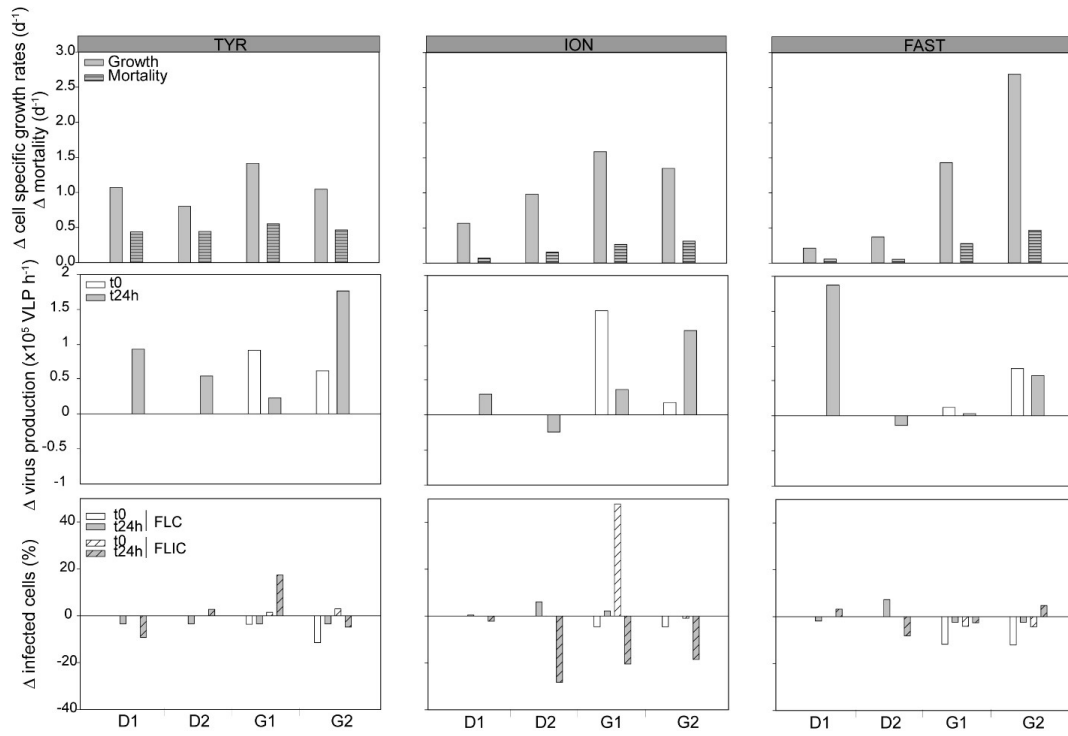
901 **Figure 5.** nMDS plot of micro-eukaryotes community composition over the course of the three
902 experiments based on Bray-Curtis dissimilarities of 18S rDNA sequences. Samples clustering at different
903 level of similarity are circled together. All circles represent clusters which are significantly different ($p <$
904 0.05) from each other based on a PERMANOVA test.

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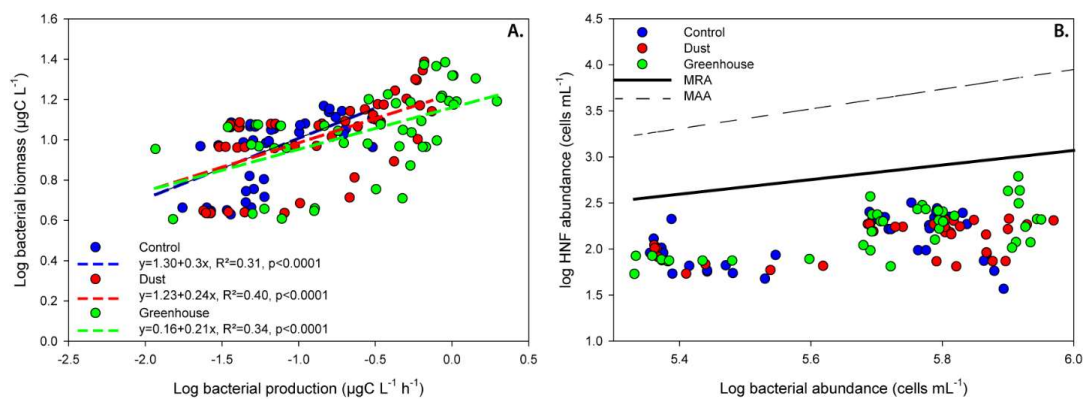


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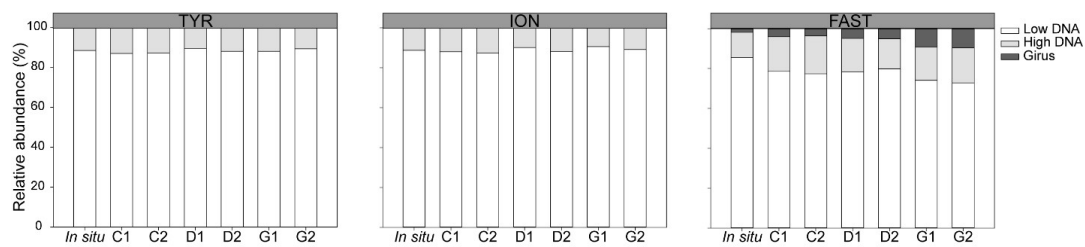
909 **Figure 1.**



910 **Figure 2.**

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913

914 **Figure 3.**

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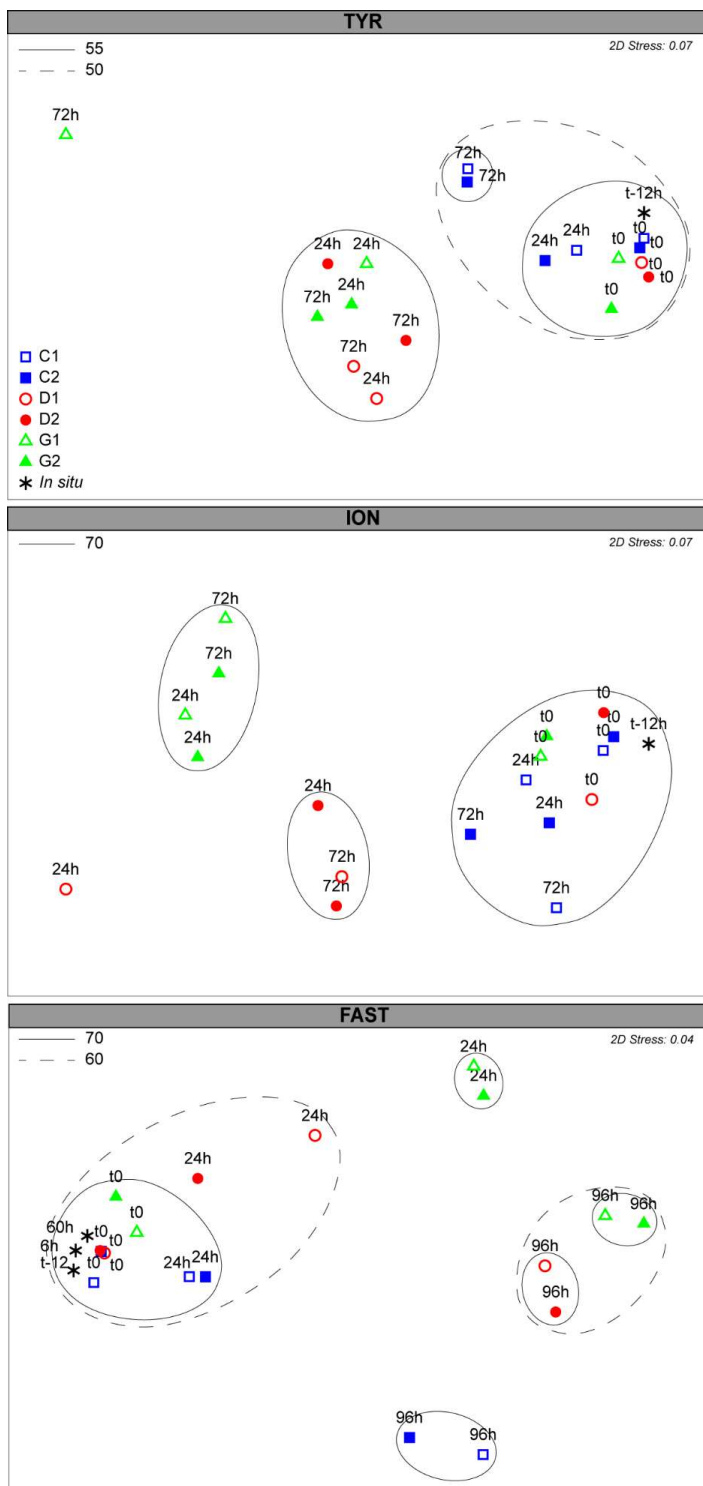


Figure 4.



Figure 5.