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

Julie Dinasquet[1,2*], Estelle Bigeard[3], Frédéric Gazeau[4], Farooq Azam[1], Cécile Guieu[4], Emilio Marañón[5], Céline Ridame[6], France Van Wambeke[7], Ingrid Obernosterer[2] and Anne-Claire Baudoux[3]

[1] Marine Biology Research Division, Scripps Institution of Oceanography, UCSD, USA

[2] Sorbonne Université, CNRS, Laboratoire d'Océanographie Microbienne, LOMIC, France

[3] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR 7144 Adaptation et Diversité en Milieu Marin, France

[4] Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, 06230 Villefranche-sur-Mer, France

[5] Department of Ecology and Animal Biology, Universidade de Vigo, Spain

[6] CNRS-INSU/IRD/MNHN/UPMC, LOCEAN: Laboratoire d'Océanographie et du Climat: Expérimentation et Approches Numériques, UMR 7159

[7] Aix-Marseille Université, CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography, UM110, France

[*]Corresponding: jdinasquet@ucsd.edu, present address: Center for Aerosol Impact on Chemistry of the Environment (CAICE), Scripps Institution of Oceanography, UCSD, USA

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Abstract

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

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1. Introduction

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

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

In the Mediterranean Sea, dust deposition stimulates PP and N_2 fixation (Guieu et al., 2014; Ridame et al., 2011) but also BP, bacterial respiration, virus production, grazing activities, and can alter the composition of the microbial community (*e.g.,* Pulido-Villena et al., 2014; Tsiola et al., 2017; Guo et al., 2016; Pitta et al., 2017; Marín-Beltrán et al., 2019). Overall, in such oligotrophic system, dust deposition appears to predominantly promote heterotrophic activity which will increase respiration rates and CO_2 release.

Anthropogenic CO_2 emissions are projected to induce an increase in seawater temperature and an accumulation of CO_2 in the ocean, leading to its acidification and an alteration of ocean carbonate chemistry (IPCC, 2014). In response to ocean warming and increased stratification,

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

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

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2. Material & Method

2.1 Experimental set-up

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

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

2.2. Growth rates, mortality, and top down controls

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

2.3. Viral abundance, production and life strategy

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

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

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

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

$$FLIC = 100 \times VPL / BS \times HB_i \quad (1)$$

$$FLC = 100 \times VPLG / BS \times HB_i \quad (2)$$

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

2.4 DNA sampling, sequencing and sequence analysis

To study the temporal dynamics of the microbial diversity, water samples (3 L) were collected in acid-washed containers from each minicosm at t0, t24h, and at the end of the experiments (t72h at TYR and ION and t96h at FAST). Samples were filtered onto 0.2 µm PES filters (Sterivex©) and stored at -80 °C until DNA extraction. Nucleic acids were extracted from the filters using a phenol-chloroform method and DNA was then purified using filter columns from NucleoSpin® PlantII kit (Macherey-Nagel©) following a modified protocol. DNA extracts were quantified and normalized at 5ng μL^{-1} and used as templates for PCR amplification of the V4 region of the 18S rRNA (~380 bp) using the primers TAReuk454FWD1 and TAReukREV3 (Stoeck et al., 2010) and the V4-V5 region of the 16S rRNA (~411 bp) using the primers 515F-Y (5'-GTGYCAGCMGCCGCGGTAA) and 926R-R (5'-CCGYCAATTYMTTTRAGTTT) (Parada et al., 2016). Following polymerase chain reactions, DNA amplicons were purified, quantified and sent to Genotoul (https://www.genotoul.fr/, Toulouse, France) for high throughput sequencing using paired-end 2x250bp Illumina MiSeq. Note that although we used universal primer, Archaea were mostly not detected and the prokaryotic heterotrophic communities corresponded essentially to Eubacteria, therefore the taxonomic description referred to the general term 'bacterial communities'

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

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

2.5 Statistics

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

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3. Results

3.1. Microbial growth, mortality and top-down controls

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

3.2. Viral dynamics and processes

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

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

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

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

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

3.3. Microbial community composition

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

3.3.1. Bacterial community composition

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

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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., *Synechoccocus*
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

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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).

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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

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

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

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

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

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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

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

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

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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 *Emiliania 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

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

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

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

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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

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

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

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

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

5. Conclusion

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

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

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

6. Data availability

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

7. Author contributions

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

8. Competing interests

The authors declare that they have no conflict of interest.

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9. Special issue statement

This article is part of the special issue 'Atmospheric deposition in the low-nutrient–low-chlorophyll (LNLC) ocean: effects on marine life today and in the future (ACP/BG inter-journal SI)'. It is not associated with a conference.

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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 *a* (µg L^{-1})[1]	0.063	0.066	0.072
BP (ng C L^{-1} h^{-1})[2]	11.6	15.1	34.6
Bacterial abundance (x10^5 cells mL^{-1})[1]	4.79	2.14	6.15
Viral abundance (x 10^6 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 (x 10^4 VLP mL^{-1} 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 [1]Results presented in Gazeau et al. 2020
865 [2]Results 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 ± 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	µapp BP	mean ± sd	0.076 ± 0.025	0.066 ± 0.018	0.116 ± 0.008	0.194 ± 0.02	0.164 ± 0.019	0.1503 ± 0.003
		period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
TYR	µapp syn	mean ± sd	nd	nd	nd	nd	0.014 ± 0.05	0.033 ± 0.003
		Period					2 - 3	2 - 3
TYR	µapp picoeuk	mean ± sd	nd	nd	nd	nd	0.024 ± 0.004	nd
		period					2 - 3	
ION	µapp BP	mean ± sd	0.042 ± 0.007	0.041 ± 0.005	0.09 ± 0.02	0.14 ± 0.006	0.13 ± 0.01	0.14 ± 0.03
		Period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
ION	µapp syn	mean ± sd	nd	nd	0.011± 0.001	0.015 ±0.001	0.038± 0.002	0.045 ± 0.008
		Period			0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
ION	µapp picoeuk	mean ± sd	0.018 ± 0.001	0.012 ± 0.007	0.043 ± 0.014	0.034 ± 0.014	0.057 ± 0.012	0.053 ± 0.008
		Period	0.5 - 3	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
FAST	µapp BP	mean ± sd	0.020 ± 0.002	0.026± 0.003	0.089 ± 0.014	0.090 ± 0.007	0.12 ± 0.005	0.16 ± 0.014
		Period	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5	0 - 0.5
FAST	µapp syn	mean ± sd	0.022 ± 0.002	0.024 ± 0.002	0.039 ± 0.001	0.045 ± 0.003	0.064 ± 0.001	0.063 ± 0.001
		Period	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2	0.5 - 2
FST	µapp picoeuk	mean ± sd	0.020 ± 0.002	0.012 ± 0.001	0.023± 0.004	0.026 ± 0.001	0.040 ± 0.002	0.034 ± 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 raw represents the
885 bacterial cell specific growth rates and relative mortality rates at t24h after dust addition. The second
886 raw represents the relative viral productions at t24h and at T0 for the G treatments. The last raw
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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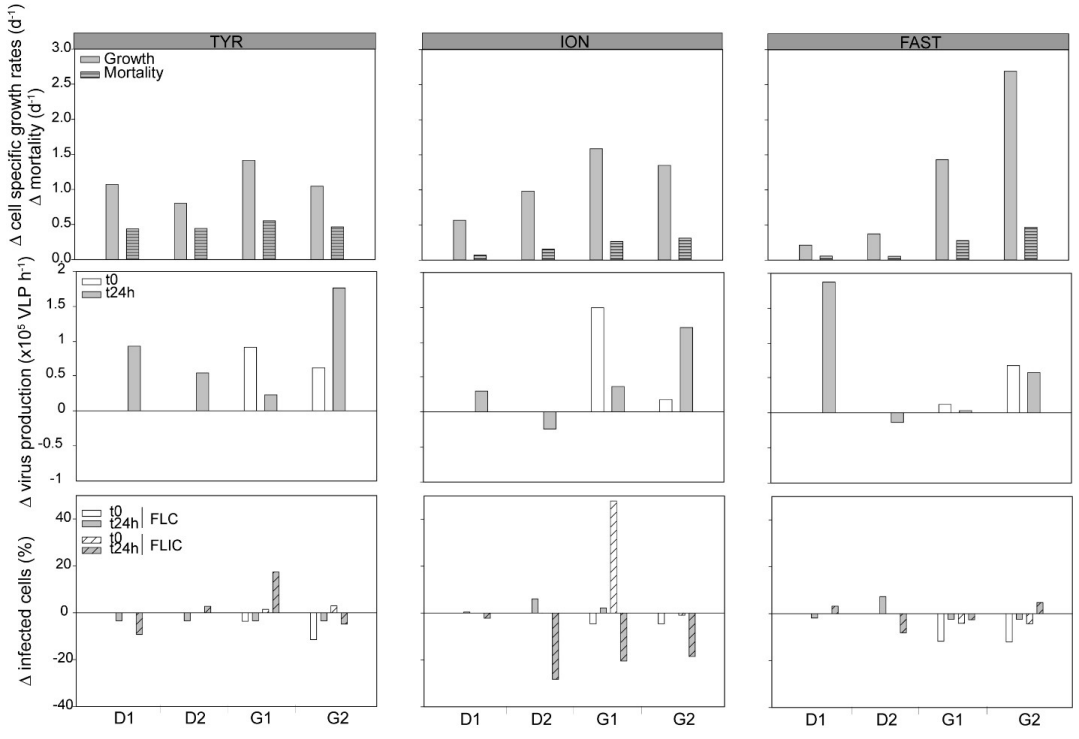

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909 **Figure 1.**

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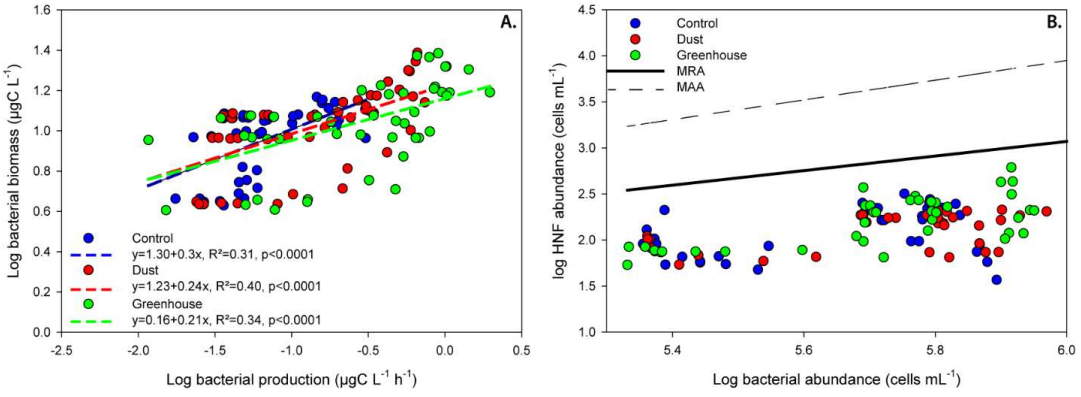

910 **Figure 2.**

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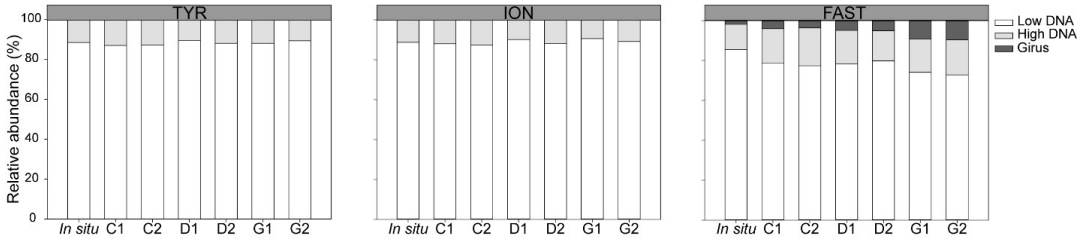

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914 **Figure 3.**

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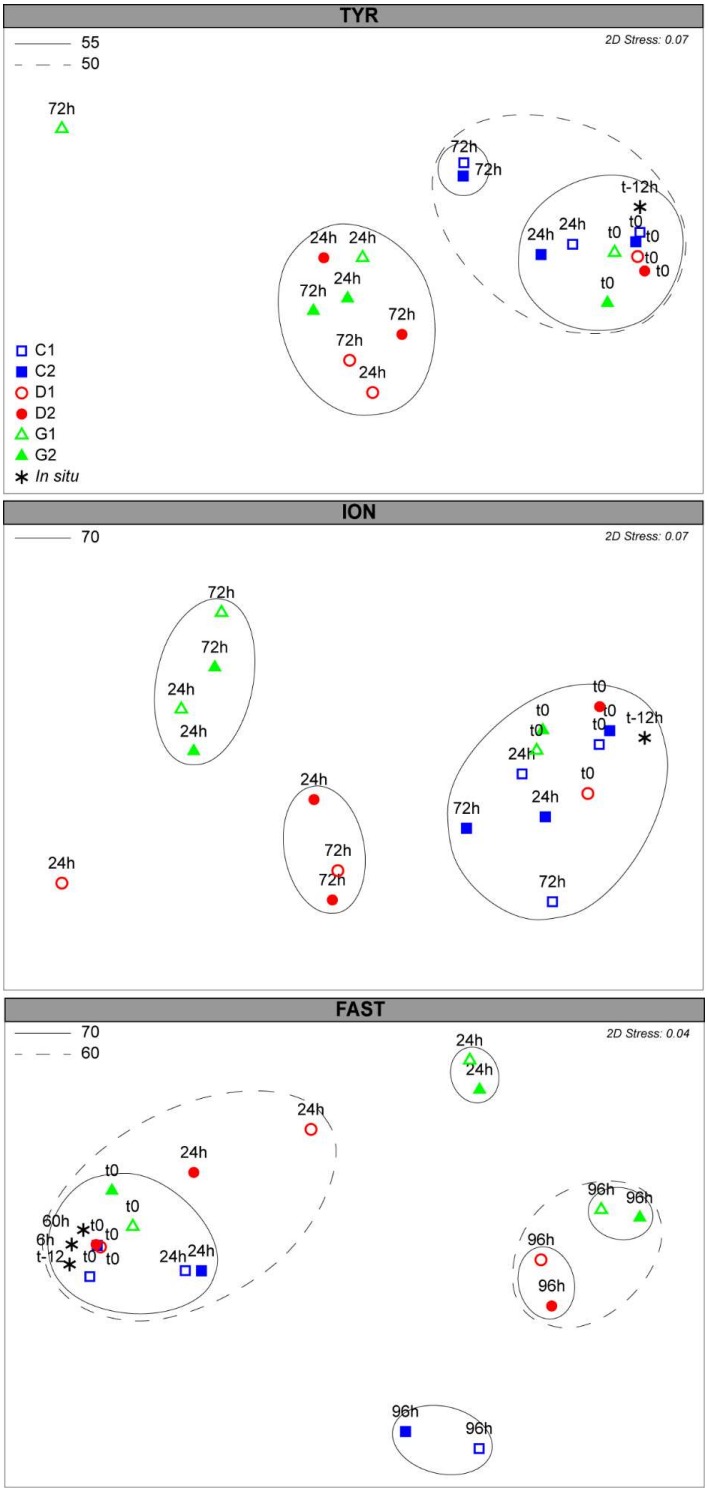

Figure 4.

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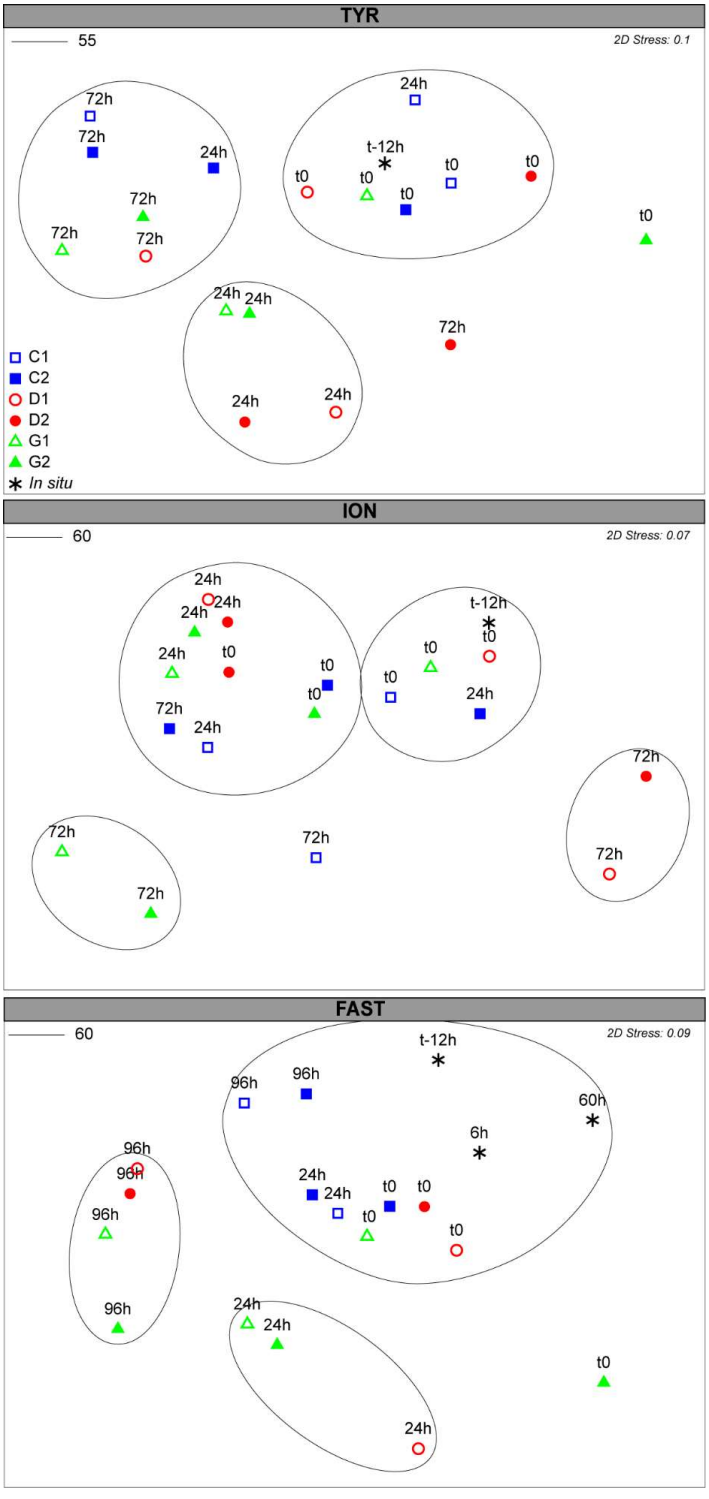

Figure 5.