Impact of grazing, resource availability and light on prokaryotic growth and diversity in the oligotrophic surface global ocean

by

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Originality-Significance Statement:

We manipulated natural microbial communities in order to get insight into what controls growth and community composition of prokaryotes in the global oligotrophic ocean. The reduction of grazing pressure, by itself, essentially caused an increase in prokaryotic growth and a moderate decrease in community richness, while the increase in resource availability, by itself, enhanced growth at the level of community but systematically reduced populations of well-known oligotrophic taxa such as SAR11 and *Prochlorococcus*. By contrast, light exposure did not result in a significant re-structuration of the prokaryotic community. There was, however, an overall negative effect of light exposure on growth rates and community richness which, interestingly, seemed to be related to a poor acclimation of prokaryotic communities to the high incident irradiances associated to relatively deep mixed layers.

Summary

The impact of grazing, resource competition and light on prokaryotic growth and taxonomic composition in subtropical and tropical surface waters was studied through 10 microcosm experiments conducted between 30ºN and 30ºS in the Atlantic, Pacific and Indian oceans. Under natural sunlight conditions, significant changes in taxonomic composition were only observed after the reduction of grazing by sample filtration in combination with a decrease in resource competition by sample dilution. Sunlight exposure significantly reduced prokaryote growth (11±6%) and community richness (14±4%) compared to continuous darkness but did not significantly change community composition. The largest growth inhibition after sunlight exposure occurred at locations showing deep mixed layers. The reduction of grazing had an expected and significant positive effect on growth, but caused a significant decrease in community richness (16±6%), suggesting that the coexistence of

many different OTUs is partly promoted by the presence of predators. Dilution of the grazer-free prokaryotic community significantly enhanced growth at the level of community, but consistently and sharply reduced the abundance of *Prochlorococcus* and SAR11 populations. The decline of these oligotrophic bacterial taxa following an increase in resource availability is consistent with their high specialization for exploiting the limited resources available in the oligotrophic warm ocean.

Introduction

The abundance and impact of marine microbes on biogeochemical processes depend on the balance between their growth and mortality rates (Strom, 2008; Kirchman, 2016). The growth rates of prokaryotes living in the pelagic realm are largely limited by the availability of inorganic nutrients and/or organic carbon (Carlson and Ducklow, 1996; Caron et al., 2000; Martínez-Garcia et al., 2010; Hale et a.l, 2017), while the main sources of mortality are viral lysis and grazing by protists (Fuhrman and Noble, 1995; Pernthaler, 2005; Kirchman, 2016). Besides controlling the standing stock of prokaryotic communities, predators and viruses may also affect community composition likely through selective grazing and host specificity (Jürgens and Matz, 2002; Pernthaler, 2005; Corno and Jürgens,2008; Cram et al., 2016), although some theoretical models predict that protistan predation should have little effect on bacterial community composition (Thingstad and Lignell 1997; Thingstad, 2000). An experimental study by Baltar et al. (2016) concluded that protist predation does not significantly alter bacterioplankton community composition in the Mediterranean Sea. Depending on the environmental characteristics, microbial communities may be controlled by bottom-up factors (i.e. nutrient availability), top-down factors (grazing or viral lysis), as well as by temperature (Sunagawa et al., 2015; Morán et al., 2017) and light (Ruiz-González

et al., 2013; Richert et al., 2015, Sánchez et al., 2017) in a changing balance. In oligotrophic waters, it has been suggested that bacterial abundance and production are fundamentally determined by nutrient supply (Sanders et al., 1992), whereas other authors have found that grazing pressure on bacteria is also a relevant regulatory factor (Caron et al., 2000; Gasol et al., 2002; Silva et al., 2019).

Compared to the role of nutrients and predators on microbial dynamics, the effect of light on prokaryotes has only been extensively studied in the last two decades (see review by Ruiz-González et al., 2013). Sunlight affects marine prokaryotes in different ways: some organisms, such as cyanobacteria, need light for survival as well as for growth, others, such as the aerobic anoxygenic phototrophic (AAP) bacteria or proteorhodopsin-containing organisms, are stimulated by light (Kolber et al., 2000; Bejá et al., 2001; Gómez-Consarnau et al., 2007; Straza and Kirchman, 2011, Ferrera et al. , 2017), and others, such as members of the SAR11 clade, can be sensitive to solar UV radiation (Alonso-Sáez et al., 2006; Ruiz-González et al., 2012, Matallana-Surget et al., 2012). These multiple effects are likely to translate into complex prokaryotic community responses to variations in sunlight exposure (Langenheder et al., 2006; Manrique et al., 2012; Richert et al., 2015). The magnitude of such alterations probably depends not only on the spectral quality and intensity of the incident radiation but also on nutrient availability (Morán et al. 2001) and the previous light exposure history, both largely modulated by water column vertical mixing (Bertoni et al., 2011; Matallana-Surget et al., 2012; Ruiz-González et al., 2012; 2013, Galí et al., 2013).

To the best of our knowledge, the experimental assessment of the importance of top-down and bottom-up controls jointly with light as regulating factors of prokaryotic community composition and growth, has not been systematically assessed in the oligotrophic surface ocean. The permanent stratification of tropical and subtropical oceans reduces

nutrient supply to the upper layers (Longhurst, 2010), originating a large nutrient-depleted habitat where light intensity and depth penetration are large (Tedetti and Sempéré, 2006). These conditions favor the selection of oligotrophic (Lauro et al., 2009; Overmann and Lepleux, 2016), and high-irradiance acclimated taxa (Alonso-Saez et al., 2006; Kataoka et al., 2009; Santos et al., 2011; Ruiz-Gonzalez et al., 2012, 2013). *Pelagibacter* (SAR11) and *Prochlorococcus* are two well-known genera representative of the oligotrophic lifestyle (Overmann and Lepleux, 2016). These two genera typically dominate the surface waters of tropical and subtropical oceanic biomes (Partensky et al., 1999; Morris et al., 2002) and share a set of adaptations, such as the ability to exploit light and small cell and genome sizes, allowing them to thrive in extremely diluted and illuminated environments (Biller et al., 2015; Giovanonni, 2017).

To evaluate the importance of top-down and bottom-up controls as well as solar radiation on prokaryotic growth and taxonomic community composition in surface waters of the tropical and subtropical oceans, we conducted microcosm experiments at 10 stations located between 30 ºN and 30ºS in the Atlantic (4 experiments), Pacific (4 experiments) and Indian (2 experiments) oceans from December 2010 to June 2011. We manipulated grazing pressure through 0.8 μm sample filtration, resource availability through dilution of the filtered samples with 0.2 μm filtered seawater, and solar radiation by exposing filtered and diluted samples either to the natural full sunlight spectrum or to total darkness. Growth rates at the community level were estimated from biomass and production data, while community composition was explored using high-throughput 16S rRNA amplicon sequencing. We hypothesize that resource competition and solar radiation are key determinants of community composition, while grazing mostly affects growth of prokaryotes inhabiting these regions.

Results

Initial conditions

Seawater for the experiments was collected from 3 m depth at 10 sampling sites (Fig. 1a). A relatively wide range of initial conditions was observed at the sampling sites for the measured environmental variables (Table 1). Chlorophyll-*a* concentration ranged from 0.03 μg L^{-1} in the South Atlantic (station 3) to 0.21 μg L^{-1} in the western tropical Pacific (station 9) (Table 1). Phosphate concentration also varied 10-fold from 0.02 μmol L^{-1} in the Indian Ocean to 0.32 μmol L^{-1} in the equatorial Pacific (Table 1). By contrast, nitrate concentrations varied two orders of magnitude, from 0.03 μmol L^{-1} in the North Pacific to 2.28 μmol L^{-1} in the equatorial Pacific (Table 1). Heterotrophic prokaryotic abundance varied by ca. one order of magnitude (Table 1) and was highest in the North Atlantic (station 2). The mixed layer depth (MLD) varied largely from as shallow as 8 m in the North Atlantic (station 1) to 100 m in North Pacific (station 8).

There were no significant differences in the initial prokaryotic assemblages among experiments or ocean basins (Fig. 1 b) (Permutation test, $p>0.05$). The initial prokaryotic communities were dominated by Subsection I Cyanobacteria and the SAR11 clade representing, on average, 51% and 16% of the 16S rRNA-gene sequences, respectively (Fig. 1b). The lowest richness, Shannon diversity index (H') and Pielou evenness index (J') corresponded to station 5, in the Indian ocean, where phosphate concentration was also the lowest (Table 1), and the community was overwhelmingly dominated by subsection I cyanobacteria and SAR11 clade, jointly representing 88% of the reads (Fig. 1b). *Prochlorococcus* was the dominant cyanobacterial taxon (representing >90% of the cyanobacterial sequences) in all stations, excepting stations 1 and 9, where *Synechococcus*

contributed 37% and 90%, respectively, to the pool of cyanobacterial sequences (details not shown). The relative abundance of the SAR11 clade was comparatively low in the eastern tropical North Pacific (station 9), and eastern tropical North Atlantic (station 1), coinciding with the shallowest MLD (Table 1). The contribution of archaea to the prokaryotic community was systematically low, contributing, on average, <1% of total sequence abundance.

Effect of grazing, dilution and light exposure on prokaryotic growth

The estimated growth rates at time zero were <0.3 d^{-1} except in the equatorial Pacific, where initial rates were ca. 2 d^{-1} (Fig. S1). An appreciable increase in prokaryotic growth rate over the first 24 h of incubation in unmanipulated surface seawater exposed to light (thereafter LC treatment) was observed in 7 out of 10 experiments (Fig. S1). Maximum growth rates mostly occurred in the filtered and diluted treatments exposed to light (thereafter LFD treatment) or darkness (thereafter DFD treatment).

In order to summarize the effect of the different treatments, we calculated the effect of filtration (light filtered to light control, LF/LC response ratio), the effect of dilution (light filtered diluted to light filtered, LFD/LF response ratio) and the effect of light on the filtered and diluted samples (light filtered diluted to dark filtered diluted, LFD/DFD response ratio) by averaging the response ratios derived for each time point (Fig. 2). A significant positive effect of filtration on growth rates was observed in 5 out of 10 experiments (Wilcoxon test, $p<0.05$), while dilution enhanced prokaryotic growth rates in 2 out of 10 experiments (Wilcoxon test, $p<0.05$) (Fig. 2). Interestingly, dilution caused a significant decrease in growth rates in experiment 3 (South Atlantic Ocean), and experiment 7 (equatorial Pacific Ocean) (Wilcoxon test, $p<0.05$) (Fig 2). Light exposure significantly reduced growth in 3 out

of 10 experiments conducted in the equatorial and North Atlantic and Pacific Oceans (Wilcoxon test, $p<0.05$) (Fig 2). The magnitude of growth inhibition by light was significantly correlated with the mixed layer depth (Table S1), the deeper the MLD, the higher the inhibition (Fig 3).

When pooling the response ratios of the 10 experiments growth rates, on average significantly increased 3.1-fold after filtration (Z-test, $p=0.011$), and 1.7-fold (Z-test, $p=0.022$) after dilution; and decreased 0.9-fold upon light exposure (Z-test, $p=0.025$) (Fig. 4). The magnitude of the increase in prokaryotic growth associated to grazing reduction was positively correlated with the initial prokaryote abundance (Table S1)

Effect of filtration, dilution and light exposure on bacterial community composition and diversity

Based on the time-course changes in growth (Fig. S1), we infer that shifts in community composition mostly occurred within the first 24-48 h, and that the prokaryotic community remained relatively stable afterwards. The most noticeable alteration after 72 h of incubation associated to the combination of filtration and dilution (LFD versus LC) was the consistent and sharp decrease in the relative abundance of cyanobacterial and/or SAR11 reads (Fig. 5), which resulted in significant differences in community composition (Fig. 6) (Permutation test, $p=0.013$). There was a significant effect of the sample origin on the final community composition (Fig. 6) (Permutation test, $p<0.001$). Filtration alone (LF versus LC) did not cause significant changes in community composition (Permutation test, $p=0.570$) (Fig. 6), favoring different groups depending on the origin of the sample, like Rhodobacterales (experiments 1-N-Atl and 2-Eq-Atl), Flavobacteriales (experiment 4-S-Ind), Alteromonadales (experiments 1-N-Atl, 2-Eq-Atl, 8-N-Pac) or Caulobacterales (experiment

196 3-S-Atl) (Fig. 5). On the other hand, the dilution of filtered samples (LFD versus LF)
197 eventually favored or hindered a particular group (Fig. 5), but did not globally cause
198 significant changes (Permutation test, p=0.164) (Fig. 6). The effect of light exposure (LFD
199 versus DFD) on prokaryotic community composition was not significant (Permutation test,
200 p=0.979) (Figs. 5, 6). On average, OTU richness at the end of the experimental incubation,
201 significantly decreased after filtration (0.83-fold) and light exposure (0.85-fold) (Table S2,
202 Fig. 4). Shannon diversity and Pielou evenness significantly decreased with filtration ca. 0.9-
203 fold (Table S2, Fig 4). The decrease in richness associated to filtration was positively
204 correlated with the initial nitrate concentration, while that associated to dilution was
205 negatively related with phosphate concentration (Table S1).

206 *Effect of filtration and dilution on the relative abundance of specific OTUs*

207 A differential analysis of the sequence abundance data, as implemented in DESeq2, detected
208 nine differentially abundant OTUs ($p<0.045$, FDR<0.1) associated with the filtration
209 treatment (i.e. LC versus LF treatment) (Fig. 7a). The same analysis detected eight
210 differentially abundant OTUs associated with the dilution treatment (i.e. LF versus LFD
211 treatment) (Fig. 7b). By contrast, none of the OTUs showed a significant difference in
212 abundance when comparing LFD versus DFD ($p>0.02$, FDR>0.32). The sequences of two
213 Rhodobacterales OTUs showed a positive effect of filtration increasing their abundance in
214 the LF treatment compared to the LC by up to 6-fold (Fig 7a). An alphaproteobacterium
215 belonging to the *Thalassospira* genus, showing a relatively low abundance in the LC
216 treatment, also significantly increased its abundance upon filtration. Several other OTUs
217 showing low to moderate abundances in the LC treatment and belonging to different bacterial
218 taxa were negatively affected by filtration (Fig. 7a). The dilution of the grazer-free

community favored the increase in the abundance of two Rhodobacterales OTUs, affiliated to genera *Marinovum* and *Maritimibacter*, and a Caulobacterales OTU affiliated to the genus *Hyphomonas* (Fig. 7b). Notably, the dilution negatively affected two OTUs that were abundant in the LF treatment, including a *Prochlorococcus* OTU (representing on average 90% of total *Prochlorococcus* abundance), and a SAR11 OTU (representing on average 93% of total SAR11 abundance) (Fig. 7). A less abundant SAR11 OTU, an alphaproteobacterium OTU affiliated to the *Sphingobium* genus, and a Flavobacteriales OTU affiliated to the NS2b group also showed a reduction in sequence abundance upon dilution (Fig. 7b).

Discussion

Methodological considerations

We manipulated natural microbial communities from surface waters of the global subtropical and tropical ocean in order to get insight into what controls prokaryote growth and community composition in these well-illuminated, mostly oligotrophic regions comprising 70% of the ocean's surface. It is important to note that the filtration and dilution procedures aimed at exploring the effect of grazing and resource availability have some limitations (Gasol and Morán, 1999; Fuchs et al., 2000). Regarding filtration, for example, some predators may pass through the filter pores, and even though grazing pressure is undoubtedly reduced, it is not wholly eliminated. Filtration also excludes larger particles and cells, including primary producers, which may cause a reduction of resource availability during the incubation as compared to the unmanipulated control, and thus the impact of reducing grazing pressure on growth can be underestimated. Filtration may also cause cell breakage and release dissolved substances not present in the unmanipulated seawater, which may compensate for the aforementioned resource reduction. Moreover, the filtered and diluted

treatment would most likely result in an increase in resource availability as compared to the filtered treatment, just because a similar amount of nutrients would be available for only 1/5th of the original prokaryotic community (Fuchs et al., 2000), thus relaxing competition. However, we must notice here that an accompanying consequence of dilution with 0.2 µm filtered seawater is the increase in the virus to prokaryotes ratio. Consequently, we cannot discard an increase in prokaryotic cell lysis (Wilcox and Fuhrman, 1994, Larsen et al., 2004) in the filtered and diluted treatment compared with the filtered treatment, which would also underestimate the impact of resource availability on prokaryotes. Considering all these constraints, our conclusions would be on the conservative side concerning the effect of grazing and resource availability reduction.

Role of acclimation in the response of prokaryotes to light exposure

On average, the impact of light exposure on prokaryotic growth in our study was moderately low as previously observed in coastal waters of the Southern Ocean (Richert et al., 2015) or the Mediterranean Sea (Sánchez et al., 2017). The overall negative effect (Fig. 4) was mostly driven by the sharp negative impact observed in one of the North Pacific experiments (Fig. 2), associated with a very deep mixed layer depth (MLD) (Fig. 3). Such pattern strongly suggests that the ability of prokaryotes inhabiting the surface layers of the oceans to stand high levels of solar radiation depends on their previous exposure to radiation (see Bertoni et al., 2011; Ruiz-González et al., 2013; and references therein). The MLD influences the average light (including both PAR and UVR) exposure, and relates to the rate of vertical transport, which determines the residence time of a given organism within the zone of exposure to damaging radiation (Neale et al., 2003). In this regard, deep mixed layers would likely result in microorganisms staying for very short periods on the high radiation exposure

265 zone as to photoacclimate. We clearly show that some prokaryotes in North and Equatorial
266 Atlantic and Pacific waters were not able to cope with increased sunlight during 3 days of
267 exposure at the high irradiance intensities associated to on-deck incubations.

268 Although light exposure caused a slight decrease in prokaryotic richness (Fig. 4), it
269 had no significant effects on prokaryotic community composition during the experiments
270 (Figs. 5, 6), as previously reported for other marine sites (Winter et al., 2001; Schwalbach et
271 al., 2005; Piquet et al., 2010). Unexpectedly, cyanobacterial taxa did not show a significant
272 response to light exposure, suggesting that they are able to survive in dark conditions, at least
273 for short periods, conceivably owing to their ability to use organic substrates (Zubkov et al.,
274 2003; Scanlan et al., 2009; Muñoz-Marín et al., 2013). Schwalbach et al. (2005) found a
275 sharp decline in cyanobacterial taxa abundance during longer incubations (5-10 days) in total
276 darkness. With the only exception of an experiment in the South Indian Ocean, the
277 contribution of Rhodobacterales to the prokaryotic community was similar or higher in the
278 LFD than in the DFD treatments (Fig. 5). This is consistent with the capability for aerobic
279 anoxygenic photosynthesis (AAP) present in many representatives within this group (Buchan
280 et al., 2005; Wagner-Döbler and Biebl, 2006; Moran et al 2007; Brinkhoff et al., 2008).
281 Experimental studies have demonstrated that members of the *Roseobacter* clade benefit from
282 light exposure (Alonso-Sáez et al., 2006, Ruiz-González et al., 2012; Sánchez et al., 2017).

283 *Grazing pressure favors prokaryotic diversity*

284 Grazing reduction promoted an expected significant increase in prokaryotic growth (Fig. 2,
285 Fig. 4), in accordance with the previously suggested bacterial growth top-down control under
286 oligotrophic conditions (Caron et al., 2000; Gasol et al., 2002; Pernthaler, 2005, Silva et al.,
287 2019). Consistent with theoretical models (Thingstad and Lignell, 1997; Thingstad, 2000),

experimental data (e.g. Richert et al., 2015; Baltar et al., 2016) and field observations (e.g. Storesund et al., 2016), grazing appears to have a limited influence on the community composition in our experiments (Figs. 5, 6). This is in contrast with empirical evidence of a large impact of predators on prokaryotic community structure in freshwater ecosystems (e.g, Simek et al., 2001; Pernthaler et al., 2001), which supports the notion that the magnitude of the influence of predation on prokaryotes depends on the characteristics of the system (Pernthaler, 2005; Corno and Jürgens, 2008). Comparatively, more consensus exists about the positive role of predation on prokaryotic richness (Pernthaler, 2005; Zhang et al., 2007; Corno and Jürgens, 2008; Ram et al., 2016). Here, we also found a significant reduction in prokaryotic richness (ca. 20%), Shannon diversity (ca. 17%) and evenness (ca. 10%) when predators were removed (LF versus LC) (Fig. 4). The abundance of prokaryotes in the LF treatment did not significantly differ from that in the LC (paired T-Test, p=0.06) at the beginning of the experimental incubation, which strongly supports that the observed decrease in richness is not associated to the potential exclusion of large prokaryote cells by filtration. This effect on richness might be related to the top-down control of fast-growing opportunistic taxa by grazers (Pernthaler, 2005). The significant increase, after grazing reduction, of populations belonging to Rhodobactereaceae, the *Roseobacter* clade (i.e. *Thalassococcus* genus) and *Thalassospira* (Fig. 7a), known to include fast-growing or copiotrophic bacteria (Allers et al., 2007; Teira et al., 2009; Ferrera et al., 2011, Hütz et al., 2011; Teira et al., 2011) is coherent with this hypothesis. The bacterial taxa negatively affected by filtration, such as OM60 (NOR5) Gammaproteobacteria or *Prochlorococcus* (Fig. 7a), would likely be outcompeted by fast-growing species once grazer abundance is reduced by filtration. Moreover, the decrease in richness associated to grazing reduction was higher when nitrate concentration was higher (Table S1), which would favor phylotypes adapted to rapid growth

when nutrient concentrations are high. Once freed from top-down control, these fast-growing bacteria would outcompete grazing-resistant, but slow-growing bacteria resulting in an overall decrease of richness. Accordingly, grazing would act as a key force sustaining richness in these oligotrophic systems, by favoring slow-growing or oligotrophic lineages and, consequently, diminishing competitive exclusion (Zhang et al., 2007; Gifford et al., 2013). A recent review on adaptations of oligotrophic bacteria highlights their characteristically low loss rates by top-down agents such as protistan grazers or viruses (Overmann and Lepleux, 2016; and references therein).

Increase in resource availability negatively affects oligotrophic bacteria

Prokaryotic community composition significantly changed, as compared to the unmanipulated control (LC), only in the filtered and diluted (LFD) treatment, suggesting that both top-down and bottom-up forces contribute to shape prokaryotic assemblages in surface oligotrophic waters. Interestingly, neither community composition nor richness were significantly affected by the dilution itself (LFD vs LF) (Figs. 4,6), which implies that, paradoxically, resource availability alone has a relevant but limited role in controlling prokaryotic communities in the oligotrophic ocean as previously concluded from both empirical data (Strom, 2000; Gasol et al., 2002) and theoretical models (Thingstad and Lignell, 1997). It is important to note that the total amount of resources was not manipulated here; we only modified its availability by reducing prokaryotic abundance through dilution. To our knowledge, this is the first experimental study where the effect of resource availability on prokaryotic populations has been systematically assessed by combining filtered (i.e., grazer-free) and diluted seawater short-term incubations with high throughput sequencing analyses in the oligotrophic ocean. Even though our resource manipulation caused only minor

changes at the community level, significant changes could be appreciated at the level of individual OTUs (Fig. 7b). The relative sequence abundance of the two most abundant populations, assigned to the SAR11 clade (on average, 12% of total sequences in unmanipulated samples) and the genus *Prochlorococcus* (on average, 11% of total sequences in unmanipulated samples), decreased ca. 4 and ca. 9-fold respectively, in the filtered and diluted (LFD), compared to the filtered treatment (LF). Calvo-Díaz et al. (2011) had also observed a decrease in *Prochlorococcus* abundance accompanied by an increase in heterotrophic bacteria during short-term bottle incubations. These authors speculated that, among other factors, the potential increase in the availability of substrates due to seawater manipulation could favor heterotrophic versus autotrophic prokaryotes. In the same line, previous experiments with surface seawater in the Atlantic Ocean revealed systematic negative responses of SAR11 bacteria to the addition of organic nutrients, alone or combined with inorganic nutrients, suggesting that they might be outcompeted by other fast-growing bacteria upon enrichment (Teira et al., 2010). By contrast, other experimental studies did not observe a decrease in SAR11 abundance after dilution of non-filtered (i.e. grazers are present) seawater (Ferrera et al., 2011; Cram et al., 2016), which may be explained by the tight control exerted by grazers on fast-growing bacteria.

Both SAR11 and *Prochlorococcus* are well known representatives of the oligotrophic lifestyle in the marine realm (Overmann and Lepleux, 2016). A member of the *Sphingobium* genus was also negatively affected by dilution (Fig. 7b), which agrees with the widespread adaptation of sphingomonads to oligotrophic environments (Lauro et al., 2009; Aylward et al., 2013). Oligotrophic bacteria are typically very abundant and exhibit a series of adaptations that allow them to succeed in very diluted environments, including their small

sizes, streamlined genomes, high grazing and viral infection resistance, or slow but constant growth irrespective of substrate concentration (Cottrell and Kirchman, 2016; Overmann and Lepleux, 2016; Dadon-Pilosof et al., 2017). In addition, oligotrophic bacteria present a reduced transcriptional control compared to copiotrophic bacteria that preclude them to sense and react to environmental fluctuations (Lauro et al., 2009; Gifford et al., 2013; Cottrell and Kirchman, 2016; Overmann and Lepleux, 2016). Our data nicely agree with such diverging trophic strategies. The increase in resource availability associated to dilution favored copiotrophic bacteria adapted to respond to perturbations (Fig. 7b), such as the Rhodobacterales *Maritimibacter and Marinovum* or the Caulobacterales *Hyphomonas* (Brinkhoff et al., 2008; Hogle et al., 2016), which would presumably outcompete oligotrophic populations. A less abundant member of the Flavobacteria-NS2b marine group (on average, 0.3% of the sequences in the unmanipulated samples) could also have an oligotrophic lifestyle, as it showed a ca. 5-fold decrease in sequence abundance after dilution (Fig. 7b). Although there is not much information about the ecology of the NS2b marine group, Alonso-Sáez et al. (2015) showed that this bacterial group follows similar temporal dynamics than SAR11 populations, which suggests that it may also be well adapted to oligotrophic conditions. Korlevic et al. (2015) also suggested that the Flavobacteria-NS2b clade could be adapted to oligotrophic conditions in an extensive study in the Adriatic Sea.

Conclusion

The manipulation of natural microbial communities from surface waters of the global subtropical and tropical ocean revealed an overall negative effect of light exposure on growth rates and community richness which, interestingly, seems to be related to a poor acclimation of prokaryotic communities to high incident irradiances associated to relatively deep mixed

layers. By contrast, light exposure did not result in a significant re-structuring of the prokaryotic community. The reduction of grazing pressure by itself caused essentially an increase in prokaryotic growth and a moderate decrease in community richness, Shannon diversity and evenness, while the increase in resources alone enhanced growth at the level of community and systematically reduced populations of well-known oligotrophic taxa such as SAR11 and *Prochlorococcus*. The responses to dilution of grazer-free prokaryotic communities described here, strongly suggest that a reduction in resource competition in the absence of predators may negatively affect prokaryotic lineages well adapted to the oligotrophic growth conditions prevailing in the surface ocean

Experimental procedures

Sample collection and experimental setup.

Experiments were carried out at 10 stations located in the tropical and subtropical Atlantic, Indian and Pacific oceans between 14th December 2010 and 14th July 2011, during the Malaspina 2010 circumnavigation expedition (http://www.expedicionmalaspina.es/), on board the R/V Hespérides (Figure 1a). Conductivity–Temperature–Depth (CTD) casts were carried out at each station with a Sea-Bird Electronics 911 plus probe attached to a rosette equipped with Niskin bottles starting around 10:00 local time. Profiles of underwater photosynthetically active radiation (PAR) were obtained with a 4π Biospherical QCP2300-HP sensor attached to the CTD. At each sampling site seawater samples were taken a 3 m depth for chemical (nutrients, chlorophyll-*a* concentrations) and biological (heterotrophic prokaryotic abundance, prokaryotic community taxonomic composition) characterization as

403 part of the Malaspina sampling routine. Samples for phosphate and nitrate measurements
404 were frozen and their concentrations were determined by standard colorimetric methods with
405 a Technicon autoanalyzer (Cabello et al 2016). Chlorophyll-*a* concentration was
406 fluorometrically determined after biomass concentration onto 0.2 μm pore size polycarbonate
407 filters and extraction in 90% acetone (Estrada et al 2016). The mixed layer depth was
408 estimated as the depth where local potential density exceeded by 0.1 kg m^{-3} the value of the
409 shallowest data point and obtained from Fernández-Castro et al., (2014).

410 *Experimental setup*

411 Seawater for the experiments was collected from 3 m depth using 30-L Niskin bottles and
412 filtered through a 200 μm mesh to remove large zooplankton. Ultraviolet (UVA and UVB)
413 radiation transparent 3-L carboys made of low density polyethylene were used for the
414 incubations. Each experiment consisted of 3 treatments (in duplicate): a filtered treatment
415 through 0.8 μm pore size polycarbonate filters to reduce predators while maintaining most
416 free-living prokaryotes and exposed to sunlight (LF, standing for light + filtration), a filtered
417 and diluted treatment (0.8 μm filtered seawater diluted (1:5) with 0.2 μm filtered seawater)
418 to reduce both predators and resource competition and exposed to sunlight (LFD, standing
419 for light + filtration + dilution) and a filtered and diluted treatment kept under dark conditions
420 (DFD, standing for dark + filtration + dilution). A control, consisting of unmanipulated
421 seawater exposed to sunlight (LC, standing for light control) was also incubated in order to
422 check for changes in bacterial community composition associated with sample manipulation.
423 LC, LF and LFD samples were incubated on deck under natural light conditions while the
424 DFD treatment was also incubated on deck under dark conditions, by carefully covering the
425 carboys with two layers of black tape. The experimental carboys were kept at near *in situ*

426 temperature (± 1°C) by circulating surface seawater through the incubation tank. The
427 incubations lasted 3 days and samples were taken every 12-24 h for heterotrophic prokaryotic
428 biomass (HPB) (as estimated by flow cytometry) and leucine incorporation rate
429 measurements. Empirically derived leucine-to-carbon conversion factors were used to
430 estimate heterotrophic prokaryotic production (HPP) (Teira et al., 2015). Growth rates (GR)
431 at the community level were calculated at each time point simply by dividing HPP by HPB
432 (Kirchman, 2016). DNA samples for prokaryotic community composition analyses were
433 taken from all treatments at the end of the incubations.

434 *Flow cytometry analyses*

435 Samples were fixed and processed with a FACSCalibur flow cytometer (BD-Biosciences)
436 with a blue laser emitting at 488 nm. Samples of 1.2 mL seawater were fixed with a
437 paraformaldehyde-glutaraldehyde mix (1% and 0.05% final concentrations, respectively) and
438 stored at -80ºC until analysis in the laboratory within a maximum of seven months after the
439 end of the cruise. Samples were stained with SYBRGreen I, at a final concentration of
440 1:10.000, for 15 min in the dark at room temperature. The average flow rate used was 12 µL
441 min^{-1} and acquisition time ranged from 30 to 260 seconds depending on cell concentration
442 in each sample. Data were inspected in a green fluorescence (FL1) versus light side scatter
443 (SSC) plot and analyzed as detailed as in Gomes et al. (2015). Molecular Probes latex beads
444 (1 µm) were always used as internal standards. The biovolume of prokaryotic cells was
445 estimated using the calibration obtained by Calvo-Díaz and Morán (2006) relating relative
446 light side scatter (population SSC divided by bead SSC) to cell diameter assuming spherical
447 shape. Cell biovolume was finally converted into carbon biomass with the Gundersen et al.
448 (2002) equation: cell biomass (fg C $cell^{-1}$) = 108.8 * V0.898.

449 *Leucine incorporation rates*

450 The [^{3}H]leucine incorporation method (Kirchman et al., 1985), modified as described by
451 Smith and Azam (1992), was used to determine leucine incorporation rates. From each
452 experimental carboy, six 1.5 mL vials (4 replicates and 2 killed controls) were filled with 1.2
453 mL of seawater. A total of 120 µL of cold 50% trichloroacetic acid (TCA) was added to the
454 killed controls. After 15 minutes, 20 nmol L^{-1} of L-[4,5-^{3}H] leucine (144.2 Ci $mmol^{-1}$,
455 Amersham) was added to all samples, which were incubated for 2.5-6 h in the same
456 incubation tank and under the same light conditions as the corresponding experimental
457 carboys. Incubations were terminated by adding TCA (5% final concentration) to the
458 samples. The prokaryotic cells were pelleted by two successive centrifugation steps (12000
459 rpm, 10 min), including a washing step with 1 mL of 5% TCA following Kirchman et al.
460 (1985) with slight modifications (Smith and Azam, 1992). Scintillation cocktail was added
461 to the pellets and after 18 h, the radioactivity was determined in a liquid scintillation counter
462 (Wallac-PerkinElmer).

463 *High-Throughput sequencing*

464 In order to characterize the initial prokaryotic community at each sampling site (sample from
465 station 7 was lost) 6-12 L of surface seawater (3 m depth) was sequentially filtered through
466 a 200-µm and a 20-µm mesh to remove large plankton. Further filtering was done by serially
467 pumping water through 47-mm polycarbonate (Nucleopore Whatmann) membrane filters of
468 3 µm and 0.2 µm pore size with a peristaltic pump (Masterflex, EW-77410-10). The filters
469 were then flash-frozen in liquid N_2 and stored at −80°C until DNA extraction. The time span
470 from bottle closing to filter freezing was ~4 h and, except for the time needed to empty the
471 rosette bottles, the water was kept at 4°C. DNA extractions from the 0.2 µm filter were

performed using the standard phenol–chloroform protocol (Massana et al. 1997). At the end of each experiment, water from treatment duplicates was pooled and 1-2 L was filtered through a 0.2 µm pore-size polycarbonate filters (Nuclepore Whatmann, 47-mm filter diameter). Filters were then stored at -80ºC until DNA extraction. Microbial community DNA was extracted from the 0.2 µm filter using the Ultra Clean Soil DNA isolation kit (MoBio Laboratories, Inc.) and quantified in a Nanodrop. Samples from the end of experiments 6 and 7 were not available for sequencing. The different extraction protocols for the field samples and the experimental samples precluded us to make statistical comparisons between both sets of samples. Nevertheless, we include data from field samples to provide information about the initial prokaryotic communities.

Prokaryotic diversity was assessed in the 0.2-3 µm fraction of initial and experiment samples by amplicon sequencing of the hypervariable V4-V5 (~400 bp) region of the 16S rRNA gene with the Illumina MiSeq platform (iTags) using paired-end reads (2×250 bp) and primers 515F-Y - 926R targeting both Archaea and Bacteria (Parada et al., 2016). Amplicon libraries were sequenced at the Research and Testing Laboratory facility (Lubbock, TX, USA; rtlgenomics.com/). Reads were processed following an in-house pipeline (Logares, 2017). Briefly, raw reads were corrected using BayesHammer (Nikolenko et al., 2013) following Schirmer et al. (2015). Corrected paired-end reads were subsequently merged with PEAR (Zhang et al., 2014) and sequences >200 bp were quality-checked and de-replicated using USEARCH (Edgar 2010). Operational Taxonomic Units (OTUs) were delineated at 97% similarity using UPARSE V8 (Edgar 2013). To obtain OTU abundances, reads were mapped back to OTUs at 97% similarity. Chimera check and removal was performed both *de novo* and using the SILVA reference database (Quast et al., 2013). Taxonomic assignment

was generated by BLASTing (Altschul, et al. 1990) OTU representative sequences against the SILVA database. In order to compare both alpha and beta diversity among experimental treatments, the raw OTU table was subsampled using "rrarefy" (Vegan package in R) to the number of reads present in the sample with the lowest amount of reads, which was 7,747. Sequences are publicly available at the European Nucleotide Archive (http://www.ebi.ac.uk/ena) under the accession numbers PRJEB25570 (sequences from experiments) and PRJEB25224 (sequences from field samples).

Statistical analyses

To compare the impact of experimental manipulations on growth, we first calculated the response ratios at each sampling time as the quotient between the mean growth rates (from duplicates)of two different treatments. The relative error of each quotient was estimated as the square root of the sum of the squares of the relative errors in the individual variables. To account for the diverse time-courses observed in growth rates (Fig. S1), we calculated the time-averaged response ratios for each experiment. The effect of grazing reduction (i.e. effect of filtration) was estimated by dividing a given response variable in LF by that in LC (LF/LC), the effect of resource competition reduction (i.e. effect of dilution) by dividing a given response variable in LF by that in LFD (LF/LFD) and the effect of light by dividing a given response variable in LFD by that in DFD (LFD/DFD). The non-parametric Wilcoxon test (two-tailed) was applied to compare time-averaged response ratios derived for each experiment against a constant value of one in order to detect significant responses to the different treatments. The Z-test was used to compare the mean response ratios (pooling the data from all experiments) against a constant value of one in order to detect significant

responses to the different treatments. The p-value was standardized as proposed by Good (1982) in order to overcome the low number of samples.

The sequence abundances of the subsampled OTU table were transformed using the centered log ratio (clr) (Fernandes et al., 2014; Gloor et al., 2017) using the web-based program Calypso 8.72. Zeros were replaced by the minimum value that is larger than 0 divided by 2. Variance partitioning by redundancy analysis (RDA) filtering for the top 100 most abundant OTUs was used to analyze community composition variation against sampling site and experimental treatment. Permutation tests of the factors included in Redundancy Analysis (RDA) (experiment and treatment) were conducted to test for significance. The DeSeq2 procedure (Love et al 2014), based on negative binomial generalized linear model, was used to detect differentially abundant OTUs between experimental treatments using the web-based program Calypso 8.62. The input for DeSeq2 was the raw (not subsampled) data set. As recommended for this method we removed rare OTUs from the data set (i.e. those OTUs contributing <0.01% of the total sequence abundance). Benjamini–Hochberg–Yekutieli procedure was used to control false discovery rate (FDR) (Benjamini and Yekutieli 2001).

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847 **Figure Legends**

848 Figure 1. Map of locations where sampling for experiments was conducted (A) ,and relative
849 contribution of the major taxonomic groups of prokaryotes to the global community based
850 on number of 16S rRNA gene sequences in surface water at the different locations (B).

851 Figure 2. Time-averaged response to filtration (LF/LC), dilution (LDF/LF) and light
852 exposure (LFD/DFD) of growth rate in each of the 10 experiments. Eq, equatorial, Atl,
853 Atlantic, Ind, Indian, Pac, Pacific. Error bars represent the propagated standard error (SE).
854 Asterisks indicate a significant effect of filtration (mean LF/LC differs from 1), dilution
855 (mean LFD/LF differs from 1), or light exposure (mean LFD/DFD differs from 1) on specific
856 growth rate using the non-parametric Wilcoxon test.

857 Figure 3. Relationship between the growth rate response to light exposure and the mixed
858 layer depth (m) in the 10 experiments. The black line represent the fitted potential model.

859 Figure 4. Box plots showing the response to filtration (LF/LC), dilution (LDF/LF) and light
860 exposure (LFD/DFD) of growth rate (GR), Richness (S), H' Diversity (Shannon index) and
861 J' Evenness (Pielou index) in the experiments (10 for GR, 8 for S; H' and J'). Fifty percent
862 of the data are included within the limit of the boxes and the caps represent 10th and 90th
863 percentiles The thick black line represents the average for all the experiments. Asterisks
864 indicate a significant effect of filtration (LF/LC differs from 1), dilution (LFD/LF differs
865 from 1) or light exposure (LFD/DFD differs from 1) on specific growth rate, richness,
866 Shannon diversity or evenness using Z-tests.

867 Figure 5. Relative contribution of major taxonomic groups of bacteria to community structure
868 (in number of sequences) in the light + unmanipulated (LC), light + filtration (LF), light
869 +filtration + dilution (LFD) and dark + filtration +dilution (DFD) treatments at the end of the
870 experiments. Note that data are not available for experiments 6 and 7.

871 Figure 6. Redundancy analysis (RDA) biplot, constrained to visualize the variance in OTU
872 abundance, explained by treatment at the end of the experiments. Squares and solid line
873 represent the light + unmanipulated (LC) treatment, inverted triangles and dashed line
874 represent light + filtration (LF) treatment, circles and crossed circles and dotted lines
875 represent light +filtration + dilution (LFD) and dark + filtration +dilution (DFD) treatments,
876 respectively. The DFD is highlighted by light grey shadowing.
877 Figure 7. Fold-change versus mean (±SE) abundance in the subsampled data set of the OTUs
878 identified to be significantly different in abundance between (a) light + unmanipulated (LC)
879 and light + filtration (LF) treatments, or (b) light + filtration (LF) and light +filtration +
880 dilution (LFD) treatments by DESeq2 ($p<0.05$, FDR<0.1). A negative fold-change value
881 denotes lower abundance and a positive fold change value denotes higher abundance in LC
882 compared to LF or LF compared to LFD.
883
884 Figure S1. Time-course of growth rates for the light + unmanipulated (LC), light + filtration
885 (LF), light + filtration + dilution (LFD) and dark + filtration + dilution (DFD) treatments in
886 each of the 10 experiments. Eq, equatorial, Atl, Atlantic, Ind, Indian, Pac, Pacific. Error bars
887 represent the standard deviation (SD) from duplicates. Note that error bars are not visible
888 when smaller than the symbols.

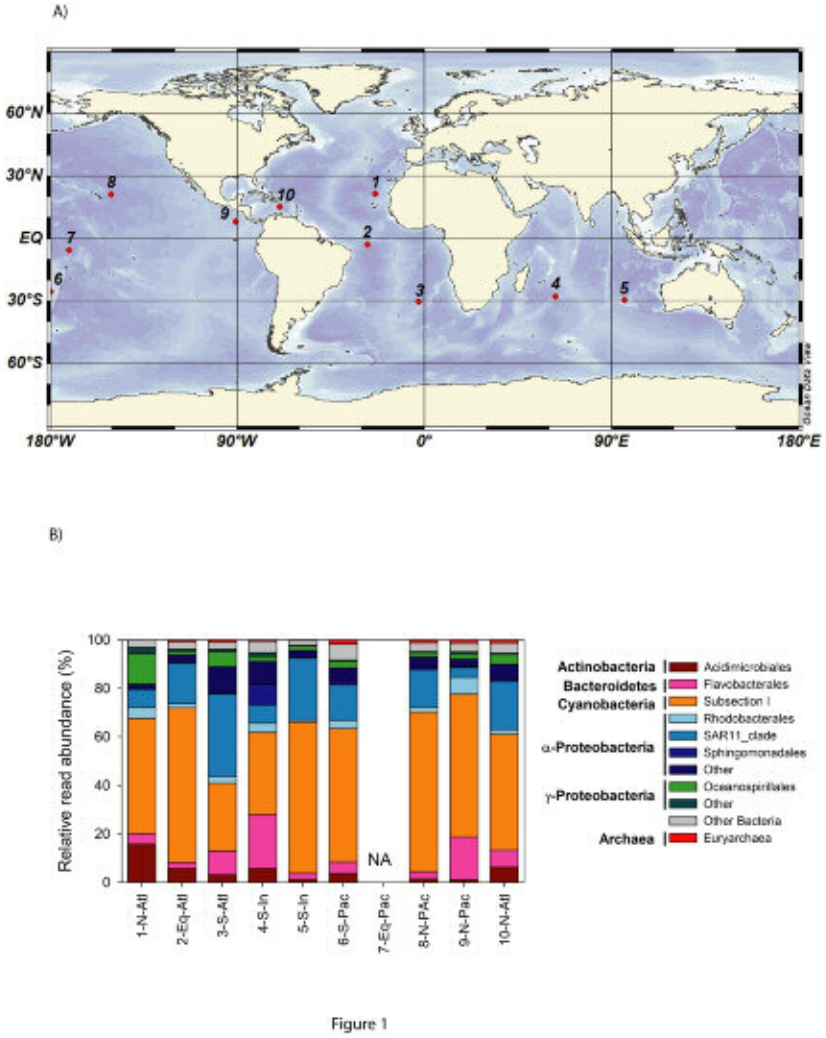

Figure 1

Figure 1. Map of locations where sampling for experiments was conducted (A) and relative contribution of the major taxonomic groups of prokaryotes to the global community based on number of 16S rRNA gene sequences in surface water at the different locations (B).

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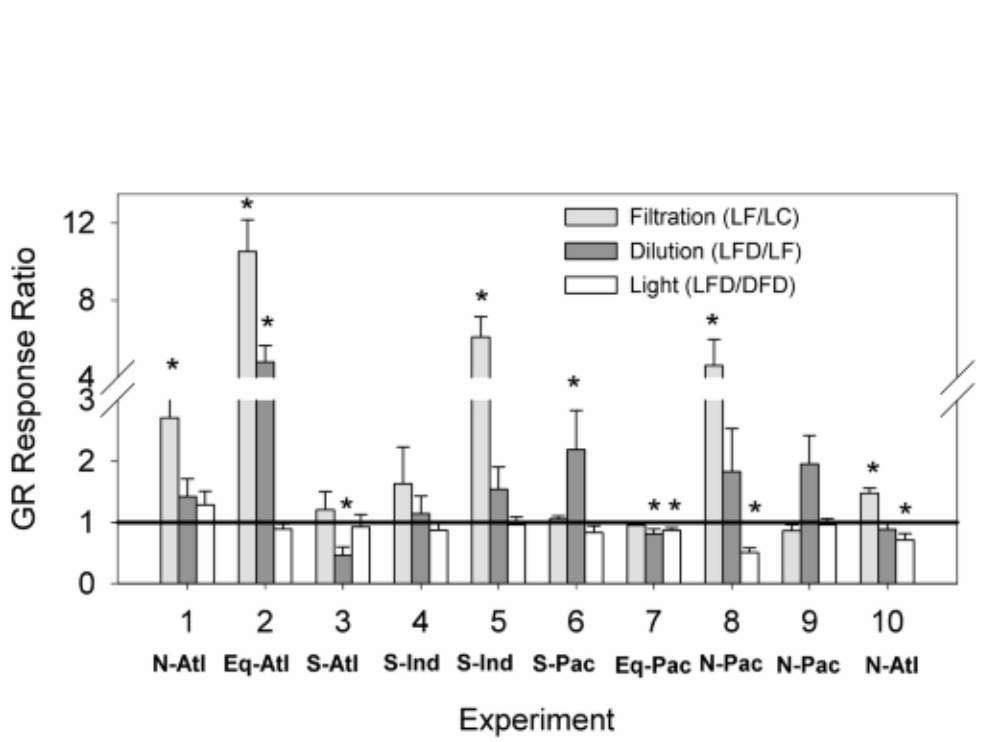

Figure 2. Time-averaged response to filtration (LF/LC), dilution (LDF/LF) and light exposure (LFD/DFD) of growth rate in each of the 10 experiments. Eq, equatorial, Atl, Atlantic, Ind, Indian, Pac, Pacific. Error bars represent the propagated standard error (SE). Asterisks indicate a significant effect of filtration (mean LF/LC differs from 1), dilution (mean LFD/LF differs from 1), or light exposure (mean LFD/DFD differs from 1) on specific growth rate using the non-parametric Wilcoxon test.

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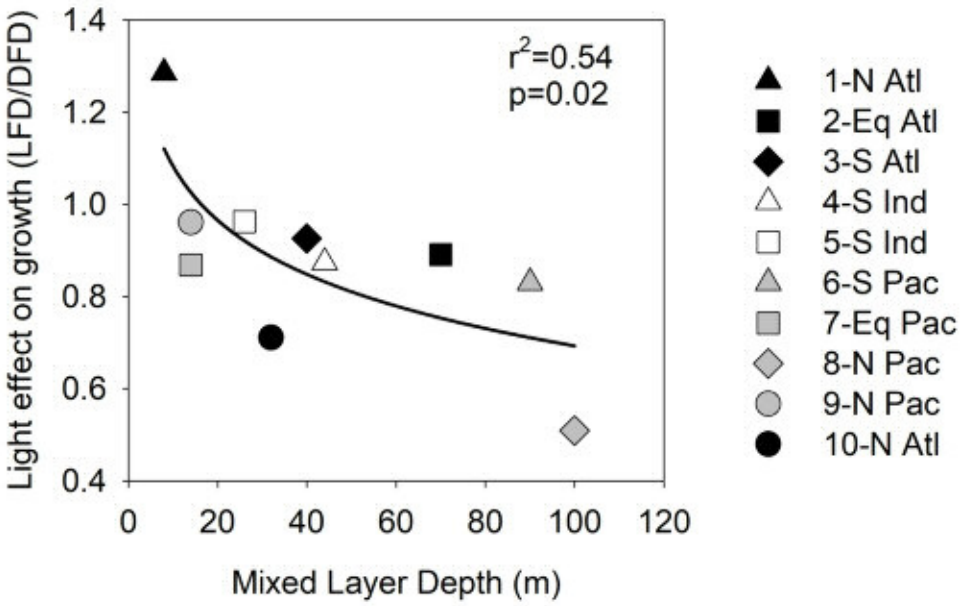

Figure 3. Relationship between the growth rate response to light exposure and the mixed layer depth (m) in the 10 experiments. The black line represent the fitted potential model.

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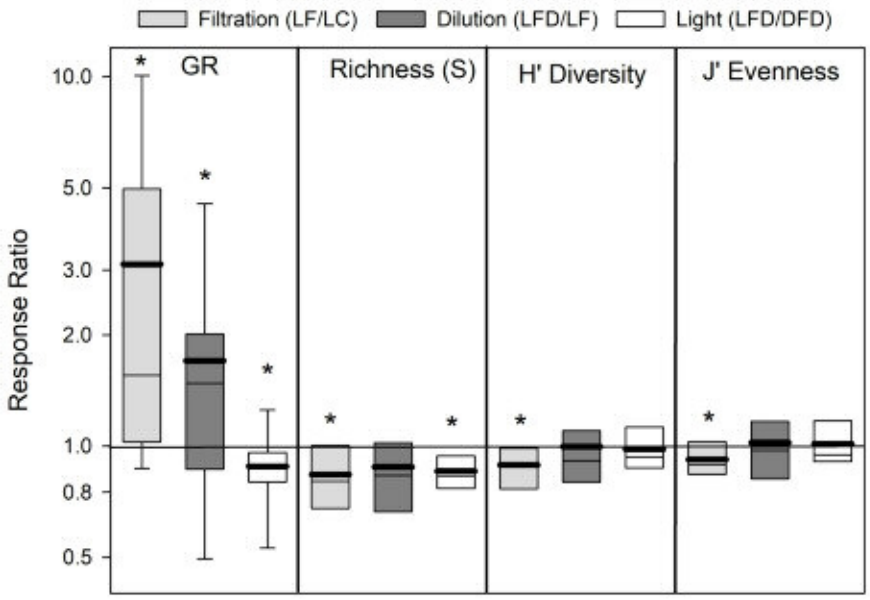

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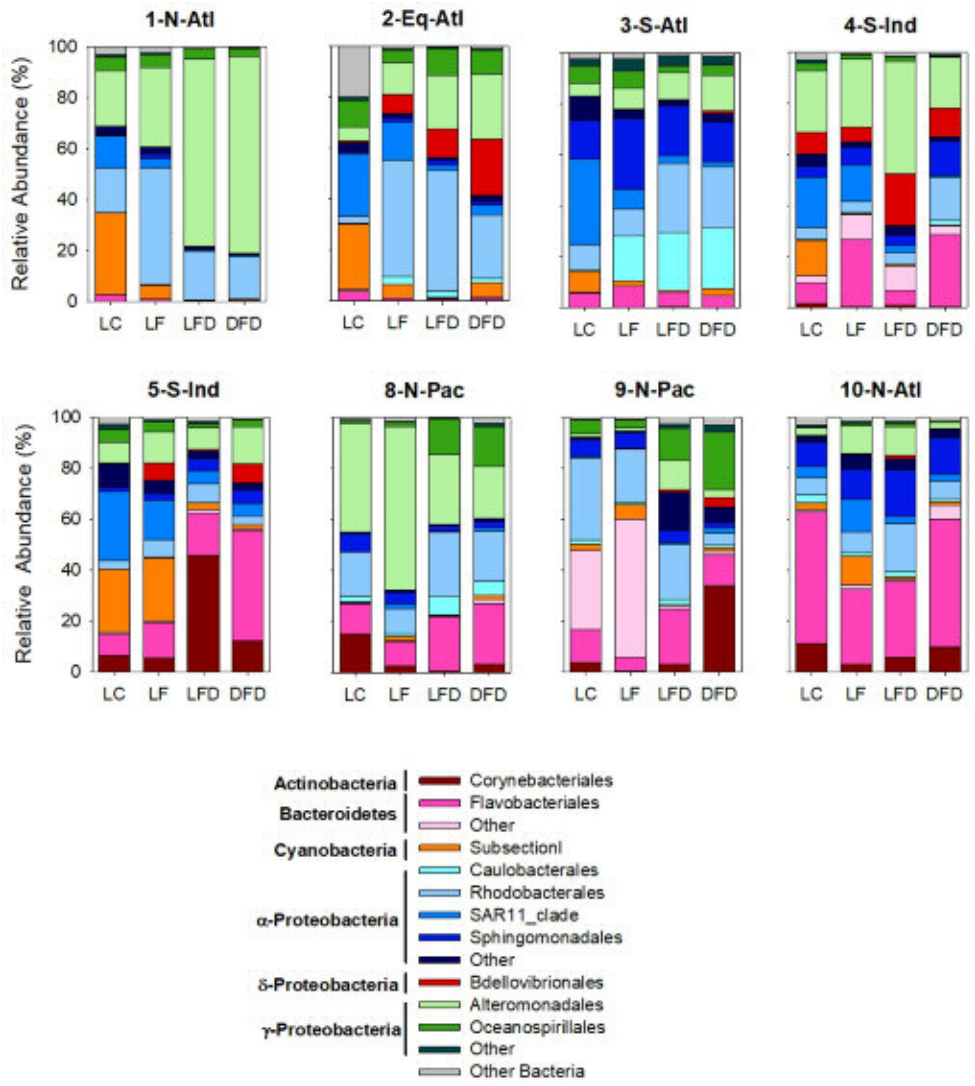

Figure 5. Relative contribution of major taxonomic groups of bacteria to community structure (in number of sequences) in the light + unmanipulated (LC), light + filtration (LF), light +filtration + dilution (LFD) and dark + filtration +dilution (DFD) treatments at the end of the experiments. Note that data are not available for experiments 6 and 7.

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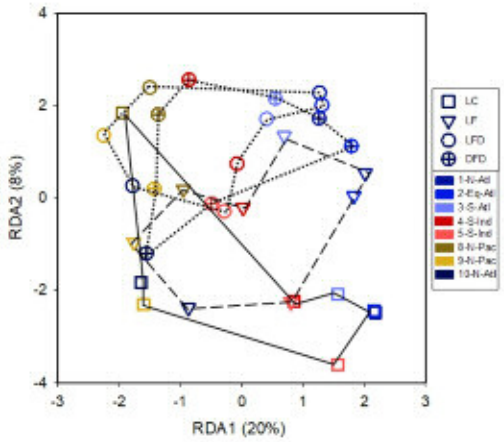

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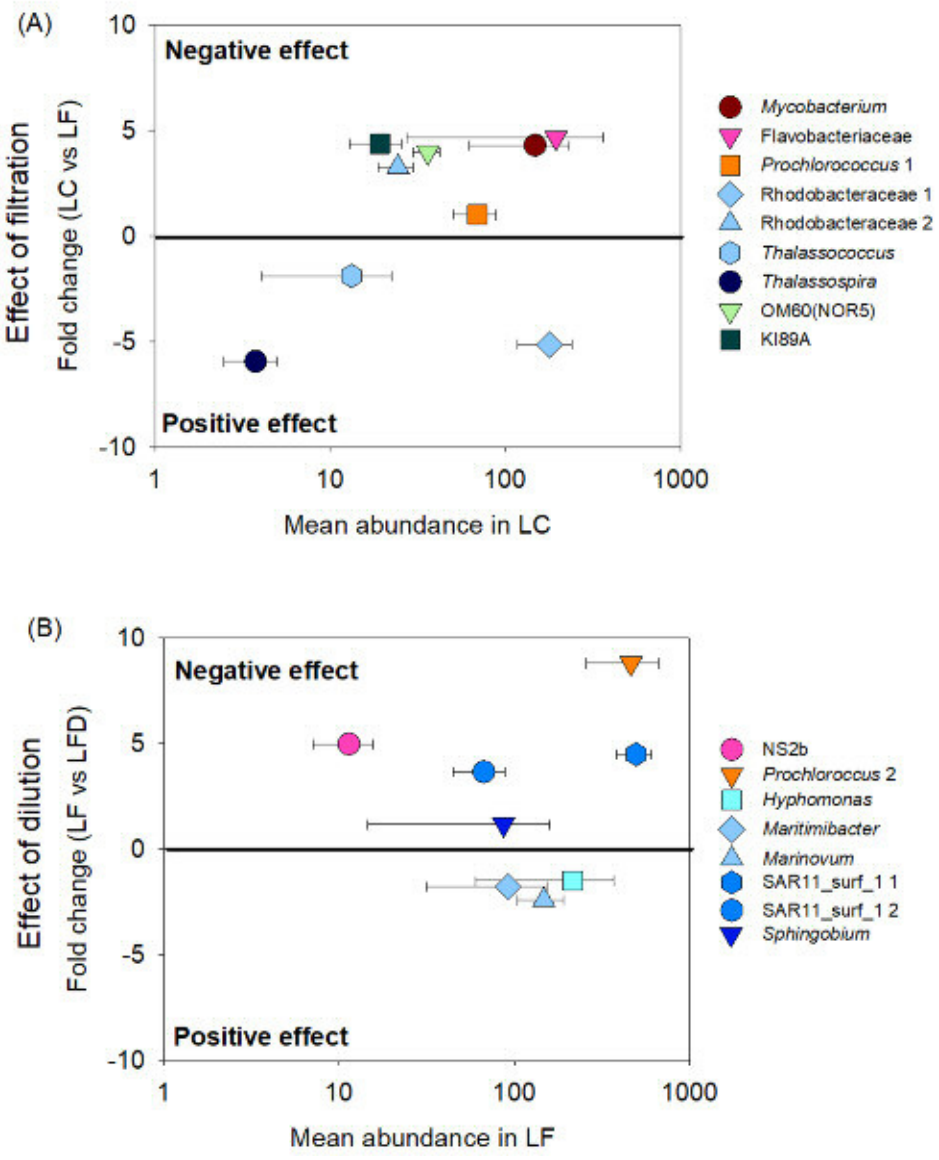

Figure 7. Fold-change versus mean (±SE) abundance in the subsampled data set of the OTUs identified to be significantly different in abundance between (a) light + unmanipulated (LC) and light + filtration (LF) treatments, or (b) light + filtration (LF) and light +filtration + dilution (LFD) treatments by DESeq2 ($p<0.05$, FDR<0.1). A negative fold-change value denotes lower abundance and a positive fold change value denotes higher abundance in LC compared to LF or LF compared to LFD.

177x227mm (150 x 150 DPI)

Table 1. Environmental conditions at the sampling sites. Temperature (Temp), Surface Photosynthetic Active Radiation (SPAR), chlorophyll-a concentration (Chla), phosphate concentration (PO_4^-), heterotrophic prokaryote abundance (HPA), mixed layer depth (MLD), number of OTUs (S). Shannon diversity index (H'), Pielou eveness index (J'). Discrete measurements derive from 3 m samples. NA. not available. SPAR represents the mean incident light during the three days of incubation.

EX-Ocean	Temp °C	SPAR µE m^{-2} s^{-1}	Chla µg L^{-1}	PO_4^- µmol L^{-1}	NO_3^- µmol L^{-1}	HPA cell mL^{-1}	MLD m	S	H'	J'
1-N-Atl	24.8	1636	0.18	NA	0.509	706199	8	167	2.79	0.55
2-Eq-Atl	27.5	1562	0.15	0.078	NA	1601136	70	176	1.99	0.38
3-S-Atl	22.5	1478	0.03	0.170	0.361	280620	40	171	2.97	0.58
4-S-In	25.9	866	0.09	0.033	0.262	357757	44	207	3.41	0.64
5-S-In	21.7	1222	0.07	0.019	0.191	635132	26	136	1.74	0.35
6-S-Pac	24.0	NA	0.13	0.089	0.143	507637	90	263	2.78	0.50
7-Eq-Pac	28.3	579	0.18	0.319	2.280	481133	14	NA	NA	NA
8-N-Pac	24.0	1249	0.09	0.083	0.028	924691	100	198	2.11	0.40
9-N-Pac	28.2	293	0.21	0.229	0.377	888244	14	146	2.81	0.56
10-N-Atl	28.7	579	0.09	0.068	0.340	932430	32	225	2.86	0.53