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## Plankton communities of the five "Iles Eparses" (Western Indian Ocean) considered to be pristine ecosystems

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Abstract: Coral reef environments are generally recognized as being the most threatened of fragile marine ecosystems. They are highly susceptible to stress and disturbance, especially to anthropogenic pressure. However, it is extremely difficult to distinguish the effects of climate change from other forcing factors, mainly because it is difficult to study ecosystems that are isolated from human pressure. The five Iles Eparses (Scattered Islands) are located in the Western Indian Ocean (WIO) and form the 5th district of the French Southern and Antarctic Lands (TAAF). They are considered to be pristine ecosystems as they are occupied only by a small group of military personnel. This study described the plankton assemblages for the first time, by determining the abundances of microbial (virus, bacteria, heterotrophic protists and phytoplankton) and metazooplankton communities in various lagoon and ocean sites around each island. The Europa lagoon has extensive, productive mangrove forests. Their particular structure and functioning, with the highest nutrient concentrations (nitrogen forms, dissolved organic carbon), explain bacterial production and growth rates that are higher than those reported for the other islands. The marine ecosystem of Tromelin, which lies outside the Mozambique Channel, had the lowest biological productivity, with the lowest nutrient concentrations and bacterial growth rates. Comparison with a sampling station in Mayotte lagoon, considered to be the reference for an anthropized island, showed that the patterns of microbial assemblages in the Iles Eparses were different from those found in Mayotte lagoon.



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Dr Marc BOUVY  
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Montpellier, 22 January 2015

Dear Editor,

Please find enclosed the MS entitled “Plankton communities in the five Iles Eparses (Western Indian Ocean) considered to be pristine ecosystems” written by M. Bouvy and colleagues, that we wish to submit as a research article in the journal “Acta Oecologica” in the framework of “Eparses 2014”.

We hope that you will find our work interesting and acceptable for publication in your journal.

Please let us know if you need complementary information.

Sincerely yours

Marc BOUVY, for the authors

# Plankton communities in the five Iles Eparses (Western Indian Ocean) considered to be pristine ecosystems

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## Highlights:

- The microbial and zooplankton assemblages in the five Iles Eparses were studied
- Bacterial growth rates and grazing rates by HNF were determined for various sites
- Bacterial production and growth rates were higher in lagoons with mangroves

1 Plankton communities in the five Iles Eparses  
2 (Western Indian Ocean) considered to be  
3 pristine ecosystems

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29 Mozambique Channel

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## Abstract

Coral reef environments are generally recognized as being the most threatened of fragile marine ecosystems. They are highly susceptible to stress and disturbance, especially to anthropogenic pressure. However, it is extremely difficult to distinguish the effects of climate change from other forcing factors, mainly because it is difficult to study ecosystems that are isolated from human pressure. The five Iles Eparses (Scattered Islands) are located in the Western Indian Ocean (WIO) and form the 5<sup>th</sup> district of the French Southern and Antarctic Lands (TAAF). They are considered to be pristine ecosystems as they are occupied only by a small group of military personnel. This study described the plankton assemblages for the first time, by determining the abundances of microbial (virus, bacteria, heterotrophic protists and phytoplankton) and metazooplankton communities in various lagoon and ocean sites around each island. The Europa lagoon has extensive, productive mangrove forests. Their particular structure and functioning, with the highest nutrient concentrations (nitrogen forms, dissolved organic carbon), explain bacterial production and growth rates that are higher than those reported for the other islands. The marine ecosystem of Tromelin, which lies outside the Mozambique Channel, had the lowest biological productivity, with the lowest nutrient concentrations and bacterial growth rates. Comparison with a sampling station in Mayotte lagoon, considered to be the reference for an anthropized island, showed that the patterns of microbial assemblages in the Iles Eparses were different from those found in Mayotte lagoon.

## 55 1. Introduction

56 The conservation and sustainable use of marine resources are priority goals in a growing  
57 number of national and international policy agendas (Spalding et al., 2007). Biogeographic  
58 classification is essential for developing ecologically representative systems in protected areas  
59 to protect a complete range of biodiversity – genes, species, populations and communities –  
60 throughout the trophic chain. A recent report analyzed the effects of anthropogenic activities  
61 in the oceans worldwide, focusing on stressors that can be evaluated at global scale (Halpern  
62 et al., 2008). According to these authors, all the oceanic ecosystems analyzed (coral reefs,  
63 mangroves, seagrass meadows, seamounts, rocky reefs, soft shallow areas, continental shelf  
64 areas, slope areas, pelagic waters and the deep sea) may be affected by anthropogenic  
65 activities to varying degrees. Special attention should be paid to the smallest living marine  
66 organisms as marine microbes provide essential ecosystems functions and are threatened by  
67 pollution (Nogales et al., 2011). It is now recognized that marine microbial components are  
68 associated with the channeling of a large proportion of carbon fluxes through the microbial  
69 food web (Estrada and Vaqué, 2014). Where there is eutrophication or pollution pressure, the  
70 composition and structure of microbial communities are basic indicators of the ecosystem  
71 status, providing information on the type of factors regulating the dynamics of these  
72 communities (Fuhrman, 1999; Suttle, 2005).

73 Coastal marine habitats at the land-sea interface are threatened by human activities at sea and  
74 on shore, and are, therefore, among the most heavily degraded (Costanza et al., 1997). Coral  
75 reef environments are generally recognized as being among the most threatened of the fragile  
76 marine ecosystems, and are highly susceptible to stress and disturbance, especially to  
77 anthropogenic pressure (Mellin et al., 2008) and climate change (Miller et al., 2009). Studies  
78 of coral reef systems to understand the causes, effects and consequences of direct  
79 anthropogenic pressure are generally conducted in anthropized zones. However, it is  
80 extremely difficult to distinguish the effects of climate change from other forcing factors,  
81 mainly because it is difficult to study ecosystems that are isolated from human pressure.  
82 “Pristine” coral reef ecosystems are often located on uninhabited islands.

83 The five Iles Eparses (Scattered Islands) are located in the Western Indian Ocean (WIO) and  
84 form the 5<sup>th</sup> district of the French Southern and Antarctic Lands (TAAF). Several studies of  
85 these remote ecosystems were performed recently, which established ecological baselines for  
86 pristine coral reef systems. However, most previous studies have dealt with reef fish  
87 inventories (Chabanet, 2002; Quod et al., 2004; Chabanet and Durville, 2005) following the  
88 extensive coral bleaching event in 1998, and only a few studies have considered the

89 biodiversity, structure and functioning of the marine microbial communities in these islands  
90 (for example, the nutrient status was studied by Riaux-Gobin et al., 2011). The structure of  
91 the plankton foodweb in these ecosystems considered to be pristine ecosystems, must be  
92 understood in order to protect them from future human threats. The lack of "reference  
93 environments" raises serious problems: (1) limited knowledge about the diversity and  
94 functions of microbial communities from unaffected coastal sites, (2) lack of knowledge on  
95 the sensitivity of reference communities (e.g. bacteria, phyto-and zooplankton) to local  
96 environmental forcing (nutrient inputs, organic and mineral pollution, etc).

97 As part of the international program "Eparses 2011-2013", a survey was carried out from  
98 April 5 to 23, 2011 by several scientific teams aboard the N/O Marion Dufresne II, the TAAF  
99 supply vessel, to collect data on many aspects of terrestrial and marine biodiversity in the Iles  
100 Eparses. This study focused on plankton microorganisms, based on samples taken from  
101 various lagoon and ocean stations in each of the five islands (see Table 1), as well as from a  
102 station in Mayotte lagoon, which is considered be a typical anthropized island in the  
103 geographic zone.

104 The overall aim of the project was to determine whether there were differences between such  
105 "pristine" ecosystems in the spatial distribution, composition and structure of biological  
106 compartments owing to environmental conditions in each island ecosystem. This preliminary  
107 study characterized the plankton assemblages by (1) determining the abundances of microbial  
108 communities (virus, bacteria, protists and phytoplankton) and metazooplankton in the lagoon  
109 and ocean sites around each island, and (2) exploring relationships between environmental  
110 conditions and biological components at regional scale. The main control factors of bacterial  
111 communities (nutrient enrichment *versus* predation) were determined by bioassay  
112 experiments.

113

## 114 2. Material and Methods

### 115 2.1. Study sites and samplings

116 The Iles Eparses (Scattered Islands) are small coral reef islands located in the Indian Ocean  
117 close to Madagascar, and became the 5th district of the French Southern and Antarctic Lands  
118 (TAAF) in February 2007. Four of these islands lie in the Mozambique Channel, west of  
119 Madagascar (from south to north: Europa, Bassas da India, Juan de Nova and Glorieuses) and  
120 the fifth (Tromelin island) lies about 450 kilometers east of Madagascar (Figure 1). The  
121 islands have been classified as "Marine Protected Areas", and all except Bassas da India have



122 a meteorological station. Each island except Bassas da India, has an airstrip more than  
123 1,000 m long for use by small groups of military personnel.

124 Samples were taken during a single period (April 5 to 23, 2011) from 22° 21'S to 12° 46'S  
125 and 39° 44'E to 54° 31'E (Figure 1, Table 1) from 16 stations. There was one ocean station  
126 and two or three stations (depending on the lagoon area) for each island. Samples were taken  
127 at a depth of 0.5 m using a Niskin bottle, transferred immediately to acid-washed  
128 polyethylene bottles and kept in the dark at *in situ* temperatures until processed in the  
129 laboratory on board within 2 hours. A total of 25 parameters were measured to characterize  
130 the physical, chemical and biological environment of the water column. Metazooplankton was  
131 collected using a WP2 plankton net (80 µm mesh-size) equipped with a Hydrodata flowmeter.  
132 The net was hauled vertically from near bottom to surface at ocean and deep lagoon stations,  
133 and horizontally (at a depth of 0.5 m) at shallow stations. After collection, metazooplankton  
134 samples were rapidly preserved in a 4% buffered formaldehyde solution.

135

### 136 *2.2. Physical and chemical parameters*

137 At each sampling station, a CTD profiler (YSI 600 XLM) was deployed to record  
138 temperature, depth, pH and dissolved oxygen profiles. Dissolved organic carbon (DOC)  
139 analyses were performed on 30 ml subsamples collected in pre-combusted (450°C overnight)  
140 glass vials, preserved with 35 µl of 85% phosphoric acid. Samples were stored in the dark  
141 until analysis using a Shimadzu TOC VCPH analyzer (Rochelle Newall et al., 2008).  
142 Chlorophyll concentrations were determined by [fluorometry after](#) filtration onto Whatman  
143 GF/F fiberglass filters and direct extraction using methanol (Yentsch and Menzel, 1963).  
144 Samples for measuring dissolved nutrients (SiO<sub>4</sub>, NH<sub>4</sub>-N, NO<sub>3</sub>-N, NO<sub>2</sub>-N, PO<sub>4</sub>-P) were  
145 filtered onto Whatman GF/F fiberglass filters, stored at -20°C and analyzed as described by  
146 Strickland and Parsons (1972). Sampled water was filtered through a pre-combusted GF/F  
147 Whatman filters to determine particulate organic nitrogen (PON) and particulate organic  
148 carbon (POC), using a nitrogen carbon analyzer after acid decarbonation.

149

### 150 *2.3. Biological parameters*

151 For bacterial and viral abundances, samples were fixed with prefiltered (0.02 µm) buffered  
152 formaldehyde (2% final concentration), stored in liquid nitrogen (-196°C) and analyzed on  
153 return to Montpellier University. Total bacterial cells (TB) were enumerated by flow  
154 cytometry using the method described by Marie et al. (1997). One milliliter of fixed  
155 subsamples was incubated with SYBR Green I (Molecular Probes, Eugene, OR, USA) at a

156 final concentration of 1/375 for 15 min at 4°C in the dark. For each subsample, three replicate  
157 counts were performed using a FACSCalibur flow cytometer (Becton Dickinson, San Jose,  
158 CA, USA) equipped with an air-cooled argon laser (488 nm, 15 mW). Stained bacterial cells,  
159 excited at 488 nm, were enumerated according to their right angle light scatter (RALs) and  
160 green fluorescence (FL1) was measured using a 530/30 nm filter. These cell parameters were  
161 recorded on a four-decade logarithmic scale mapped onto 1024 channels. Fluorescent beads  
162 (1-2 µm, Polysciences, Warrington, PA, USA) were systematically added to each sample.  
163 Standardized RALS and FL1 values (cell RALS and FL1 divided by 1 µm beads RALS and  
164 FL1 respectively) were used to estimate the relative size and nucleic acid content of bacterial  
165 cells respectively (Troussellier et al., 1999). List-mode files were analyzed using BD  
166 Cellquest Pro software. The number of virus-like particles (VLPs) contained in triplicates of  
167 50-200 µl samples was determined after particles had been retained on 0.02 µm pore-size  
168 membranes (Anodisc) and stained with SYBR Gold (Patel et al., 2007). On each slide, VLPs  
169 were counted in 15-20 fields using an epifluorescence microscope, with final numbers giving  
170 a precision of <10% at 95% confidence limit. Culturable heterotrophic bacteria (CB) were  
171 counted by plating 100 µL of serial dilutions of each sample on marine agar plates (Marine  
172 Agar; Difco, Detroit). After 4 days' incubation at *in situ* room temperature (close to 27°C),  
173 colony forming units (CFU) were counted (it was established that the counts did not increase  
174 for longer incubation periods).

175 Bacterial Production (BP) was estimated from the DNA synthesis rates measured by (3H-  
176 methyl) thymidine (3H-TdR) incorporation using the microcentrifuge method (Smith and  
177 Azam, 1992). On board, a sample aliquot (1.4 ml) was added to a sterile polystyrene snap cap  
178 tube containing a final saturating concentration of 20 nM of <sup>3</sup>H-TdR (specific activity 53 Ci  
179 mmol<sup>-1</sup>, Amersham). Triplicate live samples and a control were run for each assay. Killed  
180 controls were prepared by adding 70 µl of 100% of trichloroacetic acid (TCA) 15 min before  
181 the addition of <sup>3</sup>H-TdR. Bacterial growth was measured in the dark at *in situ* temperature for a  
182 short incubation time (no longer than 1 h). Incorporation was terminated by adding 70 µl of  
183 100% TCA. Samples were stored for at least 2 h at 4°C and then centrifuged at 14000 g for  
184 15 min. The precipitates were rinsed three times with 5% TCA and once with 70% ethanol  
185 and were resuspended in 1.5 ml of liquid scintillation cocktail (Ultima Gold LLT, Perkin  
186 Elmer) before determining the radioactivity using a liquid scintillation counter (Beckman LS  
187 6500).

188 Pico and nano-phytoplankton samples were fixed with paraformaldehyde (2% final  
189 concentration), and counted using a FACS Aria Flow cytometer (Becton Dickinson, San Jose,

190 CA, USA) equipped with an HeNe air-cooled laser (633 nm, 20 mW). Cells excited at 633 nm  
191 were detected and enumerated according to their FALS and RALS properties and their orange  
192 fluorescence (576/26 nm) and red fluorescence ( $> 650$  nm) from phycoerythrin and  
193 chlorophyll pigments, respectively. Fluorescent beads (1-2 $\mu$ m for pico and 2-6-10-20 $\mu$ m for  
194 nano) were systematically added to each sample. List-mode files were analyzed using BD  
195 FACSDiva software. To enumerate heterotrophic (HNF) and pigmented nanoflagellates  
196 (PNF), water samples were fixed with paraformaldehyde (2% final concentration) and stored  
197 at 4°C for 24 h. Twenty-five millilitres of preserved water samples were then stained with  
198 DAPI (final concentration, 15 mg ml<sup>-1</sup>) for 15 min, filtered onto a black Nuclepore filter (0.8  
199 mm pore size), stored at -20°C, and counted using an epifluorescence microscope (Nikon  
200 Eclipse TE200) with UV excitation (Boenigk et al., 2004, modified). Pigmented  
201 nanoflagellates were discriminated by blue and green fluorescence under UV excitation.  
202 For microzooplankton (ciliates) and microphytoplankton (dinoflagellates, diatoms)  
203 abundances, water samples (500 mL) were concentrated by gravity filtration onto a 5 $\mu$ m  
204 porosity filter (polycarbonate membrane, Nuclepore), and fixed with alcalin lugol iodine (2%  
205 final concentration). The remaining 50 mL was then stored at 4°C in the dark until analysis in  
206 the laboratory. Microorganisms were enumerated in an Utermöhl settling chamber (Hydro-  
207 Bios combined plate chamber) using a reverse microscope (Zeiss Axiovert, magnification  
208 x400) for ciliates, and an inverted microscope (Olympus IX70), equipped with digital camera  
209 (Moticam MoticamPro) for phytoplankton.  
210 Metazooplankton were counted under a stereomicroscope (Olympus SZX200), using a  
211 Dolfuss counting chamber and were identified as described by Tregouboff and Rose (1957),  
212 and Conway et al (2003). The abundance of the various taxa was discriminated by group,  
213 genus or species.

214

#### 215 *2.4. Bacterial growth rates and grazing rates by HNF*

216 Water samples were taken at 0.5 m depth at the various stations for each island. Two bioassay  
217 series were performed to compare the responses of the bacterial community to inorganic  
218 enrichment with 100% of predators (using  $<50$   $\mu$ m-filtered water) and with 1% of predators  
219 (using 99% of 0.22  $\mu$ m-filtered water and 1% of  $<50$   $\mu$ m-filtered water). The samples were  
220 homogenized and distributed equally into 2 series of 3 x 100 ml Whirl-Pak® polyethylene  
221 sterile bags. At time zero (t<sub>0</sub>), inorganic nitrogen (mixture of 2.5  $\mu$ M as NH<sub>4</sub>Cl and 1.5  $\mu$ M as  
222 NaNO<sub>3</sub>), inorganic phosphorus (1.5  $\mu$ M as NaH<sub>2</sub>PO<sub>4</sub>) and 200  $\mu$ M as glucose were added in  
223 combination. All assays were performed in triplicate with a total of 6 Whirlpaks per station.

224 All Whirlpaks were incubated for 24 hours on board in a tank filled with a seawater circuit to  
225 ensure that the water temperature remained fairly constant during the experiments.  
226 Subsamples were removed at time zero (t0) and after 24 h (t24) incubation to enumerate the  
227 bacterial abundance (see above). The bacterioplankton growth rates in each triplicate were  
228 calculated as  $\mu = (\ln N_{24} - \ln N_0)/t$ , where t was the incubation time and N24 and N0 were the  
229 bacterial concentrations at the end and at the beginning of incubation. The grazing rates were  
230 calculated as the difference between the apparent growth rate ( $\mu+g$ ) and the net growth rate  
231 ( $\mu$ ).

232

### 233 *2.5. Data processing*

234 The differences between sites for all parameters were tested using the non parametric Mann-  
235 Whitney U-test. Differences were considered as significant at  $p < 0.05$  (Sigma Stat version 3.5).  
236 The relationships between environmental parameters and biological variables were studied  
237 using multivariate analysis, with data from the 16 sampling stations. Principal component  
238 analysis (centered PCA) was performed for each of two data sets: an Environmental System  
239 based on 8 parameters, and a Biological System based on 12 variables. The results of the two  
240 analyses were combined by co-inertia analysis, which allows two tables with a different  
241 number of variables to be compared (Dolédéc and Chessel, 1994). Two sets of factor scores  
242 were obtained for the sampling points: scores of the rows “seen by the environmental  
243 parameters”, and scores of the rows “seen by the biological variables”. The significance of the  
244 co-inertia analysis was tested after randomizing the results, by a repeated random permutation  
245 of the rows of both tables, and a comparison of these results obtained with a standard PCA.  
246 The resulting distribution of 2000 replicated matches of the two arrays gave an estimated  
247 significance of  $p < 0.001$  for the difference from the original value. Cluster classification of  
248 observation scores from the first factorial planes of the co-inertia analysis (Ward’s criterion  
249 aggregation) was performed to classify the 16 stations. All this data processing was  
250 performed using ADE-4 software (Thioulouse et al. 1997).

251

## 252 **3. Results**

### 253 *3.1. Environmental parameters*

254 The surface temperature ranged from 26.9°C (Europa lagoon) to 30.1°C (Juan de Nova  
255 lagoon) with mean values similar for the lagoon and ocean stations (Table 1). There was little  
256 variation in salinity, with average values of 35.34 and 35.05, for lagoon and ocean sites. There

257 was little variation in pH with values ranging from 7.95 to 8.02 (average of 7.98 and 8.01 in  
258 lagoon and ocean sites, respectively). The dissolved oxygen concentrations ranged between  
259 4.27 mg l<sup>-1</sup> at Glorieuses lagoon (G3) to 9.43 mg l<sup>-1</sup> at Europa lagoon (E1), except for Bassas  
260 da India lagoon where a high concentration was reported (B1: 10.96 mg l<sup>-1</sup>) (Table 1).  
261 Low dissolved nutrient concentrations were found, for all nutrients, without significant  
262 differences between the sites (p>0.05; Table 2). Dissolved phosphorus concentrations were  
263 below the detectable limits (threshold 0.010 μM). Silicate concentrations did not vary  
264 significantly (p>0.05) between the stations, with an average of 2.41 and 1.90 μM for ocean  
265 and lagoon sites, respectively. Ammonium concentrations accounted for the larger  
266 contribution of nitrogen forms in ocean sites with an average of 0.16 μM (Table 2). The  
267 highest concentrations of nitrite and nitrate were reported in the Europa lagoon (0.19 μM).  
268 The mean values of DOC concentrations averaged 103 μM and 96.4 μM in ocean and lagoon  
269 sites respectively, with the highest concentrations for the Europa stations. Particulate organic  
270 nitrogen averaged 24.1 and 34.5 μg l<sup>-1</sup> in ocean and lagoon sites, respectively, while  
271 particulate organic carbon averaged 171.5 and 182.8 μg l<sup>-1</sup>. There were higher particulate  
272 organic nitrogen forms in the Europa stations, especially in the lagoon. The particulate  
273 organic C/N averaged 7.3 and 5.4 in ocean and lagoon sites, respectively, with the highest  
274 values in Europa and Bassas da India ocean sites.

275

### 276 *3.2. Biological variables*

277 The culturable bacteria (CB) density varied from 330 to 60,000 CFU ml<sup>-1</sup> (colony forming  
278 unit) with lower values reported in Europa sites (Table 3). The bacterial abundance averages  
279 were similar (9 x 10<sup>5</sup> ml<sup>-1</sup> for ocean sites and 12 x 10<sup>5</sup> ml<sup>-1</sup> for lagoon sites). The highest  
280 abundances of total bacteria (TB) were found in Europa lagoon, and in the Mayotte lagoon  
281 which was considered to be a polluted site (not part of the Iles Eparses). The highest values  
282 for bacterial production, (BP) were found in the Europa lagoon (close to 400 pmole l<sup>-1</sup> h<sup>-1</sup>)  
283 whereas the mean of the ocean sites was only 27 pmole l<sup>-1</sup> h<sup>-1</sup>. Virus like particle (VLP)  
284 concentrations were significantly different (mean of 2.86 x 10<sup>7</sup> ml<sup>-1</sup> for the ocean sites and a  
285 mean of 15.46 x 10<sup>7</sup> ml<sup>-1</sup> for the lagoon sites (t-test; p<0.006), with the highest values  
286 reported in Juan de Nova lagoon (stations J1, J2 and J3).

287 Among the phytoplankton, the dominant groups in terms of abundance were the  
288 picoeukaryotes (Pico) and the picocyanobacteria (Cyano) mainly *Synechococcus* and  
289 *Prochlorococcus*. Picoeukaryotes and picocyanobacteria abundances were similar in ocean  
290 and lagoon sites (mean of 21 x 10<sup>3</sup> ml<sup>-1</sup> and 23 x 10<sup>3</sup> ml<sup>-1</sup>, respectively) whereas

291 picoeukaryotes abundances were significantly higher in lagoon sites, especially in the Europa  
292 lagoon (t-test;  $p < 0.05$ ). There were very few nanophytoplankton cells (Nano) and pigmented  
293 nanoflagellates (PNF), especially in ocean sites (mean of 1.06 and  $1.60 \times 10^2 \text{ ml}^{-1}$ ,  
294 respectively). Microphytoplankton densities were higher in lagoon sites (mean of 11,715 cells  
295  $\text{l}^{-1}$ ) than in ocean sites (mean of 2,190 cells  $\text{l}^{-1}$ ) with the highest abundances found in the  
296 Europa and Juan de Nova lagoon stations (Table 3). The mean chlorophyll-a concentrations,  
297 considered here as a proxy of total phytoplankton biomass, were generally low and  
298 statistically different (t-test;  $p < 0.05$ ) between the type of ecosystem ( $0.181 \mu\text{g l}^{-1}$  in ocean and  
299  $0.507 \mu\text{g l}^{-1}$  in lagoon sites).

300 The heterotrophic nanoflagellates (HNF) abundances were low and similar in both types of  
301 site. The ciliate community was identified as two groups, with aloricate abundances higher  
302 than loricate abundances, especially in lagoon sites (no loricate organisms were found in Juan  
303 de Nova and Tromelin ocean sites) (data not shown). Ciliate abundances were very low for all  
304 the stations (Table 3). Metazooplankton numbers varied from 607 (G1, Glorieuses lagoon) to  
305  $6008 \text{ ind.m}^{-3}$  (Mayotte lagoon) with similar means in ocean and lagoon sites (1824 and 2583  
306  $\text{ind.m}^{-3}$  in ocean sites and lagoon sites, respectively). Copepods were the most abundant in all  
307 sites (>75% abundance) except for Bassas de India (39%) where meroplankton larvae were  
308 dominant (45%) (data not shown).

309

### 310 *3.3. Bacterial growth rates and HNF grazing rates*

311 The 24 h bioassay experiments were conducted for each island enumerating the bacteria for  
312 each treatment (presence or absence of predators, with or without enrichment). The results  
313 showed that the nanoflagellate abundance did not increase during incubation in the various  
314 assays. Bacterial growth rates in the presence (gross rate;  $\mu+g$ ) or absence (net rate;  $\mu$ ) of  
315 predators, and grazing rates of bacteria by predators ( $g$ ) in the different nutrient conditions  
316 (with or without added nutrients) are given in Table 4. With no added nutrients (control),  
317 bacterial growth rates were higher for the Europa lagoon (E2:  $4.25 \text{ d}^{-1}$ ) and Bassas lagoon  
318 (B1:  $4.17 \text{ d}^{-1}$ ), and values were lower for ocean sites (from  $0.48 \text{ d}^{-1}$  in GO to  $2.73 \text{ d}^{-1}$  in BO).  
319 Grazing rates by predators were generally lower than growth rates (Figure 2) and net bacterial  
320 growth rates ( $\mu$ ) in the absence of predators were greater than in the presence of predators  
321 ( $\mu+g$ ) (Table 4). With enrichment, net growth rates ( $\mu$ ) were higher in both ocean and lagoon  
322 sites than without enrichment. With the exception of the Tromelin ocean station (TO), growth  
323 rates were clearly higher with enrichment but there was no close correspondence between  
324 growth and grazing rates values (Figure 2). Net growth of the bacterial communities from

325 ocean stations (BO, EO, JO, GO) and Mayotte was clearly higher with enrichment and  
326 absence of predators (values of  $\mu$  close to  $5 \text{ d}^{-1}$ )

327

### 328 *3.4. Co-inertia analysis*

329 The two PCAs on environmental and biological variables were performed on all data sets (16  
330 stations; 8 environmental parameters; 12 biological variables). The first two eigenvalues of  
331 the co-inertia analysis accounted for 90.9% of the total variability (Figures 3 and 4),  
332 indicating that the analysis focused on the first 2 axes. The values of the projected variables of  
333 the Environmental and Biological tables on the axes (F1, F2) of the co-inertia analysis (Iner E  
334 and Iner B) were close to the values of projected variables on the same axes of the standard  
335 (PCA) analysis (Var E and Var B) (Table 5). The factorial plane of the co-inertia for the  
336 Biological table explained 88.9% of the variance, and the factorial plane for the  
337 Environmental table explained 87.9% of the variance. The co-inertia analysis, therefore,  
338 demonstrated a co-structure between the 2 data sets. Figures 4 and 5 represent the factorial  
339 planes of the variables (columns) and stations (lines) in the Environmental and the Biological  
340 System, respectively.

341 In the Environmental System (Figure 3), the first axis (F1) showed an opposition between the  
342 organic nutrient context (POC, PON, DOC) and the silicate concentration (SI). Ward's  
343 aggregation recognized 4 groups of stations. The first group ENV-1 comprised the Europa  
344 lagoon stations (E1, E2 and E3) and had significantly higher concentrations of organic  
345 nutrient (PON, POC and DOC), whereas the second group ENV-2 (JNO, EO and BO) was  
346 more associated with ammonium ( $\text{NH}_4$ ). The third group (JN3, G1) was in opposition with  
347 the two first groups without specific information, whereas the fourth group (ENV-4) was  
348 characterized by low organic concentrations, high inorganic concentrations ( $\text{NO}_3$ ,  $\text{NO}_2$ ), and  
349 high silicate concentrations. Consequently, the factorial plane defined by the first 2 axes in  
350 this environmental system distinguished stations according to nutrient richness (Axis F1).

351 In the Biological System (Figure 4), the F1 axis showed the association of the bacterial  
352 variables (TB, BP) and the phytoplankton variables (CHLO, NANO, PNF), opposed to  
353 cyanobacteria concentrations (CYANO) and culturable bacteria (CB). The factorial plane  
354 highlighted the neutral position of metazooplankton (ZPK), ciliates (CIL) and heterotrophic  
355 nanoflagellates (HNF). In this system, Ward's aggregation produced by cluster analysis on  
356 the scores of stations identified 3 main groups. Group BIO-1 comprised the Europa lagoon  
357 stations as for the Environmental system (see above), with higher values of total bacterial  
358 abundance (TB) and production (BP) linked to high autrophic algal biomass (CHLO, PNF,

359 NANO). The second group BIO-2 comprised all ocean stations and two lagoon stations (JN1  
360 and G3), and had significantly higher concentrations of picocyanobacteria (CYANO) with the  
361 genera *Prochlorococcus* and *Synechococcus*, and culturable bacteria (CB). In the third group  
362 BIO-3, Bassas and Mayotte lagoons were in a neutral position, characterized by higher  
363 concentrations of metazooplankton, ciliates and heterotrophic nanoflagellates (ZPK, CIL,  
364 HNF). Thus, the mean values of biological characteristics in the 3 groups of stations varied  
365 according to biological richness (Axis F1).

366 The correlation between the new environmental and biological ordination of the stations,  
367 reflecting the degree of association between the Environmental and Biological systems, was  
368 highly significant, with R-values of 0.828 and 0.677 for the 2 factorial planes (Axis F1  
369 Environment/Axis F1 Biology; Axis F2 Environment/Axis F2 Biology). There was a good fit  
370 for all these results between the 2 new ordination sets.

371

## 372 4. Discussion

### 373 4.1. Regional context

374 In the Western Indian Ocean (WIO), the Mozambique Channel is dominated by southward  
375 migrating eddy trains with large anticyclones of 300 km in diameter (Quarty and Srokosz,  
376 2004). Many studies conducted in this zone were based on mesoscale features with physical  
377 and biological approaches demonstrating the importance of the frontal areas and the cyclonic  
378 and anticyclonic eddies (Ménard et al., 2014; Debourges-Dhaussy et al., 2014). Various  
379 studies have shown the importance of eddies for increasing nutrient concentrations and  
380 primary production, attracting zooplankton and top-predators around these zones  
381 (Weimerskirch et al., 2004). However, it is now recognized that coral reefs are one of the  
382 coastal ecosystems most threatened by climate change and anthropogenic pressures (Hoegh-  
383 Guldborg et al., 2007; Sandin et al., 2008). The WIO, therefore, provides a unique  
384 environmental gradient for examining the interactive effects of environmental variation,  
385 climate change, connectivity, resilience and adaptation of coral communities (McClanagan et  
386 al., 2014). However, little attention has been paid to microbial communities in coral reefs, and  
387 their role in the nutrition of reef organisms, or in the transfer of dissolved organic matter from  
388 microorganisms to predators (Dinsdale et al., 2008). So far as we are aware, there are very  
389 few microbial studies of the coral reef lagoons located in the WIO, with only one study of the  
390 nutrient status of the Iles Eparses (Riaux-Gobin et al., 2011) and a few studies on microbial  
391 ecology in Mayotte lagoon (Vacelet et al., 1999; Gourbesville and Thomassin, 2000;



392 Houlbrèque et al., 2006). The coral reef lagoons in Madagascar are very different (e.g. Great  
393 Reef of Toliara). However, very few studies of aquatic microorganism dynamics have been  
394 conducted in this zone, except for the phytoplankton components (Vasseur et al., 2000) and  
395 recently for bacterial and viral interactions (Bouvy et al., 2015). This study should, therefore,  
396 provide information about the relationships between environmental conditions and the main  
397 plankton compartments of the Iles Eparses, considered here to be pristine systems at a  
398 regional scale.

399

#### 400 *4.2. Nutrient context and plankton structure*

401 The water temperature, salinity and pH were uniform, with no stratification along the water  
402 column at any of the lagoon or ocean stations. The Mozambique Channel is subject to  
403 anticyclonic and cyclonic mesoscale eddies throughout the year with a southward water  
404 migration (Schouten et al., 2003). Roberts et al. (2014) reported that there was no significant  
405 difference in surface temperature in April along the Channel. This was confirmed by our  
406 results obtained in April 2011 with surface temperatures varying between 28.1°C and 29.8°C.  
407 On average, nutrient concentrations were low, similar to those reported in oceanic zones, with  
408 undetectable levels of orthophosphate. Most of the WIO is nutrient-limited (especially  
409 phosphates) with little or no upwelling along most of the East African coast (Porter et al.,  
410 2013) and prevailing downwelling (McClanahan, 1988). However, mesoscale eddies can  
411 occasionally increase nutrient concentration and primary production (Weimerskirch et al.,  
412 2004). There is very little human activity in the WIO region, especially in the Iles Eparses  
413 and nutrient concentrations in mangroves are mainly derived from the release of nutrients  
414 and organic matter from mangrove litter during leaching and decomposition. This study  
415 produced the first measurements of virioplankton and protozoan concentrations in the WIO.  
416 Virioplankton concentrations were similar to those found in Pacific near-shore oceanic coral  
417 reefs (Seymour et al., 2005; Pattern et al., 2011; Bouvy et al., 2012a). Virioplankton  
418 abundances (min-max, 1.4 – 34.4 x 10<sup>7</sup> VLPs ml<sup>-1</sup>) were within the usual range (10<sup>7</sup> – 10<sup>8</sup> ml-  
419 1) for temperate productive systems (Weinbauer, 2004). VLP concentrations were  
420 significantly higher in the lagoon than in the ocean sites, confirming that viral abundances  
421 tend to be greater in productive, nutrient rich environments (Weinbauer et al., 1993). The  
422 bacterial densities were similar to those occurring in near-shore through to oceanic coral reefs  
423 (Seymour et al., 2005; Dinsdale et al., 2008; Patten et al., 2008). The highest chlorophyll  
424 values were observed in the lagoons (especially Europa) with an average of 0.507 µg l<sup>-1</sup>,

425 while significantly lower values, close to concentrations recorded in South Pacific coral reef  
426 lagoon, were found in ocean sites (Rochelle-Newall et al., 2008). These results were  
427 confirmed by the statistical difference in algal concentrations between the two types of  
428 systems. The phytoplankton composition, dominated by picoeucaryotes (Pico) and  
429 picocyanobacteria (Cyano), was in the range reported by surveys in tropical lagoons (Ferrier-  
430 Pages and Furla, 2001; Houlbr eque et al., 2006; Bouvy et al., 2012b) and in oceanic waters  
431 (Flombaum et al., 2013). Our results confirmed the importance of picoplankton (defined here  
432 as cells  $<3\mu\text{m}$ ), primarily found in oligotrophic areas of the oceans, where they contribute to  
433 nutrient remineralization (Azam et al., 1983) and may account for up to 95% of primary  
434 production (Raven, 1998). On average, picocyanobacteria and picoeukaryotes were  
435 significantly less abundant in oceanic waters than in the lagoons. However, their  
436 concentrations were lower in Europa mangrove waters as they are believed to be outcompeted  
437 by other phytoplankton in high-nutrient waters (Partensky et al., 1999).

438 It is now accepted that nanoflagellates are commonly the most abundant group of coastal  
439 marine protists in nanoplankton communities (70-80%  $< 5 \mu\text{m}$ ), with a count of heterotrophic  
440 nanoflagellates (HNF) and pigmented nanoflagellates (PNF) of between  $10^2$  and  $10^3 \text{ cells ml}^{-1}$   
441 (Massana 2011). There were relatively low concentrations of both groups in the Iles Eparses,  
442 with no significant differences between lagoon and ocean sites. The low abundances of  
443 nanoflagellates were also in the range reported for the Mayotte reef (Houlbr eque et al. 2006)  
444 and in the Great Reef of Toliara, Madagascar (Bouvy et al., 2015).

445 Overall, aloricate ciliates were more abundant than loricate ciliates in the Iles Eparses,  
446 confirming that oligotrophic marine waters generally have significantly more aloricate ciliates  
447 than tintinnids (Quevedo et al., 2003). There was no significant difference in total ciliate  
448 concentrations between the lagoon and ocean ecosystems, with abundances generally lower  
449 than those found in other coastal localities (Jyothibabu et al. 2008; Liu et al 2012 in the  
450 southeastern Arabian Sea and the Bay of Bengal, respectively). Recently, Fournier et al.  
451 (2012) reported abundances of ciliates in French Polynesian Atoll lagoons (with a mean of  
452  $740 \text{ cell l}^{-1}$ ) that were significantly larger than those reported in Iles Eparses lagoons (mean of  
453  $44 \text{ cell l}^{-1}$ ). These low concentrations of heterotrophic protists may significantly affect the  
454 flow of organic matter in the microbial food web in the Iles Eparses ecosystems.

455 The mean total metazooplankton abundance in the Iles Eparses ( $0.6$  to  $6 \times 10^3 \text{ ind m}^{-3}$ ) was  
456 lower than those found in a French Polynesian Atoll (between  $5 \times 10^3 \text{ ind m}^{-3}$  and  $23 \times 10^3 \text{ ind}$   
457  $\text{m}^{-3}$ ; Pagano et al., 2012) and in the coral reef lagoon of New Caledonia (mean of  $3.5 \times 10^5 \text{ ind}$   
458  $\text{m}^{-3}$ ; Carassou et al., 2010). There was no significant difference between the two types of

459 ecosystem (mean of  $1.8 \times 10^3$  and  $2.5 \times 10^3$  ind  $m^{-3}$ , respectively in ocean and lagoon sites).  
460 Our results showed that copepod nauplii (copepodids) and adult copepods accounted for a  
461 large proportion of the total density of zooplankton (close to 75%). This proportion is lower  
462 in atoll lagoons of the Tuamotu archipelago (French Polynesia), where copepods account for  
463 nearly 35% of the total zooplankton abundance whereas meroplankton account for up to 74%,  
464 owing to the importance of pearl farming (Le Borgne et al., 1989; Carassou et al., 2010;  
465 Pagano et al., 2012).

466

#### 467 *4.3. Influence of nutrient and predator levels (HNF) on the bacterial growth rates and* 468 *grazing rates*

469 The enrichment experiments were performed in nutrient conditions comparable to those  
470 observed in some of the Iles Eparses in 2009 (Riaux Gobin et al. 2011), and also to those  
471 reported in Ahe atoll lagoon (Bouvy et al. 2012b) and in the Great Reef of Toliara (Bouvy et  
472 al. 2015). The study also measured bacterial growth rates and bacterial grazing rates by  
473 nanoflagellates, as it is now commonly accepted that nanoflagellates are the most important  
474 grazers on bacteria in most environments (e.g. Sanders *et al.* 1992; Tsai *et al.* 2011). Our  
475 results showed a large range of bacterial growth rates with different patterns in lagoonal and  
476 oceanic conditions. Bacterial growth rates were higher when the nanoflagellate concentration  
477 was reduced by 99%, confirming that nanoflagellates are the main bacterial predators (see  
478 above). Overall, all bacterial growth rates ( $\mu$ , table 4) were relatively high in the upper range  
479 of data reported in other ocean ecosystems (Tsai et al., 2011; Bouvy et al., 2012b; Bouvy et  
480 al., 2015). The highest growth rates were reported in lagoon ecosystems with  $4.25 \text{ d}^{-1}$  in  
481 Europa, which also had the highest bacterial production and dissolved and particulate organic  
482 matter. Microbial communities are adapted to intertidal zones and are subject to highly  
483 variable salinity, floating, light and temperature conditions, which give rise to the high  
484 diversity that characterizes mangrove ecosystems (Feller et al., 2010). In the other  
485 environments studied, the growth rates of bacterial communities can be expected to be limited  
486 by dissolved inorganic and organic matter, given that mineral limitation of growth rates is  
487 widespread in various ecosystems including atoll systems (e.g. Torreton et al., 2000; Bouvy et  
488 al., 2012b). Our results showed that bacterial growth rates were higher with added nutrients  
489 for each station, especially for the ocean stations at Juan de Nova (JO) and Europa (EO),  
490 indicating that nutrient limitation is a major factor for bacterial communities in the conditions  
491 encountered in the Iles Eparses. Furthermore, a high ratio between heterotrophic bacteria and  
492 picoautotrophic cells was reported at all stations (H/A; mean of 20.1), especially in the

493 Europa mangroves, suggesting that these microbial communities can act as CO<sub>2</sub> sources  
494 (Duarte and Agusti, 1998). The greater heterotrophic effect (such as external eutrophication)  
495 could, therefore, be related to changes in the relative contribution of the various microbial  
496 components, or to an increase of nutrient concentrations.

497 Prey abundance and water temperature are usually considered to be among the most important  
498 factors regulating the grazing activity of nanoflagellates (Choi 1994). Our experiments  
499 showed that grazing rates by nanoflagellates increased with increasing bacterial growth rates,  
500 indicating that bacterial and nanoflagellate dynamics were closely coupled at certain lagoon  
501 stations (J2, E2 and B1). In the tropical conditions encountered in the Iles Eparses, water  
502 temperature is certainly not the main factor controlling bacterial and nanoflagellate activities.  
503 Moreover, our study did not consider alternative sources of bacterial mortality, such as lysis  
504 by viruses. Very few studies have been carried out on viruses in atoll lagoons (Seymour et al.,  
505 2005; Dinsdale et al., 2008; Patten et al., 2011; Bouvy et al., 2012a), and very little is known  
506 about the response of tropical bacterioplankton to the presence of viruses.

507

#### 508 *4.4. Relationships between biological components and trophic variables*

509 Multivariate analysis demonstrated clear differences between nutrient levels and biological  
510 productivity in the Iles Eparses. Co-inertia analysis coupled with a Ward's aggregation clearly  
511 defined a group with the three stations sampled in Europa lagoon, characterized by high  
512 nutrient levels associated with high bacterial dynamics. In the Environmental system,  
513 particulate organic carbon (POC), particulate nitrogen (PON) and dissolved organic carbon  
514 (DOC) were the parameters that had the strongest correlation with the Europa lagoon (ENV-  
515 1), confirming the role of mangroves as a provider of nutrients and organic matter for the  
516 biological compartments (Saenger, 2002). Microbial communities, especially bacteria (TB  
517 and BP), are, therefore, fundamental in these sites (BIO-1) for the mineralization of organic  
518 matter and its transformation into nutrients, as confirmed by the correlation found in the  
519 Biological system. The release of ammonium (NH<sub>4</sub>) into the overlying water following high  
520 rates of remineralization in the mangrove sediment may support the high bacterioplankton  
521 activities in the Europa lagoon, as demonstrated by Miyajima et al. (2001). Pigmented  
522 nanoflagellates (PNF) and nanophytoplankton (NANO) were strongly linked to bacterial  
523 abundances in the Europa lagoon, suggesting a high trophic coupling between bacteria and  
524 nanoplankton. Co-inertia analysis also revealed a group (ENV-2) with three southern ocean  
525 stations (JNO, EO, BO), characterized by higher nutrient richness than the other ocean  
526 stations (TO and GO). However, all the ocean stations were grouped into one group (BIO-2)

527 for the biological variables reflecting the large contrast in terms of functioning between  
528 lagoon and ocean ecosystems. The ocean stations were characterized by higher concentrations  
529 of nitrate and nitrite, and by picocyanobacteria (PICO) which played a major role in ocean  
530 ecosystems. These data confirmed that these pico-autotrophic cells can represent a substantial  
531 fraction of marine primary production (Flombaum et al. 2013). Our study also confirmed that  
532 picocyanobacteria were outcompeted by other phytoplankton in high nutrient waters as  
533 mangroves (Partensky et al. 1999).

534 Finally, Mayotte lagoon has a particular biological composition which differs from the Iles  
535 Eparses. It has higher concentrations of heterotrophic groups (HNF, CIL and ZPK) associated  
536 with high microalgae abundance (ALG), suggesting an omnivorous network with a  
537 dominance of the herbivorous food chain, as observed in coastal upwelling systems (e.g.  
538 Vargas and Gonzales, 2004). As reported by Gourbesville and Thomassin (2000), Mayotte  
539 lagoon is subject to organic and inorganic pollution from sewage, which probably stimulates  
540 primary production and the microheterotrophic pathway and their transfer to metazooplankton  
541 (mainly copepods and appendicularians; data not shown).

542 Two of the Iles Eparses had very different ecological functioning:

543 - The Europa lagoons with large and productive mangrove forests are clearly  
544 distinguished with higher nutrient concentrations (nitrogen forms, dissolved organic  
545 carbon) than those reported in other islands. Mangroves are transitional coastal  
546 ecosystems in tropical and sub-tropical regions with biologically important, productive  
547 ecosystems (Kathiresan and Qasim, 2005). These intense nutrient pressures influence the  
548 structure and dynamics of the microbial compartments. The high bacterial production and  
549 growth rates are linked to the presence of mangroves, owing to the high concentrations of  
550 dissolved and particulate organic matter (POC, PON, DOC; Table 2) that are released into the  
551 lagoon waters driven by tides and freshwater flow (Silveira et al., 2011).

552 - The marine ecosystem of Tromelin had the lowest biological productivity, with the  
553 lowest nutrient concentrations and bacterial growth rates. Bacterial communities appeared to  
554 be adapted to the oligotrophic conditions as enrichment had no significant effect on the  
555 growth rates. This may be because Tromelin is outside the Mozambique Channel, and so the  
556 marine system is not subject to the frontal areas and cyclonic and anticyclonic eddies  
557 characterizing the Mozambique Channel.

558 In conclusion, this survey provided the first regional study giving a preliminary insight into  
559 the spatial distribution of the plankton communities in the Iles Eparses. The coral reef lagoons

560 off the Iles Eparses are particularly well preserved, with low nutrient levels, while those in  
561 Mayotte can be considered to be an anthropized, polluted ecosystem with a predominance of  
562 herbivore networks. The Europa lagoon had productive bacterial and pigmented  
563 nanoflagellate communities related to the presence of mangroves. Picocyanobacteria were the  
564 main component found at the oligotrophic ocean stations (low phosphate concentrations). The  
565 Iles Eparses can, therefore, be considered to be pristine ecosystems and should be protected  
566 from human pressure and pollution. Ecological changes generally take place over the long  
567 term and each new generation of scientists and the general public alike fail to recognize the  
568 changes that have taken place gradually over time (Katikiro, 2014). Although there is a lack  
569 of ecological data on this area of the West Indian Ocean, identifying changes occurring in the  
570 ecosystem over time will show how the environmental baseline (established by this study) has  
571 shifted to such an extent that it no longer includes species that were found in the past. In this  
572 context, data mining is necessary and should focus essentially on the genetic diversity and  
573 functioning of microbial communities in the Iles Eparses, for which there have been very few  
574 studies.

575

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584

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*Legend of the figures*

Figure 1: Location of the Iles Eparses (Europa, Bassas da India, Juan de Nova, Glorieuses and Tromelin; black dots) in West Indian Ocean. See also Mayotte island in Mozambique Channel (black square)

Figure 2: Growth rates of bacteria ( $\text{day}^{-1}$ ) *versus* grazing rates of bacteria by predators ( $\text{day}^{-1}$ ) in the different lagoon and oceanic sites from experimental procedures, with nutrient added (black square) and in absence of nutrient addition (Control: gray circle). Standard deviation is reported from triplicates analysis. Abbreviation of the 10 stations: TO: Tromelin ocean; GO: Glorieuses ocean; JO: Juan de Nova ocean; EO: Europa ocean; BO: Bassas da india ocean; G2: Glorieuses lagoon; J2: Juan de Nova lagoon; ML: Mayotte lagoon; E2: Europa lagoon; B1: Bassas da India lagoon.

Figure 3: Co-inertia analysis with the position of the environmental parameters on the F1 x F2 plane. Position of the sites were linked to environmental parameters co-inertia weights, with identification of 4 groups by Ward's aggregation (ENV-1; ENV-2, ENV-3 and ENV-4). See abbreviations in Table 1 for the sites. Abbreviations of parameters: PON: particulate organic carbon; POC: particulate organic nitrogen; C/N: ratio of particulate organic compounds; DOC: dissolved organic carbon;  $\text{NH}_4$ : ammonia;  $\text{NO}_3$ : nitrate;  $\text{NO}_2$ : nitrite; Si: silicate.

Figure 4: Co-inertia analysis with the position of the biological variables on the F1 x F2 plane. Position of the sites was linked to biological variables co-inertia weights, with identification of 3 groups by Ward's aggregation (BIO-1; BIO-2 and BIO-3). See abbreviations in Table 1 for the sites. Abbreviations for variables: TB: total bacteria abundance; BP: bacterial production; CB: culturable bacteria; VLP: virus like particles; CHLO: chlorophyll-a; NANO: nanophytoplankton; PICO: picoeukaryotes; CYANO: picocyanobacteria; PNF: pigmented nanoflagellates; ALG: microalgal density; HNF: heterotrophic nanoflagellates; CIL: total ciliates (loricates and aloricates); ZPK: metazooplankton

Table 1: List of stations studied in the five Iles Eparses and in Mayotte island in West Indian Ocean in April 2011. Sampling data, site code, geographical coordinates and some physical parameters (temperature, salinity, dissolved oxygen amount and pH) are reported as average along the water column (undet : not determined).

	Parameters Units	Code	Latitude South	Longitude East	Temp °C	Salinity ppt	Oxygen mg l <sup>-1</sup>	pH
Sampling data	EUROPA							
5 April	ocean	EO	22° 20' 120	40° 19' 634	undet	undet	undet	undet
6 April	lagoon	E1	22° 20' 996	40° 22' 351	27.3	35.85	9.43	7.96
6 April	lagoon	E2	22° 20' 877	40° 22' 877	26.9	35.92	6.99	7.98
6 April	lagoon	E3	22° 20' 515	40° 22' 344	27.0	35.93	nd	nd
	BASSAS DA INDIA							
8 April	ocean	BO	21° 26' 150	39° 42' 644	29.2	35.22	5.26	8.00
9 April	lagoon	B1	21° 26' 827	39° 42' 644	28.6	35.05	10.96	7.99
	JUAN DE NOVA							
11 April	ocean	JO	17° 02' 167	42° 44' 745	29.8	35.5	6.03	8.01
12 April	lagoon	J1	17° 01' 901	42° 44' 943	30.1	35.41	5.61	7.98
12 April	lagoon	J2	17° 01' 388	42° 45' 361	30.1	35.44	4.43	7.97
12 April	lagoon	J3	17° 03' 708	42° 47' 477	30.1	35.47	5.55	7.95
	MAYOTTE							
15 April	lagoon	ML	12° 46' 395	45° 14' 699	29.2	35.13	7.99	8.01
	GLORIEUSES							
17 April	ocean	GO	11° 34' 745	47° 15' 907	29.2	35.00	6.41	8.02
18 April	lagoon	G1	11° 33' 641	47° 18' 182	28.8	34.67	6.91	7.95
18 April	lagoon	G2	11° 33' 230	47° 18' 502	29.1	34.94	5.45	7.98
18 April	lagoon	G3	11° 32' 503	47° 19' 151	28.8	34.92	4.27	7.99
	TROMELIN							
23 April	ocean	TO	15° 53' 988	54° 30' 876	28.1	34.47	6.91	8.02
	<i>Mean of ocean sites</i>				<i>29.1</i>	<i>35.05</i>	<i>6.15</i>	<i>8.01</i>
	<i>Mean of lagoon sites</i>				<i>28.7</i>	<i>35.34</i>	<i>6.29</i>	<i>7.98</i>

Table 2: Mean of the chemical parameters of the 16 studied sites (lagoon and oceanic stations) located in the Iles Eparses and in Mayotte lagoon.

PO<sub>4</sub> : dissolved phosphorus ; SI(OH)<sub>4</sub> : silicates ; NO<sub>2</sub> : nitrite ; NO<sub>3</sub> : nitrate ; NH<sub>4</sub> : ammonia ; PON : particulate organic nitrogen ; POC : particulate organic carbon ; C/N : ratio between particulate organic forms ; DOC dissolved organic carbon. (nd: non detectable).

Parameters	Code	PO <sub>4</sub>	SI(OH) <sub>4</sub>	NO <sub>2</sub>	NO <sub>3</sub>	NH <sub>4</sub>	PON	POC	C/N	DOC
Units		µM	µM	µM	µM	µM	µM	µM		µM
<b>EUROPA</b>										
ocean	EO	nd	1.94	0.04	0.12	0.16	21.70	222.4	10.25	136.3
lagon	E1	nd	1.59	0.05	0.23	0.49	54.55	250.2	4.59	149.8
lagon	E2	nd	1.51	0.04	0.21	0.07	47.94	311.4	6.50	142.5
lagon	E3	nd	1.57	0.04	0.12	0.37	47.11	260.9	5.54	168.5
<b>BASSAS DA INDIA</b>										
ocean	BO	nd	2.90	0.05	0.07	0.08	22.32	238.3	10.54	95.2
lagon	B1	nd	2.34	0.07	0.20	0.25	26.66	143.2	5.37	79.6
<b>JUAN DE NOVA</b>										
ocean	JO	nd	2.04	0.07	0.05	0.40	31.41	171.9	5.47	104.6
lagon	J1	0.06	2.40	0.11	0.10	0.15	31.88	161.1	5.05	87.8
lagon	J2	nd	1.65	0.04	0.05	0.07	27.89	138.5	4.97	78.1
lagon	J3	nd	1.26	0.03	0.05	0.04	36.13	188.4	5.21	77.2
<b>MAYOTTE</b>										
lagon	ML	nd	2.79	0.06	0.26	0.13	32.59	121.2	3.72	73.4
<b>GLORIEUSES</b>										
ocean	GO	nd	nd	nd	nd	0.04	27.28	119.9	4.39	91.9
lagon	G1	nd	1.43	0.05	0.02	0.01	38.85	208.4	5.36	71.5
lagon	G2	nd	1.83	0.02	0.03	0.01	24.80	140.3	5.66	71.1
lagon	G3	nd	2.15	0.02	0.12	0.06	17.85	127.1	7.12	77.1
<b>TROMELIN</b>										
ocean	TO	nd	2.73	0.04	0.05	0.13	17.98	107.9	6.00	87.1
<b>Mean of ocean sites</b>		nd	2.41	0.05	0.07	0.16	24.1	171.5	7.3	103.0
<b>Mean of lagoon sites</b>		nd	1.90	0.05	0.14	0.15	34.5	182.8	5.4	96.4

Table 3: Mean of the biological variables of the 16 studied sites (ocean and lagoon) located in the Iles Eparses and in Mayotte lagoon. Concentrations of each variable are reported: CB : culturable bacteria ; TB : total bacterial ; BP : bacterial production ; VLP : virus like particles ; Pico : picoeukaryotes : Cyano : picocyanobacteria ; Nano : nanophytoplankton ; HNF : heterotrophic nanoflagellates ; PNF : pigmented nanoflagellates ; Chloro : chlorophyll-a ; ZpK : metazooplankton.

Parameters	Code	CB	TB	BP	VLP	Pico	Cyano	Nano	HNF	PNF	Chloro	Microalga	Ciliates	ZpK
Units		ml <sup>-1</sup>	10 <sup>5</sup> ml <sup>-1</sup>	pmole l <sup>-1</sup> h <sup>-1</sup>	10 <sup>7</sup> ml <sup>-1</sup>	10 <sup>3</sup> ml <sup>-1</sup>	10 <sup>3</sup> ml <sup>-1</sup>	10 <sup>2</sup> ml <sup>-1</sup>	10 <sup>2</sup> ml <sup>-1</sup>	10 <sup>2</sup> ml <sup>-1</sup>	µg l <sup>-1</sup>	l <sup>-1</sup>	l <sup>-1</sup>	m <sup>3</sup>
<b>EUROPA</b>														
ocean	EO	330	10.69	4.1	3.10	54.14	40.1	1.32	1.35	0.67	0.184	3004	22	2452
lagon	E1	3150	17.76	397.8	9.55	33.40	8.31	4.69	6.21	9.21	0.529	10712	38	1065
lagon	E2	860	21.91	377.1	6.16	57.59	4.95	4.48	4.95	14.4	0.522	12136	36	1051
lagon	E3	2000	20.20	404.5	12.70	47.39	4.64	2.73	3.43	7.93	0.684	7152	50	1529
<b>BASSAS DA INDIA</b>														
ocean	BO	35000	9.33	7.1	1.40	47.11	34.6	1.06	3.79	1.18	0.340	2928	68	2307
lagon	B1	3600	9.47	55.9	13.90	32.86	39.3	2.01	5.79	3.86	0.581	4625	28	33
<b>JUAN DE NOVA</b>														
ocean	JO	30450	9.04	27.5	1.54	0.30	18.1	1.50	2.48	1.80	0.164	650	2	1313
lagon	J1	60000	5.16	7.1	34.41	33.18	24.4	1.25	1.93	1.07	0.265	12560	2	2569
lagon	J2	14000	11.49	6.5	24.41	93.23	78.5	2.95	4.97	2.37	0.555	68770	28	4611
lagon	J3	4900	10.69	42.3	22.20	87.94	72.5	3.26	2.36	1.29	0.759	3456	42	3217
<b>MAYOTTE</b>														
lagon	ML	19600	20.14	78.3	7.61	78.27	26.9	2.69	2.03	2.25	0.429	2700	66	6008
<b>GLORIEUSES</b>														
ocean	GO	35650	9.26	2.8	4.68	2.76	20.5	1.35	5.94	2.12	0.162	2508	44	2282
lagon	G1	8200	5.71	57.4	9.29	57.44	54.1	1.84	3.60	5.63	0.625	2512	50	607
lagon	G2	19000	6.94	146.5	21.31	146.5	112.0	3.68	7.50	4.29	0.526	9004	130	3749
lagon	G3	12000	8.21	25.4	7.22	25.35	8.71	0.55	3.15	1.35	0.152	3344	30	731
<b>TROMELIN</b>														
ocean	TO	17750	8.94	1.3	3.59	1.26	1.92	0.07	3.82	2.97	0.054	1860	40	767
<b><i>Mean of ocean sites</i></b>		<b>23836</b>	<b>9.45</b>	<b>27</b>	<b>2.86</b>	<b>21.11</b>	<b>23.1</b>	<b>1.06</b>	<b>3.37</b>	<b>1.60</b>	<b>0.181</b>	<b>2190</b>	<b>35</b>	<b>1824</b>
<b><i>Mean of lagoon sites</i></b>		<b>12647</b>	<b>12.02</b>	<b>134</b>	<b>15.46</b>	<b>62.62</b>	<b>62.6</b>	<b>2.79</b>	<b>7.24</b>	<b>5.72</b>	<b>0.507</b>	<b>11715</b>	<b>44</b>	<b>2514</b>



Table 4: Bacterial growth rates in presence ( $\mu+g$ ) or absence ( $\mu$ ) of HNF (respectively in 100% and 1% fraction), and grazing rates of bacteria by predators ( $g$ ) in the different experimental conditions (control and with nutrient added; see Material and methods). Experiments were performed in triplicates

Site	Fraction Rate	100% $\mu+g$ ( $\text{day}^{-1}$ )		1% $\mu$ ( $\text{day}^{-1}$ )		$g$ ( $\text{day}^{-1}$ )	
		mean	std	mean	std	mean	std
<b>EO (ocean)</b>	Control	1.12	0.03	2.10	0.22	0.97	0.23
	+ nutrient	3.15	0.02	5.26	0.17	2.10	0.15
<b>E2 (lagon)</b>	Control	0.01	0.00	4.25	0.18	4.24	0.24
	+ nutrient	1.91	0.23	6.61	0.07	4.66	0.30
<b>BO (ocean)</b>	Control	0.85	0.07	2.73	0.03	1.88	0.07
	+ nutrient	3.30	0.13	5.10	0.09	1.80	0.20
<b>BL (lagon)</b>	Control	-0.96	0.14	4.17	0.18	5.13	0.13
	+ nutrient	1.40	0.25	6.32	0.46	4.88	0.37
<b>JO (ocean)</b>	Control	0.50	0.04	1.54	0.08	1.03	0.09
	+ nutrient	2.15	0.04	4.67	0.06	2.52	0.07
<b>J2 (lagon)</b>	Control	0.46	0.09	3.14	0.07	2.67	0.05
	+ nutrient	2.73	0.08	6.57	0.19	3.83	0.14
<b>ML (lagon)</b>	Control	1.51	0.07	2.18	0.02	0.65	0.09
	+ nutrient	2.06	0.06	3.95	0.05	1.88	0.08
<b>GO (ocean)</b>	Control	1.03	0.05	0.48	0.11	0.55	0.11
	+ nutrient	2.27	0.09	2.43	0.16	0.16	0.05
<b>G2 (lagon)</b>	Control	0.80	0.05	1.15	0.24	0.34	0.19
	+ nutrient	1.08	0.04	2.30	0.34	1.21	0.38
<b>TO (ocean)</b>	Control	0.32	0.01	0.84	0.21	0.52	0.21
	+ nutrient	0.42	0.13	1.06	0.06	0.63	0.09

Table 5: Comparison of inertia from the 2 data sets based on Environmental (E) and Biological (B) variables resulting from the co-inertia analysis. Two co-inertia axes (F1 and F2) are selected. Var E and Var B: inertia of each table projected on the co-inertia axes. Iner E and Iner B: maximal projected inertia of each table. Covar: covariance of the 2 sets of coordinates projected on the co-inertia axes. R-value represents the correlation between the 2 new sets of coordinates resulting from the co-inertia analysis

Axis	Var E	Var B	Iner E	Iner B	Covar	R-value
F1	2.621	4.137	2.908	4.747	2.706	0.828
F2	1.504	2.561	2.146	2.692	1.330	0.677

Figure 1 : Bouvy et al.

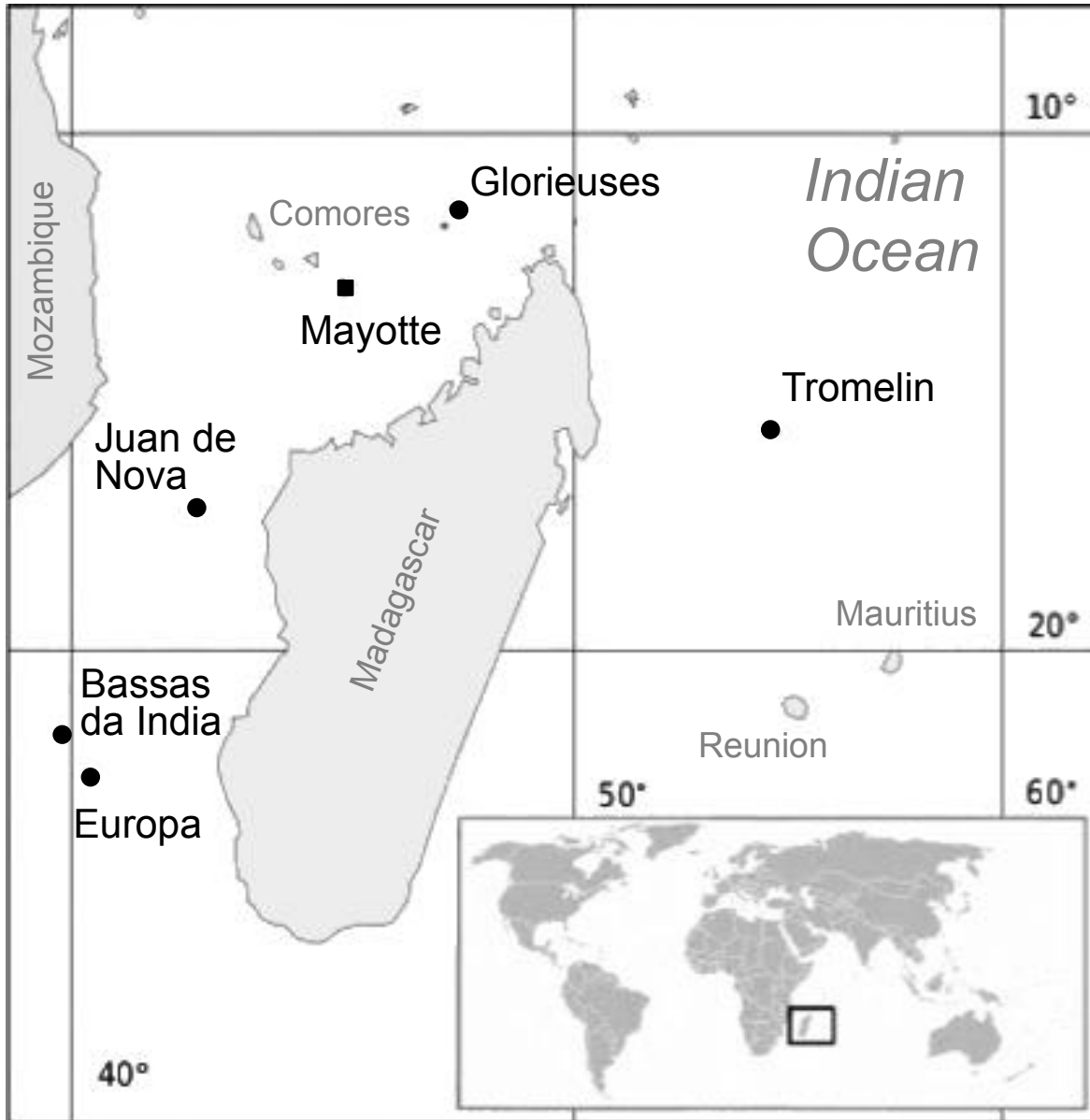


Figure 2: Bouvy et al.

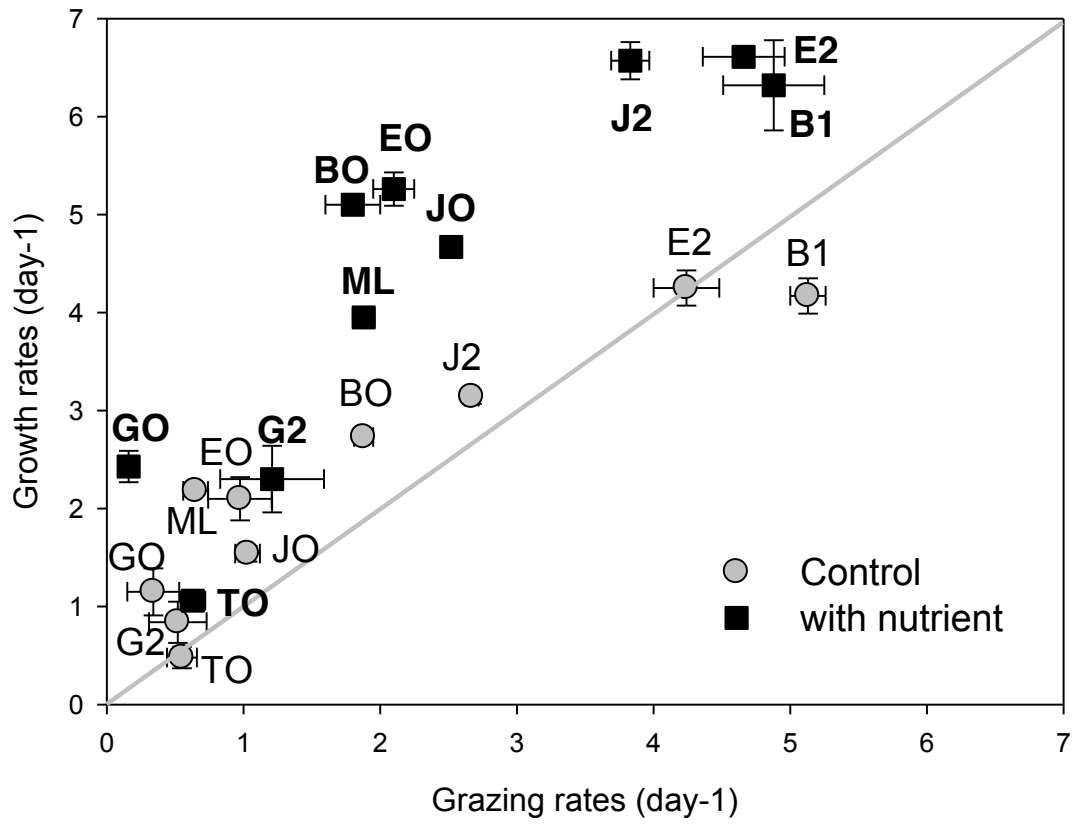


Figure 3: Bouvy et al.

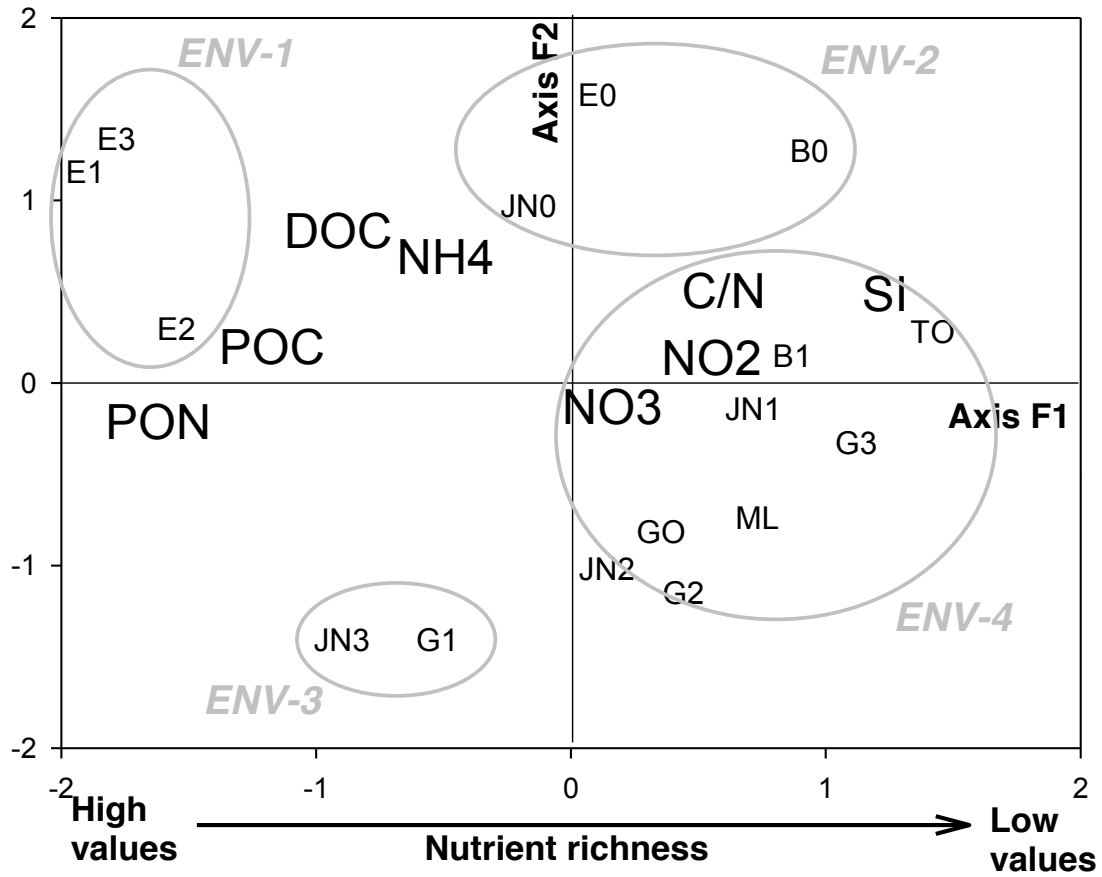


Figure 4: Bouvy et al.

