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.

Center for MARine Biodiversity, Exploitation & Conservation

UMR 248 : IRD- Ifremer- Université Montpellier – CNRS

Dr Marc BOUVY
marc.bouvy@ird.fr

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

Bouvy M.^{1*}, Got P.¹, Domaizon I.², Pagano M.³, Leboulanger C.¹,
Bouvier C.¹, Carré C.¹, Roques C.¹, Dupuy C.⁴

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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28 *Keywords:* microorganisms, distribution, enrichment experiment, nutrient limitation, islands,
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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.

1. Introduction

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

Coastal marine habitats at the land-sea interface are threatened by human activities at sea and on shore, and are, therefore, among the most heavily degraded (Costanza et al., 1997). Coral reef environments are generally recognized as being among the most threatened of the fragile marine ecosystems, and are highly susceptible to stress and disturbance, especially to anthropogenic pressure (Mellin et al., 2008) and climate change (Miller et al., 2009). Studies of coral reef systems to understand the causes, effects and consequences of direct anthropogenic pressure are generally conducted in anthropized zones. 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. “Pristine” coral reef ecosystems are often located on uninhabited islands.

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). Several studies of these remote ecosystems were performed recently, which established ecological baselines for pristine coral reef systems. However, most previous studies have dealt with reef fish inventories (Chabanet, 2002; Quod et al., 2004; Chabanet and Durville, 2005) following the extensive coral bleaching event in 1998, and only a few studies have considered the

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

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

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

2. Material and Methods

2.1. Study sites and samplings

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

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

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

2.2. Physical and chemical parameters

At each sampling station, a CTD profiler (YSI 600 XLM) was deployed to record temperature, depth, pH and dissolved oxygen profiles. Dissolved organic carbon (DOC) analyses were performed on 30 ml subsamples collected in pre-combusted (450°C overnight) glass vials, preserved with 35 µl of 85% phosphoric acid. Samples were stored in the dark until analysis using a Shimadzu TOC VCPH analyzer (Rochelle Newall et al., 2008). Chlorophyll concentrations were determined by [fluorometry after](#) filtration onto Whatman GF/F fiberglass filters and direct extraction using methanol (Yentsch and Menzel, 1963). Samples for measuring dissolved nutrients (SiO₄, NH₄-N, NO₃-N, NO₂-N, PO₄-P) were filtered onto Whatman GF/F fiberglass filters, stored at -20°C and analyzed as described by Strickland and Parsons (1972). Sampled water was filtered through a pre-combusted GF/F Whatman filters to determine particulate organic nitrogen (PON) and particulate organic carbon (POC), using a nitrogen carbon analyzer after acid decarbonation.

2.3. Biological parameters

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

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

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

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

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

2.4. Bacterial growth rates and grazing rates by HNF

Water samples were taken at 0.5 m depth at the various stations for each island. Two bioassay series were performed to compare the responses of the bacterial community to inorganic enrichment with 100% of predators (using <50 μ m-filtered water) and with 1% of predators (using 99% of 0.22 μ m-filtered water and 1% of <50 μ m-filtered water). The samples were homogenized and distributed equally into 2 series of 3 x 100 ml Whirl-Pak® polyethylene sterile bags. At time zero (t₀), inorganic nitrogen (mixture of 2.5 μ M as NH₄Cl and 1.5 μ M as NaNO₃), inorganic phosphorus (1.5 μ M as NaH₂PO₄) and 200 μ M as glucose were added in combination. All assays were performed in triplicate with a total of 6 Whirlpaks per station.

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

2.5. Data processing

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

3. Results

3.1. Environmental parameters

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

was little variation in pH with values ranging from 7.95 to 8.02 (average of 7.98 and 8.01 in lagoon and ocean sites, respectively). The dissolved oxygen concentrations ranged between 4.27 mg l⁻¹ at Glorieuses lagoon (G3) to 9.43 mg l⁻¹ at Europa lagoon (E1), except for Bassas da India lagoon where a high concentration was reported (B1: 10.96 mg l⁻¹) (Table 1).

Low dissolved nutrient concentrations were found, for all nutrients, without significant differences between the sites ($p > 0.05$; Table 2). Dissolved phosphorus concentrations were below the detectable limits (threshold 0.010 μM). Silicate concentrations did not vary significantly ($p > 0.05$) between the stations, with an average of 2.41 and 1.90 μM for ocean and lagoon sites, respectively. Ammonium concentrations accounted for the larger contribution of nitrogen forms in ocean sites with an average of 0.16 μM (Table 2). The highest concentrations of nitrite and nitrate were reported in the Europa lagoon (0.19 μM). The mean values of DOC concentrations averaged 103 μM and 96.4 μM in ocean and lagoon sites respectively, with the highest concentrations for the Europa stations. Particulate organic nitrogen averaged 24.1 and 34.5 $\mu\text{g l}^{-1}$ in ocean and lagoon sites, respectively, while particulate organic carbon averaged 171.5 and 182.8 $\mu\text{g l}^{-1}$. There were higher particulate organic nitrogen forms in the Europa stations, especially in the lagoon. The particulate organic C/N averaged 7.3 and 5.4 in ocean and lagoon sites, respectively, with the highest values in Europa and Bassas da India ocean sites.

3.2. Biological variables

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

Among the phytoplankton, the dominant groups in terms of abundance were the picoeukaryotes (Pico) and the picocyanobacteria (Cyano) mainly *Synechococcus* and *Prochlorococcus*. Picoeukaryotes and picocyanobacteria abundances were similar in ocean and lagoon sites (mean of $21 \times 10^3 \text{ ml}^{-1}$ and $23 \times 10^3 \text{ ml}^{-1}$, respectively) whereas

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

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

3.3. Bacterial growth rates and HNF grazing rates

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

ocean stations (BO, EO, JO, GO) and Mayotte was clearly higher with enrichment and absence of predators (values of μ close to 5 d⁻¹)

3.4. Co-inertia analysis

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

In the Environmental System (Figure 3), the first axis (F1) showed an opposition between the organic nutrient context (POC, PON, DOC) and the silicate concentration (SI). Ward's aggregation recognized 4 groups of stations. The first group ENV-1 comprised the Europa lagoon stations (E1, E2 and E3) and had significantly higher concentrations of organic nutrient (PON, POC and DOC), whereas the second group ENV-2 (JNO, EO and BO) was more associated with ammonium (NH₄). The third group (JN3, G1) was in opposition with the two first groups without specific information, whereas the fourth group (ENV-4) was characterized by low organic concentrations, high inorganic concentrations (NO₃, NO₂), and high silicate concentrations. Consequently, the factorial plane defined by the first 2 axes in this environmental system distinguished stations according to nutrient richness (Axis F1).

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

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

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

4. Discussion

4.1. Regional context

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

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

4.2. Nutrient context and plankton structure

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

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

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

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

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

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

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

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

Europa mangroves, suggesting that these microbial communities can act as CO₂ sources (Duarte and Agusti, 1998). The greater heterotrophic effect (such as external eutrophication) could, therefore, be related to changes in the relative contribution of the various microbial components, or to an increase of nutrient concentrations.

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

4.4. Relationships between biological components and trophic variables

Multivariate analysis demonstrated clear differences between nutrient levels and biological productivity in the Iles Eparses. Co-inertia analysis coupled with a Ward's aggregation clearly defined a group with the three stations sampled in Europa lagoon, characterized by high nutrient levels associated with high bacterial dynamics. In the Environmental system, particulate organic carbon (POC), particulate nitrogen (PON) and dissolved organic carbon (DOC) were the parameters that had the strongest correlation with the Europa lagoon (ENV-1), confirming the role of mangroves as a provider of nutrients and organic matter for the biological compartments (Saenger, 2002). Microbial communities, especially bacteria (TB and BP), are, therefore, fundamental in these sites (BIO-1) for the mineralization of organic matter and its transformation into nutrients, as confirmed by the correlation found in the Biological system. The release of ammonium (NH₄) into the overlying water following high rates of remineralization in the mangrove sediment may support the high bacterioplankton activities in the Europa lagoon, as demonstrated by Miyajima et al. (2001). Pigmented nanoflagellates (PNF) and nanophytoplankton (NANO) were strongly linked to bacterial abundances in the Europa lagoon, suggesting a high trophic coupling between bacteria and nanoplankton. Co-inertia analysis also revealed a group (ENV-2) with three southern ocean stations (JNO, EO, BO), characterized by higher nutrient richness than the other ocean stations (TO and GO). However, all the ocean stations were grouped into one group (BIO-2)

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

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

Two of the Iles Eparses had very different ecological functioning:

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

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

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

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

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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 (day^{-1}) *versus* grazing rates of bacteria by predators (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; NH_4 : ammonia; NO_3 : nitrate; 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 ⁻¹	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
	Mean of ocean sites				29.1	35.05	6.15	8.01
	Mean of lagoon sites				28.7	35.34	6.29	7.98

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.

PO₄ : dissolved phosphorus ; SI(OH)₄ : silicates ; NO₂ : nitrite ; NO₃ : nitrate ; NH₄ : 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 ₄	SI(OH) ₄	NO ₂	NO ₃	NH ₄	PON	POC	C/N	DOC
Units		μM	μM	μM	μM	μM	μM	μM		μM
EUROPA										
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
BASSAS DA INDIA										
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
JUAN DE NOVA										
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
MAYOTTE										
lagon	ML	nd	2.79	0.06	0.26	0.13	32.59	121.2	3.72	73.4
GLORIEUSES										
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
TROMELIN										
ocean	TO	nd	2.73	0.04	0.05	0.13	17.98	107.9	6.00	87.1
Mean of ocean sites		nd	2.41	0.05	0.07	0.16	24.1	171.5	7.3	103.0
Mean of lagoon sites		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 ⁻¹	10 ⁵ ml ⁻¹	pmole l ⁻¹ h ⁻¹	10 ⁷ ml ⁻¹	10 ³ ml ⁻¹	10 ³ ml ⁻¹	10 ² ml ⁻¹	10 ² ml ⁻¹	10 ² ml ⁻¹	µg l ⁻¹	l ⁻¹	l ⁻¹	m ³
EUROPA														
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
BASSAS DA INDIA														
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
JUAN DE NOVA														
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
MAYOTTE														
lagon	ML	19600	20.14	78.3	7.61	78.27	26.9	2.69	2.03	2.25	0.429	2700	66	6008
GLORIEUSES														
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
TROMELIN														
ocean	TO	17750	8.94	1.3	3.59	1.26	1.92	0.07	3.82	2.97	0.054	1860	40	767
Mean of ocean sites		23836	9.45	27	2.86	21.11	23.1	1.06	3.37	1.60	0.181	2190	35	1824
Mean of lagoon sites		12647	12.02	134	15.46	62.62	62.6	2.79	7.24	5.72	0.507	11715	44	2514

Table 4: Bacterial growth rates in presence ($\mu+g$) or absence (μ) 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% $\mu+g$ (day ⁻¹)		1% μ (day ⁻¹)		g (day ⁻¹)	
		mean	std	mean	std	mean	std
EO (ocean)	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
E2 (lagon)	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
BO (ocean)	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
BL (lagon)	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
JO (ocean)	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
J2 (lagon)	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
ML (lagon)	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
GO (ocean)	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
G2 (lagon)	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
TO (ocean)	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.