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Macroalgae as a tool for assessing the ecological status of coral reefs under the Water Framework Directive: A case study on the reef flats of La Réunion (Indian Ocean)

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ABSTRACT

The monitoring of macroalgae is required by the Water Framework Directive (WFD) to achieve good ecological status for coastal waters and specific questions arise for tropical ecosystems belonging to the outermost European regions. To assess the suitability of macroalgae as a biological quality indicator for La Réunion reef flats (France), we performed multivariate analyses linking the abundance and composition of macroalgae to water physico-chemistry. Three hydrological groups of stations were identified according to dissolved inorganic nitrogen (DIN) concentrations and DIN/PO_4 ratios. Some indicator species were found at the N-enriched stations (*Bryopsis pennata, Caulerpa lamourouxii, Chaetomorpha vieillardii, Derbesia* sp., *Blennothrix lyngbyacea, Sphacelaria tribuloides*), and others at the non-impacted stations (*Anabaena* sp1, *Blennothrix glutinosa, Codium arabicum, Neomeris vanbosseae*). Another key result was the significant increase in red algal cover at the most N-enriched station. Our findings are discussed in the context of the application of the WFD in the outermost French regions.

1. Introduction

France, as part of the European community, enacted the Water Framework Directive (WFD, 2000/60/EC) which commits European Union member states to achieve good qualitative and quantitative status for all water bodies including coastal waters. Regarding European coasts, the work of several task groups resulted in the definition of various indicators that can potentially be used for assessing environmental status (see a review in Birk et al., 2012). Among these indicators, the abundance of opportunistic macroalgae and species shift in floristic composition have been used successfully as descriptors of human-induced eutrophication (e.g. Bermejo et al., 2012; Guinda et al., 2014; Blanfuné et al., 2017), indicator species most sensitive to pollution being gradually replaced by highly resistant, nitrophilic or opportunistic species (Arévalo et al., 2007; Guinda et al., 2008). The monitoring of macroalgae (and angiosperms) is now required by the WFD (Article 1.1.4, Annexe V). The assessment of cover and species richness of perennial species of macroalgae compared to that of opportunists is a common basis for all the indices proposed in Europe (Table 1).

Specific questions arise for tropical ecosystems including European outermost regions (ORs) and especially coral reefs (Le Moal, 2012; Le Moal et al., 2016), due to the intrinsic natural variability of these ecosystems, their exposure to extreme natural disturbances and their low resilience (Mora et al., 2016). Disturbances of coral reefs are caused by a complex combination of stress factors including those arising from climate change, disease, predation, destructive fishing practices, invasive species, storms and changes in water quality (Cooper et al., 2009; Diaz-Pulido et al., 2016). Over the last several decades, anthropogenic activities have dramatically increased nutrient loading along coastlines and greatly accelerated the deterioration of coastal marine ecosystems (Nixon, 1995; Bricker et al., 2008; Howarth et al., 2011). On some coral reefs, nutrient and sediment inputs have increased severalfold over the last 150 years (e.g. Richmond, 1993; McCulloch et al., 2003) altering biodiversity (Duprey et al., 2016) and leading to trophic dominance by assemblages of macroalgae (Bruno et al., 2009; Koch et al., 2013; Ainsworth et al., 2016). Reported responses of coral reef macroalgae to nutrient enrichment are summarized in Table 2. However, little is known regarding the suitability of macroalgae as a

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Table 1
Principal biological indices using macroalgae to assess the ecological status of coastal water bodies in the Water Framework Directive.

Indices and references	Metrics used
Ecological Evaluation Index (EEI) Orfanidis et al., 2001, 2003, 2011	Mean coverage of perennial (ESGI) and opportunistic (ESGII) species. Two different Ecological Status Group (ESGI and ESGII) was created depending on morphological, ecological and physiological characteristics of the species (Littler and Littler, 1980).
Littoral community cartography (CARLIT) Ballesteros et al., 2007; Blanfuné et al., 2017	Stress-tolerance of the macroalgal community per geomorphological habitat.
Reduced List Species (RSL) Wells et al., 2007	Specific richness, % Rhodophyta, % Chlorophyta, % opportunistic species, and ratio ESGI/ESGII.
Quality of Rocky bottoms index (CFR) Juanes et al., 2008; Guinda et al., 2008; Guinda et al., 2014	Coverage and richness of characteristic macroalgae, fraction of opportunistic species.
Cover Characteristic species Opportunistic species (CCO) Ar Gall et al., 2016	Total cover of macroalgal communities, number of characteristic species per topographic level and the cover of opportunistic species.
Marine Macroalgae assessment tool (MarMAT) Neto et al., 2012	Species richness, geomorphology, % Chlorophyta, number of Rhodophyta, number of opportunists/perennial, proportion of opportunists and coverage of opportunists.
The monitoring of opportunistic macroalgal blooms Patrício et al., 2007; Scanlan et al., 2007.	Total available intertidal area for opportunistic macroalgae growth (ha), areal coverage (ha), % cover and biomass.

biological quality indicator, nor about the feasibility of developing an index compatible with European intercalibration requirements. Although the productivity of certain groups of macroalgae (e.g. *Cladophora*, *Enteromorpha*, *Ulva*, Turf) is nutrient-limited and increases with nutrient availability (Lapointe, 1997; Teichberg et al., 2008; Den Haan et al., 2016), macroalgal biomass may be restrained by grazing (Edmunds and Carpenter, 2001; Burkepile and Hay, 2009, 2010), by competition or by light availability (Fong and Paul, 2011). Conversely, overfishing (Jackson et al., 2001) or die-off of herbivores (e.g. sea urchins; Liddell and Ohlhorst, 1986) causes persistent shifts from an original dominance by corals to a preponderance of fleshy seaweeds (Hughes et al., 2007; Bruno et al., 2009). Furthermore, episodic events such as tropical storms and coral bleaching lead to changes in the coral-algal competition and significantly affect the floristic composition and abundance (Hughes, 1994; Osborne et al., 2011).

In La Réunion, a young volcanic island in the Mascarene archipelago, the degradation of coral reefs (decrease in coral cover, algae blooms) has been observed since the 1980s and has been partly explained by a chronic enrichment in nutrients (Cuet et al., 1988; Naïm, 1993; Naïm et al., 2013). There are no perennial rivers in the vicinity of these fringing reefs, so that nutrient enrichment is mainly attributed to submarine groundwater discharge (SGD). The highly permeable volcanic (basaltic) aquifer is characterized by high levels of nitrogen (N) derived from anthropogenic sources (Cuet et al., 2011; Tedetti et al., 2011; Guigue et al., 2015). N supply caused by SGD increases the N:P ratio in reef waters, which was hypothesized to favor the observed increase in abundance and biomass of macroalgae (Cuet et al., 2011). Algal blooms occur during Austral summer and decrease with the onset of the cool season (Naïm et al., 2013), but the GCRMN (Global Coral Reef Monitoring Network) monitoring in La Réunion has revealed a significant increase in algal cover over the last 10 years (1998–2008) at most stations (Tourrand et al., 2013). In certain cases, the algae represent early successional stages, with opportunistic species responding to the availability of new space after environmental disturbances, while in other cases, the increase in algae is associated with a shift in coral community structure (Obura et al., 2017).

In this paper, we present algal community structure and composition along transects perpendicular to the coast on four reef flats in La Réunion. Transects were distributed along a nutrient enrichment gradient. Due to the short sampling duration (eight months), temporal patterns in the data, both inter-annual and seasonal, could not be discerned but will be important to consider in future work on the indicator/index development. In this preliminary study, we tested parameters currently in use in temperate EU countries (species composition, % opportunistic/perennial species, % functional groups, % cover) (Table 1) to identify potential algal bioindicators of nutrient enrichment in coral reefs. We expected algae communities to show higher cover and lesser diversity with decreasing distance from the coast and increasing nutrient enrichment. Our findings are discussed in the context of the application of WFD in French outermost regions.

2. Material and methods

2.1. Study area

La Réunion, a volcanic island of the Mascarene archipelago, lies in the South-West Indian Ocean (21°07′–19°40′ S, 55°13′–61°13′ E), 800 km off the east coast of Madagascar. The discontinuous and narrow (500 m wide at most) fringing reefs - from north to south, Saint-Gilles/La Saline, Saint-Leu, Etang-Salé and Saint-Pierre - are located along the dry, leeward west coast (Fig. 1). Their total length is 25 km and they cover an area of 18 km^2. Saint-Gilles/La Saline and Saint-Leu are characterized by carbonate-rich sediments, while Etang-Salé and Saint-Pierre are characterized by black sand from the nearby active volcano.

2.2. Sampling design

Groundwater flow varies along the shoreline depending on the geological structure of the coastal plain (see Tedetti et al., 2011 for more details) and is mainly conspicuous inshore (Cuet et al., 2011). Sites and stations within sites were selected to represent an enrichment gradient in nitrogen caused by SGD. Salinity, nutrient concentration, algal cover and specific composition were recorded at Saint-Gilles/La Saline (TOB and TE, Fig. 1), the most extensive reef in La Réunion, and at Saint-Leu (SL), Etang-Salé (ES) and Saint-Pierre (SP). Water depth does not exceed 1.50 m at high tide on the stations.

At Saint-Gilles/La Saline, two contrasting sites were chosen. TOB was previously identified as a reference site unaffected by SGD and mainly under oceanic influence (Andral et al., 2010), while the back reef zone at TE is particularly N-enriched by SGD (Chauvin et al., 2011). At Etang-Salé, the study site was established near localized submarine springs that are found in the southern part of the reef (Cuet and Naïm, 1992). The Saint-Leu and Saint-Pierre sites were chosen according to preliminary data showing low salinity and high nitrate concentration near the shore that were recorded at the beginning of the study (low-groundwater level conditions). For comparison purpose with TOB, an additional site unaffected by SGD was selected at Saint-Leu (SLNI) for water sampling only.

At each site, except Etang-Salé (see below), sampling was performed along coral strips extending from the reef flat to the beach,

Table 2
Review on the use of macroalgae as nutrient enrichment indicators in coral reefs, including the main results of our study (in bold).

Bioindicators	Techniques	Responses with nutrients enrichment
Community structure		
Taxonomic richness	Taxonomic inventory	● Increase macroalgal species richness (Burkepile and Hay, 2009) ● Increase in red and green algae richness (Fabricius et al., 2005) ● Decrease in species richness (Scherner et al., 2013; Amaral et al., 2018) ● Increase in non-native species richness (Lapointe and Bedford, 2011) ● **Increase in opportunistic species richness (this study)** ● **Increase in some cyanobacteria species (this study)**
% cover	Video or photo transects	● Increase in macroalgal cover (Cuet et al., 1988; Naïm, 1993; Hunter and Evans, 1995; Stimson et al., 1996; Van woesik et al., 1999; Stimson and Larned, 2000; Stimson et al., 2001; Fabricius and De'Ath, 2004; Fabricius et al., 2005; De'ath and Fabricius, 2010; Lapointe et al., 2010; Fabricius et al., 2012; Naïm et al., 2013) ● **Increase in red algae cover** (Lapointe et al., 1987; Horrocks et al., 1995; Fabricius et al., 2005, 2012; Burkepile and Hay, 2009; Lapointe and Bedford, 2011; Scherner et al., 2013; **this study**) ● Increase (Thacker et al., 2001; Fabricius et al., 2012) or decrease (Scherner et al., 2013) in brown algae cover ● Increase in non-native species cover (Lapointe and Bedford, 2011) ● Increase in green algae cover (Fabricius et al., 2005; Scherner et al., 2013) ● Increase in cyanobacteria cover (Miller et al., 1999) ● **Increase** (Smith et al., 2001; **this study**) and decrease (Björk et al., 1995; Fabricius and De'Ath, 2001; Fabricius et al., 2005) **in CCA cover** ● Decrease in calcareous algae cover (including CCA) (Scherner et al., 2013) ● Increase in opportunistic species abundance (Amaral et al., 2018) ● Macroalgae blooming (Smith et al., 1981; Lapointe and O'Connell, 1989; Lapointe, 1997; Lapointe et al., 2004; Barile and Lapointe, 2005; Lapointe et al., 2005a,b, 2011; Smith et al., 2005; Lapointe and Bedford, 2010; Teichberg et al., 2010)
Biomass	Quadrats	● Increase in algal biomass (Smith et al., 1981; Smith et al., 2001; Lapointe et al., 2004; Burkepile and Hay, 2009; Fabricius, 2011; Amaral et al., 2018)
Biochemical and physiological measurements		
Nitrogen concentration	Spectrophotometric assay or elemental analyzer	● Increase: macroalgal tissue N concentration reflects nutrient enrichment because N uptake and growth are temporally decoupled via storage (Lapointe, 1997; Costanzo et al., 2000; Koop et al., 2001; Cohen and Fong, 2006; Lin and Fong, 2008; Lapointe et al., 2010; Teichberg et al., 2010; Lapointe and Bedford, 2011; Cox et al., 2013)
Ratio C:N:P or ratio N:P	Elemental analyzer (N, C) and colorimetric assay (P)	● Increase or decrease depending on species and environmental factors: the changes in carbon, phosphorus and nitrogen levels in organisms can identify prominent nutrient sources (Lapointe et al., 1987; Lapointe, 1997; Larned, 1998; Koop et al., 2001; Umezawa et al., 2002; Barile, 2004; Lapointe et al., 2005a, 2010, 2011; Lourenço et al., 2005; Teichberg et al., 2010; Lapointe and Bedford, 2011; Barile, 2018)
Nitrogen stable isotope signature ($\delta^{15}N$)	Mass spectrophotometry	● Increase with terrestrial nitrogen load to the reef (Lapointe, 1997; Umezawa et al., 2002; Lapointe et al., 2004, 2005b; Costanzo et al., 2005; Cohen and Fong, 2006; Garrison et al., 2007; Lin et al., 2007; Lin and Fong, 2008; Teichberg et al., 2008; Dailer et al., 2010, 2012; Lapointe and Bedford, 2010; Teichberg et al., 2010; Lapointe et al., 2010, 2011; Lapointe and Bedford, 2011; Viana et al., 2011; Cox et al., 2013; Lapointe et al., 2015; Abaya et al., 2018; Barile, 2018)
Alkaline phosphatase activity (APA)	Spectrophotometric assay	● Increasing in some macroalgae under high N concentration and P limitation (Schaffelke, 2001; Lapointe et al., 1992; Lapointe, 1997; Koop et al., 2001). APA enables macroalgae to increase their phosphorus supply by using organic P.
Amino acids	HPLC	● Citrulline is identified as a N-storage product in some red algae. Increase in concentration was a common response to nutrient increase (Bird et al., 1982; Horrocks et al., 1995; Jones et al., 1996; Costanzo et al., 2000; Koop et al., 2001)
Pigments	Spectrophotometric assay	● Increase in phycoerythrin and/or chlorophyll *a* contents (Jones et al., 1996; Costanzo et al., 2000; Koop et al., 2001)

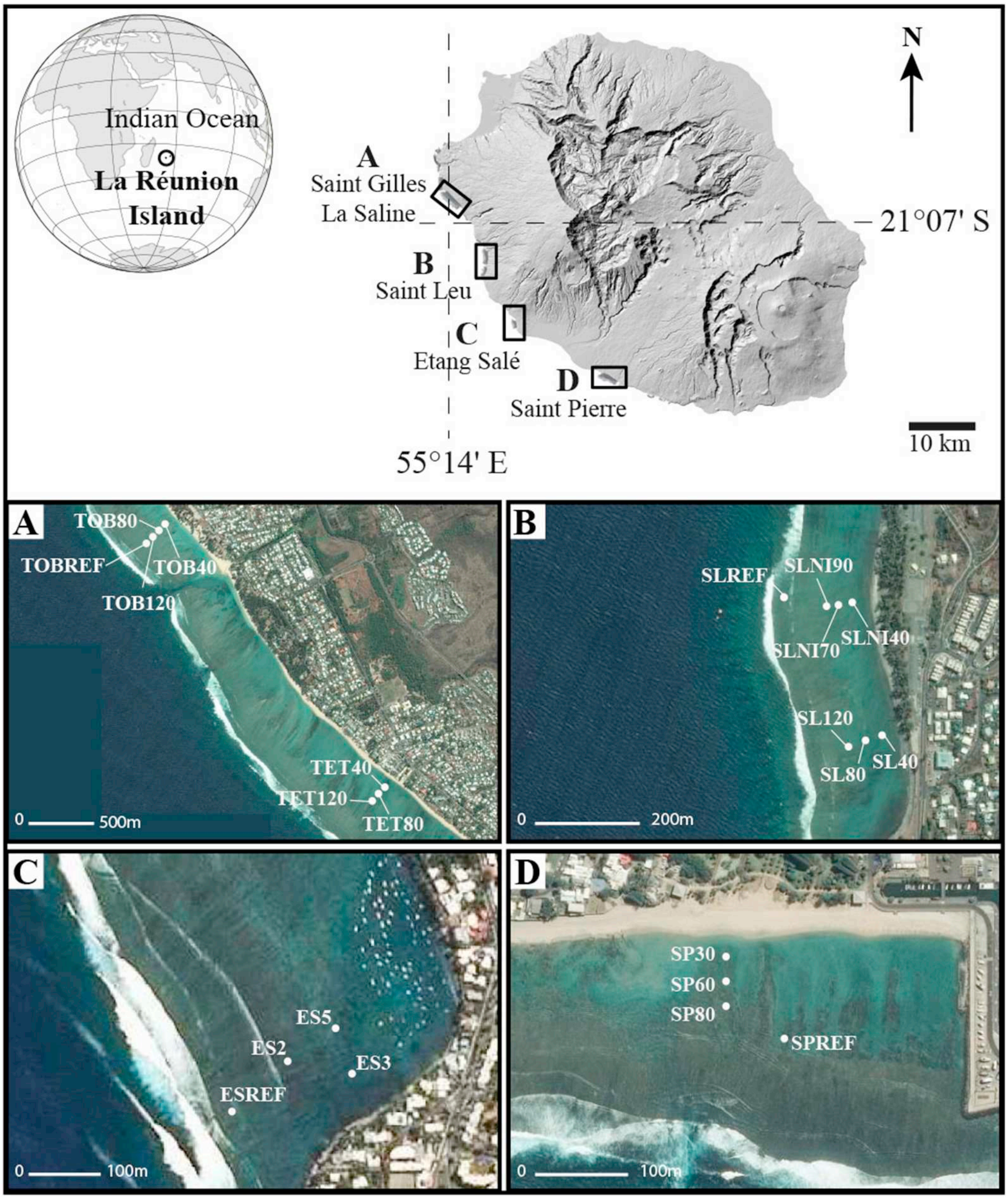

Fig. 1. Localization of the monitoring sites in La Réunion: Saint Gilles/La Saline (TOB and TE), Saint Leu (SL and SLNI), Etang-Salé (ES) and Saint Pierre (SP). For each site, the stations were positioned along coral strips extending from the reef flat to the beach perpendicular to the coastline (except Etang Salé, see text).

perpendicular to the coastline (Fig. 1). Three stations were positioned at increasing distance from the shore (40 m, 80 m and 120 m), the farthest station being assumed to be the least impacted by SGD. At Etang-Salé, one of the stations (ES3) was positioned close to the main spring mouth, while the two other stations were positioned upstream (ES2) and downstream (ES5) of ES3, respectively. In addition, in each of the four sites, sampling was performed at an additional reference station (noted REF) that was as far as possible from the beach and therefore little impacted by SGD, to account for possible differences between incoming water masses.

Sampling took place from December 2010 (beginning of the warm and rainy season) to July 2011 (dry and cool season). It was performed every month (8 dates) at 4 stations (TE40, TE80, TE120 and TOBREF) to better capture the temporal variability, but every two months only (4 dates) at the other stations due to technical constraints. It was not possible to assess abundance and composition of macroalgae at ESREF, due to swell conditions near the reef front. More information about the sampling is given in Supplementary Material S1.

2.3. Field data

2.3.1. Water sampling and analysis

Sampling was systematically performed in the morning at low tide. Salinity was measured in situ using a multiparameter probe YSI Professional Quatro Plus (resolution ± 0.01; accuracy ± 0.1). Samples for nutrient analysis were taken subsurface, i.e. at ~0.1 m depth, using 2 L PE bottles previously washed with 1 M HCl and Milli-Q water. Bottles were opened below the water surface to avoid sampling of the surface microlayer and rinsed three times before filling. Samples were immediately filtered through Millipore HAWP (silicates) or GF/F filters (ammonium, nitrates, nitrites, phosphates) and stored in a cooler (following GT DCE Réunion “Physico-Chimie et Phytoplancton”, 2016). Back at the laboratory, samples were frozen until analysis, except for silicates, for which samples were stored at 4 °C. Ammonium (NH_4) analyses were performed manually according to the indo-phenol blue method (Aminot and Kérouel, 2004). Nitrates (NO_3), nitrites (NO_2), phosphates (PO_4) and silicates (Si) were measured using a

Bran + Luebbe Autoanalyzer II and standard analysis methods (Aminot and Kérouel, 2007). Dissolved inorganic nitrogen (DIN) is the sum of nitrates, nitrites and ammonium. The DIN/P ratio is the ratio of DIN to phosphates.

2.3.2. Floral assemblages

2.3.2.1. Specific composition. At each station, the composition of algal assemblages (presence/absence) was assessed following the "Belt Transect" method (60 m × 2 m) (Hill and Wilkinson, 2004). Transects were positioned parallel to the shore. Five taxonomic groups were considered: Bacillariophyta, Cyanobacteria, brown algae (Phaeophyceae), green algae (Chlorophyta) and red algae (Rhodophyta). Samples of selected algae and cyanobacteria specimens were preserved in a solution of formaldehyde buffered in seawater (3%) for later microscopic examination. For macroalgae, samples were sorted, photographed, given preliminary identification and pressed for collection on the same day. At least one specimen from each encountered species was processed to form a voucher collection. Macroalgae identification was done according to available reference lists for La Réunion (Payri, 1985; Ballesteros, 1994). Detailed morphological and anatomical examinations were performed using pressed specimens and formaldehyde preserved samples. The identification of cyanobacteria concerned phenotype determination only, using available monographs and determination manuals (Anagnostidis and Komarek, 1985, 1988; Komárek and Anagnostidis, 1999, 2005; Komárek, 2013). Currently accepted names were checked using the Algaebase (Guiry and Guiry, 2018; http://www.algaebase.org). The identified species were grouped in eight functional groups for analyses: ACG (articulated calcified group), CCA (crustose coralline algae), CBG (corticated branched group), FG (filamentous group), FG macroalgae (filamentous macroalgae excluding diatoms and cyanobacteria), TLG (thick leathery group), TSG (tubular or sheet group) and VG (vesiculous group) according to the studies of Littler and Littler (1980, 1984), Littler et al. (1983), Steneck and Watling (1982), Steneck and Dethier (1994), and Cheal et al. (2010).

2.3.2.2. Algal cover

The percentage cover of macroalgae and cyanobacteria was estimated using photoquadrats. For each station, 7 to 10 photoquadrats of 0.25 m^2 (50 cm × 50 cm) were placed randomly on either side of the transect and then pictured using a digital camera. Occurring species in each quadrat were recorded on a waterproof data sheet. At the laboratory, the photographs were downloaded to a computer, renamed with a unique location code, and processed to improve image quality. Each photo was analyzed for percentage cover using CPCE (Coral Point Count with Excel extensions, Kohler and Gill, 2006), a software program for stratified random point analyses on digital photography. Using a specific tool of the software, we manually delineated each species or group of species (when the identification at species level was not possible) to estimate their percent cover for all photos. At each sampling date, the percentage cover was estimated for each station, except ES2 in April and June, and SLREF in December and June, when sampling was impossible due to too much swell near the reef crest (Supplementary material S1).

2.4. Statistical analyses

2.4.1. Water physico-chemistry

We characterized each station on the basis of the water physico-chemistry (salinity, silicates, nitrates, nitrites, ammonium, phosphates, DIN/P ratio), using PCA and hierarchical clustering. We focused on the values recorded in December, February, April and June when sampling was complete, except at the SL site for which missing values in December were replaced by the values obtained at the SLNI site (possibly minimizing SGD impact at SL). The within-group normalized PCA (Dolédec and Chessel, 1987) that was performed to highlight differences caused by SGD across stations is described in Supplementary material S2. We then performed hierarchical clustering of the stations (Ward aggregation method and Euclidean distances) in order to define groups with similar water physico-chemistry. Raw data were centered and standardized (all sampling dates and stations taken together) prior to classification to account for the heterogeneity of the nature of the variables. Classification was performed using the average of the four values obtained for each of the variables and the stations (for December, February, April and June). Comparing means (given ± SD) between groups was performed using the Mann-Whitney *U* test.

2.4.2. Floral assemblages versus water physico-chemistry

In order to identify ecological indicators of water quality, we performed multivariate analysis to relate information on algae communities to water physico-chemistry. Correspondence analyses (CA) were performed on different types of variables: (1) presence/absence, and (2) species diversity: overall diversity, taxonomic, functional groups diversity, and various percentages and ratios in relation with literature (% perennial species, % opportunistic species, % ESGI, % ESGII, and all ratios, Table 1) (Turquet et al., 2014). Principal component analysis (PCA) were performed for the algal cover: overall algal cover, taxonomic, functional group cover and various percentages and ratios (Turquet et al., 2014).

First, we performed CA and PCA on all combinations of observations by stations and dates. However, the analysis of seasonal variability, using intra-class CA and PCA, revealed the very small impact of temporal compared to spatial variability in the ordination results. Consequently, we present all the CA and PCA analyses based on average values at station level only.

Statistical analyses were performed in R (version 3.0.0, R Development Core Team, 2013), with the package ade4 (Chessel et al., 2004; Dray and Dufour, 2007).

3. Results

3.1. Macroalgae and cyanobacteria identification

Throughout the study, 1989 observations were done and 65 species or groups of species (when identifying the specific level is not possible in the field) were surveyed (Table 3).

One diatom assemblage (Bacillariophyta) mainly composed of *Halamphora*, *Licmophora* and *Grammatophora* (Gilles Gasiole, obs.) was surveyed, as well as fourteen cyanophyta, of which three were identified at the genus level (*Hydrocoleum, Leptolyngbya, Spirulina*) and two species remained unidentified (*Anabaena* sp1 and *Oscillatoria* sp.) pending molecular work. With regard to the macroalgae, 5 species of brown algae (Phaeophyceae), 28 green algae (Chlorophyta) and 17 red algae (Rhodophyta) were surveyed (Table 3). The small filamentous red algae like *Pterocladiella caerulescens*, some Gelidiales and some Rhodymeniales were gathered in one single group named RAT (Red Algae Turf). Some other macroalgae were identified only at the genus level pending molecular work (*Carpopeltis, Codium*, *Derbesia, Ulva*) or to simplify the survey for taxa in which species identification based on morphological data is problematic (*Dictyota*, *Hydrolithon, Hypnea, Lobophora, Neogoniolithon, Padina*, *Peysonnelia*).

For percentage cover estimation based on photographs, some species were grouped together to limit identification errors (Table 3): the *Caulerpa* (*Caulerpa* spp.) and *Dictyosphaeria* (*Dictyosphaeria* spp.) genera. A red algae turf formed mainly by *Amphiroa fragilissima* and *Jania adhaerens* was called *Amphiroa* Turf (AT). This turf constitutes very dense patches intertwined with other red algae such as *Ceratodictyon intricatum*, *Gelidiella acerosa* and other unidentified filamentous and creeping algae that were consistently observed with low cover across samples.

Table 3
List of species or groups of species monitored during the study with their taxonomic affiliation, their functional groups belonging and their ecological status. Species proposed as bioindicator for La Réunion reef flats are indicated in bold letters.

Species	Code used	Functional groups[a]	Ecological status[b]
Bacillariophyta (1)	DIATO	FG	Seasonal
Cyanobacteria (14)	CYANO	FG	
Anabaena sp1	ANA_SP1	FG	Opportunistic
Blennothrix glutinosa	BLE_GLUT	FG	Opportunistic
Blennothrix lyngbyacea	**BLE_LYNG**	**FG**	**Opportunistic**
Blennothrix major	BLE_MAJO	FG	Opportunistic
Hydrocoleum spp.	HYD_SPP	FG	Opportunistic
Leptolyngbya hendersonii	LEP_HEND	FG	Opportunistic
Leptolyngbya spp.	LEP_SPP	FG	Opportunistic
Lyngbya majuscula	LYN_MAJU	FG	Opportunistic
Lyngbya sordida	LYN_SORD	FG	Opportunistic
Oscillatoria sp.	OSC_SP	FG	Opportunistic
Phormidium laysanense	PHO_LAYS	FG	Opportunistic
Spirulina spp.	SPI_SPP	FG	Opportunistic
Symploca hydnoides	SYM_HYDN	FG	Opportunistic
Symplocastrum coccineum	SYM_COCC	FG	Opportunistic
Brown algae (5)	BROWN		
Dictyota spp.	DIC_SPP	TSG	Perennial
Lobophora spp.	LOB_SPP	TLG	Perennial
Padina spp.	PAD_SPP	TSG	Perennial
Sphacelaria tribuloides	**SPH_TRIB**	**FG**	**Seasonal**
Turbinaria ornata	TUR_ORNA	TLG	Perennial
Green algae (28)	GREEN		
Anadyomene wrightii	ANA_WRIG	TSG	Perennial
Boergesenia forbesii	BOE_FORB	VG	Perennial
Boodlea composita	BOO_COMP	TSG	Seasonal
Bornetella sphaerica	BOR_SPHA	TSG	Perennial
Bryopsis pennata	**BRY_PENN**	**FG**	**Opportunistic**
Caulerpa lamourouxii	**CAU_LAMO**	**CBG**	**Opportunistic**
Caulerpa nummularia	CAU_NUMM	CBG	Perennial
Caulerpa serrulata	CAU_SERR	CBG	Perennial
Caulerpa sertularioides	CAU_SERT	CBG	Seasonal
Caulerpa webbiana	CAU_WEBB	CBG	Perennial
Caulerpa spp.	CAU_SPP	CBG	–
Chaetomorpha vieillardii	**CHA_VIEI**	**FG**	**Opportunistic**
Chlorodesmis hildebrandtii	CHL_HILD	FG	Perennial
Cladophoropsis sundanensis	CLA_SUND	FG	Perennial
Codium arabicum	COD_ARAB	CBG	Perennial
Codium sp.	COD_SP	CBG	–
***Derbesia* sp.**	**DER_SP**	**FG**	**Opportunistic**
Dictyosphaeria cavernosa	DICT_CAVE	VG	Perennial
Dictyosphaeria verluysii	DICT_VERL	VG	Perennial
Dictyosphaeria spp.	DICT_SPP	VG	Perennial
Ernodesmis verticillata	ERN_VERT	TSG	Perennial
Halimeda discoidea	HAL_DISC	ACG	Perennial
Neomeris annulata	NEO_ANNU	TSG	Perennial
Neomeris vanbosseae	NEO_VANB	TSG	Perennial
Phyllodictyon anastomans	PHY_ANAS	TSG	Perennial
***Ulva* sp.**	**ULV_SP**	**TSG**	**Opportunistic**
Valonia aegagropila	VAL_AEGA	VG	Perennial
Valonia ventricosa	VAL_VENT	VG	Perennial
Red algae (17)	RED		
Actinotrichia fragilis	ACT_FRAG	ACG	Perennial
Amphiroa fragilissima	AMP_FRAG	ACG	Perennial
Carpopeltis sp.	CAR_SP	TLG	Perennial
Ceratodictyon intricatum	CER_INTR	FG	Perennial
Digenea simplex	DIG_SIMP	CBG	Perennial
Galaxaura rugosa	GAL_RUGO	ACG	Perennial
Ganonema farinosum	GAN_FARI	CBG	Seasonal
Gelidiella acerosa	**GEL_ACER**	**CBG**	**Perennial**
Gracilaria canaliculata	**GRA_CANA**	**CBG**	**Opportunistic**
Hydrolithon spp.	HYDRO_SPP	CCA	Perennial
Hypnea spp.	HYP_SPP	CBG	–
Jania adhaerens	JAN_ADHA	ACG	Perennial
Lithophyllum kotschyanum	LIT_KOTS	CCA	Perennial
Neogoniolithon spp.	NEO_SPP	CCA	Perennial

(*continued on next page*)

Table 3 (*continued*)

Species	Code used	Functional groups[a]	Ecological status[b]
Peyssonnelia spp.	PEY_SPP	TLG	Perennial
Red Algae Turf[c]	**RAT**	**FG**	**Perennial**
Amphiroa Turf[d]	AT	ACG	Perennial

[a] Functional groups: ACG: articulated calcified group; CBG: corticated branched group; CCA: crustose coralline algae; FG: filamentous group; TLG: thick leathery group; TSG: tubular or sheet group; VG: vesiculous group.

[b] Algae belong to different Ecological Status Group (ESG; Wells et al., 2007): slow-growing perennial (ESGI); fast-growing opportunistic (ESGII); seasonal growing during austral summer or winter depending on species (ESGII).

[c] Red Algae Turf (RAT) is composed mainly by Gelidiales and Rhodymeniales.

[d] Amphiroa Turf (AT) is formed mainly by *Amphiroa fragilissima* and *Jania adhaerens* which constitutes very dense patches intertwined with other red algae such as *Ceratodictyon intricatum, Gelidiella acerosa*,

3.2. *Water physico-chemistry*

Raw data are given in Table S2 (Supplementary material S2). The results of the within-group normalized PCA are shown in Fig. S2. Briefly, salinity, silicate and nitrate concentrations, as well as the DIN/P ratio, correlate well with the first axis of the PCA, salinity being opposed to the three other parameters. The positive linear relationship between silicate and nitrate concentrations is particularly significant ($R^2 = 0.87$; $p < 0.001$). Phosphate concentration is the only parameter correlated with PC2.

Three main groups were identified using hierarchical clustering, two of them splitting into two sub-groups (Fig. 2). Group G1 consists of TE40, which is opposed to all other stations. This station is the most N-enriched, and has the highest DIN/P ratio (5.8 ± 2.6 µM and 56 ± 32 respectively). Group G2 consists of all Saint-Pierre stations including the reference one and the two other TE stations (sub-group 2.1), as well as the two SL stations closest to the beach and ES3, the closest ES station to the submarine spring (sub-group 2.2). Group G2 is moderately N-enriched compared to TE40 (1.5 ± 0.7 µM), and has a lower DIN/P ratio (16 ± 8) with no difference between sub-groups 2.1 and 2.2. However, sub-groups 2.1 and 2.2 have slightly different phosphate concentrations (0.09 ± 0.02 µM and 0.11 ± 0.02 µM respectively; p = 0.002). Group G3 consists of all other stations. TOB site is associated with SLNI70 and SL120 (sub-group 3.1). These stations are opposed to some extent to sub-group 3.2 consisting of the ES site (except ES3 belonging to group G2) and the SLNI site except SLNI70. DIN concentrations and the DIN/P ratio are significantly lower in group G3 (0.8 ± 0.3 µM and 7 ± 2 respectively) than group G2 ($p < 0.001$ for both). DIN concentrations are not significantly different between sub-groups 3.1 and 3.2, but phosphate concentrations are slightly higher in sub-group 3.1 than 3.2 (0.13 ± 0.03 µM and 0.11 ± 0.02 µM respectively; p = 0.046). Therefore, the DIN/P ratio is lower in sub-group 3.1 than 3.2 (6 ± 1 and 7 ± 2 respectively; p = 0.021).

3.3. *Floral assemblages versus water physico-chemistry*

3.3.1. *Species composition*

The floral assemblages were described based on a set of 18 stations over four sites (Fig. 1, Supplementary material S1), representing the three hydrological groups G1, G2 and G3 (Fig. 2). The floral assemblages of each hydrological group are summarized in Table S3 (Supplementary material S3).

The correspondence analysis (CA) on specific composition data (presence/absence) provides a distribution of data variability up to 38.6% on the first two axes 1 and 2 (Fig. 3). In spite of this relatively low percentage of explained variance, some separation of the three

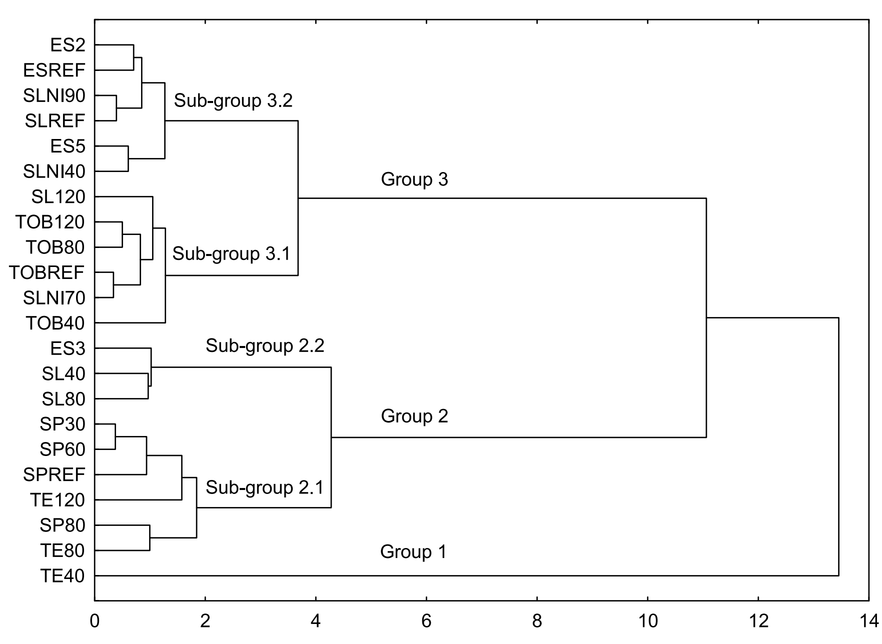

Fig. 2. Dendrogram showing hierarchical clustering of the stations (Ward aggregation method and Euclidean distances).

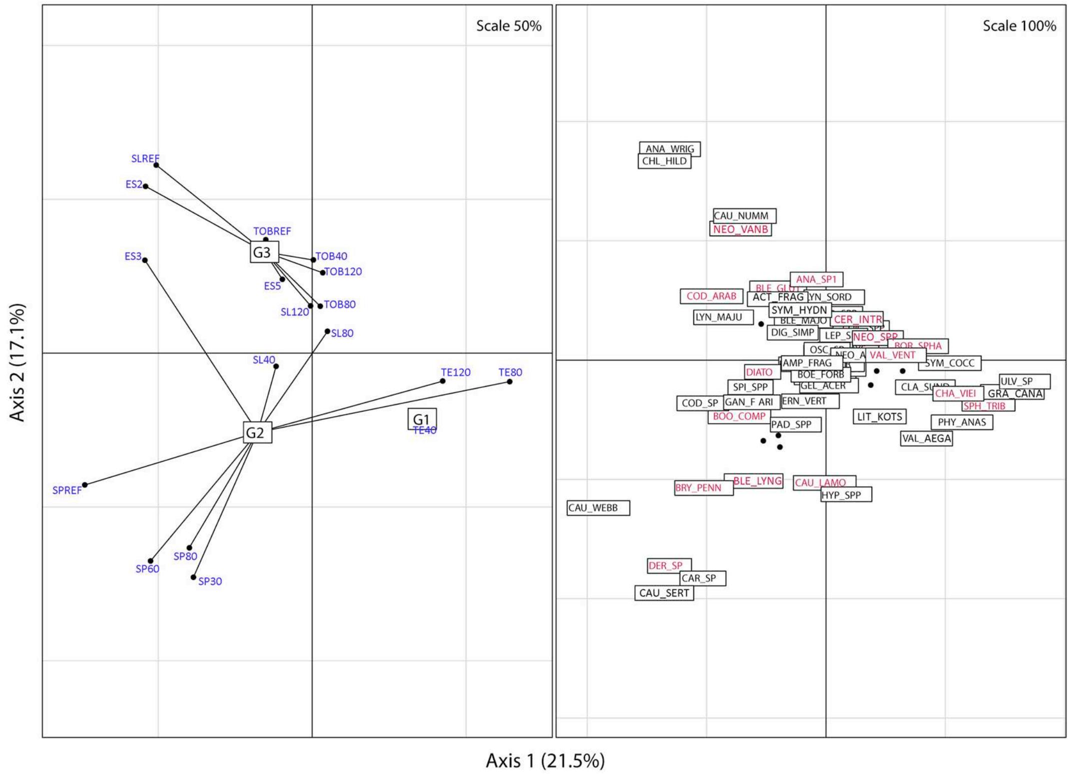

Fig. 3. Correspondence analysis on specific composition data (presence/absence). Left: projection of the stations (in blue) and hydrological groups (G1, G2, G3). Right: projection of the species with, in red, the species that contribute significantly (> 50% cumulative relative contribution to axis 1 and 2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

hydrological groups is observed. Axis 1 opposes G3 and G2 on the left side, to group G1 (TE40) and stations TE80 and TE120 on the right side (representing 40%, 70% and 66% respectively). Axis 2 overall opposes group G3 positioned on the positive side of the axis, and groups G1 and G2 (mainly SP30, SP60 and SP80 representing 64%, 51% and 41% respectively), except for stations ES3, SL40 and SL80. Therefore, floral assemblages clearly differ between groups G1 and G3. Within G2 however, some stations (TE80 and TE120) are close to group G1 (TE40) and some others (ES3, SL40 and SL80) close to group G3. In addition, an effect of the sites is likely, as the SP site is clearly opposed to the other stations of group G2. Sixteen species contribute significantly (> 50% cumulative relative contribution to axis 1 and 2) to our analysis: three cyanobacteria (*Anabaena* sp1, *Blennothrix glutinosa, Blennothrix lyngbyacea*), the diatoms, one brown algae (*Sphacelaria tribuloides*), two red algae (*Ceratodictyon intricatum, Neogoniolithon* spp.) and nine green algae (*Boodlea composita, Bornetella sphaerica, Bryopsis pennata, Caulerpa lamourouxii, Chaetomorpha vieillardii, Codium arabicum, Derbesia* sp.*, Neomeris vanbosseae, Valonia ventricosa*) (Fig. 3, in red). TE stations were characterized by a high frequency of *Chaetomorpha vieillardii* and *Sphacelaria tribuloides,* and SP stations by *Blennothrix lyngbyacea, Bryopsis pennata*, *Caulerpa lamourouxii* and *Derbesia* sp., while group G3 was characterized by a high frequency of two cyanobacteria (*Anabaena* sp1, *Blennothrix glutinosa*) and two green algae (*Neomeris vanbosseae* and *Codium arabicum*).

Correspondence analysis on diversity data (taxonomic groups, functional groups and ratios) did not allow a clear differentiation of the three hydrological groups (data not show).

3.3.2. Algal cover

Algal cover data are summarized in Supplementary material S4. *Amphiroa* turf (AT) is the most abundant group (reaching > 80% cover at SP30 and SP60, and 67.8% in February at ES3) (Table S4, Fig. S4-1). As a result of the extensive AT cover on the rubbles, the highest algal percentage cover was measured at the SP site (49.4–86.4% at SP30, 44.8–83.7% at SP60) followed by stations ES3 (70.7% in February) and TE40 (50.7% in January). Then, the predominant species were diatoms, *Neogoniolithon* spp. and *Hydrolithon* spp. A bloom of diatoms observed in February at SL80 was responsible for a 95% algal cover.

Principal component analysis (PCA) represents 40.2% of the variability on the first two axes 1 and 2 (Fig. S4-2). G1, composed of the TE40 station (represented at 84%), contributes half of the variance explained on axis 1. The other groups G2 and G3 do not show a clear separation on axis 1 and 2 (Fig. S4-2). Among the species that contribute significantly (> 50% cumulative relative contribution to axis 1 and 2) to the analysis (Fig. S4-2, in red), the communities associated with G1 were characterized by a high cover of red algae (RA) (91% cumulative relative contribution), and especially *Neogoniolithon* spp., *Gelidiella acerosa*, *Hydrolithon* spp. and the Red Algae Turf (RAT) (91%, 86%, 81% and 74% cumulative relative contribution, respectively) (Fig. S4-2). Communities associated with TOB120 and TOBREF stations were characterized by a high cover of green algae (GA), especially *Boergesenia forbesii* (65% cumulative relative contribution), and one cyanobacteria *Anabaena* sp1. (45.7% cumulative relative contribution) (Fig. S4-2).

4. Discussion

4.1. Water physico-chemistry

Salinity is clearly opposed to Si concentrations along the first axis of the within-group normalized PCA, whose first factor therefore represents terrestrial freshwater influence (Garrison et al., 2003; Street et al., 2008; Cuet et al., 2011; Tedetti et al., 2011). The positive linear relationship found between Si and NO_3 concentrations provides evidence of nitrogen (N) input from terrestrial sources into the marine environment. With the exception of the TOB site, the closest stations to the beach as well as ES3 (the closest station to the Etang-Salé submarine spring) have the highest DIN, and especially NO_3 concentrations (up to $4.7 \pm 1.9\,\mu M$ at TE40), showing that the NO_3-enriched basaltic aquifer (Cuet et al., 2011; Tedetti et al., 2011) is a significant source of N to the reefs as found in other coastal areas (e.g. Garrison et al., 2003; Kim et al., 2003; Paytan et al., 2006; Bowen et al., 2007; Street et al., 2008).

According to terrestrial freshwater influence, three main groups were identified using hierarchical clustering, two of them splitting into two sub-groups according to PO_4 concentrations. PO_4 concentrations are uncorrelated with the first factor of the PCA. The source is therefore mostly oceanic, as previously found at the TE site (Cuet et al., 2011). Accordingly, the average PO_4 concentration is low ($0.11 \pm 0.03\,\mu M$) and typical of the oligotrophic ocean environment (Atkinson and Falter, 2003). Slight differences between sites or stations within a single site may be due to the metabolic activity of benthic communities.

Finally, due to the low spatial variability of the PO4 concentrations, the more or less marked N-enrichment due to freshwater inputs mainly leads to a gradual increase in the DIN/P ratio whose values characterize the three main groups identified using hierarchical clustering. At the most N-enriched station TE40 (group G1), the DIN/P ratio is 56 ± 32, suggesting that macroalgae are PO4-limited. The N/P ratio is in effect of the order of 30 in benthic primary producers (Atkinson and Smith, 1983). High alkaline phosphatase activity (APA) can however compensate for PO_4-limitation of macroalgae in coral reef systems that are subject to significant N-inputs (Schaffelke and Klumpp, 1997; Schaffelke, 2001; Schaffelke et al., 2005). In contrast, within group G3, which includes the stations less influenced by terrestrial N-inputs, with an average NO_3 concentration of $0.4 \pm 0.2\,\mu M$, the DIN/P ratio is 7 ± 2. As a result, macroalgae are clearly limited in nitrogen.

4.2. Species composition as bioindicator

Floral assemblages were distinctly different in groups G1 (the most N-enriched station TE40) and G3 (the stations less influenced by terrestrial N-inputs), suggesting that floristic composition could be a useful descriptor of human-induced N enrichment. However, floral assemblages clearly differed according to some other factors within group G2 (moderately N-enriched). The three stations close to group G3 in Fig. 3 (ES3, SL40 and SL80) form the sub-group 2.2, which differs from the other stations of group G2 by slightly higher phosphate concentrations. Within the sub-group 2.1, floral assemblages of TE and SP are clearly different, suggesting a strong influence of the site in addition to nutrient enrichment. Indeed, a number of environmental variables were not considered in this study, such as biotic (e.g. coral cover, biomass of herbivorous fishes) and abiotic (water movement, light, substrate) variables, which have been shown to influence the structure of macroalgal communities in other studies (Burkepile and Hay, 2010; De'ath and Fabricius, 2010).

No taxonomic or functional trends were observed for specific composition, in contrast to previous studies (Fabricius et al., 2005; Wells et al., 2007; Neto et al., 2012). Species of the same functional group may respond differently to similar stressors as the functional group approach was used originally to predict productivity and other ecological attributes (e.g. grazing resistance, competitive abilities and reproductive effort) and not water quality (Orfanidis et al., 2011). Consequently, Orfanidis et al. (2011) developed a specific functional classification for the Mediterranean coast using twelve traits relevant to nutrient and light responses. A similar analysis for tropical marine flora could provide relevant results. Functional traits of macroalgae may be more predictive than taxonomic indicators, as Teresa and Casatti (2017) have demonstrated for fish.

Four species of green algae (*Bryopsis pennata, Caulerpa lamourouxii, Chaetomoropha vieillardii, Derbesia* sp.) were characteristic of impacted stations (group G1 and sub-group 2.1). The occurrence of these opportunistic species often increases consecutively to ecosystem degradation in relation to land-based nutrient inputs (Lapointe and Bedford, 2010; Lapointe et al., 2005a,b; Smith et al., 2005; Teichberg et al., 2010). Furthermore, the genera *Caulerpa* and *Chaetomorpha* are commonly used in pollution biomonitoring studies throughout the world (García-Seoane et al., 2018). However, our study showed that some other green algae were characteristic of non-impacted stations (*Neomeris vanbosseae* and *Codium arabicum*). This result can be related to the physiology of these perennial species, with slow growth (low nutrient uptake; Wallentinus, 1984), in contrast to opportunistic species with fast growth and high productivity (Littler and Littler, 1980). Our results confirm the interest of using the classification opportunistic/ perennial macroalgae in coral reefs. Three different categories should be considered in upcoming monitoring: slow-growing perennial species, fast-growing opportunistic species and seasonal species (Martínez et al., 2012).

With regard to the cyanobacteria, our study showed that some species were characteristic of non-impacted stations (*Anabaena* sp1, *Blennothrix glutinosa*). This result goes against many publications on coral reefs that consider that the presence of cyanobacteria is the sign of a degradation of the ecosystem (Miller et al., 1999; Diaz-Pulido and Garzón-Ferreira, 2002; De Bakker et al., 2017). It is possibly explained by the slightly elevated phosphate level observed at the non-impacted stations (see 3.2). Many cyanobacteria, including *Anabaena* genus (Komárek, 2013) and *Blennothrix glutinosa* (Palińska et al., 2015), can fix atmospheric N_2 so their growth is unlikely to be limited by nitrogen but rather by phosphate availability (Kuffner and Paul, 2001). In contrast, *Blennothrix lyngbyacea* is not a diazotroph species (Palińska et al., 2015) and it was characteristic of impacted stations (SP30 and SP60 mainly), presumably due to the high N:P ratio. This species is known to respond to eutrophication by building extensive mats (Charpy et al., 2010, 2012a,b). It is therefore likely to be a bioindicator species, but further studies are required to better characterize the environmental factors that trigger blooms of this cyanobacteria. A recent study (Johnstone et al., 2010) allowed the identification of the main triggers of *Lyngbya majuscula* blooms, including availability of dissolved nutrients, especially dissolved P and Fe, and others factors such as light and temperature using an integrated Bayesian Network.

Finally, our study demonstrated the importance of accurate taxonomic identification to species level to use macroalgae as bioindicators. Higher taxonomic ranks have more power to detect anthropogenic impacts on coral reefs (Jimenez et al., 2010; Van Wynsberge et al., 2017). The use of molecular methods (e.g. metabarcoding) on future studies could improve taxonomic resolution and it was already proposed and tested by several authors (Baird and Hajibabaei, 2012; Taberlet et al., 2012; Reimer et al., 2018).

4.3. Algal cover as bioindicators

Algal cover is an important parameter to take into account when considering the impact of nutrient enrichment. Macroalgal blooms are more and more common in coral reef environments. They are directly linked to an excess of anthropogenic nutrients (Teichberg et al., 2010; García-Seoane et al., 2018 for reviews; Table 2) but also to the effects of climate change (temperature increase) (Gao et al., 2017).

During our study, the cover of erect red algae appears to be a good bioindicator of the N-enrichment gradient since the highest red algal cover (mainly *Gelidiella acerosa* and the Red Algal Turf) was observed at the most N-enriched station TE40 (group G1). This is in accordance with earlier observations at La Réunion. Between 1985 and 1990, the La Saline reef flat, highly impacted by N-enriched submarine groundwater discharge, was invaded by the red algae *Gracilaria canaliculata* (Naïm et al., 2013). Nitrogen supply is known to promote the growth and the abundance of red algae in coral reefs (Costanzo et al., 2000; Lin and Fong, 2008) and several studies demonstrated an increase of red algae cover with nutrient enrichment (Table 2).

A high abundance of CCA (crustose coralline algae) was also observed at TE40 possibly due to N-enrichment at this site, as shown by a previous study (Smith et al., 2001). However, other studies (Björk et al., 1995; Fabricius and De'Ath, 2001; Fabricius et al., 2005) showed, on the contrary, a decrease in CCA with nutrient enrichment. This contrasting results could be explained by other biotic factors (coral cover, biomass of herbivorous fishes, etc.) that influence the structure of macroalgal communities (Burkepile and Hay, 2010; De'ath and Fabricius, 2010; Keith et al., 2014). Herbivory is clearly one of the most important factors structuring algal community composition and species diversity. At the TE site, the higher abundance of herbivorous fishes compared to the other stations (Nicolas Loiseau, com. pers.) may have favored the high CCA abundance, as previously demonstrated by Burkepile and Hay (2009).

4.4. Perspectives and recommendations

This first study in the framework of WFD in French overseas territories coral reefs has enabled us to propose a first list of 10 bioindicator species for La Réunion reef flats (Table 3, in bold). The high frequency of occurrence and/or high cover of these bioindicator species clearly reflect N-enrichment of the reef flats by submarine groundwater discharge, although these species are not always conspicuous, possibly depending on the PO_4 concentration of overlaying waters. However, a long-term monitoring is highly recommended to confirm these preliminary results since coral reefs represent a highly dynamic ecosystem more and more frequently exposed to extreme natural disturbances (e.g. cyclones, bleaching). The frequency and the intensity of these disruptive events can impact the structure of the algal community including species richness and life-history strategy (opportunistic vs. perennial). The successional sequence of algae and the role of abiotic and biotic factors in mediating (facilitating or inhibiting) the succession of species after disturbances should be well understood to confirm bioindicator species.

Similar studies have to be conducted in other French overseas territories (Guadeloupe, Martinique, Mayotte), since the list of bioindicator species will be specific for each region, but the methodology should be improved, especially the estimation of algal cover. Measuring relative abundance (< 5%; 5–25%; 25–50%, 50–75% and > 75%) on belt-transects to approximate each species cover, as is done with the CARLITT method or the CFR (Table 1), is effective and much easier to implement than photoquadrats in coral ecosystems.

Finally, the macroalgae bioindicator approach should be used in addition to global and multi-taxonomic monitoring of coral reefs (e.g. GCRMN). A multi-bioindicator and multi-taxa approach is expected to provide a more integrative and complementary view of coral reef ecosystem health.

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