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Selection of parameters for seagrass management: Towards the development of integrated indicators for French Antilles

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Abstract :

Seagrass beds are increasingly impacted by human activities in coastal areas, particularly in tropical regions. The objective of this research program was to study seagrass beds characteristics under various environmental conditions in the French Antilles (FA, Caribbean Sea). A total of 61 parameters, from plant physiology to seagrass ecosystem, were tested along a gradient of anthropogenic conditions, distributed across 11 sites and 3 islands of the FA. A selection of 7 parameters was identified as relevant for the monitoring of seagrass meadows in the framework of public policies. They combined “early warning indicators” (e.g. nutrients and some trace metals) and long-term responding parameters (e.g. shoot density) adapted to management time scales. The ecological status of seagrass meadows was evaluated using a PCA. This work is a first step towards monitoring and management of seagrass meadows in the FA.

Highlights

► A panel of seagrass meadows descriptors were studied along a gradient of anthropogenic conditions in Caribbean region. ► Bioindication capacity of two native seagrass species has been confirmed. ► The most relevant parameters for monitoring local seagrass beds health and water quality were identified. ► An ecological status of the seagrass meadows was provided using a multimetric approach.

Keywords : Biological indicators, Caribbean Sea, Ecological status, Management, Pressure-impact relationship, Seagrass

1. Introduction

Seagrasses form rich and significant coastal habitats across tropical and temperate regions worldwide (Green and Short, 2003; Short et al., 2011) and support a wide range of ecological functions and services (Orth et al., 2006). Because of their position at the land-sea interface, they are at the forefront of the fast-changing environmental conditions induced by human activities in coastal areas (Short et Wyllie-Echeverria 1996; Orth et al., 2006). Increasing anthropogenic activities resulting from population growth, including deforestation, tourism, aquaculture and industrial activities combined with inadequate sewage treatment plants, are leading to the degradation of water quality and clarity (e.g. increase in nutrients, organic matter and sediment inputs). These threats are the major causes of the global decline of seagrass beds (Short et al., 2011; Waycott et al., 2009). After degradation or even disappearance, the recovery process is long and not systematic (Godet et al., 2008; O'Brien et al., 2018; Santos et al., 2019). Restoration methods are complicated and expensive, and their implementation is often limited to some species and small areas (Cunha et al., 2012; Katwijk et al., 2016). They also involve decreasing the sources of degradation, but long-term success is not guaranteed. In this context, the conservation and protection of seagrass beds are essential to maintain sustainability and ecosystem services (Mtwana Nordlund et al., 2016; Ruiz-Frau et al., 2017). These objectives require a better understanding of the ecological status and evolution of seagrass beds and challenges ecosystem management methods.

Depending on management issues and objectives, several monitoring strategies can be implemented: (1) general ecosystem monitoring under a pressure panel, (2) diagnosis of the ecological status of the environment (bioindication), (3) impact assessment, using stress indicators related to specific pressures, and (4) assessment of ecosystem resilience and effectiveness of management measures (Roca et al., 2016). This involves the use of different approaches and specific diagnostic tools that should be planned for in the design phase of monitoring programs (Legg and Nagy, 2006; Yoccoz et al., 2001). This is particularly important because no single indicator can meet all the management objectives and can be misleading if taken in isolation (Martínez-Crego et al., 2010; Prado et al., 2010; Roca et al., 2016). The choice of the most relevant parameters according to the type of seagrass meadow, specific objectives and the development of robust indicators, while optimizing the protocols, represents a major management challenge (Arthur et al., 2008; Madden et al., 2009; Kilminster et al., 2015; Roca et al., 2016).

In French overseas territories of the Caribbean region (French Antilles, FA), seagrass beds' management actions respond to several public policies with specific challenges set by the strategy for the establishment and management of Marine Protected Areas (MPA, MEDDTL 2012), the

European Water Framework Directive (WFD, European Commission), the French Coral Reefs Initiative (Ifrecor) and the French National Observatory of Biodiversity (FOB) (Fig. 1). In the context of the WFD's implementation, several multimetric indicators have been developed in Europe for monospecific seagrass beds of *Posidonia oceanica* (Romero et al., 2007; Gobert et al., 2009; Lopez y Royo et al., 2010), *Cymodocea nodosa* (Oliva et al., 2012; Orlando-Bonaca et al., 2015) and *Zostera* sp. (García-Marín et al., 2013; Neto et al., 2013). The local specificities of tropical seagrass beds (i.e. plurispecific) and their geographical location (isolated islands) prevent the transposition of WFD indicators to the French overseas.

Seagrass beds in the Caribbean cover about 66000 km² (Miloslavich et al., 2010) and nine species are documented (van Tussenbroek et al., 2010; Short et al., 2011). Their surface area in the FA accounts for 217 km² and five seagrass species are reported: *Thalassia testudinum* and *Syringodium filiforme* (which are the two dominant species), *Halodule wrightii*, *Halophila decipiens,* and *Halophila stipulacea* (which is an invasive species), (Willette and Ambrose, 2012; Maréchal et al., 2013; Willette et al., 2014; Ifrecor, 2016).

Like most Caribbean regions, the FA territories are faced with the development of human populations and their activities, leading to increased eutrophication, pollution and sedimentation in coastal areas (Diez et al., 2019). Since 2011, the region experiences recurrent massive coastal standing of the pelagic brown macroalgae *Sargassum* (van Tussenbroek et al., 2017; Wang et al., 2019), to which are added the increasing power and frequency of hurricanes, as evidenced by the 2017 dramatic hurricane season (Pillet et al., 2019; Walcker et al., 2019).

Identifying the link between sources of disturbance and the ecological status of coastal habitats is key for the development of diagnostic tools for marine ecosystems (Marbà et al., 2013). This is particularly true as the selection of parameters to discriminate healthy from unhealthy seagrass beds can be very subjective, even when recommendations are provided by experts (Wood and Lavery, 2000). In order to provide factual guidance for decision-making, especially for indicators, the objectives of our work are multiple and as follows : (1) to study the response of seagrass meadows to several parameters along a gradient of anthropogenic pressures (i.e. nutrient inputs, organic matter, metal pollution and sedimentation); (2) to investigate the bioindication capacity of the two native and long-lived Caribbean seagrass species: *T. testudinum* and *S. filiforme,* for which very little work has yet been carried out for the development of bioindication tools; (3) to select the most relevant parameters for the construction of multimetric indicators based on the management objectives of the FA public policies and implementation capacities.

2. Materials and methods

2.1. Study area and sampling sites

The study was carried out on selected FA territories of the Lesser Antilles: Guadeloupe, Saint-Martin and Saint-Barthélemy islands (Fig. 2). Guadeloupe is one of the largest volcanic islands of the Lesser Antilles (1,780 km^2 with its dependencies). Saint-Martin (54 km^2 for the French part) and Saint-Barthélemy (24 km^2) are old volcanic islands covered in limestone and located in the north of the arc of the Lesser Antilles. Study stations were selected according to: (1) the well-developed presence in adjacent coastal areas of the two dominant and indigenous seagrass species: *T. testudinum* and *S. filiforme*; (2) an anthropogenic gradient of water quality at the scale of these islands; (3) the availability of historical ecological (e.g. seagrass density and canopy height), physicochemical (water temperature, salinity, dissolved O_2, turbidity, nitrate) and phytoplankton data, and (4) regional distribution (as the FA islands are distributed along the Caribbean arc).

Potential anthropogenic pressure was estimated based on the proximity and intensity of the disturbances, using pressures data and expert knowledge (Table 1, Table S1). Based on these criteria, 11 stations were sampled both during 2017 and 2018 dry seasons with the aim to account for inter-annual variability (Fig. 2, Table 1).

2.2. Parameters selection for the experiment

General trends in the sensitivity of seagrass beds and ecological responses to anthropogenic disturbance have been studied in recent years (Table 2) (Martínez-Crego et al., 2008; van Katwijk et al., 2011; Roca et al., 2016; Yang et al., 2018). As responses trend of parameters based on the literature (Table 2) must be validated across our study region (Martínez-Crego et al., 2008), we have selected parameters with complementary specificities, ranging from plant physiology to the seagrass bed ecosystem (Table 2). At physiological level, descriptors such as $\delta^{13}C$ and $\delta^{15}N$ isotopes, nutrients (N, P) and trace metals reflect physiological processes and are recognized as "early warning indicators". Morphological descriptors provide information on plant characteristics which are sensitive to environmental conditions. Structural parameters, such as meadows cover and shoot density, were measured in order to characterize meadow's configuration and population's integrity. Moreover, we also collected information about associated communities as it brings key information about water quality (taxa and cover of macroalgae, epiphytes and cyanobacteria) and estimation of the habitat function with the diversity and abundance of macrofauna. We also analyzed silt & clay, organic matter and carbonate contents in sediments for habitat characterization.

All parameters were then measured at local seagrass meadows to build a dataset. The objective was to select a set of parameters responding to anthropogenic disturbances, which could also be used to describe the ecological functioning of the meadow. Our scientific approach is holistic. Thus, our hypothesis is that we will be able to select the most powerful parameters to build multimetric indicators, which are now frequently used for their robustness in bioindication and health monitoring of seagrass beds (Wood and Lavery, 2000; Romero et al., 2007; Arthur et al., 2008). Given the difficulties of collecting continuous data on the sources of disturbance and their intensity, this proposed multimetric approach will also allow and contribute to the a posteriori evaluation of the evolution of environmental conditions.

2.3. Sampling design, data collection, and analyses

2.3.1. Sampling design

The sampling design was adapted from the Seagrass-Watch (McKenzie et al., 2001) and SeagrassNet (Short et al., 2006) protocols and complies with monitoring of seagrass beds in the FA (GTN Herbiers Ifrecor-DCE, 2017 for a review). Three linear transects of 50 meters-long each were deployed and monitored using the Line Intercept Transect (LIT) and the belt transect (1 m wide band along each transects) and quadrats (ten by transect) methods. Sampling was done by SCUBA diving or snorkeling depending on depth conditions (Table 1). Ten specimens of *T. testudinum* and *S. filiforme*, when present, were collected at the start, middle and end of each transect (three collecting zones per transect, nine zones at each station). Morphometric measurements, physiological analysis and characterization of leaf epiphytes were performed on each sample. Sediment samples were collected with minicorers (3 cm in diameter and 5 cm long) in the middle section of each transect. Samples of seagrasses and sediments were immediately refrigerated until measurements and further analysis.

2.3.2. Sediment characteristics

Minicorers were emptied and sediments were dried at 60 °C for 48 hours. Organic matter contents were calculated according to mass loss after combustion at 450 °C for 5 hours. Carbonate contents were determined following Jiang et al. (2019). The amount of silt and clay (<63 µm; Blott and Pye, 2001) was assessed on sieved samples using a laser diffractometer (MASTERSIZE 2000) and data were analyzed using the Malvern V5.61 software.

2.3.3. *Seagrass meadow descriptors and physiological descriptors*

The density of *T. testudinum* and *S. filiforme* was estimated using 10 x 20 cm quadrats (CARICOMP 1994, Bouchon et al., 2003). Seagrass abundance and cover were estimated using 50 x 50 cm meshed quadrats. For each transect, fragmentation was assessed according to the LIT method (GTN Herbiers

Ifrecor-DCE, 2017). The collected seagrasses specimens were rinsed with distilled water and measured with the precision of ± 0.5 mm using a ruler. For *T. testudinum*, the Leaf Area Index (LAI, $m^2\ m^{-2}$) was calculated according to the following equation:

$$\mathrm{LAI} = \frac{\mathrm{LL} \times \mathrm{LW} \times \mathrm{Lves}}{1\,000\,000} \times \mathrm{Shoots}$$

(with LL: leaf length (mm), LW: leaf width (mm), Lves: number of leaves per shoot, Shoots: shoots density m^{-2}). The presence of grazing marks and necrosis on *T. testudinum* leaves was recorded. Visible epiphytes were removed (see below) and leaves were wiped clean. Leaves and rhizomes from each harvesting area and species were dried separately at 60°C for 48 hours and the mass of dry leaves was weighed. For each species, leaves and rhizomes from the nine harvesting zones (at each station) were pooled and grounded to powder using an agate planetary mill (Pulverisette, 05.20, Fritsch).

Analyses of C & N contents and $\delta^{13}C$ & $\delta^{15}N$ isotopes were performed using an elemental analyzer (Flash EA 2000, Thermo Scientific) coupled to an Isotope Ratio Mass Spectrometer (Delta V+ with a conflo IV interface, Thermo Scientific) at the Pôle Spectrométrie Océan (PSO Plouzané, France). Measurements of $\delta^{13}C$ and $\delta^{15}N$ were expressed as relative values per thousand (‰). Analytical accuracies based on replicated measurements of acetanilide (Thermo Scientific) were 0.03 ‰ for $\delta^{13}C$, 0.06 ‰ for $\delta^{15}N$, 0.2 % for C and 0.1 % for N. The contents in phosphorus (P) and trace elements (ETs) in the form of cadmium (Cd), copper (Cu), lead (Pb), iron (Fe), nickel (Ni), zinc (Zn), chromium (Cr), manganese (Mn) and mercury (Hg) were specifically measured in the tissues of the climax species *T. testudinum.* As a long-lived species, it has high integrative capacity (Fourqurean et al., 1997; Burkholder et al., 2007; Govers et al., 2014b; Holmer et al., 2016) which is why we chose it as a model species for physiological parameters including metal analyses that were not performed for *S. filiforme*. For this purpose, 250 mg of ground leaves and rhizomes of *T. testudinum* were calcined in an oven at 500°C for 8 hours before being digested with HNO_3 (65 %), HCl (32 %) and HF (40 %) at 90°C. The measurements were performed using an ICP-MS (ICP Q-MS-X series 2, Thermo Scientific) at the PSO. The accuracy of the analysis was determined using the certificate material reference (BCR670).

2.3.4. Benthic associated macrofauna and flora and epiphyte communities

The benthic macrofaunal diversity was assessed using ten 50 x 50 cm quadrats (for sessile epifauna) and across belt transects (for large macrofauna). Macroalgae and cyanobacteria covers were visually estimated in each quadrat. The total species richness of the associated faunal communities was calculated as the sum of the data collected from both quadrats and belt transects. In addition, the

diversity and % cover of epiphytes were estimated for each leaf, before being scraped off, dried and weighed.

2.4. Statistical analysis

Prior to statistical analyses, data were tested for variance homogeneity and normality of distributions of residues. If necessary, data were transformed into logarithms to meet variance analyses type assumptions. Linear regressions were performed to calculate the coefficient of determination (R^2) and linear correlation (Pearson Correlation test, Cor) to assess the relationships between parameters. ANOVAs (1-way, 2-way nested and 3-way nested) were used to identify significant differences ($\alpha = 0.05$) in each parameter between stations, years and the potential anthropogenic pressure gradient. When ANOVA was significant between stations, a post hoc comparison of sample means was performed using the Tukey multiple comparison test. This step makes it possible to discard the parameters that do not show significant differences between stations. Then, parameters of 2018 field campaign showing significant differences between sites were included in a first Principal Component Analysis (PCA) to explore their behavior in a continuous way (following the protocol of Martínez-Crego et al., 2008) and perform a new step for selection of parameters. On the basis on this analysis, and in order to avoid redundancy, a new set of parameters was selected, including physiological parameters on *T. testudinum* leaves (less destructive and more sensitive parameters) strongly correlated ($r \leq 0.80$) with the first component of the PCA, and with the environmental gradient of anthropogenic pressures (see Results). Some key structural parameters (density and cover of seagrasses) were also included in this selection for the implementation of a second PCA, in order to establish a first classification of sites according to seagrass meadows status. All statistical tests and analyses were performed using R v3.4.3.

3. Results

3.1. Seagrass meadow, plant, and physiological descriptors

3.1.1. Morphological, structural and landscape parameters

The characteristics of seagrass meadows are presented in Fig. 3 (all morphological data are detailed in Table S2).

Mean LAI varied from 0.20 to 3.79 and there was no significant pattern depending on years ($p > 0.05$, Fig. 3C). Most of the seagrass leaves had grazing marks (about 30 %), except samples from Marigot (1.39 %), Petite-Terre (2.91 %) and Colombier (3.54 %) (Table S2). The necrosis percentage in *T. testudinum* leaves also appeared to be station-specific with trends stable in time (Fig. 3B).

For the seagrass density and cover analysis, quadrats with values = 0 were excluded. Most of the meadows were continuous and rarely fragmented (Table S3), but the seagrass cover was spatially heterogeneous (Table S4). Mean shoot density ranged from 111.11 m^{-2} to 1173.21 m^{-2} for *T. testudinum* and values were stable across the two years of the study, except for Passe à Colas ($p < 0.01$) and Tintamarre ($p < 0.001$) (Fig. 3D). For *S. filiforme*, the mean shoot density varied between 300 and 2897.62 m^{-2} (Fig. 3E). For both species, densities were consistent with other values observed in the region (Cortés et al., 2010; van Tussenbroek et al., 2014; Chalifour, 2017; Créocean, 2017).

3.1.2. Stable isotopic ratio, nutrients and ETs contents in seagrass tissues

Although leaves and rhizomes were both analyzed, we choose to present the results for leaves only. The values obtained for rhizomes are available as supplementary data in Tables S8 and S9.

$\delta^{13}C$ values in *T. testudinum* leaves varied between -12.50 and -6.60 ‰. Leaves and rhizomes values appeared strongly correlated ($R^2 = 0.61$, $p < 0.001$, Fig. 4A). $\delta^{15}N$ ranged from -2.73 to 9.41 ‰ in *T. testudinum* leaves (Fig. 4B). There was no significant difference between the two years of sampling for isotopic ratio. The correlation between the two parts of the plant was also strongly positive and significant for $\delta^{15}N$ ($R^2 = 0.54$, $p < 0.001$, Fig. S1). For stations located in low-impact areas, the $\delta^{15}N$ signal was relatively stable (mean = 1.40 ± 0.71 ‰) whereas it was more heterogeneous for the most impacted stations (mean = 3.89 ± 2.27 ‰). The overall range of $\delta^{15}N$ in *S. filiforme* leaves was also large (from -1.62 to 6.56 ‰, Table S9) and strongly correlated to $\delta^{15}N$ content in *T. testudinum* leaves ($R^2 = 0.56$, $p < 0.001$, Fig. S2).

Nitrogen content in *T. testudinum* leaves varied from 1.20 to 2.80 % and was relatively stable across the two years, except in samples from Colombier and Marigot (Fig. 4C, $p < 0.001$). The N values in leaves of *T. testudinum* (Fig. 4C) and *S. filiforme* ($p < 0.001$, Table S9) were significantly larger in the remote island of Petite-Terre compared to other stations located further away from anthropogenic influence such as Tintamarre Island and Passe à Colas. For *T. testudinum*, N was on average 41 % higher in leaves than in rhizomes. Phosphorus contents in *T. testudinum* leaves were between 0.11 and 0.34 % and were also stable across years, except in samples from Christophe Islet and Marigot ($p < 0.001$, Fig. 4E).

Most of the targeted ETs in *T. testudinum* showed spatial variations (Fig. 4). Mn values in leaves generally increased across the gradient (min: 6.08 $\mu g.g^{-1}$, max: 398.76 $\mu g.g^{-1}$; Fig. 4F, Table S6) and were consistent between the two sampling periods, except in samples from Petit-cul-de sac, Christophe Islet, Galion and Marigot ($p < 0.001$). Fe (Fig. 4G) and Zn (Fig. 4H) contents in leaves were stable across the two years but showed large and significant differences between the least impacted

and the most impacted stations (e.g. Tintamarre *vs.* Marigot) (Fig. 4G, Fig. 4H and Table S6). Our results also highlighted that Mn, Ni, Cd and Pb contents were more abundant in leaves than in rhizomes (Fig. 4F, Fig. 4G, Tables S8 and S10).

3.1.3. Benthic associated fauna, flora and epiphyte communities

The assessment of the seagrass associated communities is synthesized in Table 3 and detailed data is available in Tables S11, S12 and S13. Benthic macrofauna assemblages and abundance varied significantly across stations and islands (Table 3, Table S13). Some stations had a higher abundance of grazers, such as at Bouée verte, Passe à Colas and Christophe Islet (e.g. sea urchins densities were 6.35 ± 0.77, 5.00 ± 0.17 and 1.28 ± 0.20 per m^2, respectively).

Macroalgal cover (Table 3) and diversity (Table S12) varied considerably between sampling sites.

The epiphyte communities of *T. testudinum* leaves were dominated mainly by encrusting calcareous algae, which represented on average about 80 % of the epiphytes' relative cover (Table S11). The cyanobacteria relative cover on *T. testudinum* leaves was significantly higher in samples from Petite-Terre (30.29 %), Petit-cul-de sac (9.02 %) and Colombier (3.14 %) compared to other stations ($p < 0.05$). No trend emerged from total epiphyte cover across stations (Table 3) and there was no correlation between total epiphyte cover and epiphyte load ($R^2 = 0.08$).

3.2. Sites classification according to seagrass ecological status

Based on the results of the first PCA (Fig. S3), the physiological parameters of *T. testudinum* leaves that appeared the most correlated to the environmental gradient of anthropogenic pressures (N, C/N, Pb and Zn, Table S14) and some structural parameters (seagrass density and cover) were selected with the aim to implement a second PCA for site classification (Fig. 5). A similar response of metrics is observed, with the exception of *S. filiforme* density, on both sides of the first axis of the PCA (explaining 67 % of total variability), illustrating ecological status and the anthropogenic impact. The parameters positively correlated to this first component included N, Pb, and Zn contents in *T. testudinum* leaves, which were interpreted as markers of degraded meadows. In contrast, the parameters negatively correlated to the first component were considered indicators of the good ecological status of seagrass beds, including seagrass cover and C/N ratio.

4. Discussion

4.1. Spatial and temporal parameter variations

In this study, a large number of seagrass meadow parameters were measured including descriptors of the physiology, individuals, populations, landscapes and associated communities. By performing

stratified sampling and collecting data at a one-year interval, we identified several parameters responding to anthropogenic disturbances at the regional scale in the FA.

At the physiological level, we recorded a wide range of nutrients, ETs and stable isotopic ratio values in plant leaves (Fig. 4, Tables S9 and S10) and compared them to reference Caribbean data (Christiaen et al., 2014; Govers et al., 2014a).

$\delta^{13}C$ is known to respond specifically to light conditions: the augmentation of light availability is correlated to increases of the photosynthetic activity, leading to a $\delta^{13}C$ enrichment in leaves (Farquhar et al., 1989; Serrano et al., 2011). Our data revealed a similar pattern, except for Petit-Bourg and Galion (Fig. 4A), suggesting that other drivers influence $\delta^{13}C$, such as the balance between HCO_3^- and CO_2 used as an inorganic carbon source by seagrasses (Durako, 1993; Beer et al., 2002).
In other studies, $\delta^{15}N$ values in *T. testudinum* leaves range from 0.3 to 7 ‰ (with a mean around 3 ‰, Christiaen et al., 2014 for a review). With $\delta^{15}N$ values ranging up to 12.14 ‰ (Fig. 4B), our data represent the highest record for seagrasses in the area. The large range of values observed in samples from Galion could be linked to the environmental dynamics occurring at the mouth of a pond influenced by pulse watershed releases. Previous studied have shown that $\delta^{15}N$ data can be used to track the origin of nitrogen, which is possible at small spatial scales if N sources are limited (Fourqurean et al., 1997; Udy et al., 1999; Mutchler et al., 2007; Christiaen et al., 2014). Urban or agriculture wastewater typically leads to high $\delta^{15}N$ values in seagrass tissues from surrounding meadows (Schubert et al., 2013; Jones et al., 2018). In contrast, low values have been associated with unimpacted environments (Castro et al., 2007). There are several documented hypotheses, sometimes conflicting, about the intermediate trends and negative values of $\delta^{15}N$ in seagrass tissues, which, depending on the genus and latitude, can lead to confusion (Yamamuro et al., 2003; Christiaen et al., 2014; Walton et al., 2016). As observed elsewhere (Yamamuro et al., 2003), the $\delta^{15}N$ measured in seagrass leaves could be linked to a local dissolved inorganic nitrogen source (water and sediments). This seems to be supported by the spatial correlation observed between values of $\delta^{15}N$ content in *T. testudinum* and *S. filiforme.* Similarly, the correlation between nitrogen stable isotopic ratios measured in leaves and rhizomes reflects the seagrass capacity to assimilate these elements as nutrients through both leaves and rhizomes.

In our study, N values in *T. testudinum* leaves showed large variations compared to data from the literature (ranging from 0,91 % to 3,02 %, see Govers et al., 2014 for a review) and had a tendency to increase along the gradient of anthropogenic pressures (Fig. 4C). However, in some areas, the increase in nitrogen could be linked to natural phenomena such as high abundance of animals (about

10,000 individuals of the Lesser Antillean Iguana *Iguana delicatissima* for 1.5 km² are recorded at Petite-Terre island) or seabirds in protected area whose fecal matter can contributes to the seagrass meadow N enrichment as has already been documented in coral reefs (Lorrain et al., 2017; Graham et al., 2018) or mangrove ecosystems (McFadden et al., 2016). However, if the cyanobacteria presence is related to the high levels of nutrients in the water column (Hamisi et al., 2004), their presence can favour the assimilation of inorganic nitrogen in seagrass tissues (Yamamuro, 1999). This could also explain the high nitrogen values observed at stations where they occur (e.g Petite-Terre Island, Fig. 4C and Table S12). Thus, if the range of N values and their tendency to increase from the least to the most impacted locations (Fig. 4C, Table S6) suggest that N in *T. testudinum* and *S. filiforme* leaves could be considered a useful bioindicator of N water enrichment, it is important to refer to the environmental context of the study site to interpret these results. Except for Petite-Terre seagrass samples, leaf nitrogen content was around 17 % higher in *T. testudinum*, a climax species, than in *S. filiforme,* an opportunistic species (Table S9), thus confirming the higher sensitivity of the slow-growing species (Fourqurean et al., 1997).

The P content of *T. testudinum* was consistent with values from the literature ranging between 0.10 to 0.51 % (reviewed in Govers et al., 2014a), but fluctuated depending on stations (Fig. 4E). These results demonstrate that nutrients in seagrass leaves could be good bioindicators to detect eutrophication, especially in an environment limited in N, P and carbonate sediments (Duarte, 1990). This is a key finding as most of the studied seagrass meadows in the FA occur in similar environments (Table 1). It must be noted, however, that non-anthropogenic factors such as the decomposition of sargassum (van Tussenbroek et al., 2017) and the occurrence of upwelling (Hill and McQuaid, 2008) have been recorded as a potential source of nutrients for seagrass tissues, a parameter that was not assessed in the present study.

Our results highlighted that ETs in *T. testudinum* leaves could be promising bioindicators of metal pollution as shown by Zn, Pb, Fe, Cd and Mn trends across stations and pressures gradient, which were consistent with the range of values available in the literature for this species (Govers et al., 2014b and Vonk et al., 2018 for reviews). If some ETs (e.g: Cu, Fe, Zn, Ni) are naturally present in seagrass tissues, accumulation in the tissues has been linked to coastal pollution and shown to be toxic to the seagrass (Prange and Dennison, 2000). One hypothesis that could explain the significant augmentation of Mn, Cd, Fe, nutrients and $\delta^{15}N$ between the two years of sampling at the most anthropogenically-impacted station (Marigot) is the proximity of a wastewater discharge point and the significant land runoff and sediment remobilization during hurricane Irma (September 2017). A similar post-hurricane phenomenon has been described in the Mexican region (Whelan III et al.,

2011). However, the high values and trends observed at Marigot (increase in both nutrients and ETs co-occurring with seagrass decline) could reveal a worst case scenario.

Indeed, the wide range of values observed for the physiological parameters of *T. testudinum* leaves makes it possible to pre-identify thresholds for these parameters in response to anthropogenic pressures (Fig. 6), a first step towards the development of seagrass beds bioindicators adapted to the FA.

At the individual level, unlike other studies (e.g. Romero et al., 2007) in which leaf necrosis was correlated to the poor ecological status of *P. oceanica*, our data demonstrated that leaf necrosis for *T. testudinum* was not related to the gradient of anthropogenic disturbance.

Parameters related to the seagrasses' surrounding landscape, structure, and morphology appeared to be strongly dependent on the type of adjacent ecosystems (mangrove or coral reef), the proximity to rivers, as well as hydrodynamics (Carruthers et al., 2003) and grazing pressure (e.g. Valentine and Duffy, 2006 for a review). These parameters are, therefore, more linked to the site's specificities including productivity drivers (e.g. light condition), which likely explains the absence of spatial patterns in the gradient of anthropogenic disturbance selected for this study. As a consequence, it is not relevant to try and link theses landscape, structure and morphology parameters to a specific environmental disturbance, except in case of an exceptional climatic event, such as suggested by the declining trends observed for most of these parameters after hurricane Irma (September 2017) at Galion, Petit-cul-de-sac and Tintamarre.

Our study highlighted broad variations in the composition and abundance of the associated benthic macrofauna. The three sampling stations located in the largest *T. testudinum* meadow of the FA (Christophe Islet, Bouée verte and Passe à Colas) had a particularly high diversity and density of macrofauna, illustrating the importance of the meadows' ecological function, the ecosystem services they provide and the patrimonial interest they represent through their role as habitat (Boström et al., 2006; McCloskey and Unsworth, 2015).

The frequent occurrence of macroalgae can be considered informative of the eutrophic conditions and the sign of an ecological transition (Duarte, 1995; Burkholder et al., 2007), as Petit-Bourg and Galion stations.

The epiphyte communities found on the leaves of *T. testudinum* were dominated by encrusting calcareous red algae, a result similar to previous records (Carruthers et al., 2005; Corlett and Jones, 2007). Among this red calcareous cover, we did not detect any significant filamentous algae and we were unable to confirm the epiphyte biomass as an indicator of nutrient inputs.

4.2. Identification of the most relevant parameters and first sampling strategy recommendations for seagrass bed monitoring in the FA

The selection of parameters carried out after ANOVAs and PCAs analysis makes it possible to propose a set of relevant indicators for the monitoring of FA seagrass beds in a anthropisation context (Fig. 5, Fig. S1, Table S5, S6 and S14); this constitutes a preliminary step in the setting up of multimetric indicators.

To enhance the effectiveness of the protocols and minimize implementation costs, it is important to avoid redundancies and prioritize the most useful and reliable parameters according to the objectives of the monitoring. Several criteria also need to be considered, such as the promotion of non-destructive methodologies, when possible, as well as low-tech measurement methods producing results simple to interpret. In this study, we demonstrated that physiological parameters such as leaf N content and some ETs (i.e. Zn and Pb) represent promising "early warning indicators" for the monitoring of the *T. testudinum* and *S. filiforme* seagrass meadows of the FA in the context of WFD implementation. These parameters are also very useful for monitoring the evolution of the state of the seagrass meadows, which is key information for local (MPA) and national (FOB, Ifrecor) stakeholders. Indeed, seagrasses, particularly long-lived species, can record information about environmental conditions in their tissues (e.g. nutrients, pollutants, Fourqurean et al., 1997; Burkholder et al., 2007; Govers et al., 2014b; Holmer et al., 2016) and, to some extent, the health status of the seagrass (for instance the accumulation of some ETs can also affect seagrass health (Prange and Dennison, 2000). These sub-individual physiological parameters can respond quickly (e.g. decline) to specific disturbances and attest to the recovery process when the stressors are reduced (e.g. Roca et al., 2016). Our results confirm the bioindication capacity of *T. testudinum* and *S. filiforme* particularly the slow-growing *T. testudinum*. Bonanno and Raccuia (2018) also showed the ability of *H. stipulacea* to accumulate ETs. The similar responses observed in the three species, thus, points physiological parameters as promising indicators for long-term bioindication in the region; particularly when considering the tendency of Caribbean seagrass meadows to change in composition with a decline of the climax seagrass species progressively replaced by opportunistic and invasive species (van Tussenbroek et al., 2014; Smulders et al., 2017; Christianen et al., 2019).

For minimum technical constraints and to provide a good compromise between time, cost and effectiveness, we recommend that monitoring should at least include measurements of nitrogen in seagrass leaves, which are more sensitive than rhizomes and can be sampled in a less destructive way. Besides, as highlighted by our results, all the early warning indicators are very specific to a particular disturbance (Roca et al., 2016). This is why seagrass monitoring protocols should also include structural and demographic parameters, which are relevant for their integration capacity

(Burkholder et al., 2007; Roca et al., 2016) and compatible with management time scales. Therefore, estimates of seagrass cover or seagrass density, the latter being less subjective than the former especially for high canopy seagrass beds, which do not require laboratory work, are recommended as generic parameters for the classification of ecosystem structure, functions and seagrass habitats (Carruthers et al., 2003). Depending on the implementation protocol and the type of seagrass meadow, this protocol can be time-consuming in the field, but its efficiency has been proven for detecting long-term changes in seagrass communities faced with multiple disturbances (van Tussenbroek et al., 2014; Roca et al., 2016). Used alone, however, these measures are not sufficient to detect changes and implement management actions early enough to prevent the degradation of the meadows (van Katwijk et al., 2011; Roca et al., 2016), as testified by the declining trend of our most degraded station, Marigot (Vaslet and ATE, 2018; this study).

The approach used in our study (geolocated transects), as well as that of the SeagrassNet or Seagrass-Watch (permanent transects, McKenzie et al., 2001; Short et al., 2006), are more adapted to irregular seagrass meadows composed of pioneer or opportunistic species than to continuous seagrass meadows with long-lived species (e.g. van Tussenbroek et al., 2014). This approach is also useful to integrate landscape and spatial characteristics of the meadow and to inform about hydrodynamic processes (Patriquin, 1975) or physical disturbances (Demers et al., 2013; La Manna et al., 2015). Indeed, as the frequency of disturbances is likely to increase in the future, it can be expected that seagrass beds will become patchier and more heterogeneous with a higher abundance of *S. filiforme* and *H. stipulacea*, which are better adapted to future environmental conditions. During field monitoring, if time allows, information about the macroalgal communities should also be recorded, especially if nutrients and organic matter inputs are suspected and frequent algal-phase shifts have been recorded before (Montefalcone et al., 2015; van Tussenbroek et al., 2017).

Epiphyte communities are known to respond to eutrophication (Frankovich and Fourqurean, 1997; Zhang et al., 2014; Prado, 2018), but they do not seem to be very sensitive in our study area (Frankovich and Fourqurean, 1997; this study) and were therefore not considered as a key indicator.

Similarly, the seagrass sediment characteristics, morphometric, and associated macrofauna descriptors monitored in an annual base (as they are in several FA monitoring) did not appear essential in view of our results and the literature. These parameters can be useful if measured at the start of the monitoring program and with less frequency.

In case of multiple disturbances, the most useful strategy for identifying drivers of change is to have a holistic approach of seagrass data that is directly related to the environmental conditions (McMahon et al., 2013; Kilminster et al., 2015; Roca et al., 2016).

We recognize that more information on timeframes may be needed to better understand local conditions and to validate the selection of candidate parameters. Nevertheless at this time, when implementing public policies in the FA, the best option for monitoring seagrass beds (including long term, impact and management of effective strategies) is to combine, at least, parameters from physiological (early warning environmental change indicators) and structural (related to the integrity of the system) levels. To date, the WFD and MPA monitoring protocols implemented in the FA are relatively similar to each other and include only structural parameters (GTN Herbiers Ifrecor-DCE, 2017 for a review). While the addition of early warning indicators is justified for the regulatory seagrass beds monitoring (WFD), leading change can be difficult for MPA managers whose time and resources are often limited. They are, however, very concerned about identifying drivers of ecosystem change to take the most effective management actions locally. One solution could be to select the most relevant parameters in each category and adapt the sampling frequency, but the optimal solution would be to share seagrass monitoring actions between the various stakeholders to meet each program's objectives fully. Bringing together human and financial resources across the FA regional public policies would be strategically relevant, particularly when budgets are limited, and would make it easier to meet the needs of national reporting actions in the framework of Ifrecor and FOB.

4.3. Site classification

Our final PCA provides the first site classification based on the ecological status of seagrass meadows (Fig. 5).

The less impacted seagrass meadows were Tintamarre and Passe à Colas, which are located offshore, and relatively far from any source of disturbance (Fig. 5, Table S1). This high score can be further strengthened for Passe à Colas by the presence of local high abundance and diversity of fauna assemblages (Table 3, Table S13), attesting for the heritage value of such an ecosystem (Hyman et al., 2019). In contrast, identifying the most eutrophic and polluted seagrass beds allow us to raise an alert on their health status. Indeed, the station with the lowest rate, Marigot, seems to be in a transition to a potential collapse, which could have dramatic consequences for the area: without its seagrass meadow for water purification and sediment accretion, the ecological status of the bay could become even worse. An urgent effort to improve the water treatment system for this island, which is under high pressure from tourism (terrestrial and nautical with high environmental impact), is needed to ensure seagrass meadows conservation and the ecosystem services produced.

5. Conclusion

With continuous degradation of environmental conditions and changes in habitat structure, it is now essential to assess the status of the Caribbean seagrass meadows and the water quality to

implement proper management actions and strengthen the preservation of seagrass beds. To improve seagrass monitoring at the regional scale in the FA, we tested a panel of indicators across contrasting environmental conditions. We have identified 7 parameters providing particularly relevant information on the health of seagrass beds and water quality. For the first time, we provide a full description of several seagrass meadows in the FA which considerably improves the current understanding of how they function. We recorded a broad range of ecological status that will serve to determine thresholds of change and to identify reference sites. Moreover, quantification of anthropogenic pressures would improve the selection of parameters used for site classification. The next step of the project will be the aggregation of parameters in an integrated toolbox of indicators and protocols. A new data set, including another FA territory (Martinique Island) will be used to validate these indicators, a step that will be carried out in consultation with the relevant scientists and managers.

CRediT authorship contribution statement

F. Kerninon: Funding acquisition, project administration, conceptualization, investigation, formal analysis, writing. **C. Hellio**, **C.E. Payri** and **J-P. Maréchal**: review & editing, supervision. **J. Chalifour**, **S. Gréaux**, **S. Mège**, **J. Anthanase**, **S. Cordonnier, M-L. Rouget**, **E. Lorre** and **T. Uboldi**: Investigation. **O. Monnier**: Project administration, review & editing. **F. Le Loc'h** and **T. Alcoverro**: review & editing.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Arthur, R., Babu, Y., Lobo, A. S., Iyer, V., Moses, K. S., Santhankrishnan, M., Sen, S., Alcoverro, T. M., 2008. Scraping the bottom: Monitoring human impacts on benthic ecosystems of Tamil Nadu. UNDP/UNTRS and NCF. Chennai, 218 pages.

Beer, S., Björk, M., Hellblom, F., Axelsson, L., 2002. Inorganic carbon utilization in marine angiosperms (seagrasses). https://doi.org/10.1071/PP01185

Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Process. Landforms 26, 1237–1248. https://doi.org/10.1002/esp.261

Bonanno, G., Raccuia, S.A., 2018. Seagrass *Halophila stipulacea*: Capacity of accumulation and biomonitoring of trace elements. Science of The Total Environment 633, 257–263. https://doi.org/10.1016/j.scitotenv.2018.03.196

Boström, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science 68, 383–403. https://doi.org/10.1016/j.ecss.2006.01.026

Bouchon, C., Bouchon-Navarro, Y., Louis, M., Portillo, P., 2003. Manuel technique d'étude des récifs coralliens de la région Caraïbe. Université des Antilles et de la Guyane, 56 pages.

Burkholder, J.M., Tomasko, D.A., Touchette, B.W., 2007. Seagrasses and eutrophication. Journal of Experimental Marine Biology and Ecology 350, 46–72. https://doi.org/10.1016/j.jembe.2007.06.024

CARICOMP., 1994. CARICOMP Methods Manual-Level I. Manual of Methods for Mapping and Monitoring of Physical and Biological Parameters in the Coastal Zone of the Caribbean. CARICOMP Data Management Centre, University of the West Indies, Mona, Kingston, Jamaica.

Carruthers, T., Jacome, G., Barnes, P., 2003. Seagrass habitats of bocas del Toro, Panama. A balance between river, mangrove and coral influences. 31st scientific meeting of the association of marine laboratories of the Caribbean, Trinidad, Poster.

Carruthers, T.J.B., van Tussenbroek, B.I., Dennison, W.C., 2005. Influence of submarine springs and wastewater on nutrient dynamics of Caribbean seagrass meadows. Estuarine, Coastal and Shelf Science 64, 191–199. https://doi.org/10.1016/j.ecss.2005.01.015

Castro, P., Valiela, I., Freitas, H., 2007. Eutrophication in Portuguese estuaries evidenced by $\delta^{15}N$ of macrophytes. Mar. Ecol. Prog. Ser. 351, 43–51. https://doi.org/10.3354/meps07173

Chalifour, J., 2017. Suivi de l'état de santé des communautés coralliennes et des herbiers de la RNN de Saint-Martin, État des lieux 2016 et évolution 2007-2016, 22 pages + annexes.

Christiaen, B., Bernard, R.J., Mortazavi, B., Cebrian, J., Ortmann, A.C., 2014. The degree of urbanization across the globe is not reflected in the $\delta^{15}N$ of seagrass leaves. Marine Pollution Bulletin 83, 440–445. https://doi.org/10.1016/j.marpolbul.2013.06.024

Christianen, M.J.A., Smulders, F.O.H., Engel, M.S., Nava, M.I., Willis, S., Debrot, A.O., Palsbøll, P.J., Vonk, J.A., Becking, L.E., 2019. Megaherbivores may impact expansion of invasive seagrass in the Caribbean. J Ecol 107, 45–57. https://doi.org/10.1111/1365-2745.13021

Coleman, V.L., Burkholder, J.M., 1994. Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. Journal of Experimental Marine Biology and Ecology 179, 29–48. https://doi.org/10.1016/0022-0981(94)90015-9

Corlett, H., Jones, B., 2007. Epiphyte communities on *Thalassia testudinum* from Grand Cayman, British West Indies: Their composition, structure, and contribution to lagoonal sediments. Sedimentary Geology 194, 245–262. https://doi.org/10.1016/j.sedgeo.2006.06.010

Cortés, J., Fonseca, A.C., Nivia-Ruiz, J., Nielsen-Muñoz, V., Samper-Villarreal, J., Salas, E., Martínez, S., Zamora-Trejos, P., 2010. Monitoring coral reefs, seagrasses and mangroves in Costa Rica (CARICOMP). Rev. Biol. Trop. 58 Suppl 3, 1–22.

Créocean 2017. Suivi de l'état de santé des Réserves Naturelles Marines de Guadeloupe et Saint-Barthélemy - État des lieux 2016 et évolution 2007-2016, 114 pages.

Cunha, A.H., Marbá, N.N., Katwijk, M.M. van, Pickerell, C., Henriques, M., Bernard, G., Ferreira, M.A., Garcia, S., Garmendia, J.M., Manent, P., 2012. Changing Paradigms in Seagrass Restoration. Restoration Ecology 20, 427–430. https://doi.org/10.1111/j.1526-100X.2012.00878.

Demers, M.-C.A., Davis, A.R., Knott, N.A., 2013. A comparison of the impact of 'seagrass-friendly' boat mooring systems on *Posidonia australis*. Marine Environmental Research 83, 54–62. https://doi.org/10.1016/j.marenvres.2012.10.010

Diez, S.M., Patil, P.G., Morton, J., Rodriguez, D.J., Vanzella, A., Robin, D.V., Maes, T., Corbin, C., 2019. Marine Pollution in the Caribbean: Not a Minute to Waste. Washington, D.C.: World Bank Group.

Duarte, C., 1990. Seagrass nutrient content. Mar. Ecol. Prog. Ser. 67, 201–207. https://doi.org/10.3354/meps067201

Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 87–112. https://doi.org/10.1080/00785236.1995.10422039

Durako, M.J., 1993. Photosynthetic utilization of CO2(aq) and HCO 3 - in *Thalassia testudinum* (Hydrocharitaceae). Marine Biology 115, 373–380. https://doi.org/10.1007/BF00349834

European Commission., 2000. Directive 2000/60/EC of the European Parliament and of the council of 23 october 2000 establishing a framework for community action in the field of water policy, 72 pages.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon Isotope Discrimination and Photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40, 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Fourqurean, J.W., Moore, T.O., Fry, B., Hollibaugh, J.T., 1997. Spatial and temporal variation in C:N:P ratios, $\delta^{15}N$, and $\delta^{13}C$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. Marine Ecology Progress Series 157, 147–157.

Frankovich, T.A., Fourqurean, J.W., 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. Marine Ecology Progress Series 159, 37–50.

García-Marín, P., Cabaço, S., Hernández, I., Vergara, J.J., Silva, J., Santos, R., 2013. Multi-metric index based on the seagrass *Zostera noltii* (ZoNI) for ecological quality assessment of coastal and estuarine systems in SW Iberian Peninsula. Marine Pollution Bulletin 68, 46–54. https://doi.org/10.1016/j.marpolbul.2012.12.025

Gobert, S., Sartoretto, S., Rico-Raimondino, V., Andral, B., Chery, A., Lejeune, P., Boissery, P., 2009. Assessment of the ecological status of Mediterranean French coastal waters as required by the Water Framework Directive using the *Posidonia oceanica* Rapid Easy Index: PREI. Marine Pollution Bulletin 58, 1727–1733. https://doi.org/10.1016/j.marpolbul.2009.06.012

Godet, L., Fournier, J., van Katwijk, M., Olivier, F., Le Mao, P., Retière, C., 2008. Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: a general overview and first accurate mapping. Dis. Aquat. Org. 79, 249–255. https://doi.org/10.3354/dao01897

Govers, L.L., Lamers, L.P.M., Bouma, T.J., de Brouwer, J.H.F., van Katwijk, M.M., 2014a. Eutrophication threatens Caribbean seagrasses – An example from Curaçao and Bonaire. Marine Pollution Bulletin 89, 481–486. https://doi.org/10.1016/j.marpolbul.2014.09.003

Govers, L.L., Lamers, L.P.M., Bouma, T.J., Eygensteyn, J., de Brouwer, J.H.F., Hendriks, A.J., Huijbers, C.M., van Katwijk, M.M., 2014b. Seagrasses as indicators for coastal trace metal pollution: A global meta-analysis serving as a benchmark, and a Caribbean case study. Environmental Pollution 195, 210–217. https://doi.org/10.1016/j.envpol.2014.08.028

Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., MacNeil, M.A., 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559, 250–253. https://doi.org/10.1038/s41586-018-0202-3

Green, E.P., Short, F.T., 2003. World Atlas of Seagrasses. UNEP-WCMC.

GTN Herbiers Ifrecor-DCE., 2017. Compte – rendu de l'atelier national « Herbiers » Ifrecor-DCE. Séminaire Science-gestion, 6, 7 & 10 avril 2017, Schoelcher, Martinique. Rapport UBO-AFB-Ifrecor, 26 pages + annexes.

Hamisi, M., Lyimo, T., Muruke, M., 2004. Cyanobacterial Occurrence and Diversity in Seagrass Meadows in Coastal Tanzania. West. Indian Ocean J. Mar. Sci. 3. https://doi.org/10.4314/wiojms.v3i2.28455

Hill, J.M., McQuaid, C.D., 2008. δ13C and δ^{15}N biogeographic trends in rocky intertidal communities along the coast of South Africa: Evidence of strong environmental signatures. Estuarine, Coastal and Shelf Science 80, 261–268. https://doi.org/10.1016/j.ecss.2008.08.005

Holmer, M., Georgiev, V.G., Karamfilov, V.K., 2016. Effects of point source of untreated sewage waters on seagrass (*Zostera marina* and *Z. noltii*) beds in the South-Western Black Sea. Aquatic Botany 133, 1–9. https://doi.org/10.1016/j.aquabot.2016.05.001

Hyman, A.C., Frazer, T.K., Jacoby, C.A., Frost, J.R., Kowalewski, M., 2019. Long-term persistence of structured habitats: seagrass meadows as enduring hotspots of biodiversity and faunal stability. Proceedings of the Royal Society B: Biological Sciences 286, 20191861. https://doi.org/10.1098/rspb.2019.1861

Ifrecor, 2016. Etat des récifs coralliens et des écosystèmes associés des outre-mer français en 2015, 168 pages.

Jiang, Z., Zhao, C., Yu, S., Liu, S., Cui, L., Wu, Y., Fang, Y., Huang, X., 2019. Contrasting root length, nutrient content and carbon sequestration of seagrass growing in offshore carbonate and onshore terrigenous sediments in the South China Sea. Science of The Total Environment 662, 151–159. https://doi.org/10.1016/j.scitotenv.2019.01.175

Jones, B.L., Cullen-Unsworth, L.C., Unsworth, R.K.F., 2018. Tracking Nitrogen Source Using δ^{15}N Reveals Human and Agricultural Drivers of Seagrass Degradation across the British Isles. Front Plant Sci 9. https://doi.org/10.3389/fpls.2018.00133

Katwijk, M.M. van, Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S., Meinesz, A., Nakaoka, M., O'Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A., Verduin, J.J., 2016. Global analysis of seagrass restoration: the importance of large-scale planting. Journal of Applied Ecology 53, 567–578. https://doi.org/10.1111/1365-2664.12562

Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., O'Brien, K.R., Lyons, M., Ferguson, A., Maxwell, P., Glasby, T., Udy, J., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. Science of The Total Environment 534, 97–109. https://doi.org/10.1016/j.scitotenv.2015.04.061

La Manna, G., Donno, Y., Sarà, G., Ceccherelli, G., 2015. The detrimental consequences for seagrass of ineffective marine park management related to boat anchoring. Marine Pollution Bulletin 90, 160–166. https://doi.org/10.1016/j.marpolbul.2014.11.001

Legg, C.J., Nagy, L., 2006. Why most conservation monitoring is, but need not be, a waste of time. Journal of Environmental Management 78, 194–199. https://doi.org/10.1016/j.jenvman.2005.04.016

Lopez y Royo, C., Casazza, G., Pergent-Martini, C., Pergent, G., 2010. A biotic index using the seagrass *Posidonia oceanica* (BiPo), to evaluate ecological status of coastal waters. Ecological Indicators 10, 380–389. https://doi.org/10.1016/j.ecolind.2009.07.005

Lorrain, A., Houlbrèque, F., Benzoni, F., Barjon, L., Tremblay-Boyer, L., Menkes, C., Gillikin, D.P., Payri, C., Jourdan, H., Boussarie, G., Verheyden, A., Vidal, E., 2017. Seabirds supply nitrogen to reef-building corals on remote Pacific islets. Sci Rep 7, 3721. https://doi.org/10.1038/s41598-017-03781-y

Madden, C.J., Rudnick, D.T., McDonald, A.A., Cunniff, K.M., Fourqurean, J.W., 2009. Ecological indicators for assessing and communicating seagrass status and trends in Florida Bay. Ecological Indicators, Indicators for Everglades Restoration 9, S68–S82. https://doi.org/10.1016/j.ecolind.2009.02.004

Marbà, N., Krause-Jensen, D., Alcoverro, T., Birk, S., Pedersen, A., Neto, J.M., Orfanidis, S., Garmendia, J.M., Muxika, I., Borja, A., Dencheva, K., Duarte, C.M., 2013. Diversity of European seagrass indicators: patterns within and across regions. Hydrobiologia 704, 265–278. https://doi.org/10.1007/s10750-012-1403-7

Maréchal, J.-P., Meesters, E.H., Vedie, F., Hellio, C., 2013. Occurrence of the alien seagrass *Halophila stipulacea* in Martinique (French West Indies). Mar. Biodivers. Rec. 6, e127. https://doi.org/10.1017/S1755267213000961

Martínez-Crego, B., Alcoverro, T., Romero, J., 2010. Biotic indices for assessing the status of coastal waters: a review of strengths and weaknesses. J. Environ. Monit. 12, 1013. https://doi.org/10.1039/b920937a

Martínez-Crego, B., Vergés, A., Alcoverro, T., Romero, J., 2008. Selection of multiple seagrass indicators for environmental biomonitoring. Mar. Ecol. Prog. Ser. 361, 93–109. https://doi.org/10.3354/meps07358

McCloskey, R.M., Unsworth, R.K.F., 2015. Decreasing seagrass density negatively influences associated fauna. PeerJ 3, e1053. https://doi.org/10.7717/peerj.1053

McFadden, T.N., Kauffman, J.B., Bhomia, R.K., 2016. Effects of nesting waterbirds on nutrient levels in mangroves, Gulf of Fonseca, Honduras. Wetlands Ecol Manage 24, 217–229. https://doi.org/10.1007/s11273-016-9480-4

McMahon, K., Collier, C., Lavery, P.S., 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecological Indicators 30, 7–15. https://doi.org/10.1016/j.ecolind.2013.01.030

Miloslavich, P., Díaz, J.M., Klein, E., Alvarado, J.J., Díaz, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J.J., Weil, E., Cortés, J., Bastidas, A.C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A., Ortiz, M., 2010. Marine Biodiversity in the Caribbean: Regional Estimates and Distribution Patterns. PLoS ONE 5, e11916. https://doi.org/10.1371/journal.pone.0011916

McKenzie, L.J., Campbell, S.J., Roder, C.A., 2001. Seagrass-Watch: manual for mapping and monitoring seagrass resources by community (citizen) volunteers. Queensland Department of Primary Industries, Cairns, 94 pages.

MEDDTL., 2012. Ministère de l'Ecologie, du Développement durable, des transports et du Logement, Agence des aires marines protégées, (Mars 2012), Stratégie nationale pour la création et la gestion des aires marines protégées, 89 pages.

Montefalcone, M., Vassallo, P., Gatti, G., Parravicini, V., Paoli, C., Morri, C., Bianchi, C.N., 2015. The exergy of a phase shift: Ecosystem functioning loss in seagrass meadows of the Mediterranean Sea. Estuarine, Coastal and Shelf Science 156, 186–194. https://doi.org/10.1016/j.ecss.2014.12.001

Mtwana Nordlund, L., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass Ecosystem Services and Their Variability across Genera and Geographical Regions. PLoS ONE 11, e0163091. https://doi.org/10.1371/journal.pone.0163091

Mutchler, T., Dunton, K.H., Townsend-Small, A., Fredriksen, S., Rasser, M.K., 2007. Isotopic and elemental indicators of nutrient sources and status of coastal habitats in the Caribbean Sea, Yucatan Peninsula, Mexico. Estuarine, Coastal and Shelf Science 74, 449–457. https://doi.org/10.1016/j.ecss.2007.04.005

Neto, J.M., Barroso, D.V., Barría, P., 2013. Seagrass Quality Index (SQI), a Water Framework Directive compliant tool for the assessment of transitional and coastal intertidal areas. Ecological Indicators 30, 130–137. https://doi.org/10.1016/j.ecolind.2013.02.015

O'Brien, K.R., Waycott, M., Maxwell, P., Kendrick, G.A., Udy, J.W., Ferguson, A.J.P., Kilminster, K., Scanes, P., McKenzie, L.J., McMahon, K., Adams, M.P., Samper-Villarreal, J., Collier, C., Lyons, M., Mumby, P.J., Radke, L., Christianen, M.J.A., Dennison, W.C., 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Marine Pollution Bulletin 134, 166–176. https://doi.org/10.1016/j.marpolbul.2017.09.006

Oliva, S., Mascaró, O., Llagostera, I., Pérez, M., Romero, J., 2012. Selection of metrics based on the seagrass *Cymodocea nodosa* and development of a biotic index (CYMOX) for assessing ecological status of coastal and transitional waters. Estuarine, Coastal and Shelf Science 114, 7–17. https://doi.org/10.1016/j.ecss.2011.08.022

Orlando-Bonaca, M., Francé, J., Mavrič, B., Grego, M., Lipej, L., Flander-Putrle, V., Šiško, M., Falace, A., 2015. A new index (MediSkew) for the assessment of the *Cymodocea nodosa* (Ucria) Ascherson meadow's status. Marine Environmental Research 110, 132–141. https://doi.org/10.1016/j.marenvres.2015.08.009

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A Global Crisis for Seagrass Ecosystems. BioScience 56, 987. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Patriquin, D.G., 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquatic Botany 1, 163–189. https://doi.org/10.1016/0304-3770(75)90021-2

Pillet, V., Duvat, V.K.E., Krien, Y., Cécé, R., Arnaud, G., Pignon-Mussaud, C., 2019. Assessing the impacts of shoreline hardening on beach response to hurricanes: Saint-Barthélemy, Lesser Antilles. Ocean & Coastal Management 174, 71–91. https://doi.org/10.1016/j.ocecoaman.2019.03.021

Prado, P., 2018. Seagrass epiphytic assemblages are strong indicators of agricultural discharge but weak indicators of host features. Estuarine, Coastal and Shelf Science 204, 140–148. https://doi.org/10.1016/j.ecss.2018.02.026

Prado, P., Romero, J., Alcoverro, T., 2010. Nutrient status, plant availability and seasonal forcing mediate fish herbivory in temperate seagrass beds. Mar. Ecol. Prog. Ser. 409, 229–239. https://doi.org/10.3354/meps08585

Prange, J.A., Dennison, W.C., 2000. Physiological Responses of Five Seagrass Species to Trace Metals. Marine Pollution Bulletin 41, 327–336. https://doi.org/10.1016/S0025-326X(00)00126-0

Roca, G., Alcoverro, T., Krause-Jensen, D., Balsby, T.J.S., van Katwijk, M.M., Marbà, N., Santos, R., Arthur, R., Mascaró, O., Fernández-Torquemada, Y., Pérez, M., Duarte, C.M., Romero, J., 2016. Response of seagrass indicators to shifts in environmental stressors: A global review and management synthesis. Ecological Indicators 63, 310–323. https://doi.org/10.1016/j.ecolind.2015.12.007

Romero, J., Martínez-Crego, B., Alcoverro, T., Pérez, M., 2007. A multivariate index based on the seagrass *Posidonia oceanica* (POMI) to assess ecological status of coastal waters under the water framework directive (WFD). Marine Pollution Bulletin 55, 196–204. https://doi.org/10.1016/j.marpolbul.2006.08.032

Ruiz-Frau, A., Gelcich, S., Hendriks, I.E., Duarte, C.M., Marbà, N., 2017. Current state of seagrass ecosystem services: Research and policy integration. Ocean & Coastal Management 149, 107–115. https://doi.org/10.1016/j.ocecoaman.2017.10.004

Santos, C.B. de los, Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C.M., Katwijk, M.M. van, Pérez, M., Romero, J., Sánchez-Lizaso, J.L., Roca, G., Jankowska, E., Pérez-Lloréns, J.L., Fournier, J., Montefalcone, M., Pergent, G., Ruiz, J.M., Cabaço, S., Cook, K., Wilkes, R.J., Moy, F.E., Trayter, G.M.-R., Arañó, X.S., Jong, D.J. de, Fernández-Torquemada, Y., Auby, I., Vergara,

J.J., Santos, R., 2019. Recent trend reversal for declining European seagrass meadows. Nat Commun 10, 1–8. https://doi.org/10.1038/s41467-019-11340-4

Schubert, P.R., Karez, R., Reusch, T.B.H., Dierking, J., 2013. Isotopic signatures of eelgrass (*Zostera marina* L.) as bioindicator of anthropogenic nutrient input in the western Baltic Sea. Marine Pollution Bulletin 72, 64–70. https://doi.org/10.1016/j.marpolbul.2013.04.029

Serrano, O., Mateo, M.Á., Renom, P., 2011. Seasonal response of *Posidonia oceanica* to light disturbances. https://doi.org/10.3354/meps08955

Short, F.T, McKenzie, L.J., Coles, R.G., Vidler, K.P., Gaeckle, J.L., 2006. SeagrassNet. Manual for Scientific Monitoring of Seagrass Habitat, Worldwide Edition. University of New Hampshire Publication, 75 pages.

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Kenworthy, W.J., Nafie, Y.A.L., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Tussenbroek, B. van, Vergara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. BIOL. CONSERV. 144, 1961–1971. https://doi.org/10.1016/j.biocon.2011.04.010

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23, 17–27. https://doi.org/10.1017/S0376892900038212

Smulders, F.O.H., Vonk, J.A., Engel, M.S., Christianen, M.J.A., 2017. Expansion and fragment settlement of the non-native seagrass *Halophila stipulacea* in a Caribbean bay. Marine Biology Research 13, 967–974. https://doi.org/10.1080/17451000.2017.1333620

Udy, J., Dennison, W., Lee Long, W., McKenzie, L., 1999. Responses of seagrass to nutrients in the Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 185, 257–271. https://doi.org/10.3354/meps185257

Uku, J., Björk, M., 2001. The distribution of epiphytic algae on three Kenyan seagrass species. South African Journal of Botany 67, 475–482. https://doi.org/10.1016/S0254-6299(15)31166-2

Valentine, J.F., Duffy, J.E., 2006. The Central Role of Grazing in Seagrass Ecology, in: LARKUM, A.W.D., ORTH, R.J., DUARTE, C.M. (Eds.), SEAGRASSES: BIOLOGY, ECOLOGYAND CONSERVATION. Springer Netherlands, Dordrecht, pp. 463–501. https://doi.org/10.1007/978-1-4020-2983-7_20

van Katwijk, M., Vergeer, L., Schmitz, G., Roelofs, J., 1997. Ammonium toxicity in eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 157, 159–173. https://doi.org/10.3354/meps157159

van Katwijk, M.M., van der Welle, M.E.W., Lucassen, E.C.H.E.T., Vonk, J.A., Christianen, M.J.A., Kiswara, W., al Hakim, I.I., Arifin, A., Bouma, T.J., Roelofs, J.G.M., Lamers, L.P.M., 2011. Early warning indicators for river nutrient and sediment loads in tropical seagrass beds: a

benchmark from a near-pristine archipelago in Indonesia. Mar. Pollut. Bull. 62, 1512–1520. https://doi.org/10.1016/j.marpolbul.2011.04.007

van Tussenbroek, B.I., Cortés, J., Collin, R., Fonseca, A.C., Gayle, P.M.H., Guzmán, H.M., Jácome, G.E., Juman, R., Koltes, K.H., Oxenford, H.A., Rodríguez-Ramirez, A., Samper-Villarreal, J., Smith, S.R., Tschirky, J.J., Weil, E., 2014. Caribbean-Wide, Long-Term Study of Seagrass Beds Reveals Local Variations, Shifts in Community Structure and Occasional Collapse. PLoS ONE 9, e90600. https://doi.org/10.1371/journal.pone.0090600

van Tussenbroek, B.I., Hernández Arana, H.A., Rodríguez-Martínez, R.E., Espinoza-Avalos, J., Canizales-Flores, H.M., González-Godoy, C.E., Barba-Santos, M.G., Vega-Zepeda, A., Collado-Vides, L., 2017. Severe impacts of brown tides caused by Sargassum spp. on near-shore Caribbean seagrass communities. Marine Pollution Bulletin 122, 272–281. https://doi.org/10.1016/j.marpolbul.2017.06.057

van Tussenbroek, B.I., Lot, A., Universidad Nacional Autónoma de México (UNAM), Instituto de Ciencias del Mar y Limnología [VNV], Instituto de Biología (UNAM) [VNV], 2010. Guía de los pastos marinos tropicales del Atlántico oeste (A guide to the tropical seagrasses of the western Atlantic).

Vaslet A., ATE., 2018. Plan de gestion de la Réserve Naturelle Nationale de St-Barthélemy : 2018-2027. Partie C – Fiches actions, 194 pages.

Vonk, J.A., Smulders, F.O.H., Christianen, M.J.A., Govers, L.L., 2018. Seagrass leaf element content: A global overview. Marine Pollution Bulletin 134, 123–133. https://doi.org/10.1016/j.marpolbul.2017.09.066

Walcker, R., Laplanche, C., Herteman, M., Lambs, L., Fromard, F., 2019. Damages caused by hurricane Irma in the human-degraded mangroves of Saint Martin (Caribbean). Sci Rep 9, 18971. https://doi.org/10.1038/s41598-019-55393-3

Walton, M.E.M., Al-Maslamani, I., Haddaway, N., Kennedy, H., Castillo, A., Al-Ansari, E.S., Al-Shaikh, I., Abdel-Moati, M., Al-Yafei, M.A.A., Le Vay, L., 2016. Extreme 15N Depletion in Seagrasses. Estuaries and Coasts 39, 1709–1723. https://doi.org/10.1007/s12237-016-0103-3

Wang, M., Hu, C., Barnes, B.B., Mitchum, G., Lapointe, B., Montoya, J.P., 2019. The great Atlantic *Sargassum* belt. Science 365, 83–87. https://doi.org/10.1126/science.aaw7912

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106

Whelan III, T., Van Tussenbroek, B.I., Barba Santos, M.G., 2011. Changes in trace metals in *Thalassia testudinum* after hurricane impacts. Marine Pollution Bulletin 62, 2797–2802. https://doi.org/10.1016/j.marpolbul.2011.09.007

Willette, D.A., Ambrose, R.F., 2012. Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiota communities in the Eastern Caribbean. Aquatic Botany 103, 74–82. https://doi.org/10.1016/j.aquabot.2012.06.007

Willette, D.A., Chalifour, J., Debrot, A.O.D., Engel, M.S., Miller, J., Oxenford, H.A., Short, F.T., Steiner, S.C.C., Védie, F., 2014. Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern Caribbean. Aquatic Botany 112, 98–102. https://doi.org/10.1016/j.aquabot.2013.10.001

Wood, N., Lavery, P., 2000. Monitoring Seagrass Ecosystem Health—The Role of Perception in Defining Health and Indicators. Ecosystem Health 6, 134–148. https://doi.org/10.1046/j.1526-0992.2000.00015

Yamamuro, M., 1999. Importance of epiphytic cyanobacteria as food sources for heterotrophs in a tropical seagrass bed. Coral Reefs 18, 263–271. https://doi.org/10.1007/s003380050191

Yamamuro, M., Kayanne, H., Yamano, H., 2003. of seagrass leaves for monitoring anthropogenic nutrient increases in coral reef ecosystems. Marine Pollution Bulletin 46, 452–458. https://doi.org/10.1016/S0025-326X(02)00463-0

Yang, X., Zhang, P., Li, W., Hu, C., Zhang, X., He, P., 2018. Evaluation of four seagrass species as early warning indicators for nitrogen overloading: Implications for eutrophic evaluation and ecosystem management. Science of The Total Environment 635, 1132–1143. https://doi.org/10.1016/j.scitotenv.2018.04.227

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16, 446–453. https://doi.org/10.1016/S0169-5347(01)02205-4

Zhang, J., Huang, X., Jiang, Z., 2014. Physiological responses of the seagrass *Thalassia hemprichii* (Ehrenb.) Aschers as indicators of nutrient loading. Marine Pollution Bulletin 83, 508–515. https://doi.org/10.1016/j.marpolbul.2013.12.056

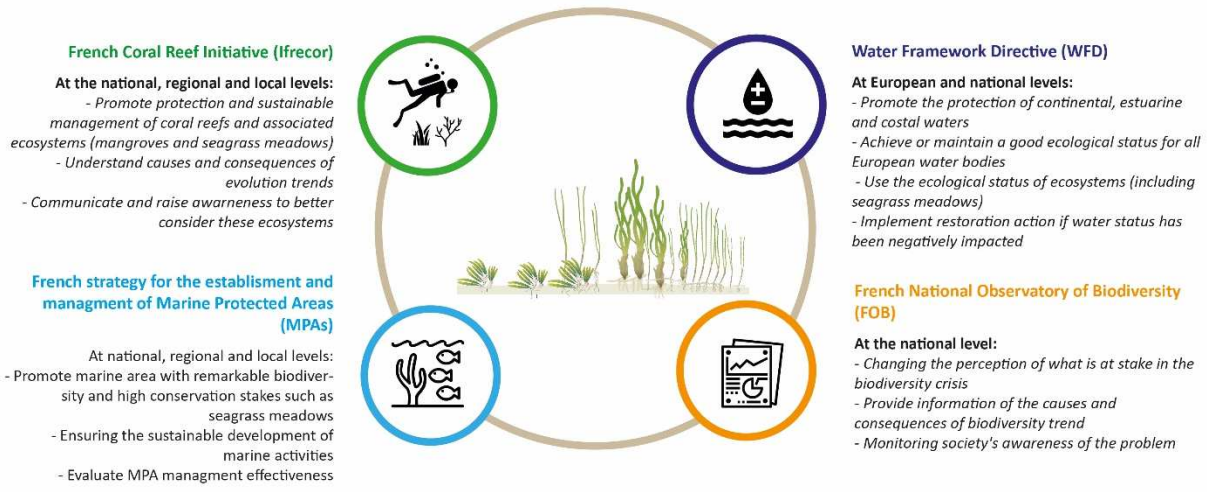

Figure 1. Schematic organization of the main public policies applying to seagrass meadows of the French Antilles.

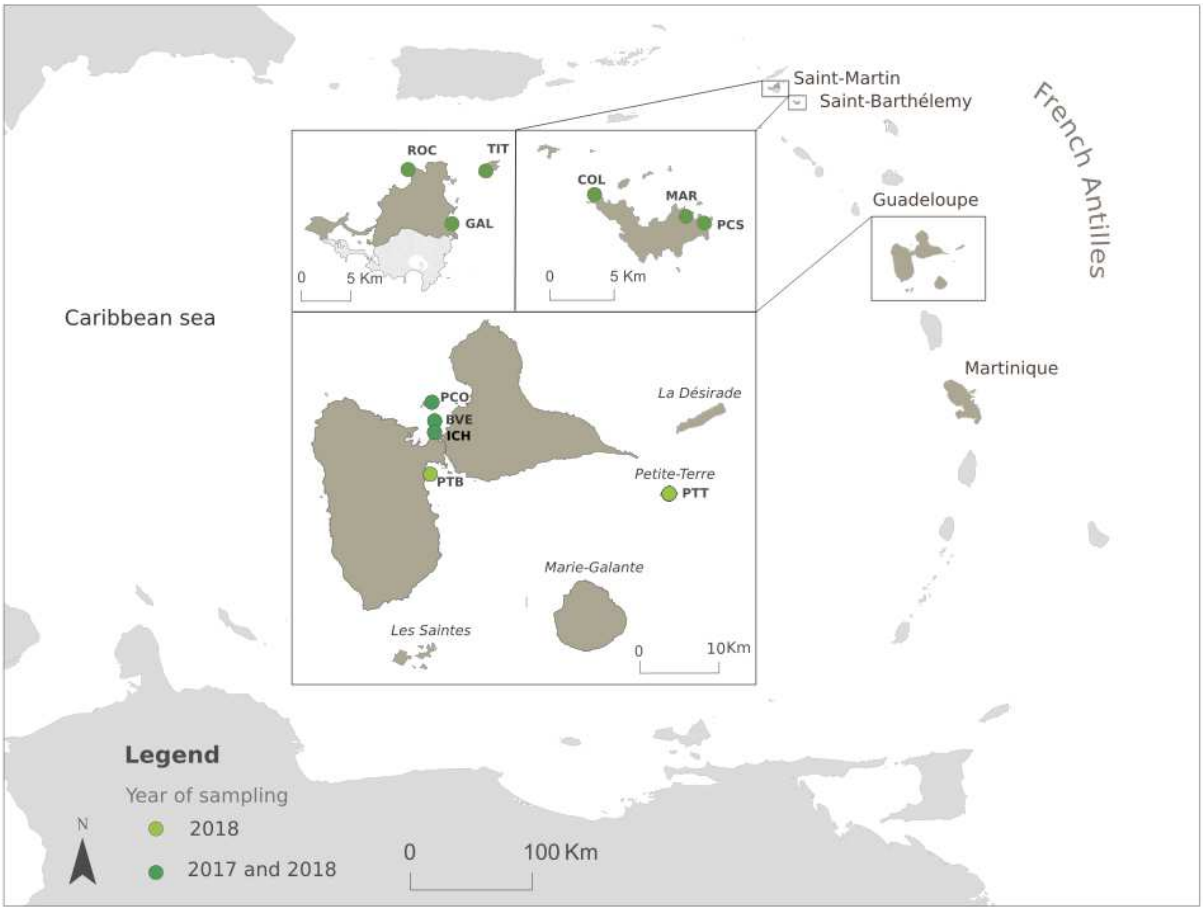

Figure 2. Map of the study area showing the 11 sampling stations across the French Antilles (in brown on the map). TIT: Tintamarre, PCO: Passe à Colas, PTT: Petite-Terre, PCS: Petit-cul-de sac, COL:

Colombier, BVE: Bouée verte, ROC: Rocher Créole, ICH: Christophe Islet, PTB: Petit-Bourg, GAL: Galion and MAR: Marigot.

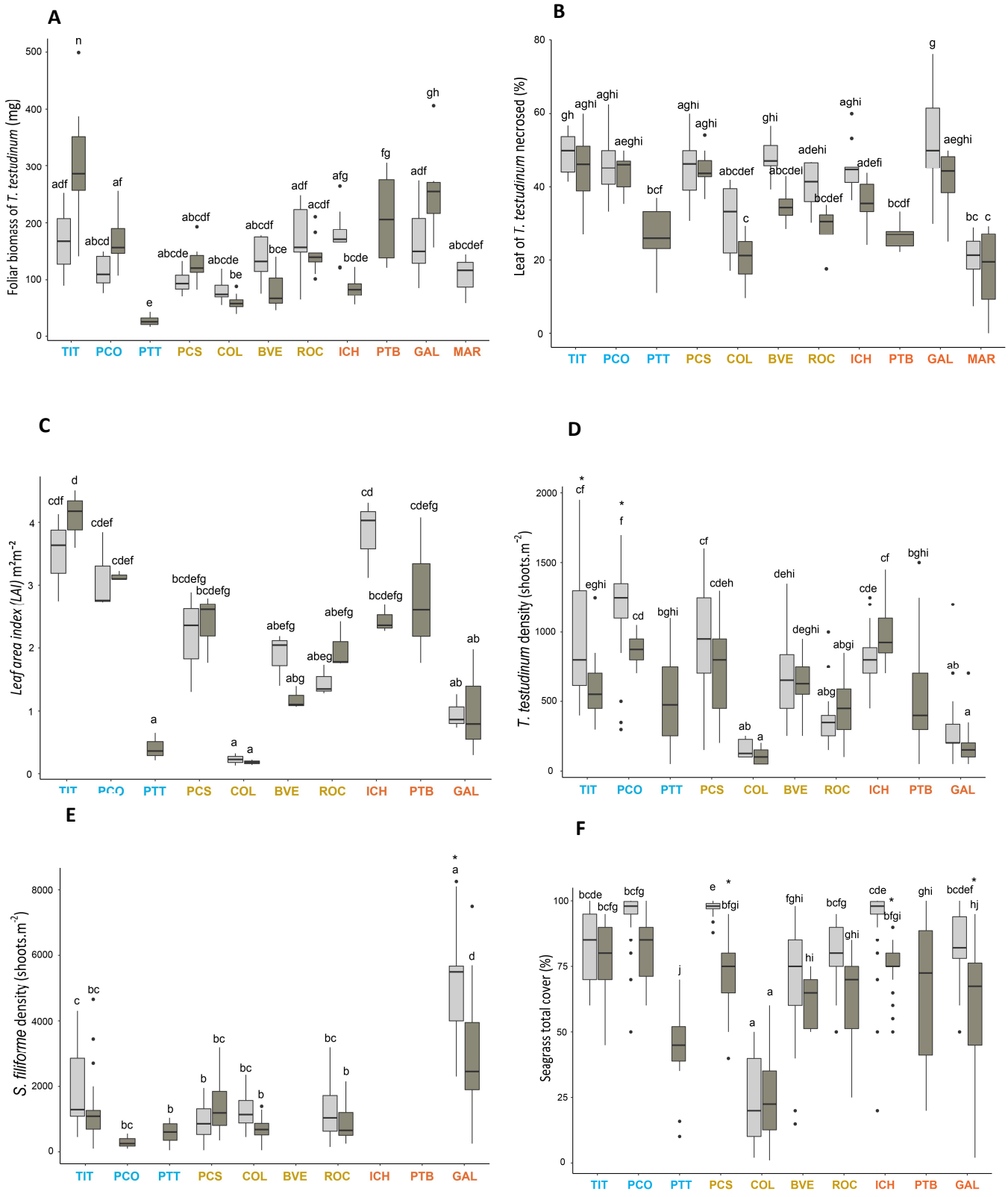

Figure 3. Morphological and structural characteristics of seagrass meadows across stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)) and year (2017 in grey and 2018 in brown).* indicates significant differences ($P < 0.05$) between the two years of sampling. Letters indicate significant differences ($P < 0.05$) across boxplots. A: Foliar biomass of *Thalassia testudinum*, B: percentage of leaves with necroses, C: Leaf area index (LAI) of *T. testudinum*, density of *T. testudinum* plants, E: density of *Syringodium filiforme* plants, E: Seagrass total cover. TIT: Tintamarre, PCO: Passe à Colas, PTT: Petite-Terre, PCS: Petit-cul-de sac, COL: Colombier, BVE: Bouée verte, ROC: Rocher Créole, ICH: Christophe Islet,

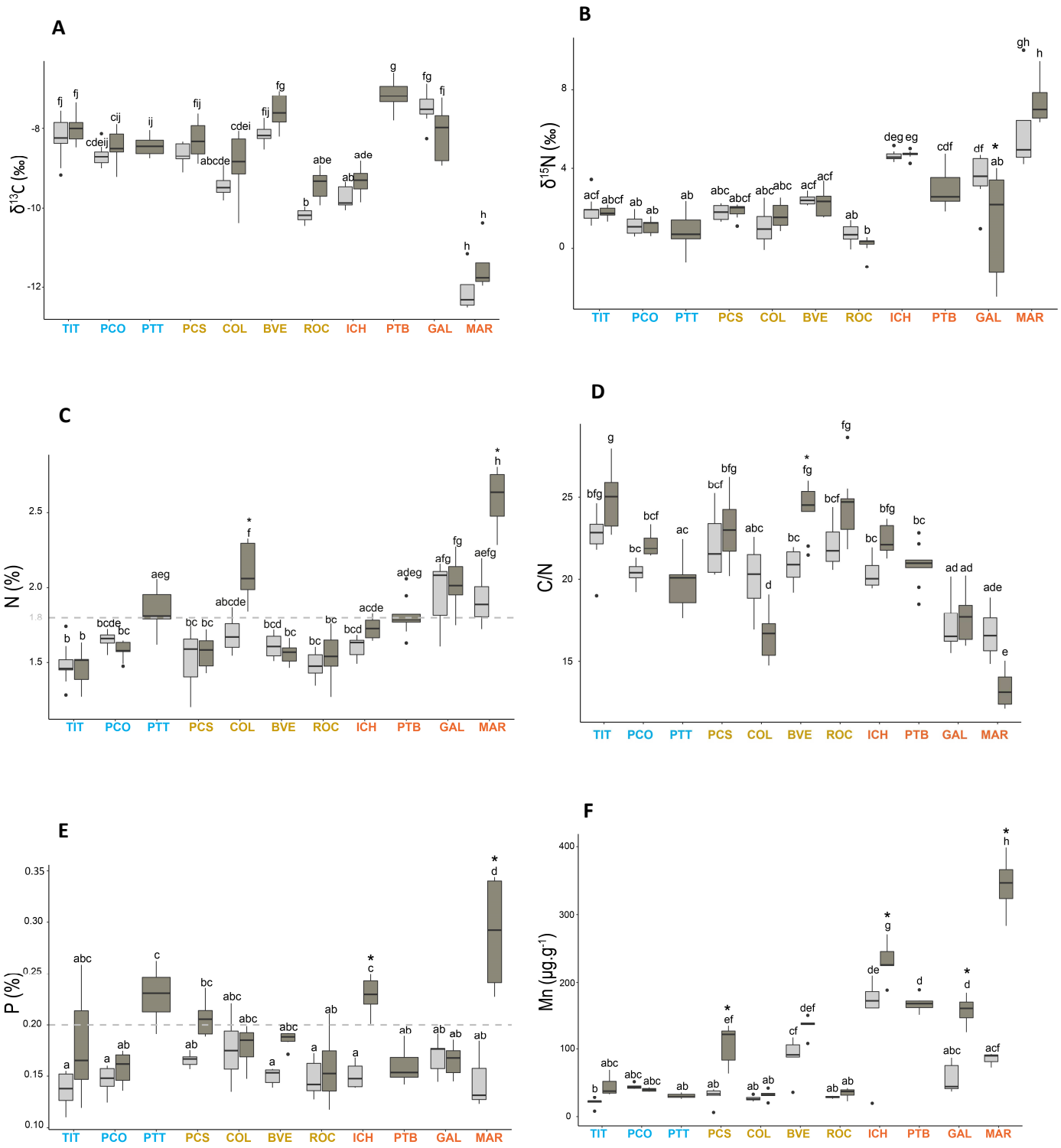

Figure 4. $\delta^{13}C$ (A), $\delta^{15}N$ (B), N (C), C/N (D), P (E), Mn (F), Fe (G), Zn (H), Cd (I) and Pb (J) contents in *T. testudinum* leaves across stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)) and year (2017 in grey and 2018 in brown).* indicates significant differences ($P < 0.05$) between the two years of sampling. Letters indicate significant differences ($P < 0.05$) across boxplots. The dotted line on Fig. 4C and Fig. 4E indicates the global threshold of nutrients limited (N < 1.8 % and P < 0.2 %) according to Duarte (1990). TIT: Tintamarre, PCO: Passe à Colas, PTT: Petite-Terre, PCS: Petit-cul-de sac, COL: Colombier, BVE: Bouée verte, ROC: Rocher Créole, ICH: Christophe Islet, PTB: Petit-Bourg, GAL: Galion and MAR: Marigot.

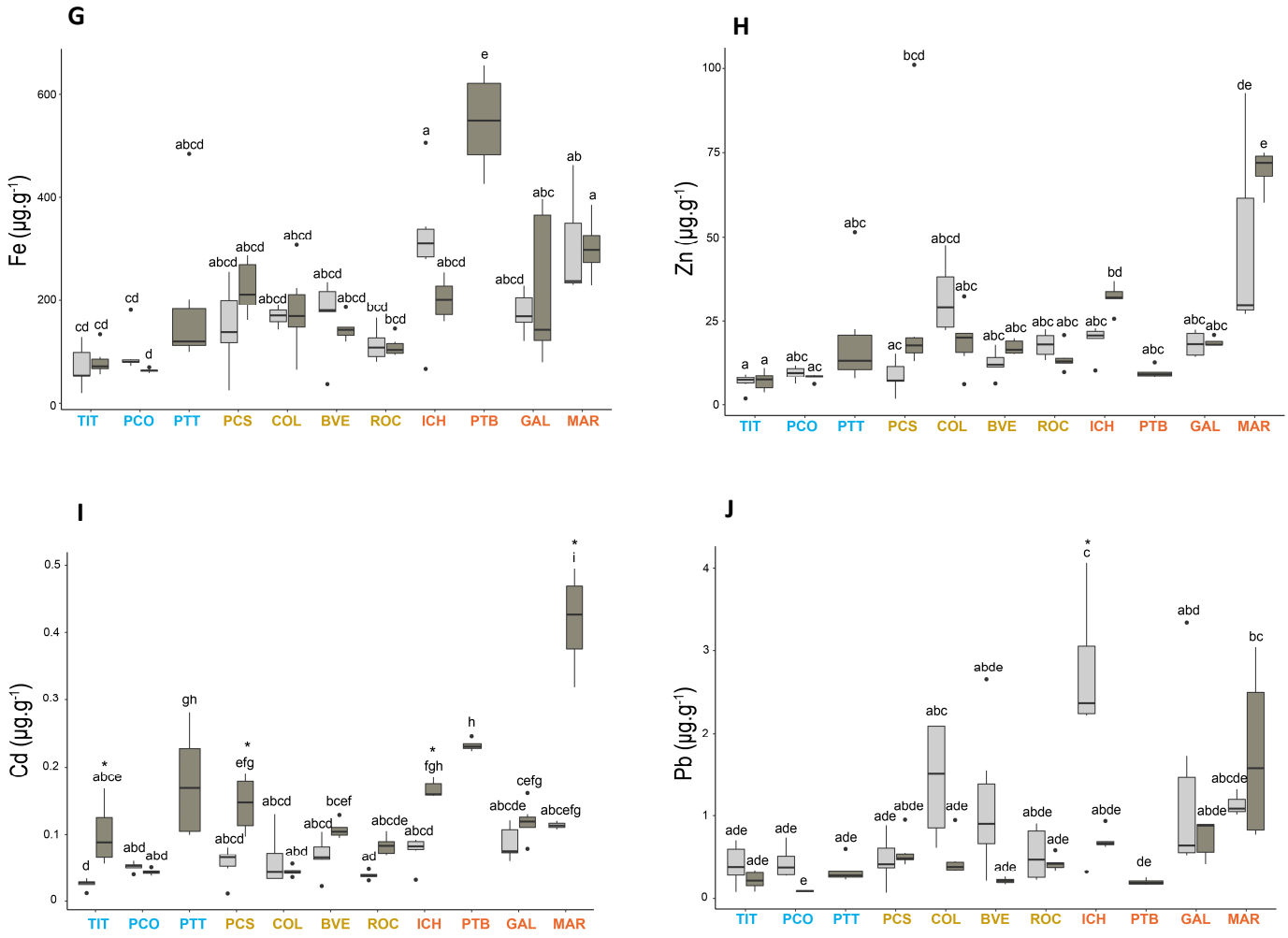

Figure 4. $\delta^{13}C$ (A), $\delta^{15}N$ (B), N (C), C/N (D), P (E), Mn (F), Fe (G), Zn (H), Cd (I) and Pb (J) contents *in T. testudinum* leaves across stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)) and year (2017 in grey and 2018 in brown).* indicates significant differences ($P < 0.05$) between the two years of sampling. Letters indicate significant differences ($P < 0.05$) across boxplots. The dotted line on Fig. 4C and Fig. 4E indicates the global threshold of nutrients limited (N < 1.8 % and P < 0.2 %) according to Duarte (1990). TIT: Tintamarre, PCO: Passe à Colas, PTT: Petite-Terre, PCS: Petit-cul-de sac, COL: Colombier, BVE: Bouée verte, ROC: Rocher Créole, ICH: Christophe Islet, PTB: Petit-Bourg, GAL: Galion and MAR: Marigot.

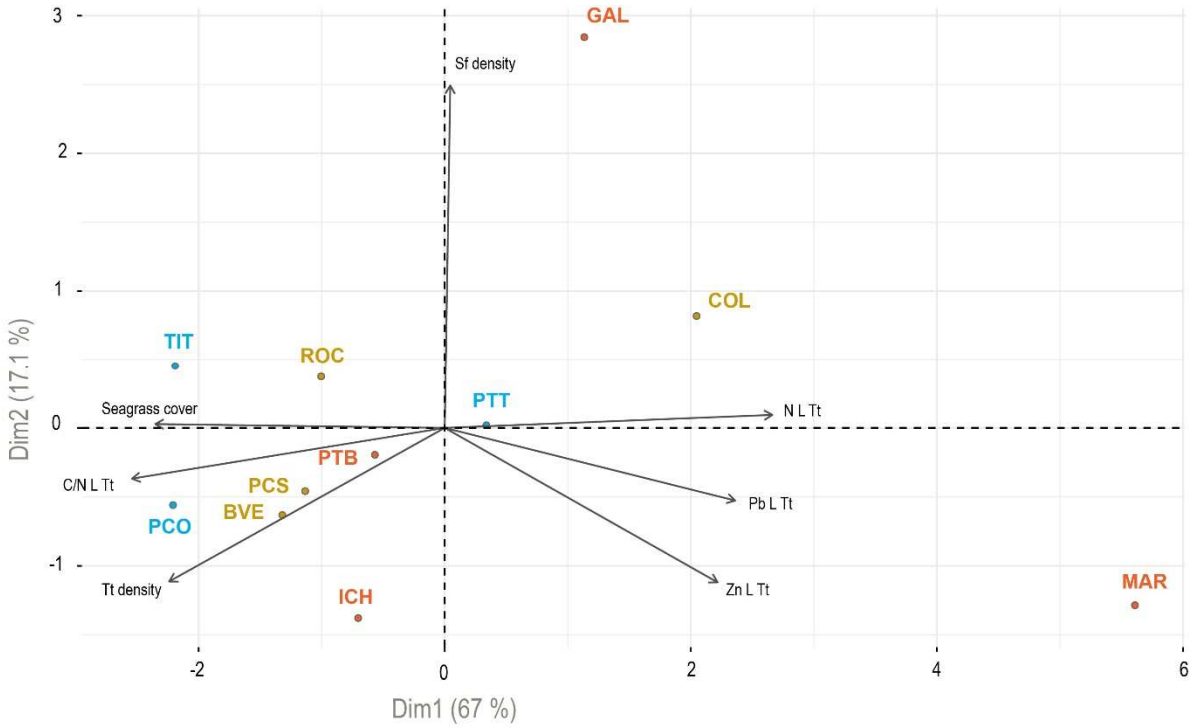

Figure 5. Biplot diagram combining the ordination plot of the sampling sites (the different colors correspond to the initial stations classification (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)) and loading factors of the 7 selected parameters. TIT: Tintamarre, PCO: Passe à Colas, PTT: Petite-Terre, PCS: Petit-cul-de sac, COL: Colombier, BVE: Bouée verte, ROC: Rocher Créole, ICH: Christophe Islet, PTB: Petit-Bourg, GAL: Galion and MAR: Marigot.

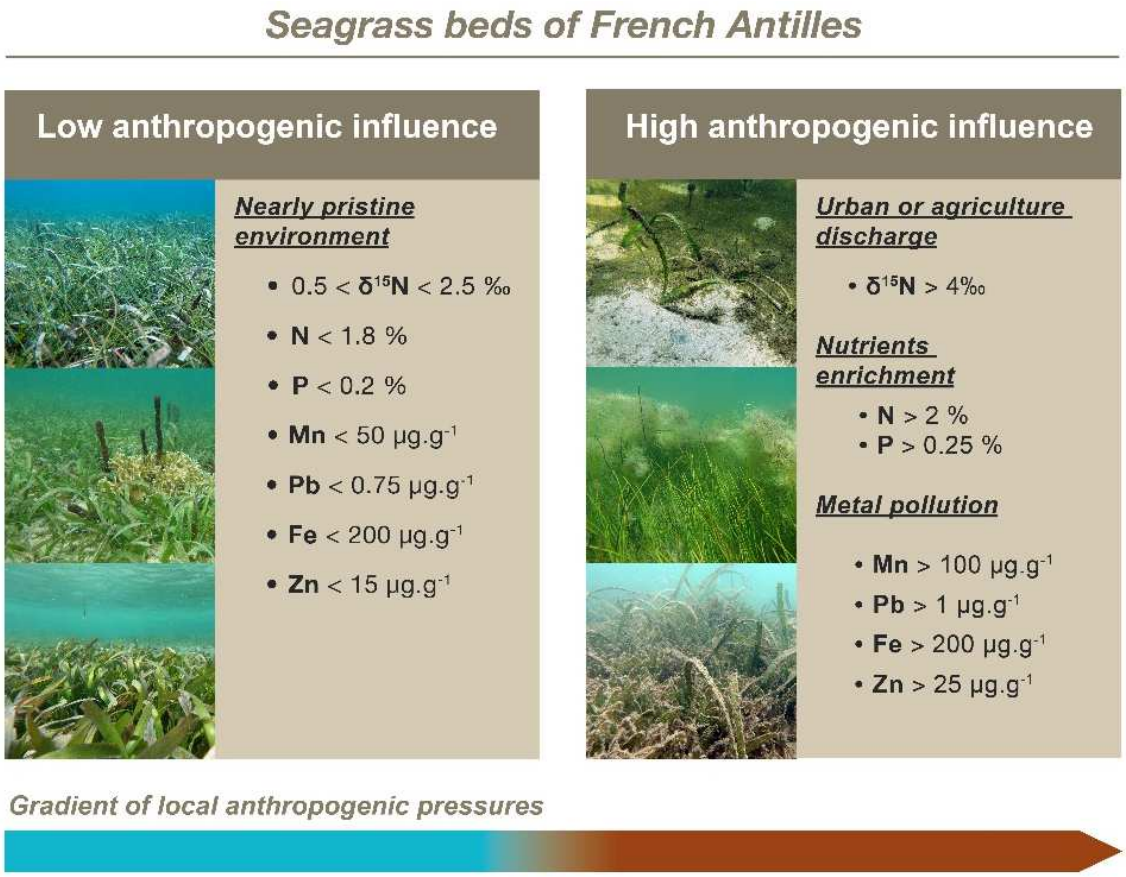

Figure 6. Conceptual diagram of thresholds estimated for physiological parameters in *T. testudinum* leaves according to the gradient of anthropogenic pressure. The colors of the arrow reflect the pressure gradient according to the initial stations classification. For N and P, the thresholds are derived from the limitation thresholds according to Duarte (1990). For $\delta^{15}N$, thresholds in nearly pristine environment were estimated by using the minimum and maximum values of the two least anthropized stations. The minimum value of the two stations with the highest mean $\delta^{15}N$ signatures was retained to define the threshold in high anthropogenic influence. For ETs, the thresholds in nearly pristine environment were estimated by rounding the maximum value of the two less anthropized stations. For the ETs, the thresholds were estimated by rounding the maximum value of the two least anthropised stations (nearly pristine environment) and the minimum value of the two most enriched stations (high anthropogenic influence).

Table 1. Specificities of the sampling stations (potential anthropogenic pressures was estimated according to the proximity and intensity of the disturbance, using pressures data and expert knowledge (Table S1): low (blue), moderate (yellow) and high (red)). For sites that were sampled twice, we consider the value, except for carbonates for which only one measure was made. Species abbreviations: Tt = *Thalassia testudinum*, Sf = *Syringodium filiforme*, Hs = *Halophila stipulacea*, Hw = *Halodule wrightii.*

Sampling station	**Island**	**Depth (m)**	**Seagrass species**	**Sediment characteristic**			**Type of local disturbances (and potential anthropogenic pressures level)**
				Silt and clay (<63 µm) %	Organic matter (%)	Carbonates (%)	
Passe à Colas (PCO)	Guadeloupe	3	Tt, Sf	15.49	4.80	91.46	Low
Tintamarre (TIT)	Saint-Martin	2	Tt, Sf	3.56	2.44	99.11	Low
Petite-Terre (PTT)	Guadeloupe	2	Tt, Sf, Hw	0.31	1.92	93.49	Some boating and recreation (low)
Bouée verte (BVE)	Guadeloupe	3	Tt	1.92	3.74	93.20	Middle of a plume of waste waters (moderate)
Rocher Créole (ROC)	Saint-Martin	7	Tt, Sf	7.20	2.71	89.07	Limited boating (moderate)
Petit cul-de-sac (PCS)	Saint-Barthélemy	2	Tt, Sf	2.04	2.44	83.05	Domestic sewages (moderate)
Colombier (COL)	Saint-Barthélemy	9	Tt, Sf, Hs	1.83	2.15	85.20	Boating (moderate)
Petit-Bourg (PTB)	Guadeloupe	1	Tt, Hs	20.48	16.20	45.31	Waste waters and urban discharge, industry (high)
Galion (GAL)	Saint-Martin	2	Tt, Sf	0.00	2.07	81.80	Waste waters, and urban discharge (high)
Christophe Islet (ICH)	Guadeloupe	2	Tt	8.38	12.45	85.64	Waste waters and urban discharge, industry (high)
Marigot (MAR)	Saint-Barthélemy	0.5	Tt, Sf	1.13	1.60	66.11	Domestic sewages (high)

Table 2. Parameters and expected responses (↑: increase, ↓: decrease) to environmental degradation according to the literature (non-exhaustive list).

Level	**Parameters**	**Response to degradation**	**References**
Physiological	N, C/N, and P content in seagrass tissues	↑	Burkholder et al., 2007; Gover et al., 2014b; Zhang et al., 2014; Holmer et al., 2016
	$\delta^{13}C$ in seagrass tissues	↓	Longstaff and Dennison, 1999; Serrano et al., 2011
	$\delta^{15}N$ in seagrass tissues	↑ / ↓	Udy et al., 1999 ; Castro et al., 2007; Schubert et al., 2013; Jones et al., 2018
	Trace metals in seagrass tissues	↑	Prange & Dennison, 2000; Gover et al., 2014b
Individual	Leaves morphological parameters (number of leaves, leaf length, leaf area, leaf biomass)	↑ / ↓	Udy et al., 1999, Zhang et al., 2014
	Leaf necrosis	↑	Romero et al., 2007, van Katwijk et al., 1997
Population	Shoot density, seagrass cover	↓	Short and Wyllie-Echeverria, 1996; Serrano et al., 2011
Landscape	Fragmentation	↑	Demers et al., 2013; La Manna et al., 2014
Communities	Macroalgae taxa	↑ / ↓	Montefalcone et al., 2015
	Macroalgae cover (%)	↑	Duarte 1995, Burkholder et al., 2007; van Tussenbroek et al., 2011
	Leaf epiphyte biomass	↑	Frankovich and Fourqurean, 1997; Zhang et al., 2014; Prado 2018
	Category of epiphytes	↑ / ↓	Martinez-Crégo et al., 2010
	Cyanobacteria cover	↑ / ↓	Coleman and Burkholder, 1994; Uku and Björk, 2001

Benthic macrofauna	↑ / ↓	Boström et al., 2006; McCloskey and Unsworth, 2015

Table 3. Benthic associated macrofauna, macroalgae, cyanobacteria and epiphyte communities (mean ± SE) for the 11 study stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)). For parameters for which two years of data were available, the mean of the two years is presented (mean ± SE), except when there was a significant difference between years (represented by * according to $P < 0.05$), in which case the values are shown for both years. Letters indicate significant differences ($P < 0.05$) across stations. Tt = *Thalassia testudinum*. NA: data not available.

Sampling station	**Benthic macrofauna species richness**	**Macroalgae total cover (%)**	**Cyanobacteria cover (seagrass and substrate) (%)**	**Total Tt leaf epiphytes cover (%)**	**Tt Leaf epiphyte load (mg.cm^{-2})**
	2018	2018	2018	2017-2018	2018
Tintamarre	9	5.30 ± 11.34^{a}	0.17 ± 0.91	21.07 ± 23.31^{eg}	10.02^{d}
Passe à Colas	19	1.82 ± 2.02^{a}	0	14.85 ± 15.76^{abc}	2.13^{ab}
Petite-Terre	1	6.03 ± 7.52^{a}	4.00 ± 2.77	20.25 ± 23.49^{defg}	1.56^{ab}
Petit cul-de-sac	2	14.90 ± 10.07^{b}	0.4 ± 1.85	16.28 ± 19.50^{abd}	3.06^{ab}
Colombier	7	7.70 ± 6.83^{a}	1.00 ± 3.71	24.38 ± 28.95^{ef}	4.09^{abc}
Bouée verte	21	1.15 ± 3.82^{a}	0.03 ± 0.18	5.00 -20.34^{ach} *	1.36^{a}
Rocher Créole	2	5.68 ± 4.27^{a}	0	24.95 ± 26.46^{f}	8.85^{cd}
Christophe Islet	14	17.48 ± 8.35^{b}	0.10 + 0.55	6.78 -17.73^{ch} *	1.31^{ab}
Petit-Bourg	12	7.90 ± 10.42^{a}	2.33 ± 8.98	17.56 ± 21.00^{bdg}	6.18^{bcd}
Galion	4	7.23 ± 12.85^{a}	0	9.74 ± 14.70^{h}	6.04^{abcd}
Marigot	NA	NA	NA	7.69 -19.00^{ach} *	NA

Supplementary material

Table S1. Details on the environmental conditions of the stations. Class of turbidity index: 1: very low (visibility > 15 m), 2: low (visibility 15 – 10 m), 3: moderate (10 - 5 m visibility), 4: important (visibility 5 - 1 m), very important: 5 (visibility < 1 m).

Sampling station	MES (mg.L^{-1})	Turbidity index	Distance from the mainland (km)
Passe à Colas (PCO)	17.53	2	5 – 7
Tintamarre (TIT)	14.13	2	3.5 - 4.7
Petite-Terre (PTT)	32.06	2	10 – 13
Bouée verte (BVE)	13.51	2	3 - 3.5
Rocher Créole (ROC)	11.11	2	0.5
Petit cul-de-sac (PCS)	13.20	3	0.04
Colombier (COL)	11.05	1	0.07 - 0.4
Petit-Bourg (PTB)	32.06	4	1
Galion (GAL)	10.43	4	0.01
Christophe Islet (ICH)	19.37	4	1
Marigot (MAR)	124.77	5	0.003

Table S2. Mean of morphological characteristic of *T. testudinum* leaves between the two years of sampling for the 11 study stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red). Letters indicate significant differences (P < 0.05) across parameters and years. * indicate significant differences (P < 0.05) across year only. NA: not available samples.

Sampling station	Leaves per shoot			Leaf length (cm)			Leaf width (cm)			Leaf area (cm²)			Grazing marks (%)		
	2017	2018		2017	2018		2017	2018		2017	2018		2017	2018	
Tintamarre	3.12^{gi}	4.04^{k}	*	11.09^{cdh}	13.43^{e}	*	1.05^{b}	1.27^{n}	*	19.23^{ij}	27.52^{l}	*	19.73^{abef}	32.70^{bcdf}	*
Passe à Colas	2.88^{eh}	3.25^{cg}	*	10.67^{ch}	11.31^{cdh}		0.89^{deg}	0.99^{ci}	*	15.91^{fg}	17.98^{gi}		23.44^{abcef}	54.49^{d}	*
Petite-Terre	NA	2.84^{e}		NA	5.33^{g}		NA	0.53^{m}		NA	5.30^{e}		NA	3.37^{a}	
Petit cul-de-sac	2.6^{f}	2.93^{ehi}	*	9.97^{bh}	13.32^{e}	*	0.88^{dgh}	0.84^{ghk}		14.61^{fh}	18.51^{gi}	*	8.75^{ae}	29.20^{bcef}	*
Colombier	3.49^{abcd}	3.65^{dj}		8.27^{ab}	7.41^{a}		0.70^{a}	0.65^{a}		9.51^{abc}	8.61^{ab}		2.49^{a}	4.25^{a}	
Bouée verte	3.49^{abd}	3.26^{cg}		9.9^{bh}	7.1^{ag}	*	0.88^{dg}	0.83^{hjk}	*	13.67^{fh}	9.91^{bc}	*	9.22^{ae}	42.31^{cd}	*
Rocher Créole	3.37^{abc}	3.83^{jl}	*	12.87^{de}	12.09^{cde}		0.95^{fi}	0.94^{ef}		19.20^{ij}	17.39^{gi}		17.37^{abef}	34.01^{bcdf}	*
Christophe Islet	3.37^{abc}	3.08^{ghi}	*	15.36^{f}	10.54^{ch}	*	0.92^{def}	0.78^{j}	*	22.21^{d}	13.55^{fh}	*	12.02^{aef}	28.86^{bcef}	*
Petit-Bourg	NA	3.94^{kl}		NA	13.61^{e}		NA	1.03^{bc}		NA	21.59^{dj}		NA	42.08^{cd}	
Galion	2.69^{ef}	3.55^{ad}	*	12.48^{cde}	16.85^{f}	*	1.04^{bc}	1.14^{l}	*	23.47^{d}	31.34^{k}	*	34.94^{bcd}	34.40^{bcdf}	*
Marigot	3.27^{bcg}	4.09^{k}	*	6.78^{ag}	10.79^{cdh}	*	0.66^{a}	0.79^{jk}	*	6.81^{ae}	12.13^{ch}	*	0^{a}	3.81^{ae}	*

Table S3. Seagrass meadow landscape parameters for the 11 study stations (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red). NA: not available data (no sampling field or enough visibility).

Sampling station	Fragmentation (%)	
	2017	2018
Tintamarre	0	7.87
Passe à Colas	0	0
Petite-Terre	NA	6.53
Petit cul-de-sac	0	2.2
Colombier	0	4.87
Bouée verte	0	10
Rocher Créole	0	0
Christophe Islet	0	4.47
Petit-Bourg	NA	0
Galion	NA	NA
Marigot	NA	NA

Table S4. Relative seagrass cover (%) (Mean of 2017 and 2018 values ± SE) by species across station (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)).

Sampling station	*T. testudinum* (%)	*S. filiforme* (%)	*H. stipulacea* (%)	*H. wrightii* (%)
Tintamarre	81.92 ± 20.03	18.08 ± 20.03	0	0
Passe à Colas	99.25 ± 3.63	0.75 ± 3.63	0	0
Petite-Terre	42.6 ± 28.16	20.66 ± 16.12	0	36.75 ± 31.78
Petit cul-de-sac	62.04 ± 24.04	37.97 ± 24.04	0	0
Colombier	3.33 ± 9.87	96.52 ± 9.85	0.14 ± 0.72	0
Bouée verte	100.00 ± 0.00	0	0	0
Rocher Créole	49.83 ± 31.20	50.17 ± 31.20	0	0
Christophe Islet	100.00 ± 0.00	0	0	0
Petit-Bourg	90.53 ± 24.96	0	9.47 ± 24.96	0
Galion	18.29 ± 22.72	77.97 ± 27.34	1.89 ± 13.74	1.85 ± 13.46

Table S5. Results of the three-way nested ANOVA evaluating the simultaneous effect of pressure gradient, station and year on structural and morphological parameters. p-values are represented by asterisks : *** P < 0.001, ** P < 0.01, * P < 0.05. L: leaves, Tt: *Thalassia testudinum*, Sf: *Syringodium filiform*e.

		Df	Sum Sq	Mean Sq	F	p-value
Structural parameters	**Seagrass cover**					
	Pressure	1	96	96	0.390	***
	Station	8	182118	22765	92.185	***
	Year	1	18295	18295	74.086	***
	Density Tt					
	Pressure	1	3558570	3558570	48.685	***
	Station	8	25572649	3196581	43.733	***
	Year	1	1169249	1169249	15.997	***
	Density Sf					
	Pressure	1	216015157	216015157	253.46	***
	Station	5	186202703	37240541	43.70	***
	Year	1	24836810	24836810	29.14	***
Morphological parameters	**Necrosis L Tt**					
	Pressure	1	96	96	0.390	***
	Station	8	182118	22765	92.185	***
	Year	1	18295	18295	74.086	***
	Grazing marks L Tt					
	Pressure	1	325	325	2.669	ns
	Station	9	22864	2540	20.862	***
	Year	1	10256	10256	84.221	***
	LAI Tt					
	Pressure	1	180367	20041	76.204	***
	Station	9	18380	18380	69.889	***
	Year	7	8710	1244	4.732	***
	Biomass L Tt					
	Pressure	1	8651	8651	4.776	*
	Station	9	427707	47523	26.240	***
	Year	1	2991	2991	1.652	ns
	Length L Tt					
	Pressure	1	3848	3848	106.837	***
	Station	9	30439	3382	93.905	***
	Year	1	175	175	4.861	*
	Width L Tt					
	Pressure	1	0.93	0.926	30.83	***
	Station	9	149.06	16.563	551.21	***
	Year	1	0.85	0.850	28.28	***
	Leaves area Tt					
	Pressure	1	4017	4017	56.09	***
	Station	9	196440	21827	304.77	***
	Year	1	1463	1463	20.43	***
	Number of leaves per shoot Tt					
	Pressure	1	14.4	14.42	28.21	***
	Station	9	524.4	58.27	114.01	***
	Year	1	148.9	148.86	291.28	***

Table S6. Three-way nested ANOVA results of physiological parameters (*T. testudinum* leaves) including the gradient of potential anthropogenic pressure, the station and the year. p-values are represented by asterisks : *** P < 0.001, ** P < 0.01, * P < 0.05.

Parameter	Df	Sum Sq	Mean Sq	F	p-value	Parameter	Df	Sum Sq	Mean Sq	F	p-value
δ^{13}C L Tt						**Fe L Tt**					
Pressure	1	7.22	7.219	70.189	***	Pressure	1	20.767	20.767	232.198	***
Station	9	151.54	16.838	33.522	***	Station	9	8.323	0.925	10.340	***
Year	1	3.30	3.302	16.395		Year	1	0.140	0.140	1.565	
δ^{15}N L Tt						**Ni L Tt**					
Pressure	1	160.21	160.21	428.042	***	Pressure	1	0.3907	0.3907	17.511	***
Station	9	131.82	14.65	39.133	***	Station	9	1.8249	0.2028	9.088	***
Year	1	0.09	0.09	0.244		Year	1	0.7047	0.7047	31.587	***
C/N L Tt						**Cu F Tt**					
Pressure	1	224.8	224.76	60.432	***	Pressure	1	1.81	1.813	30.04	***
Station	9	745.0	82.77	37.040	***	Station	9	38.99	4.332	71.77	***
Year	1	48.5	48.50	20.865	***	Year	7	17.94	17.936	297.12	***
N L Tt						**Zn L Tt**					
Pressure	1	2.102	2.1024	116.784	***	Pressure	1	13.599	13.599	194.612	***
Station	9	5.253	0.5836	32.419	***	Station	9	14.852	1.650	23.617	***
Year	1	0.295	0.2952	16.395	***	Year	7	0.198	2.833	2.833	
P L Tt						**Cd L Tt**					
Pressure	1	0.0907	0.0907	4.860	*	Pressure	1	13.546	13.546	126.545	***
Station	9	1.4121	0.1569	8.412	***	Station	9	17.327	1.925	17.985	***
Year	1	0.8814	0.8814	47.253	***	Year	7	10.203	10.203	95.314	***
Cr L Tt						**Pb L Tt**					
Pressure	1	1.031	1.0313	9.901	**	Pressure	1	22.606	22.606	114.167	***
Station	9	3.470	0.3855	3.701	***	Station	9	19.477	2.164	10.930	***
Year	1	0.291	0.2907	2.791		Year	7	12.841	12.841	64.853	***
Mn L Tt											
Pressure	1	34.73	34.73	1540.52	***						
Station	9	20.35	2.26	100.31	***						
Year	1	6.94	6.94	308.01	***						

Table S7. Stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) (‰), nutrients (N and P) (%), and C content in *T. testudinum* rhizomes (mean ± SE) across stations (mean of 2017 and 2018 data, except for P where analyses were only performed on 2018 samples). Letters indicate significant differences ($P < 0.05$) between stations. NA: not available samples. There is no significant differences between the two years of the study for $\delta^{15}N$, $\delta^{13}C$, C, N and C/N.

Sampling station	$\delta^{15}N$	$\delta^{13}C$	C	N	C/N	P
Tintamarre	1.47 ± 1.15^{bc}	-6.32 ± 0.32^{d}	32.26 ± 1.40^{cd}	0.64 ± 0.22^{ab}	55.13 ± 16.05^{ab}	0.11 ± 0.09^{ab}
Passe à Colas	0.05 ± 0.68^{ab}	-6.96 ± 0.46^{ab}	29.20 ± 2.58^{ab}	0.53 ± 0.12^{a}	57.16 ± 12.76^{ab}	ND
Petite-Terre	-0.47 ± 1.09^{a}	-7.36 ± 0.27^{ac}	30.34 ± 1.10^{abc}	0.55 ± 0.05^{a}	55.36 ± 6.05^{ab}	0.08 ± 0.01^{b}
Petit cul-de-sac	2.17 ± 1.06^{cde}	-6.97 ± 0.45^{ab}	32.12 ± 1.10^{cd}	0.64 ± 0.26^{ab}	56.73 ± 19.32^{ab}	0.14 ± 0.06^{ab}
Colombier	1.90 ± 1.04^{cd}	-7.55 ± 0.43^{c}	32.53 ± 1.13^{d}	1.02 ± 0.31^{c}	34.28 ± 10.02^{c}	0.14 ± 0.05^{ab}
Bouée verte	2.07 ± 0.99^{cde}	-6.72 ± 0.30^{bd}	31.81 ± 1.08^{acd}	0.70 ± 0.11^{ab}	46.46 ± 8.13^{ac}	0.16 ± 0.03^{ab}
Rocher Créole	0.35 ± 0.81^{ab}	-7.65 ± 0.38^{ce}	33.27 ± 1.31^{d}	0.48 ± 0.11^{a}	71.98 ± 14.99^{b}	0.11 ± 0.05^{ab}
Christophe Islet	3.63 ± 1.09^{ef}	-8.12 ± 0.33^{e}	31.85 ± 1.77^{abcd}	0.63 ± 0.14^{ab}	52.83 ± 10.79^{a}	0.17 ± 0.06^{ab}
Petit-Bourg	2.24 ± 0.86^{cde}	-6.51 ± 0.30^{bd}	31.87 ± 1.18^{abcd}	0.89 ± 0.25^{bc}	38.22 ± 9.60^{ac}	0.11 ± 0.04^{ab}
Galion	3.29 ± 2.05^{def}	-6.64 ± 0.33^{bd}	29.77 ± 2.49^{b}	1.19 ± 0.35^{c}	27.46 ± 11.99^{c}	0.23 ± 0.17^{a}
Marigot	4.87 ± 2.16^{f}	-9.03 ± 0.24^{f}	31.12 ± 1.51^{abcd}	0.77 ± 0.26^{abc}	44.38 ± 17.70^{ac}	0.14^{ab}

Table S8. Trace elements (Mn, Fe, Zn, Pb, Cd, Cr, Cu, Ni and Hg) content (µg.g^{-1}) in *T. testudinum* rhizomes (mean ± SE) across stations for 2018 samples. Letters indicate significant differences (P < 0.05) across stations. NA: not available samples. ND: non detectable, concentrations below detection limit (< 0.01 µg.g^{-1}).

Sampling station	Mn	Fe	Zn	Pb	Cd	Cr	Cu	Ni	Hg
Tintamarre	0.92 ± 0.37^{c}	90.04 ± 68.55^{a}	5.86 ± 2.34^{ac}	0.06 ± 0.03^{b}	0.01 ± 0.00^{a}	0.35 ± 0.22^{a}	1.40 ± 0.56^{a}	0.42 ± 0.22^{bc}	ND
Passe à Colas	NA	NA	NA	NA	NA	NA	NA	NA	NA
Petite-Terre	6.83 ± 0.59^{bc}	134.48 ± 26.57^{a}	2.01 ± 0.42^{a}	0.23 ± 0.05^{ab}	0.02 ± 0.01^{a}	0.91 ± 0.16^{b}	1.85 ± 0.43^{ab}	1.11 ± 0.22^{abc}	ND
Petit cul-de-sac	2.84 ± 0.72^{bc}	206.92 ± 58.89^{a}	11.15 ± 3.26^{bc}	0.72 ± 1.17^{ab}	0.05 ± 0.01^{ab}	0.45 ± 0.19^{a}	2.18 ± 0.81^{abc}	0.27 ± 0.14^{c}	ND
Colombier	14.33 ± 6.34^{abc}	486.61 ± 215.52^{a}	20.11 ± 3.58^{d}	0.32 ± 0.20^{a}	0.02 ± 0.01^{a}	0.52 ± 0.25^{a}	4.02 ± 1.80^{cd}	1.59 ± 0.66^{a}	ND
Bouée verte	11.92 ± 3.93^{abc}	517.79 ± 192.73^{a}	20.41 ± 1.89^{de}	0.28 ± 0.05^{ab}	0.03 ± 0.01^{a}	0.45 ± 0.08^{a}	1.48 ± 0.34^{ab}	1.3 ± 0.41^{ab}	ND
Rocher Créole	2.78 ± 0.83^{bc}	207.74 ± 41.53^{a}	16.07 ± 3.22^{bd}	0.27 ± 0.11^{ab}	0.05 ± 0.02^{ab}	0.49 ± 0.20^{a}	2.41 ± 0.73^{abcd}	0.64 ± 0.36^{bc}	ND
Christophe Islet	27.40 ± 19.41^{ad}	363.83 ± 166.64^{a}	27.37 ± 3.40^{e}	0.29 ± 0.08^{ab}	0.04 ± 0.02^{ab}	0.31 ± 0.09^{a}	1.35 ± 0.19^{a}	0.18 ± 0.03^{c}	ND
Petit-Bourg	45.07 ± 13.05^{d}	2613.51 ± 1194.44^{b}	12.25 ± 2.37^{bc}	0.22 ± 0.10^{ab}	0.09 ± 0.05^{b}	0.41 ± 0.17^{a}	4.5 ± 1.64^{d}	0.69 ± 0.32^{bc}	ND
Galion	19.91 ± 12.64^{abc}	930.45 ± 1653.99^{a}	17.09 ± 8.15^{bd}	0.08 ± 0.07b	0.06 ± 0.02^{ab}	0.26 ± 0.13^{a}	4.00 ± 1.52^{bcd}	1.36 ± 0.90^{ab}	ND
Marigot	34.79^{abd}	351.70^{ab}	20.67^{bde}	0.22^{ab}	0.03^{ab}	0.61^{ab}	2.71^{abcd}	1.7^{abc}	ND

Table S9. Stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) (‰), N and C (%) content in *S. filiforme* leaf (mean ± SE) across stations when the species was present (mean of 2017 and 2018). Letters indicate significant differences ($P < 0.05$) between stations. * indicate significant differences ($P < 0.05$) across year only.

Sampling station	$\delta^{13}C$	$\delta^{15}N$	C	N	C/N
Tintamarre	-8.50 ± 0.75^{b}	0.51 ± 0.79^{ab}	33.19 ± 3.56^{b}	1.19 ± 0.15^{b}	28.04 ± 2.26^{c}
Petite-Terre	-5.66 ± 0.65^{a}	1.45 ± 0.63^{a}	40.10 ± 0.62^{a}	2.08 ± 0.21^{a}	19.47 ± 1.88^{a}
Colombier	-6.00 ± 1.24^{a}	1.33 ± 0.76^{a}	32.69 ± 1.79^{b}	1.41 ± 0.21^{bcd}	23.52 ± 2.81^{b}
Petit cul-de-sac	-7.78 ± 0.69^{b}	1.29 ± 0.98^{a}	32.88 ± 3.85^{b}	1.34 ± 0.31^{b}	25.09 ± 3.22^{bc}
Rocher Créole	-8.05 ± 0.88^{b}	0.07 ± 1.00^{b}	35.70 ± 4.61^{b} *	1.37 ± 0.31^{bc}	26.78 ± 3.63^{bc}
Galion	-8.22 ± 1.36^{b}	3.61 ± 1.39^{c}	32.05 ± 2.79^{b}	1.67 ± 0.40^{cd}	19.97 ± 4.03^{a}
Marigot	-9.53 ± 2.39^{b}	5.75 ± 1.08^{d}	31.96 ± 2.55^{b}	1.94 ± 0.31^{ad}	16.63 ± 1.49^{a}

Table S10. Trace elements (Cr, Cu, Ni and Hg) content (µg.g-1) in *T. testudinum* leaves (mean ± SE) across stations for 2018 samples. Letters indicate significant differences (P < 0.05) across stations. NA: not available samples. ND: non detectable, concentrations below detection limit (< 0.01 µg.g^{-1}).

Sampling station	**Cr**			**Ni**			**Cu**			**Hg**
	2017	2018		2017	2018		2017	2018		2017-2018
Tintamarre	0.35 ± 0.30^{a}	0.46 ± 0.40^{a}	*	3.14 ± 1.01^{ab}	5.57 ± 1.48^{c}	*	0.44 ± 0.12^{e}	0.96 ± 0.24^{def}		ND
Passe à Colas	0.36 ± 0.12^{a}	0.23 ± 0.05^{a}		4.56 ± 1.17^{abc}	4.28 ± 0.33^{abc}		0.78 ± 0.23^{def}	2.02 ± 0.39^{abcf}	*	NA
Petite-Terre	NA	0.58 ± 0.10^{a}		NA	5.06 ± 0.64^{ac}		NA	7.46 ± 1.78^{h}		ND
Petit cul-de-sac	0.24 ± 0.10^{a}	0.39 ± 0.11^{a}	*	2.82 ± 1.18^{b}	3.77 ± 0.35^{abc}		0.58 ± 0.22^{de}	2.87 ± 0.71^{bc}	*	ND
Colombier	0.40 ± 0.07^{a}	0.37 ± 0.09^{a}		4.66 ± 2.84^{abc}	3.53 ± 1.37^{abc}		2.39 ± 0.45^{abc}	1.80 ± 0.46^{abcdf}		ND
Bouée verte	0.39 ± 0.22^{a}	0.24 ± 0.03^{a}		3.05 ± 1.03^{ab}	4.09 ± 0.82^{abc}		0.57 ± 0.19^{de}	3.01 ± 0.83^{c}	*	ND
Rocher Créole	0.37 ± 0.21^{a}	0.35 ± 0.06^{a}		2.99 ± 0.22^{ab}	3.77 ± 0.89^{abc}		0.83 ± 0.10^{def}	1.30 ± 0.16^{adef}		ND
Christophe Islet	0.49 ± 0.16^{a}	0.42 ± 0.14^{a}	*	2.88 ± 0.72^{b}	7.22 ± 9.14^{abc}		0.85 ± 0.22^{def}	4.52 ± 0.25^{g}	*	ND
Petit-Bourg	NA	0.37 ± 0.04^{a}		NA	3.76 ± 0.58^{abc}		NA	5.55 ± 1.01^{g}		ND
Galion	0.40 ± 0.18^{a}	0.38 ± 0.15^{a}		3.97 ± 0.65^{abc}	4.03 ± 0.46a^{bc}		0.95 ± 0.31^{def}	1.16 ± 0.45^{adef}		ND
Marigot	0.63 ± 0.41^{a}	0.43 ± 0.25^{a}	*	3.49 ± 0.64^{abc}	5.66 ± 0.91^{c}		1.44 ± 0.09^{abdef}	2.75 ± 0.45^{bc}	*	ND

Table S11. Main type of epiphytes on *T. testudinum* leaves. Letters indicate significant differences (P < 0.05) across station. NA: not available samples.

Sampling station	Relative cover of coralline algae (%)		Relative cover of macrophytes (%)	
	2017	2018	2017	2018
Tintamarre	89.37 ± 27.03	92.27 ± 23.87	0	0.06 ± 0.99
Passe à Colas	97.58 ± 13.49	89.81 ± 19.59	0.95 ± 8.33	0
Petite-Terre	NA	64.78 ± 29.29	NA	2.20 ± 10.69
Petit cul-de-sac	83.09 ± 29.3	86.84 ± 19.82	0.36 ± 3.49	0.00 ± 0.05
Colombier	85.66 ± 27.17	81.74 ± 23.43	5.99 ± 16.58	9.70 ± 15.82
Bouée verte	70.33 ± 45.1	90.6 ± 22.41	0	0.06 ± 0.87
Rocher Créole	82.66 ± 21.84	42.29 ± 47.33	0	4.80 ± 11.05
Christophe Islet	30.46 ± 42.94	74.03 ± 24.72	12.38 ± 27.42	0.20 ± 2.22
Petit-Bourg	NA	77.88 ± 26.35	NA	1.89 ± 10.84
Galion	70.89 ± 37.38	63.86 ± 41.74	10.87 ± 23.07	7.43 ± 15.71
Marigot	99.24 ± 8.7	100 ± 0.00	0	0

Table S12. Category and respective cover of macroalgae (mean of 2018 values ± SE) for station.

Sampling station	Rhizophitic calcareous macroalgae (%)	Rhizophitic non calcareous macroalgae (%)	Drift macroalgae (%)	Cyanobacteria cover % (seagrass and substrate)
Tintamarre	2.80 ± 7.23	0.13 ± 0.51	2.37 ± 6.35	0.17 ± 0.91
Passe à Colas	0.77 ± 1.18	0.10 ± 0.40	0.95 ± 1.68	0
Petite-Terre	0.95 ± 1.78	0.10 ± 0.37	4.33 ± 7.88	4.00 ± 2.77
Petit cul-de-sac	3.77 ± 3.74	0.07 ± 0.37	11.07 ± 9.65	0.4 ± 1.85
Colombier	3.03 ± 2.99	4.60 ± 6.39	0.07 ± 0.25	1.00 ± 3.71
Bouée verte	0.67 ± 3.65	0.33 ± 1.27	0.15 ± 0.39	0.03 ± 0.18
Rocher Créole	3.38 ± 2.47	1.90 ± 2.22	0.40 ± 1.04	0
Christophe Islet	7.27 ± 5.92	8.80 ± 5.99	1.42 ± 2.15	0.10 ± 0.55
Petit-Bourg	0	0	7.90 ± 10.42	2.33 ± 8.98
Galion	0	0.10 ± 0.55	7.13 ± 12.89	0

Table S13. Abundance or cover of main benthic macrofauna taxons according stations. Only 2018 data are presented (mean ± SE).

Sampling station	Cnidarians		Porifera (%)	Mollusca (nb.m^{-2})	Echinoderma (nb.m^{-2})	Crustacea (nb.m^{-2})
	Corals (%)	Anemone (nb.m^{-2})				
Tintamarre	1.33 ± 2.31	428.00 ± 366.63	0	198.68 ± 143.42	0.01 ± 0.01	0
Passe à Colas	1.33 ± 0.58	0	28.33 ± 8.08	126.71 ± 16.21	1.30 ± 0.22	0
Petite-Terre	0.33 ± 0.58	0	0	0	0	0
Petit cul-de-sac	0	2.67 ± 4.62	0	0.03 ± 0.03	0	0
Bouée verte	23.67 ± 5.69	4.00 ± 6.93	34.33 ± 12.34	416.03 ± 59.22	6.41 ± 0.78	0
Colombier	1.67 ± 0.58	0	6.67 ± 7.64	9.44 ± 9.31	0	0
Christophe Islet	0	0	20.00 ± 7.81	94.68 ± 58.98	5.25 ± 0.20	0
Petit-Bourg	0	0	2.00 ± 3.46	4.00 ± 4.00	0.83 ± 0.70	0
Galion	0	52.00 ± 73.43	0	1.33 ± 2.31	0	0.01 ± 0.01

Table S14. Correlation of parameters to PCA components incorporating parameters showing significant differences between stations (ANOVA, $P < 0.05$). Parameters with the highest correlation with Component I ($r \leq 0.80$) are noted in bold. L = leaf, R = rhizome, Tt = *Thalassia testudinum*, Sf = *Syringodium filiforme.*

	Component I	**Component II**	**Component III**
δ^{15}N L Tt	0.71	-0.10	0.61
N L Tt	**0.95**	0.22	0.04
δ^{13}C L Tt	-0.75	0.20	0.01
C L Tt	-0.49	-0.24	0.39
C/N L Tt	**-0.90**	-0.27	0.05
P L Tt	0.79	-0.41	0.16
Cr L Tt	0.39	-0.17	-0.39
Mn L Tt	0.65	0.15	0.68
Fe L Tt	0.35	0.28	0.43
Ni L Tt	0.24	-0.36	0.40
Cu L Tt	0.16	-0.55	0.20
Zn L Tt	**0.88**	-0.10	0.21
Cd L Tt	0.75	-0.06	0.39
Pb L Tt	**0.89**	0.11	0.14
δ^{15}N R Tt	0.75	0.16	0.50
N R Tt	0.56	0.76	0.02
δ^{13}C R Tt	-0.78	0.33	-0.10
C R Tt	-0.34	0.16	-0.16
C/N R Tt	-0.68	-0.47	-0.23
P R Tt	0.12	0.74	0.19
Cr R Tt	0.36	-0.66	-0.42
Mn R Tt	0.43	0.12	0.74
Fe R Tt	-0.09	0.13	0.52
Ni R Tt	0.35	-0.09	0.46
Cu R Tt	0.10	0.55	0.14
Zn R Tt	0.29	0.18	0.55
Cd R Tt	-0.12	0.46	0.48
Pb R Tt	-0.04	-0.35	-0.03
Biomass L Tt	-0.45	-0.00	0.40
Fragmentation	0.33	0.57	-0.61
Tt density	-0.74	-0.37	0.34
Sf density	-0.10	0.78	-0.45
Seagrass cover	**-0.85**	0.08	0.25
Tt relative cover	-0.58	-0.37	0.70
Sf relative cover	0.42	0.52	-0.64
Grazing marks L Tt	-0.72	0.47	0.42
Necrosis L Tt	-0.73	0.25	0.13
Canopy Tt	-0.28	0.81	0.09
Tt L area	-0.38	0.80	0.07
Tt L width	-0.49	0.66	0.18
Biomass of epibiont L Tt	0.26	0.42	-0.17
Epibiont's cover Tt	0.02	-0.53	-0.44
Shannon fauna	-0.44	-0.09	0.51
Fauna diversity	-0.54	-0.12	0.60

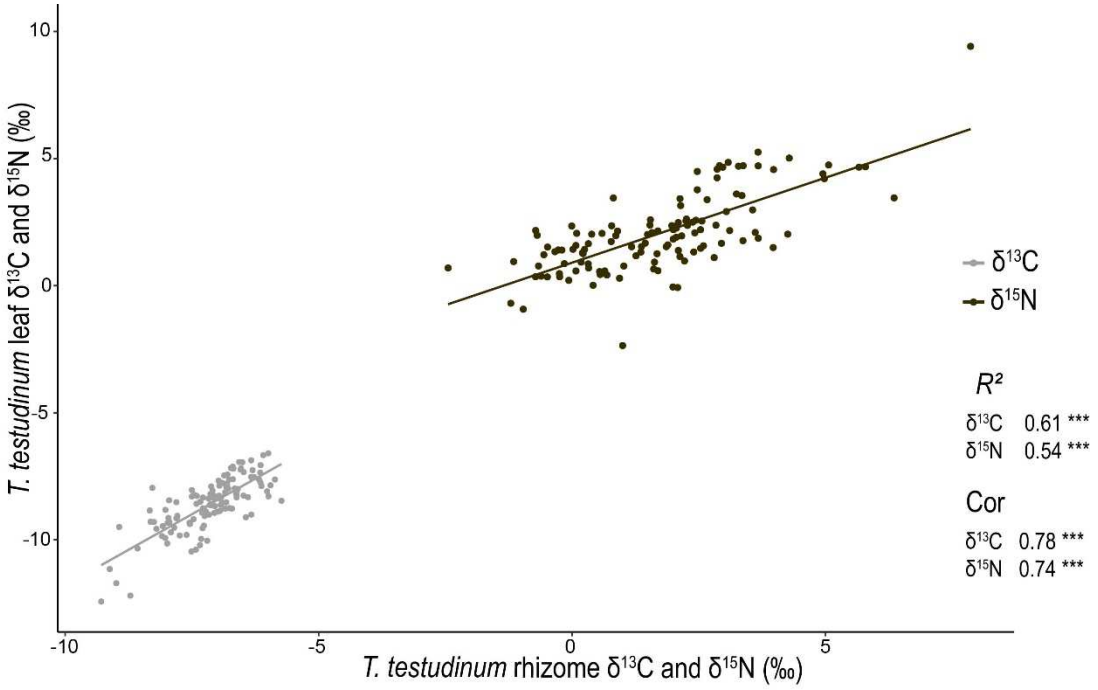

Figure S1: Correlation between leaf and rhizome values of $\delta^{15}N$ and $\delta^{13}C$ (‰) in *T. testudinum*. *** P < 0.001.

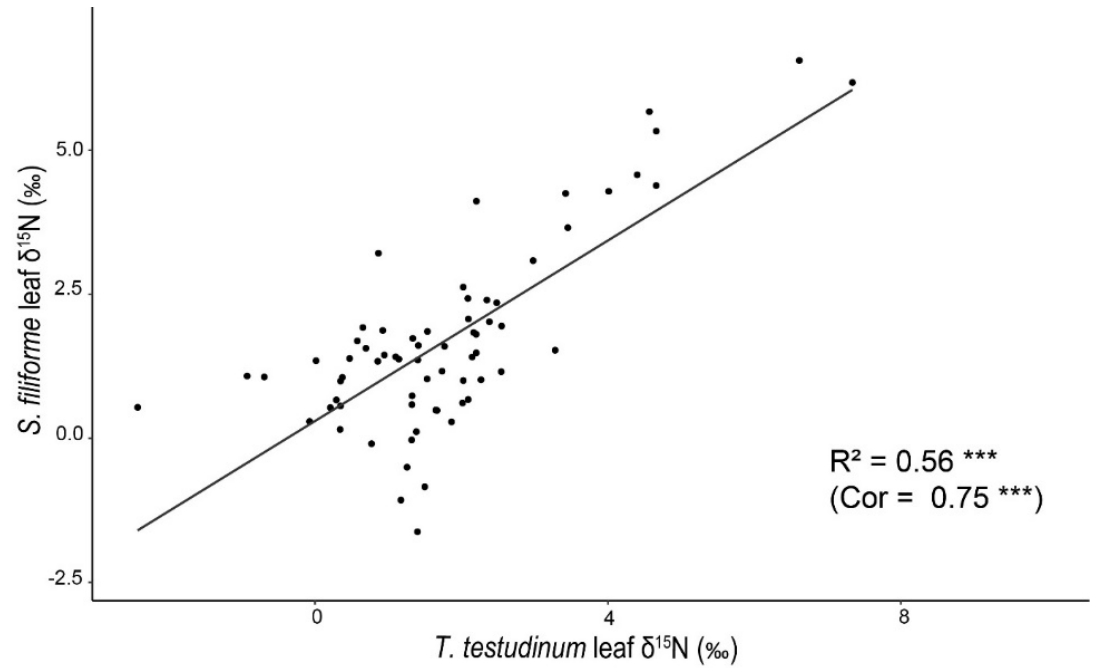

Figure S2: Correlation between leaf $\delta^{15}N$ values in *S. filiforme* and *T. testudinum* (‰). ***P < 0.001.

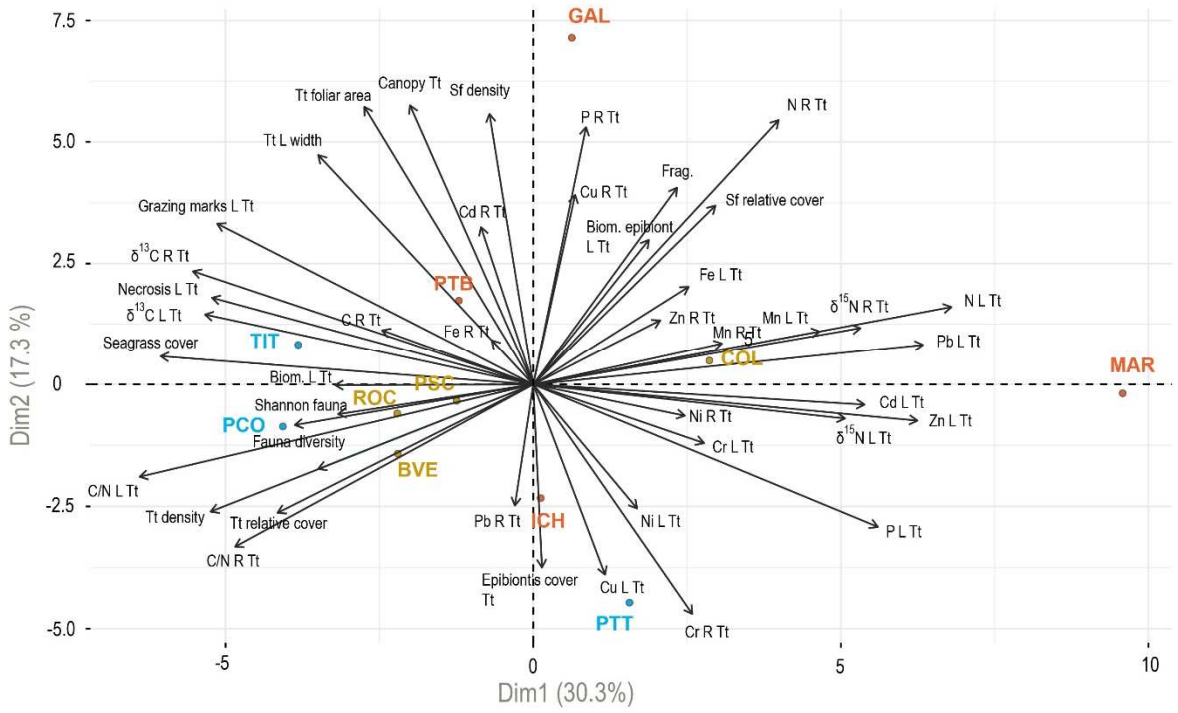

Figure S3. Biplot diagram combining the ordination plot of the sampling sites (the different colors correspond to the initial stations classification (potential anthropogenic pressures: low (blue), moderate (yellow) and high (red)) and loading factors of the 44 selected parameters from the first selection by ANOVAs analysis.