Original Articles

An optimised passive acoustic sampling scheme to discriminate among coral reefs' ecological states

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ABSTRACT

In the present era of rapid global change, innovative monitoring methods can greatly enhance our ability to detect ecological disturbances and prioritise conservation areas in a timely and cost-effective manner. While Passive Acoustic Monitoring (PAM) has recently emerged as a promising tool for monitoring ecological states in marine environments, the specifics of how to apply this method remains poorly defined. In this study we examined how different combinations of sampling settings (frequency bandwidth, time of sampling (day/night), and sample duration) influenced the ability of two acoustic indices, the Sound Pressure Level (SPL) and the Acoustic Complexity Index (ACI), to discriminate different ecological states (ecostates) of coral reefs. We applied an iterative approach to select the most efficient and consistent combinations of sampling settings to use for these two acoustic indices, depending on the stability of their discriminating power across different time scales (successive days, moon phases, and seasons), and the minimum sampling effort required for reliable ecostate assessment. The ability of SPL and ACI to discriminate ecostate-specific soundscapes was more stable and required less sampling effort at nighttime. For indices calculated in the higher frequency band (> 2 kHz), very short recording times (≤ 20 min divided into 5 s samples) were sufficient to discriminate ecostates, whereas longer recording times (≥ 200 min divided into 5 min samples) were necessary when using indices calculated in the lower frequency bands (< 1 kHz). An optimised sampling scheme, i.e. the group of the five best combinations of settings to discern among coral reef ecostates, was determined at Reunion Island, Indian Ocean, then tested at New Caledonia, Pacific Ocean. Here, the classifications obtained through visual surveys and with the optimised acoustic sampling scheme were congruent. The concordance of our results with visual fish counts confirms the potential of ecoacoustics to rapidly and reliably characterise coral reefs' ecostate, allowing managers to prioritise conservation areas among numerous sites, and detect ecological changes over time. Our study provides clear guidelines for monitoring soundscapes by means of the ecoacoustic indices most widely used in the marine realm.

1. Introduction

Coral reefs around the world are undergoing major ecological upheavals due to climate change and human impacts (Sale, 2011). To mediate these increasing threats, adaptive governance and management of coral reef ecosystems is required (Hughes et al., 2017). This involves developing reliable tools to rapidly assess and monitor the state and functioning of ecosystems across multiple spatial scales,

enhancing the capacity to detect disturbances and understand their causes, and enabling timely implementation of adaptive conservation efforts (Hoegh-Guldberg et al., 2018).

The study of soundscapes is part of ecoacoustics, where sound is considered as both a component and an indicator of ecological processes (Sueur and Farina, 2015). Soundscapes originate from three sources, biophony, geophony, and anthrophony (Pijanowski et al., 2011), and have now been characterised for a range of marine ecosystems, including polar regions (Haver et al., 2017), oceanic islands (Bittencourt et al., 2016; Haver et al., 2017), temperate reefs (Radford et al., 2010; Harris et al., 2016; Pieretti et al., 2017), and mangrove forests (Staaterman et al., 2017). These studies have focussed on both acoustic metrics and ecoacoustic indices (see review by Lindseth and Lobel, 2018), to attempt to classify different ecological states (ecostates) within these environments. Acoustic metrics describe the physical properties of the sounds such as amplitude (estimated by either the Sound Pressure Level [SPL] or Power Spectral Density [PSD]), while ecoacoustic indices, such as the Acoustic Entropy Index (H), the Acoustic Richness (AR) and the Acoustic Complexity Index (ACI) provide additional information about the soundscapes. To facilitate reading, both types are henceforth referred to as 'acoustic indices'. In the present study, we focussed on the two acoustic indices mostly used hitherto on coral reefs, these being the SPL and ACI (Pieretti et al., 2011).

On coral reefs, high values of SPL (and PSD) or ACI in the lower frequencies ($< 1\,kHz$) indicate healthy reef environments consisting of diverse and abundant reef fish assemblages, high coral cover and richness, high crustose coralline algae cover, high structural complexity or high density of mobile macro-invertebrates (Kennedy et al., 2010; Piercy et al., 2014; Kaplan et al., 2015; Bertucci et al., 2016; Freeman and Freeman, 2016; Staaterman et al., 2017). Conversely, elevated levels of these indices in the higher frequencies ($> 2\,kHz$) usually indicate more degraded ecostates, such as dead corals (Nedelec et al., 2015) and abundant macroalgae (Freeman and Freeman, 2016). This is largely because degraded habitats have higher proportions of invertebrates such as snapping shrimps, which are the dominant sound producers of higher frequencies (e.g. Radford et al., 2014; Kaplan et al., 2015; Lillis and Mooney, 2018). Moreover, Freeman et al. (2018) have recently identified that macroalgae also produce high frequency sounds through their photosynthetic activity. Indeed, oxygen (with sometimes nitrogen) gas bubbles are created on the surface of macroalgal tissue as products of photosynthesis, and these bubbles generate a short high frequency "ping" sound as they detach from the macroalgal surface (Freeman et al., 2018). As such, while PAM is widely recognised as a promising tool which may be able to detect differences in the ecostate of both temperate and tropical reef ecosystems (e.g. Kaplan et al., 2015; Freeman and Freeman, 2016; Harris et al., 2016; Pieretti et al., 2017),

the contribution of the different organisms to soundscapes, and the parametrisation of the indices reflecting their activity, need further investigation (Bertucci et al., 2016; Staaterman et al., 2017; Bolgan et al., 2018).

Previous marine PAM studies have used a range of sampling settings, varying in sample duration, frequency, and sampling effort (i.e. total recording time) to assess marine ecostates (see Lindseth and Lobel, 2018). Several of these studies have highlighted temporal variations in ecoacoustic indices due to factors such as diel, lunar, and seasonal variation (e.g., Staaterman et al., 2014; Kaplan et al., 2015), however, the degree to which variation from these sources affects the capacity of acoustic indices to discriminate among ecostates has not yet been formally evaluated. To ensure that results and differences ascribed to ecological variation are not an outcome of sampling methodology, the influence of variation in these factors must be quantified, and minimised where possible. Similarly, an estimation of the minimum sampling effort required to reliably detect differences among different ecostates would further enhance the development of PAM as an operational monitoring tool. Such an approach has been used for acoustic monitoring of tropical forests (Pieretti et al., 2015), but to our knowledge has not been applied to marine ecosystems, as marine studies have invariably focussed on ecological influences on ecoacoustic indices rather than the potential influence of the underlying sampling methodology. This study will contribute to address this shortfall.

Our main objective was to propose an optimised PAM sampling scheme which will reliably detect differences in ecostates among coral reefs. This scheme will have wide application for prioritising conservation areas and detecting the onset of disturbances (i.e. changes in ecostates).

Four main questions structured our study: i) Can visually-detected differences of coral reef ecostate also be detected by the commonly used acoustic indices SPL and ACI?; ii) Which are the combinations of acoustic sampling settings most able to consistently discriminate among ecostates across successive days, moon phases, and seasons?; iii) What is the minimum number of consecutive acoustic samples (i.e. sampling effort) required to obtain a reliable ecostate ranking?; and iv) Is the proposed acoustic sampling scheme for discriminating coral reef ecostates also applicable to coral reefs elsewhere?

2. Materials and methods

2.1. Study sites

We conducted acoustic recordings and visual ecological surveys at four sites on the outer coral reef slopes of Reunion Island, and at six sites around New Caledonia (Fig. 1). All sites were in 10–15 m depth, with gentle to moderate slopes, and characterised by coral reef matrix
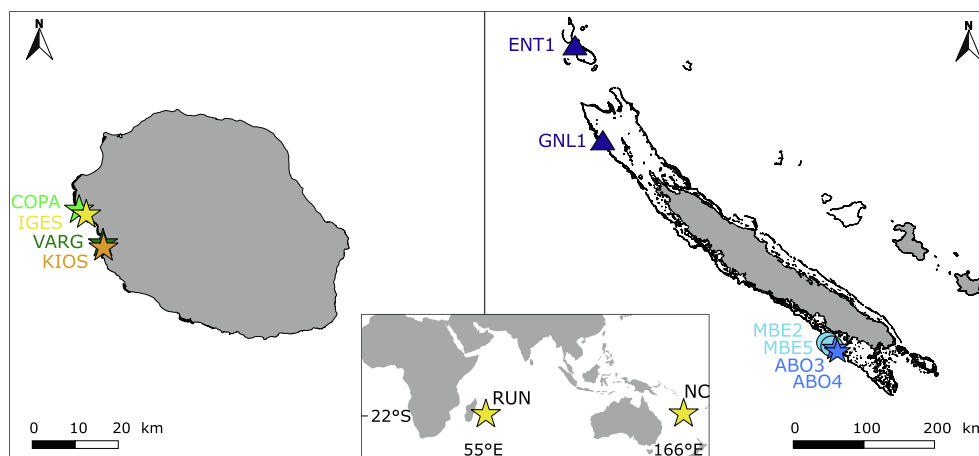

Fig. 1. Location of the coral reef sites sampled (coordinates are given in supplementary methods). Four sites were in Reunion Island (RUN), Indian Ocean; Copacabana (COPA), Igesa (IGES), Varangue (VARG), and Kiosque (KIOS). Six sites were in New Caledonia (NC), Pacific Ocean; D'Entrecasteaux (ENT1), Great Northern Lagoon (GNL1), M'berré (MBE2 and MBE5), Aboré (ABO3 and ABO4).
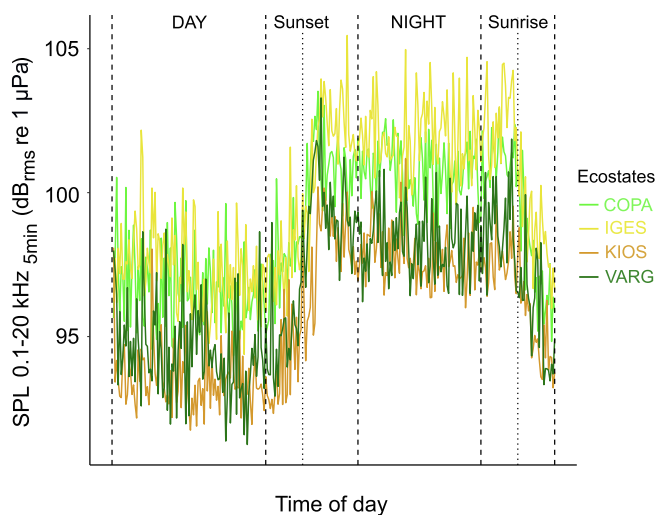
Fig. 2. Time of day variations (24 h) of SPL calculated on the whole spectrum (0.1–20 kHz) on consecutive 5 min samples for the four ecostates (COPA: Copacabana, IGES: Igesa, KIOS: Kiosque, VARG: Varangue). Similar diel trends were observed regardless of index, sample duration, frequency bandwidth, or day.

inhabited by fishes and invertebrates.

2.2. Developing optimal indices from experimental data

2.2.1. Ecological surveys

Based on existing data (Bigot et al., 2016), four Reunion Island sites were selected to represent the range of coral reef ecostates that can be found on the island's outer reef slopes. The ecostate of fish assemblage and benthic community was estimated visually at each of the four Reunion Island sites, using Underwater Visual Censuses (UVC) and Medium Scale Approach (MSA) along three 5 × 30 m belt-transects at each site (details in supplementary methods). Fish assemblages were evaluated during each of the acoustic deployments (see below), i.e. they were evaluated at Copacabana and Varangue during four consecutive moon phases in the cool season (September-October 2016) and once in the hot season (March 2017). Due to bad weather and logistical constraints, we could visually sample Kiosque and Igesa only once in the cool season (October 2016). The four Reunion Island sites were considered to represent a gradient of ecostates based on the differences in fish diversity and abundance, and benthic complexity and coverage (see supplementary methods). This visual ecostate classification using standard methodologies allowed comparison against the acoustic sampling, to determine whether similar classifications could be obtained using PAM.

2.2.2. Acoustic recorders

Underwater soundscapes were recorded using two identical acoustic recording systems. Each system consisted of a large aluminium tripod which supported a TC 4014–5 omnidirectional hydrophone (linear Frequency range: 30 Hz to 100 kHz ± 2 dB; sensitivity: − 186 dB re 1 V μPa^{-1}; RESON, Slangerup, Denmark) connected to an acquisition chain (pre-amplifier with gain set at 20 dB, acquisition card, and PC inside a waterproof container) designed by NORTEKMED S.A.S (Toulon, France). The hydrophone was fixed at the top of the tripod (approx. 1.5 m above the substrate), facing downwards to reduce capturing ambient sea surface noise. Systems were affixed to the substrate to prevent movement during recordings. Both systems were calibrated with a Brüel & Kjaer 4229 hydrophone calibrator (Nærum, Denmark) and programmed to record continuously at 100 kHz and 16 bits-depth, providing an analysis range of 0–50 kHz. Fourteen deployments of at least 72h were conducted on Reunion Island sites (five at Copacabana,

five at Varangue, two at Kiosque and two at Igesa; details below). A single deployment of 24h was conducted on each of the New Caledonian sites (coordinates of all sites are given in supplementary methods).

2.2.3. Data processing and definition of the combinations of settings tested

We began by selecting multiple different combinations of sampling settings (sample durations, acoustic indices, frequency bandwidths, and times of day) to characterise coral reef soundscapes. We then applied these combinations across different temporal scales (successive days, moon phases, and seasons) at the four different ecostates at Reunion Island, to select the combinations that were both discriminant, and robust to temporal influence. For the most discriminant and stable combinations, we then defined the minimum number of consecutive samples (i.e. sampling effort) required to obtain a reliable ecostate ranking. We called the resulting group of effective combinations the optimised sampling scheme. We finally tested the ability of this sampling scheme to discern ecostates across a range of New Caledonian outer reef slope sites known to vary in health and human impacts.

The continuous acoustic recordings resulting from each deployment were divided into four different sample durations: 30 min, 5 min, 1 min and 5 s. Each acoustic sample was individually inspected using spectrograms, and also listened to when necessary. We eliminated samples containing excessive wave or boat noise, or noise of animals probing the hydrophone. The number of "clean" samples used in the following analyses is indicated in Table S1.

Two commonly used indices were calculated for each acoustic sample: the Sound Pressure Level (SPL) and the Acoustic Complexity Index (ACI). They were calculated on four bandwidths: 0.1–0.5 kHz, 0.5–1 kHz, 1–2 kHz and 2–7 kHz, based upon recent studies on coral reefs (e.g. Kaplan et al., 2015; Bertucci et al., 2016; Freeman and Freeman, 2016; Staaterman et al., 2017). Details of calculations are given in supplementary methods.

Time of day effects were examined for day, night, dawn, and dusk. Dusk and dawn choruses are important periods of acoustic activity for fishes, urchins and snapping shrimps (e.g. Radford et al., 2008; Kaplan et al., 2015; McWilliam et al., 2017). Recording during these periods is thus encouraged by Kaplan et al. (2015) and Krause and Farina (2016) as it may allow a better detection of differences among habitats or ecostates (Radford et al., 2010, 2014). However, the present study aimed to define a robust sampling scheme that can be implemented by managers and stakeholders with the most efficiency (i.e. in the most time-effective manner), even with limited logistical capacities (i.e. a single recording device). The rapid acoustic changes during dusk and dawn periods (Fig. 2) add too much variability to the recordings, restraining their use as tools to compare ecostates. As such, we focussed on analyses on samples recorded during periods of relative soundscape stability. These being day (from 2 h after sunrise to 2 h before sunset) and night (from 3 h after sunset to 2 h before sunrise) (Fig. 2).

Accounting for the above factors, we tested 64 combinations of settings to characterise soundscapes: two acoustic indices (SPL/ACI) × two times of day (day/night) × four bandwidths (0.1–0.5 kHz, 0.5–1 kHz, 1–2 kHz and 2–7 kHz) × four sample durations (30 min, 5 min, 1 min, 5 s).

2.2.4. Temporal effects on the discriminating power of the combinations

We initially examined how temporal effects influenced soundscape classification based on the above combinations. Three scales of temporal effects were considered: seasonal, lunar and day effects.

Seasonal effects were examined for all four Reunion Island ecostates during new moon phases. This phase was chosen as it is considered the period of peak biological activity (Radford et al., 2008; Staaterman et al., 2014), which should increase discriminating power. For each ecostate, ambient sound was recorded continuously for at least three consecutive days around the new moon in both cool (September-October 2016) and hot (March-April 2017) times of year (details in

Table 1

Means (± SD) of fish and benthic metrics from the visual surveys conducted for each ecostate during new moon phase in the cool season. Rankings are in parenthesis. Mean ecological ranking indicates the average of ranking values. VARG and COPA were evaluated during new moon in September 2016, and KIOS and IGES during new moon in October 2016. Results of the surveys conducted during other moon phases and season are presented in Fig. S1.

Eco state	Fish assemblage					Benthos		Mean ecostate ranking
	Species richness	Functional richness	Hab. special. species rich.	All species abundance	Large species abundance	Availability of refuges	Coral cover (%)	
KIOS	51 ± 2 **(1)**	38 ± 2 **(1)**	29 ± 1 **(1)**	275 ± 34 **(1)**	8 ± 2 **(3)**	15 ± 2 **(2)**	17 ± 3 **(2)**	1.6
VARG	43 ± 6 **(2)**	35 ± 5 **(2)**	24 ± 3 **(2)**	210 ± 26 **(4)**	13 ± 11 **(1)**	16 ± 2 **(1)**	28 ± 2 **(1)**	1.9
COPA	42 ± 4 **(3)**	33 ± 5 **(3)**	22 ± 4 **(3)**	235 ± 63 **(2)**	4 ± 2 **(4)**	14 ± 4 **(3)**	16 ± 1 **(4)**	3.1
IGES	40 ± 7 **(4)**	30 ± 6 **(4)**	20 ± 6 **(4)**	231 ± 47 **(3)**	11 ± 4 **(2)**	11 ± 2 **(4)**	17 ± 5 **(3)**	3.4

supplementary methods). Copacabana and Varangue soundscapes were recorded simultaneously in September 2016 and March 2017, and Kiosque and Igesa soundscapes in October 2016 and April 2017.

Effects of moon phase were examined for two ecostates (Copacabana and Varangue), whose soundscapes were recorded simultaneously across four consecutive moon phases (new moon, first quarter, full moon, last quarter), from September to October 2016 (cool season). Logistical constraints did not allow us to sample Kiosque and Igesa.

Effects of sampling day were examined by recording ambient sound continuously for at least three consecutive days centred around the middle of each moon phase at each of the 14 deployments (seasonal and lunar).

2.2.5. Statistical analyses

Using all clean sound samples, we first examined, for the 64 combinations, the effect of ecostate, season, and their interaction, with sampling day as a random factor. We then examined the effect of ecostate (Copacabana and Varangue), moon phase, and their interaction on the 64 combinations, with sampling day as a random factor. These analyses were performed with linear mixed models, while main significant effects were examined further using multiple comparison analyses performed with the package multcomp (Bretz et al., 2017). We determined the discriminating power of each combination as its capacity to discriminate among groups of ecostates (from zero groups = no significant differences among ecostates, to four groups = all four ecostates are significantly different). Following these two steps, we preferentially selected the best combinations consistently having the highest discriminating power among ecostates across both seasons, as well as stability in ranking ecostates across moon phases.

We then determined the minimum number of consecutive acoustic samples required by each of these best combinations to identify the same groups of ecostates. An increasing number of consecutive samples was randomly selected from each of the four ecostates (during day or night). At each increment of the number of samples, 1000 rankings of the four ecostates were examined, corresponding to 1000 random selections per ecostate. A successful number of replicates required was reached when the ranking obtained across ecostates was consistent in 950 over the 1000 cases. In order to simulate real field sampling conditions, the number of consecutive samples included samples to remove (i.e. containing wave noise, boat noise or noise of animals probing the hydrophone). The group of best combinations, associated to the minimum required sampling effort (the "optimal combinations") collectively formed our optimised sampling scheme.

2.3. Testing the wider applicability of the selected sampling scheme

The optimised acoustic sampling scheme determined from Reunion Island data was tested on Pacific coral reefs representing a range of potentially different ecostates. Six outer reef slope sites in New Caledonia were sampled once (Fig. 1): two sites in the "M'béré" fished area, two in the "Aboré" Marine Protected Area, and two at remote

reefs at "D'Entrecasteaux" and "Great Northern Lagoon", nearly pristine areas far from New Caledonia's northern tip. We recorded soundscapes continuously for 24 h on each site using the same recording setup deployed on Reunion Island, with additional 90 min videos simultaneously recorded with two GoPro cameras (San Mateo, USA) affixed to the tripod facing outwards. Sampling was conducted in July 2017 (cooler season) across different moon phases.

Due to logistical time constraints, the ecostate of each site was assessed from the video footage rather than the underwater visual censuses used in Reunion Island. Here, we identified individual fish and estimated an index of abundance (i.e. MaxN; see supplementary methods) for each species, using the software EventMeasure (SEAGIS, Bacchus Marsh, Australia). From this we were able to calculate the five fish metrics previously used on Reunion visual data (i.e. species richness, functional richness, richness in obligate coral reef dwelling species, total abundance, large species abundance; details in supplementary methods). These metrics were used to classify the six ecostates with a hierarchical clustering. We then classified the sites using our optimised acoustic sampling scheme, and compared this classification against the one obtained using fish assemblage data.

All statistical analyses were realised with R software (Version 3.4.2, R core Team 2017), with all tests performed at a 0.95 level of significance.

3. Results

3.1. Ecological surveys at Reunion Island

Based on the visual census data, we differentiated and ranked the four sites into four ecostates (Table 1). Kiosque (KIOS) and Varangue (VARG) sites had higher fish diversity associated with more complex habitats, including higher coral cover and availability of refuges. In contrast, Copacabana (COPA) and Igesa (IGES) were characterised by less diverse fish assemblages and less complex benthic habitats.

3.2. Discriminating power of the combinations across seasons

Soundscapes from the four ecostates revealed at least two major differences following the ecological ranking from Kiosque to Igesa: activity in the higher frequency bands (> 2 kHz) increased while activity in the 0.1–0.5 kHz band decreased (Fig. 3).

Out of the 64 combinations evaluated, 36 were able to discriminate at least three groups of ecostates in both seasons (Table 2), matching the ecological differences highlighted with the visual surveys. The remaining 28 combinations were eliminated from further analysis.

Although capable of differentiating among ecostates, season significantly affected 29 out of the 36 combinations selected, with an interaction between ecostate and season detected in 22 out of the 36 cases (Table 2). These results highlighted that for some ecostates, acoustic signatures differ between hot and cool seasons. Such variance over the year is not necessarily a reason not to use these combinations, but it does suggest that comparisons among ecostates should rely on data
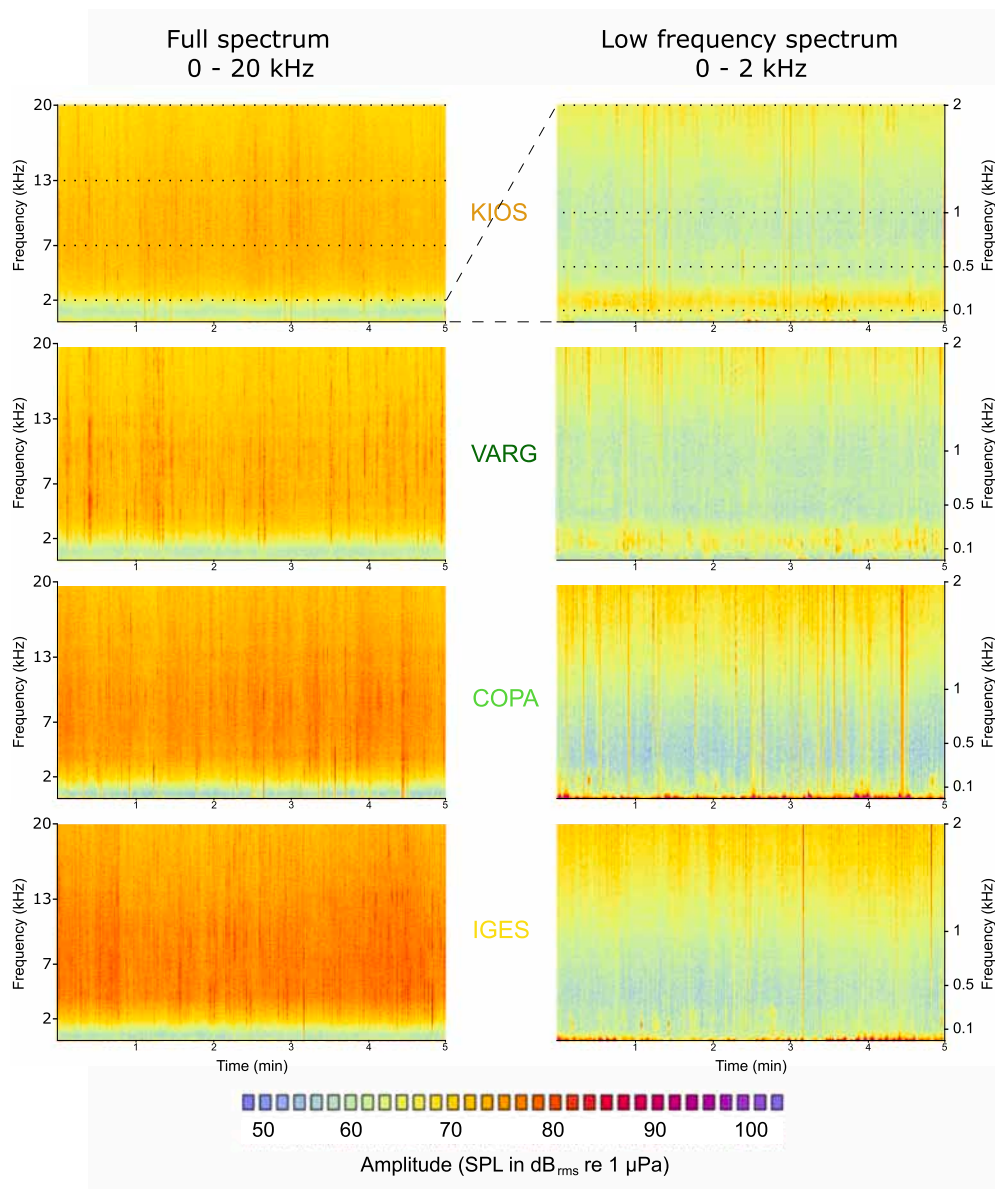
Fig. 3. Spectrograms of a 5 min sound sample recorded around midnight during new moon in the cool season at each of the four ecostates sampled at Reunion Island.

collected within a single period of year.

3.3. Discriminating power of the combinations across sampling days and moon phases

All 36 previously selected combinations successfully detected differences in ecological state between Copacabana and Varangue (Table 3). In most cases, sample duration did not affect the ranking. For example, $ACI_{night}2$-7 was significantly higher at Varangue than at Copacabana, regardless whether samples of 30 min, 5 min, 1 min or 5 s were considered (Table 3).

When the effects of moon phase and sampling day were examined across the two ecostates tested, multiple comparison analyses showed that, for 26 out of the 36 combinations, Copacabana and Varangue remained significantly different, regardless whether acoustic samples were obtained during different days and/or different moon phases (e.g., $SPL_{night}2$-7_{5s} in Fig. S2) (Table 3). These 26 "stable" combinations thus produce comparable results from samples recorded independently over several days around different moon phases (Table 3). The 10 combinations for which ranking was not stable across moon phases were

eliminated from further analyses.

Out of the 26 stable combinations, 11 were daytime combinations and 15 nighttime combinations, illustrating a slightly better stability and ability of nighttime combinations to discriminate among ecostates. In the cool season, 14 out of the 15 stable nighttime combinations (nine ACI, five SPL) discriminated the four ecostates (Tables 2 and 3), whereas in the hot season, discriminating power of nighttime combinations was slightly lower, with 12 out of the 15 stable nighttime combinations discriminating the four ecostates (Tables 2 and 3). For daytime combinations, discriminating power was also higher in the cool season, and better for ACI than SPL (Table 2 and 3).

3.4. Selection of the optimal combinations

The 26 acoustic combinations still under analysis, particularly those recorded at night, were able to discriminate among ecostates even when samples were recorded on different days or during different moon phases, but not in different seasons. To reduce this to a more practical number of combinations, we next identified which combinations performed best when sampling effort is reduced. Given seasonal variation,

Table 2
Results of the linear mixed models and multiple comparison analyses of all clean sound samples recorded in two different seasons at the four sites (i.e. ecostates) in Reunion Island. Discriminating power of combinations is indicated in both hot and cool seasons; dark blue: the combination discriminates all four ecostates; medium blue: the combination discriminates three groups of ecostates; light blue: the combination discriminates two groups; white: no significant differences among ecostates. Numbers indicate the minimum sampling effort (in minutes; inferred from the number of consecutive samples) required to obtain the ranking. *: $p \leq 0.5$; **: $p < 0.01$; ***: $p < 0.001$; NS: not significant; NA: samples sizes too low in the hot season to perform the analysis.

Index	Time of day	Bandwidth (kHz)	Sample duration	Ecostate (Fix)	Season (Fix)	Season:ecostate (Fix)	Sampling day (Random)	Hot Season	Cool Season	Selection (36 comb.)
SPL	DAY	0.1 - 0.5	30 min	NA	NA	NA	NA			
			5 min	***	***	*	NS			
			1 min	***	***	***	***			
			5 s	***	***	**	***			
		0.5 -1	30 min	NA	NA	NA	NA			
			5 min	***	***	NS	*			
			1 min	***	***	NS	***			
			5 s	***	***	NS	***			✓
		1 - 2	30 min	NA	NA	NA	NA			
			5 min	***	**	NS	*			✓
			1 min	***	***	NS	***			✓
			5 s	***	***	NS	***			✓
		2 - 7	30 min	NA	NA	NA	NA			
			5 min	***	*	NS	***			
			1 min	***	***	NS	***			
			5 s	***	***	*	***			✓
	NIGHT	0.1 - 0.5	30 min	*	NS	NS	NS			
			5 min	***	***	NS	***		250	✓
			1 min	***	***	**	***			✓
			5 s	***	***	**	***			✓
		0.5 -1	30 min	NS	NS	NS	NS			
			5 min	***	***	***	NS			
			1 min	***	***	***	***			
			5 s	***	***	***	***			✓
		1 - 2	30 min	**	NS	NS	NS			
			5 min	***	NS	***	***			
			1 min	***	NS	***	***			
			5 s	***	*	***	***		92	✓
		2 - 7	30 min	***	NS	NS	NS			
			5 min	***	**	NS	***			✓
			1 min	***	***	*	***		84	✓
			5 s	***	***	**	***	30	14	✓
ACI	DAY	0.1 - 0.5	30 min	NA	NA	NA	NA			
			5 min	**	*	NS	***			
			1 min	**	**	NS	***			
			5 s	**	*	*	***			✓
		0.5 -1	30 min	NA	NA	NA	NA			
			5 min	***	NS	NS	***			✓
			1 min	***	NS	NS	***			✓
			5 s	***	NS	NS	***			✓
		1 - 2	30 min	NA	NA	NA	NA			
			5 min	***	***	NS	***			✓
			1 min	***	***	*	***			✓
			5 s	***	***	NS	***			✓
		2 - 7	30 min	NA	NA	NA	NA			
			5 min	***	***	NS	***			✓
			1 min	***	***	NS	***			✓
			5 s	***	***	NS	***			✓
	NIGHT	0.1 - 0.5	30 min	**	NS	NS	***			
			5 min	*	*	NS	***			
			1 min	**	*	NS	***			
			5 s	**	*	NS	***			✓
		0.5 -1	30 min	***	***	***	NS			
			5 min	***	***	***	***	200		✓
			1 min	***	***	***	***			✓
			5 s	***	***	***	***			✓
		1 - 2	30 min	***	**	***	***			
			5 min	***	NS	***	***			✓
			1 min	***	NS	***	***			✓
			5 s	***	NS	***	***			✓
		2 - 7	30 min	***	***	**	***			
			5 min	***	***	**	***	25	75	✓
			1 min	***	***	**	***	20	72	✓
			5 s	***	***	**	***	20	64	✓

Table 3

Results of the linear mixed models and multiple comparison analyses of all clean sound samples recorded around different moon phases at Copacabana (COPA) and Varangue (VARG). Results of the multiple comparison indicate the relative ranking of COPA and VARG for each of the 64 combinations tested. Light grey: COPA > VARG; dark grey: VARG > COPA (at a minimum level of 0.95); white: no significant differences among ecostates; green: the relative ranking is stable when pooling samples from the four moon phases. The 36 combinations selected in Table 2 are shaded in the last column. *: p ≤ 0.5; **: p < 0.01; ***: p < 0.001; NS: not significant.

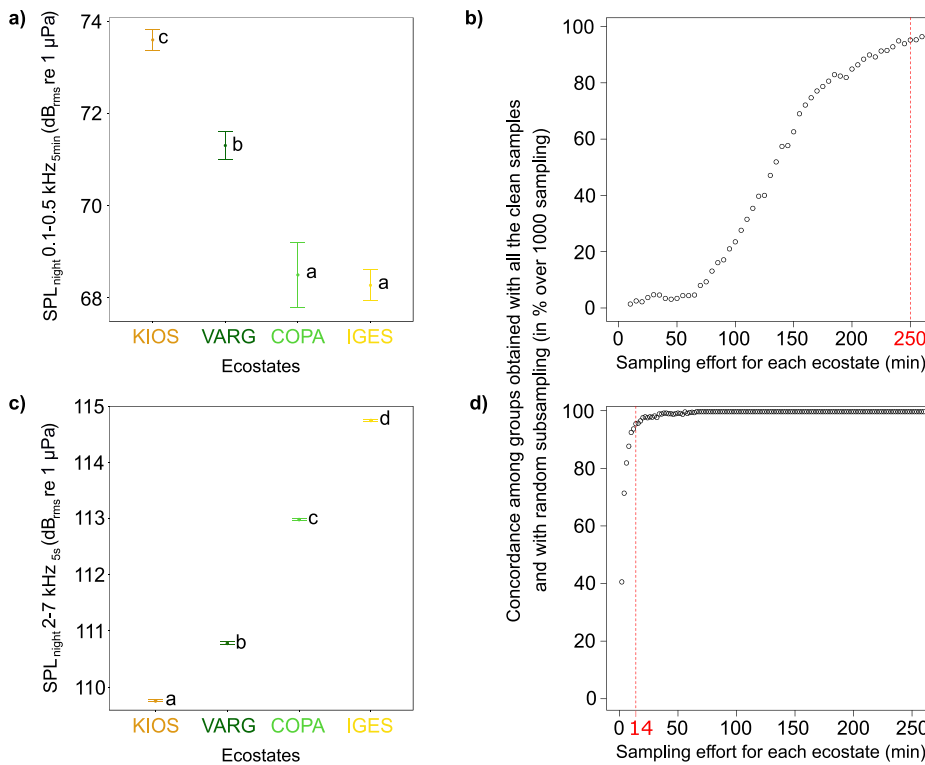| Index	Time of day	Bandwidth (kHz)	Sample duration	Eco state (fix)	Moon phase (fix)	Phase:ecostate (fix)	Sampling day (random)	Ranking stability across phases	New Moon	First Quart	Full Moon	Last Quart	Selection (26 comb.)
SPL	DAY	0.1 - 0.5	30 min	NS	NS	NS	NS						
			5 min	NS	NS	NS	***						
			1 min	NS	*	**	***						
			5 s	NS	**	*	***						
		0.5 -1	30 min	*	NS	NS	NS						
			5 min	***	NS	NS	***						✓
			1 min	***	NS	NS	***						
			5 s	***	NS	NS	***						
		1 - 2	30 min	***	*	NS	NS						✓
			5 min	***	*	NS	**						
			1 min	***	**	NS	***						
			5 s	***	**	NS	***						✓
		2 - 7	30 min	***	NS	NS	NS						
			5 min	***	NS	NS	***						
			1 min	***	*	NS	***						
			5 s	***	*	NS	***						✓
	NIGHT	0.1 - 0.5	30 min	***	NS	NS	NS						✓
			5 min	***	***	***	***						
			1 min	***	***	***	***						
			5 s	***	***	***	***						
		0.5 -1	30 min	NS	NS	NS	NS						
			5 min	***	***	*	***						
			1 min	**	***	*	***						
			5 s	***	***	*	***						
		1 - 2	30 min	***	**	NS	NS						
			5 min	***	***	NS	***						
			1 min	***	***	NS	***						✓
			5 s	***	***	NS	***						✓
		2 - 7	30 min	***	***	NS	NS						
			5 min	***	***	NS	***						✓
			1 min	***	***	NS	***						✓
			5 s	***	***	NS	***						✓
ACI	DAY	0.1 - 0.5	30 min	*	NS	NS	***						
			5 min	NS	NS	NS	***						
			1 min	NS	NS	NS	***						
			5 s	NS	NS	NS	***						
		0.5 -1	30 min	***	NS	NS	***						
			5 min	***	**	NS	***						✓
			1 min	***	*	NS	***						✓
			5 s	***	NS	NS	***						
		1 - 2	30 min	**	NS	NS	***						
			5 min	***	NS	NS	***						
			1 min	***	NS	NS	***						
			5 s	***	NS	NS	***						✓
		2 - 7	30 min	***	NS	NS	***						
			5 min	***	NS	NS	***						✓
			1 min	***	NS	NS	***						✓
			5 s	***	NS	NS	***						✓
	NIGHT	0.1 - 0.5	30 min	**	*	NS	***						
			5 min	**	*	NS	***						
			1 min	**	**	NS	***						
			5 s	***	*	NS	***						✓
		0.5 -1	30 min	***	***	**	NS						
			5 min	***	***	***	***						✓
			1 min	***	***	***	***						✓
			5 s	***	**	***	***						✓
		1 - 2	30 min	***	NS	*	***						
			5 min	***	*	*	***						
			1 min	***	*	*	***						
			5 s	***	*	*	***						✓
		2 - 7	30 min	***	*	NS	***						✓
			5 min	***	**	NS	***						✓
			1 min	***	*	NS	***						✓
			5 s	***	*	NS	***						✓

Fig. 4. Mean SPL values (± asymptotic 95%CI) calculated on all the clean samples recorded at night for the four ecostates in cool season, and results of the corresponding random subsampling analyses (1000 iterations): a) and b) for the 0.1–0.5 kHz bandwidth with a sample duration of 5 min, and c) and d) for the 2–7 kHz bandwidth with a sample duration of 5 s. Dashed red lines indicate the minimum sampling effort required to obtain the same ranking as in a) or c).

this step was conducted separately for both hot and cool seasons.

For eight out of the 26 combinations, the ranking of ecostates obtained with all the samples was also obtained with a random selection of a reduced number of consecutive samples (i.e. corresponding to a sampling effort of ≤250 min; see Fig. 4 and framed sampling efforts in Table 2).

Out of these eight combinations, we selected the five for which sampling effort was the lowest, while representing different types of indices and bandwidth, to maximise the representativeness of various aspects of the soundscape (Table 4). All five combinations involved nighttime recordings (Table 4), however acoustic rankings were identical whether daytime or nighttime samples were considered. The ranking consistency across daytime and nighttime combinations therefore allows visual data sampled at daytime to be compared with acoustic data sampled at night. The group of these five combinations of sampling settings was considered the most efficient and stable to confidently differentiate among ecostates across various temporal scales. The use of all five combinations simultaneously should therefore provide appropriate soundscape classification at other coral reef systems.

3.5. Validation of the sampling scheme: New Caledonia data

Soundscapes from New Caledonia and Reunion Island presented

marked differences (Figs. 3 and 5). In particular, activity in the 0.5–1 kHz band was higher in New Caledonia while activity in the frequency bands > 2 kHz was higher in Reunion Island. In New Caledonia, ENT1 and GNL1 presented greater activity in the 0.1–0.5 kHz band, and lower activity in the frequency bands > 2 kHz, than the other ecostates (Fig. 5).

Classifications obtained from the five optimal acoustic combinations (Fig. 6a; Table S2) and the five ecological metrics (Fig. 6b; Table S2) were congruent (Fig. 6c.). This indicates that the optimised sampling scheme developed in Reunion Island was successful in differentiating and ranking ecostates on New Caledonian reefs to the same degree as determined by visual census. In both cases, the first node separated the pristine ecostates (GNL1 and ENT1) from the others, indicating that the pristine sites were most different. Similarly, both methods also separated MPA (ABO3 and ABO4) from non-MPA ecostates (MBE2 and MBE5) (Fig. 6c). Interestingly, the acoustic classification was more sensitive to detecting differences between sites than the visual data, suggesting it may be capable of detecting more subtle ecostate differences.

4. Discussion

Coral reefs are considered the most complex and biodiverse of

Table 4
Minimum sampling effort (recording time) and acoustic ranking of Reunion Island ecostates (based on the index values) for the selected five combinations. KIOS: Kiosque; VARG: Varangue; COPA: Copacabana; IGES: Igesa.

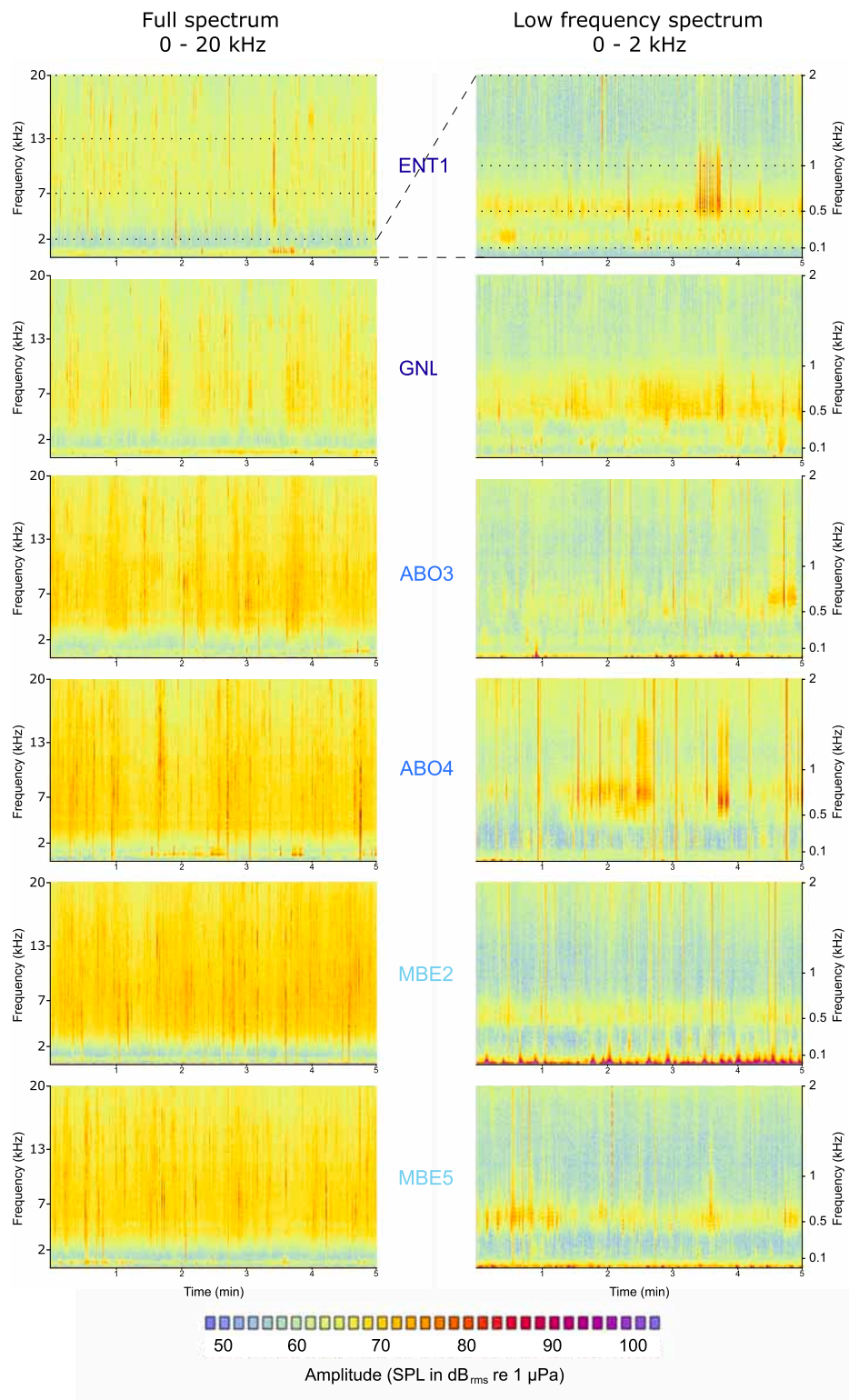| Optimal combination					Acoustic ranking of Reunion Island ecostates
Combination				Minimum sampling effort (min)	
Index	Time of day	Bandwidth (kHz)	Sample duration		
SPL	night	0.1–0.5	5 min	250	KIOS > VARG > COPA = IGES
SPL	night	1–2	5 s	92	KIOS < VARG < COPA < IGES
SPL	night	2–7	5 s	14	KIOS < VARG < COPA < IGES
ACI	night	0.5–1	5 min	200	KIOS < VARG < COPA = IGES
ACI	night	2–7	5 s	20	KIOS < COPA < IGES < VARG

Fig. 5. Spectrograms of a 5 min sound sample recorded around midnight on each of the six ecostates sampled in New Caledonia.

marine ecosystems (Moberg and Folke, 1999). Our study demonstrated that, in spite of this complexity, simple proxies such as a small suite of acoustic indices are capable of discriminating among different ecostates. We suggest that this sampling scheme could also be used to monitor simpler and less diverse marine ecosystems, equally at risk to rapid climate changes and human impacts.

For each of the five combinations selected, ecostates were identically ranked whether acoustic samples were recorded during the day or night. This important finding allowed us to compare ecostates evaluated visually at daytime with acoustic characteristics recorded at night. In both regions examined, ecostates with diverse and/or abundant fish assemblages showed highest values of SPL in the 0.1–0.5 kHz band, as per other studies (Kennedy et al., 2010; Kaplan et al., 2015; Freeman and Freeman, 2016; Staaterman et al., 2017). Similarly, more
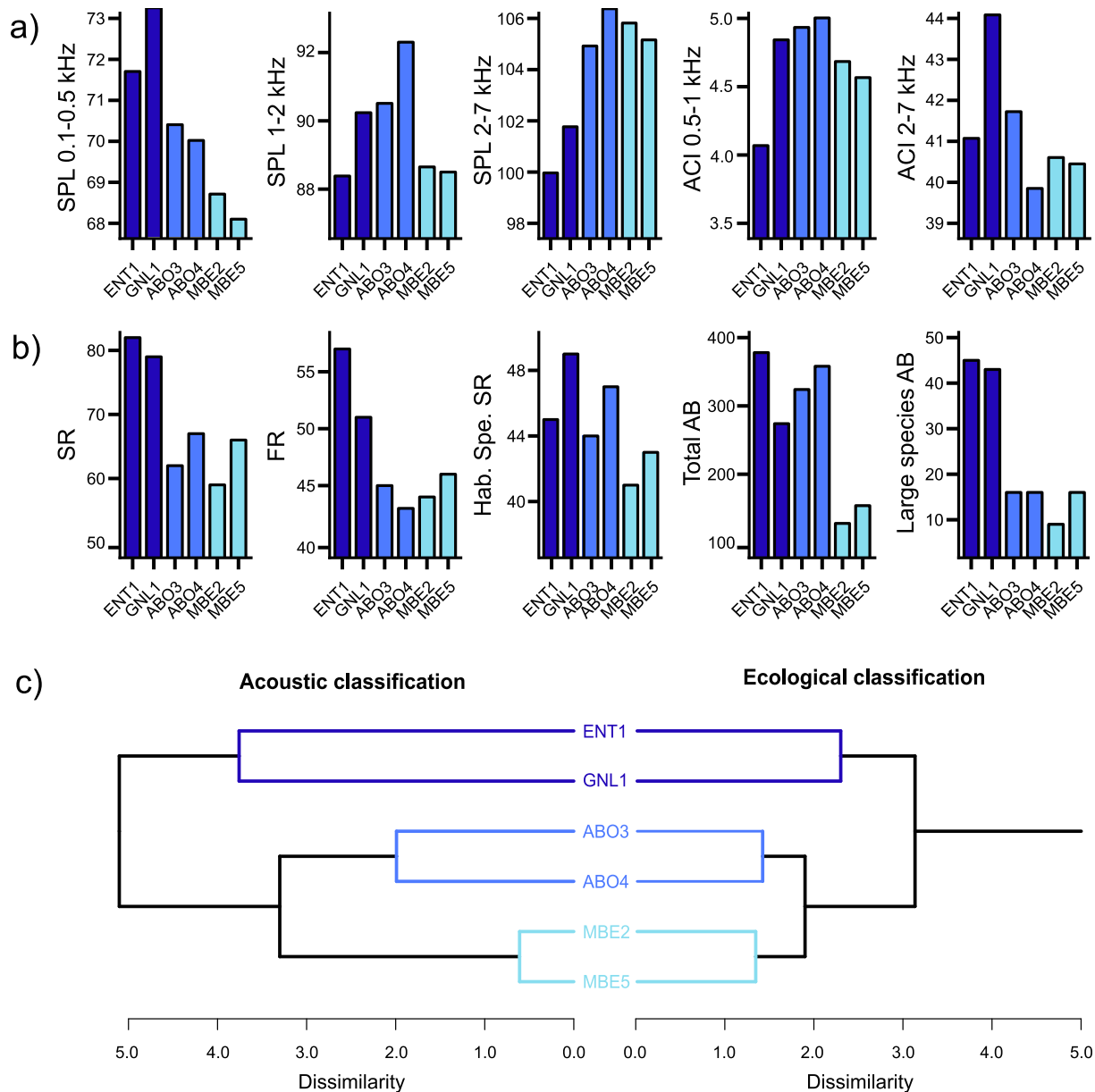
Fig. 6. a) Values of the five optimal ecoacoustic combinations (SPL in dB$_{rms}$ re 1 µPa / ACI with no units) calculated on New Caledonia acoustic data; b) Values of five ecological metrics calculated on New Caledonia visual fish data; SR: Species Richness; FR: Functional Richness; Hab.Spe.SR: habitat specialised Species Richness; AB: abundance c) Hierarchical classification trees obtained with the five ecoacoustic combinations selected in this study (left), and the five ecological metrics reflecting the state of fish assemblages (right). ENT1: D'Entrecasteaux1, GNL1: Great Northern Lagoon1, MBE2: M'berré2, MBE5: M'berré5, ABO3: Aboré3, ABO4: Aboré4.

degraded ecostates at our two locations revealed highest values of SPL in the 2–7 kHz, as in Nedelec et al. (2015) and Freeman and Freeman (2016). The three other selected combinations do not individually allow such clear ecological interpretation, however they collectively add to the power to discriminate among ecostates. In spite of marked differences in the soundscapes recorded in Reunion Island and New Caledonia, the simultaneous use of the five combinations was effective in both regions. This observation has two implications: i) further investigations are needed to understand the influence of biogeographic variations in coral reef assemblages on the ecoacoustic indices used (Bertucci et al., 2016; Staaterman et al., 2017; Bolgan et al., 2018); and ii) acoustic monitoring of marine ecosystems should not rely on a single index, but on the simultaneous use of different ecoacoustic indices calculated on several frequency bands (Sueur et al., 2014; Bolgan et al., 2018; Phillips et al., 2018). For this reason we suggest using the optimal group of five combinations simultaneously.

Two main results reinforced this view. Firstly, either SPL or ACI calculated on various frequency bands may provide complementary information. For a given index, lower frequency (< 1 kHz) combinations are only loosely correlated with higher frequency (> 2 kHz) combinations, while both are moderately correlated to medium frequency (1–2 kHz) combinations. Very similar results have been reported from the Hawaiian archipelago (Freeman and Freeman, 2016). Also, low frequency combinations could not detect significant differences between Copacabana and Igesa, whereas high frequency combinations could. Without using both frequency bands, successful differentiation among some ecostates may not be possible. Secondly, the information obtained by using both SPL and ACI indices appeared to be complementary: for a same frequency band, we obtained distinct rankings of the four Reunion Island ecostates depending on whether SPL or ACI was used. For example, in the 2–7 kHz frequency band, the site Varangue had the second lowest level for SPL but the highest level

for ACI. Similar contrasts in the information provided by amplitude level and ACI were highlighted by Bertucci et al. (2016), Staaterman et al. (2017), and Pieretti et al. (2017) in tropical and temperate reefs. It would be interesting to confirm the results obtained with the ACI in the 2–7 kHz band by applying an amplitude filter prior to its calculation as proposed by Buscaino et al. (2016) and Pieretti et al. (2017). These results emphasise the richness and complementarity of the acoustic information provided by the five combinations selected in our study.

The selected optimal combinations all relied on acoustic data sampled at night. Indeed, nocturnal combinations had marginally greater discriminating power among ecostates, required lower sampling effort and were more stable across moon phases than daytime combinations. These results agree with the findings of Radford et al. (2014) and Bertucci et al. (2016) who highlighted greater differences among reef sites when using nightly recordings, and found less variance in ACI and SPL for nighttime indices (Bertucci et al. 2016), suggesting a higher temporal stability. Nocturnal sampling may also be less impacted by anthropogenic effects such as recreational boating, and can allow other sampling to occur during the day which may affect recordings if conducted simultaneously. Recording at dusk and dawn is encouraged by Kaplan et al. (2015) and Krause and Farina (2016) as they are moments when important information about animal assemblages may be conveyed through choruses (e.g. Radford et al., 2008; Kaplan et al., 2015; McWilliam et al., 2017). However, rapid acoustic changes during dusk and dawn periods prevent the comparison of soundscapes sampled consecutively at different sites. In addition, the short dusk and dawn periods can make obtaining a minimum number of clean field recordings difficult, particularly in areas exposed to sea breezes or intense boat activity, weakening the potential to classify reef ecostates efficiently. In the present study we aimed to develop a sampling scheme which can be implemented easily, even under logistic and time constraints. Hence we recommend nighttime sampling rather than at dawn or dusk.

Although indices' values calculated with the five selected combinations had some variance among successive nights and moon phases, these variations did not compromise their capacity to discriminate among ecostates. This allows this method to be used across sites recorded during different days or even moon phases, which is typically the case during a field campaign. However, while the ranking of ecostates remained stable within each season, strong seasonal variation prevented the across-season comparisons. This is likely linked to seasonal variations in the activity, chorusing and presence of mobile fauna (e.g. McWilliam et al., 2017), and environmental changes such as upwelling events which may reduce fish sound production (Mann and Grothues, 2009). Louder activity and greater abundance of vocal animals in the hot season may increase variance and explain why we found ecoacoustic indices to have greater discriminating power during the cool season. This result must be taken with care, however, as fewer samples were available for the hot season, which could have affected the significance of the tests.

Our approach emphasized the use of two sample durations, 5 s and 5 min, which could result from large differences in the type of activity by organisms captured at lower and higher frequencies. SPL calculated for frequencies > 2 kHz are significantly correlated with the rate of snaps produced by snapping shrimps (Lillis and Mooney, 2018). As a snap lasts approximately 2 ms (Versluis et al., 2000; Bohnenstiehl et al., 2016), a single 5 s sample recorded on tropical or temperate reefs can contain tens to hundreds of snaps (Radford et al., 2010, 2014; Nedelec et al., 2015; Bohnenstiehl et al., 2016; Lillis and Mooney, 2018), providing a reasonable insight of snapping shrimp activity, and thus differentiation of ecostate. Alternatively, biophony at frequencies below 1 kHz is dominated by fish sounds (Lobel et al., 2010; Tricas and Boyle, 2014). Various activities of fishes (feeding, courtship, spawning, defence, escape) produce sounds that last from approximately 100 ms to a few seconds (Lobel et al., 2010; Tricas and Boyle 2014) and are far less frequent than shrimp snaps (Tricas and Boyle, 2014). It appears,

therefore, that 5 s samples fail to reflect the activity of fishes and that such short sample durations produce indices that are too variable to enable a reliable evaluation of differences in fish assemblages among ecostates. In contrast, a single 5 min sample can capture a large number of signals produced by fishes. Similarly, although a sampling effort of 250 min should be adopted to capture the entire reef soundscape, recording a 20 min clip appears sufficient to obtain a reliable characterisation of the high frequency soundscape. This has important implications for conducting acoustic surveys, suggesting that numerous sites can be monitored during a single night using a single recorder.

The minimal sampling durations emphasized in the present study included samples to remove (i.e. containing wave noise, boat noise or noise of animals probing the hydrophone). While boat activity was reduced in the vicinity of Reunion Island reef slopes at night, a substantial number of samples was disturbed by waves, in spite of favourable oceanic conditions during deployments. This suggests that sampling effort could be reduced under calm sea states.

The time-consuming step of data screening and cleaning is still a major limitation for a wide implementation of PAM. While geophony or anthropony may not influence indices like the ACI (e.g. Buscaino et al., 2016), these sounds strongly affect the values of other indices such as amplitude (i.e. SPL or PSD), in particular in the frequency bands below 2 kHz (Hildebrand, 2009). For example, in our study, discriminating Varangue from Copacabana with SPL calculated on the 0.1–0.5 kHz bandwidth would have been more difficult without removing disturbed samples, as Copacabana was more exposed to waves which augmented low frequency sound levels. Ongoing advances in automated detection and classification of biophony (e.g. Lin et al., 2017; Ibrahim et al., 2018), geophony and anthropony (e.g. Phillips et al., 2018) are expected to bring effective tools for cleaning ambient sound samples soon.

In conclusion, this study provides a tested and validated optimised sampling scheme to compare the ecostate of coral reefs across the Indo-Pacific using PAM. This can facilitate the prioritisation of conservation targets, and aid in the detection of disturbances (i.e. ecostate changes). The successful application of the five complementary combinations optimised at Indian Ocean Reunion Island on West Pacific New Caledonian reefs suggests their wide applicability, and their capacity to detect ecological differences among sites with different species assemblages. We encourage additional studies in other regions to use this method and examine the use of further ecoacoustic indices. It is hoped that uptake of this methodology in the future will provide another tool for classifying reefs and allow remote sampling of reef ecostates at wider spatial scales.

5. Author's contributions

SE and JHB conceived the ideas; SE, JHB, AB and FC designed methodology; SE, IUB, WDR and LV collected the data; SE, TS, IUB, GM and LV performed data handling; AB, SE, and FC analysed the data; SE, JHB and WDR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

6. Data accessibility

All the acoustic data used in this study represents > 800 GB: reasonable selections of sound files will be available from SE (simon_e-lise@hotmail.com) upon request.

Declaration of Competing 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105627.

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