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NOTE

Coral-associated Symbiodiniaceae dynamics during the 2016 mass bleaching event in New Caledonia

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Abstract The ecological success of shallow water corals hinges on their association with photosynthetic Symbiodiniaceae algae. This is affected by environmental drivers among which sea temperature is pivotal. In 2016, a prolonged heat wave challenged New Caledonia reefs triggering a severe bleaching event. Here, we tracked 72 coral colonies comprising two species of *Pocillopora* and *Porites* from a cross-shelf gradient during the event and subsequent recovery period. Symbiodiniaceae association over time was assessed using the ITS2 marker. Bleaching prevalence and photosynthetic efficiency showed that 83% of *Pocillopora* and 29% of *Porites* colonies were affected, with corals from a mid-shelf site having been most impacted. The majority of tracked colonies recovered by December 2016, with a recorded 33% mortality of *Pocillopora,* while *Porites* showed higher resilience. Consistent with previous studies, genotyping data suggest stable, species- and site-specific associations between corals and Symbiodiniaceae.

Keywords Symbiodiniaceae · Coral bleaching · Species-specificity · Next-generation sequencing · ITS2 · *SymPortal*

Introduction

Coral reef ecosystems rely on the relationship between scleractinian corals and their associated microorganisms, comprising photosynthetic algae of the family Symbiodiniaceae and bacteria, among other entities such as endolithic algae, virus, fungi, and archaea (Blackall et al. 2015; LaJeunesse et al. 2018). This association is challenged by stress conditions and, particularly, it might be disrupted under thermal stress which can lead to coral bleaching (Lesser 2011). The breakdown of coral-algae symbiosis leaves the coral hosts deprived of their nutritional needs (Davy et al. 2012) and, if

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this relationship is not promptly reestablished, the host experiences impaired metabolic efficiency, and ultimately, mortality (Rädecker et al. 2021). If the host survives, a change/displacement of symbionts can occur, with compatible taxa proliferating over others. These can include genotypes more tolerant with respect to the prevailing environmental condition.

Resolving diversity and distribution of Symbiodiniaceae harbored within different corals genetically is a key for identifying taxa that may facilitate holobiont adaptation and enhance resilience to prevalent stressors, such as heat (Hume et al. 2019; Osman et al. 2018). Growing evidence suggests co-evolution of Symbiodiniaceae and their hosts, resulting in high host specificity (Terraneo et al. 2019, 2023; Hume et al. 2020; Pootakham et al. 2021) and fidelity (*i.e.*, specificity trough time and different environments) (Thornill et al. 2006; Stat et al. 2009; Howells et al. 2019; Keshavmurthy et al. 2020), with maintenance of the same symbionts following prolonged stress.

New Caledonia coral reefs escaped mass bleaching for the past 30 years (Benzoni et al. 2017). However, during the austral summer of 2016, the El Niño Southern Oscillation coupled with strong westerly wind variability affected reefs around la Grande-Terre, Entrecasteaux Reefs, and Île des Pins (Payri et al. 2018). The first bleaching reports in New Caledonia dated to early February 2016, with sea surface temperatures exceeding 1–2 °C monthly averages and reaching 4–8 °C degree heating weeks between February and May 2016 (https://coralreefwatch.noaa.gov/satellite/dhw.php).

This study assessed Symbiodiniaceae assemblage, diversity, and photosynthetic performances across > 30 coral colonies during and after the bleaching event. Two *Pocillopora* species (*Pocillopora acuta* and *Pocillopora damicornis*—sensu Schmidt-Roach et al. 2014) and two *Porites* species (*Porites cylindrica* and *Porites* sp.) were sampled at the peak of the bleaching episode in February 2016 and for the following 11 months. Photosynthetic efficiency was assessed in situ and next-generation sequencing employed to characterize ITS2 type profiles as proxies for algal genotypes to characterize Symbiodiniaceae diversity and spatiotemporal dynamics.

Materials and methods

Field work

A total of 42 *Porites* and 30 *Pocillopora* colonies were tagged underwater in February 2016 right after the onset of the mass bleaching event. Colonies were selected on 20 m permanent transects at 2 m depth at four sites on a cross-shelf gradient (Fig. 1 a, b). Colonies were photographed in situ to provide visual bleaching prevalence records following Hill & Wilkinson (2004). Bleaching prevalence boxplots were visualized using ggplot2 in R (Wickham 2016) (Fig. 1d–f).

A total of 85 *Pocillopora* and 105 *Porites* fragments were collected from tagged colonies at four timepoints in 2016 for molecular analyses, starting at the peak of the hot sea temperature in February ($n = 70$), followed by April ($n = 42$), July ($n = 35$) and December ($n = 43$) (Online Resource 1). At each site and sampling time, we measured photosynthetic efficiency (F_v/F_m) of photosystem II of tagged corals using a diving pulse-amplitude modulated fluorometer (PAM) (Walz Gmbh, Germany) (Jones et al. 1998) (Online Resources 2, 3 for details).

Sea temperature (ST) time series were recorded using thermographs ReefTEMPS/GOPS deployed at each permanent transect (Fig. 1c) and are available at https://www.reeftemps.science (Varillon et al. 2018). Per each site, mean daily ST was extrapolated using MATLAB software (https://it.mathworks.com/products/matlab.html), based on one recording per hour (Online Resource 4).

Molecular laboratory analyses

DNA was extracted from corals using DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) at Institut de Recherche pour le Développement (New Caledonia). To barcode *Pocillopora*, PCR amplifications of the mitochondrial open reading frame (mtORF) were performed as detailed in Online Resource 2. Symbiodiniaceae type profiles were characterized using ITS2 amplicons for Illumina MiSeq at King Abdullah University of Science and Technology (Saudi Arabia) (Online Resource 2 for details).

Bioinformatic data processing and statistical analyses

Symbiodiniaceae NGS ITS2 data were analyzed using the *SymPortal* online framework (https://symportal.org) following the pipeline summarized in Hume et al. (2019) (Online Resources 5, 6). Symbiodiniaceae ITS2 diversity was analyzed with respect to coral host genus, coral host species, sampling locality, and sampling time as potential drivers for assemblage differences using permutational multivariate analysis of the variance (PERMANOVA) on Bray–Curtis matrices of the ITS2 type profile relative abundances using PRIMER 7 (Primer-E, UK) with the add-on PERMANOVA + package (Anderson et al. 2008). Canonical analysis of principal coordinates (CAP) for each single factor was also performed as a validation (Anderson et al. 2003). Coral-associated ITS2 type profiles were visualized as stacked bar plots using ggplot2 in R (Wickham 2016).

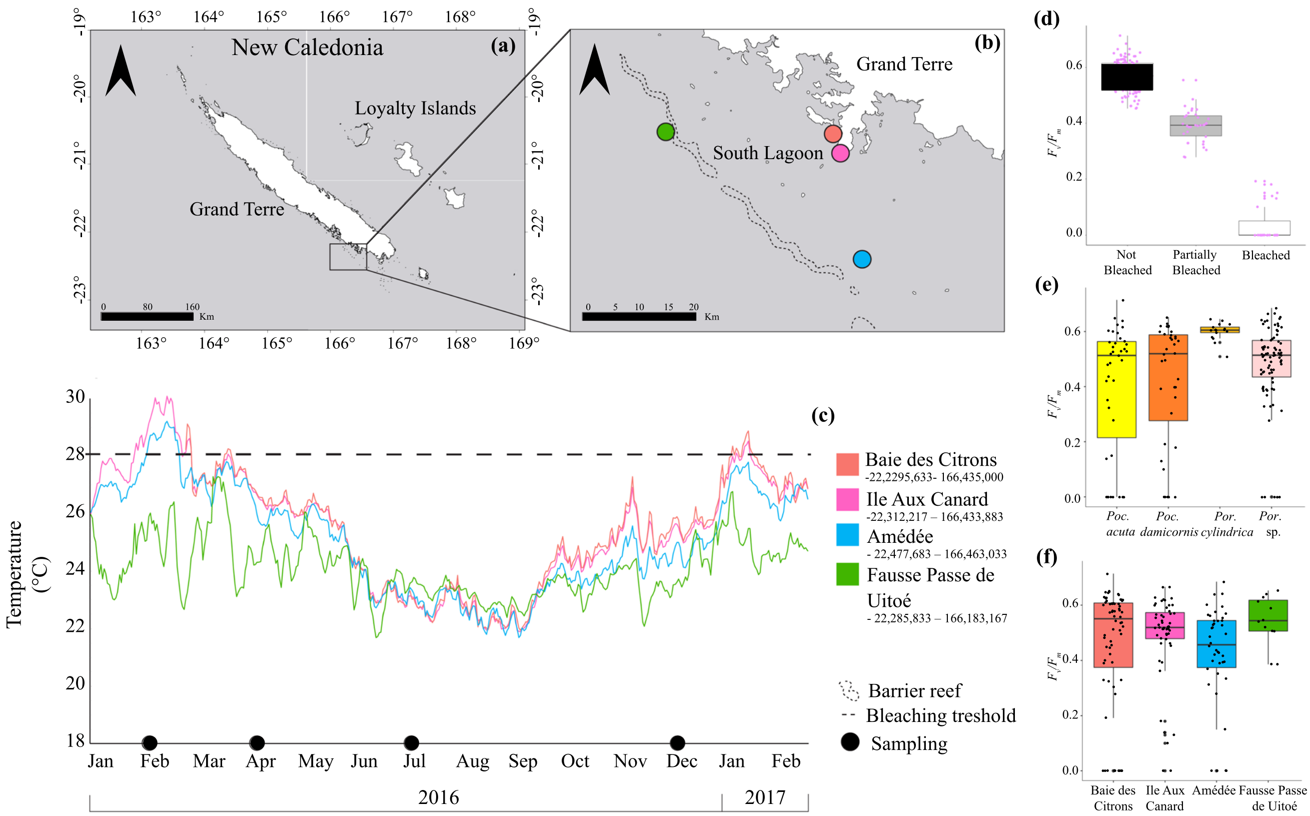

Fig. 1 **a** New Caledonia map with **b** zoom in on the four sampling sites. **c** Daily average sea temperature in 2016 at the collection sites. **d**–**f** Photosynthetic efficiency (Fv/Fm) measured using a diving PAM fluorometer for **d** in situ bleaching severity of coral colonies, **e** coral species, **f** surveyed sites

Results and discussion

In February 2016, https://coralreefwatch.noaa.gov/ identified the seas around New Caledonia as coral bleaching hotspot (Benzoni et al. 2017). Our in situ measurements confirmed that 2016 was the hottest year on record at all sampling sites (Online Resources 2, 4).

Genotyping confirmed the presence of *Poc. acuta* and *Poc. damicornis,* with a cross-shelf trend in species frequency, and no occurrence at the outer barrier site (Online Resource 1). Using the growth form, we identified six colonies of *Por. cylindrica* at Baie des Citrons and 36 of a massive *Por.* sp., distributed across all four sites. Species boundaries for massive *Porites* remain challenging (Terraneo et al. 2021), thus we decided to treat *Por.* sp. as a single species and discuss hereafter the potential for a species complex.

Different susceptibility and recovery patterns were uncovered (Figs. 1, 2). *Pocillopora* was the most adversely affected over the 11-month period. Notably, 33% of *Pocillopora* colonies died, displaying no significant species-specific trend, as opposed to only one massive *Por.* sp. Conversely, *Por. cylindrica* remained unaffected. Overall, the majority of colonies showing bleaching signs in February 2016 had recovered by December 2016. However, the offshore site exhibited an inverted trend, possibly linked to temperature fluctuations throughout the year.

Massive and encrusting corals are generally considered more tolerant to environmental stress compared to branching ones. Various factors contribute to difference in bleaching susceptibility and mortality among corals exhibiting different growth forms. Our results showed that *Pocillopora* had higher bleaching and mortality rates compared to *Porites*, regardless of the growth form in the latter. This can be related to the fact that the two genera belong to two distinct evolutionary lineages (complex and robust, respectively). Coral tissue is superficial in *Pocillopora*, while goes deeper into *Porites* porous skeleton, allowing for more nutrient reserves (Fox et al. 2021).

ITS2 genotyping highlighted the Symbiodiniaceae genus *Cladocopium* as the most represented in our samples (Fig. 2). This result is consistent with previous studies that assessed symbiont assemblages in the Pacific (e.g., LaJeunesse et al. 2003; Magalon et al. 2007). *Pocillopora* has been previously found specifically in association with *Cladocopium* species, *i.e., C. laturosum* and *C. pacificum*, over large distances in the tropical and subtropical Pacific,

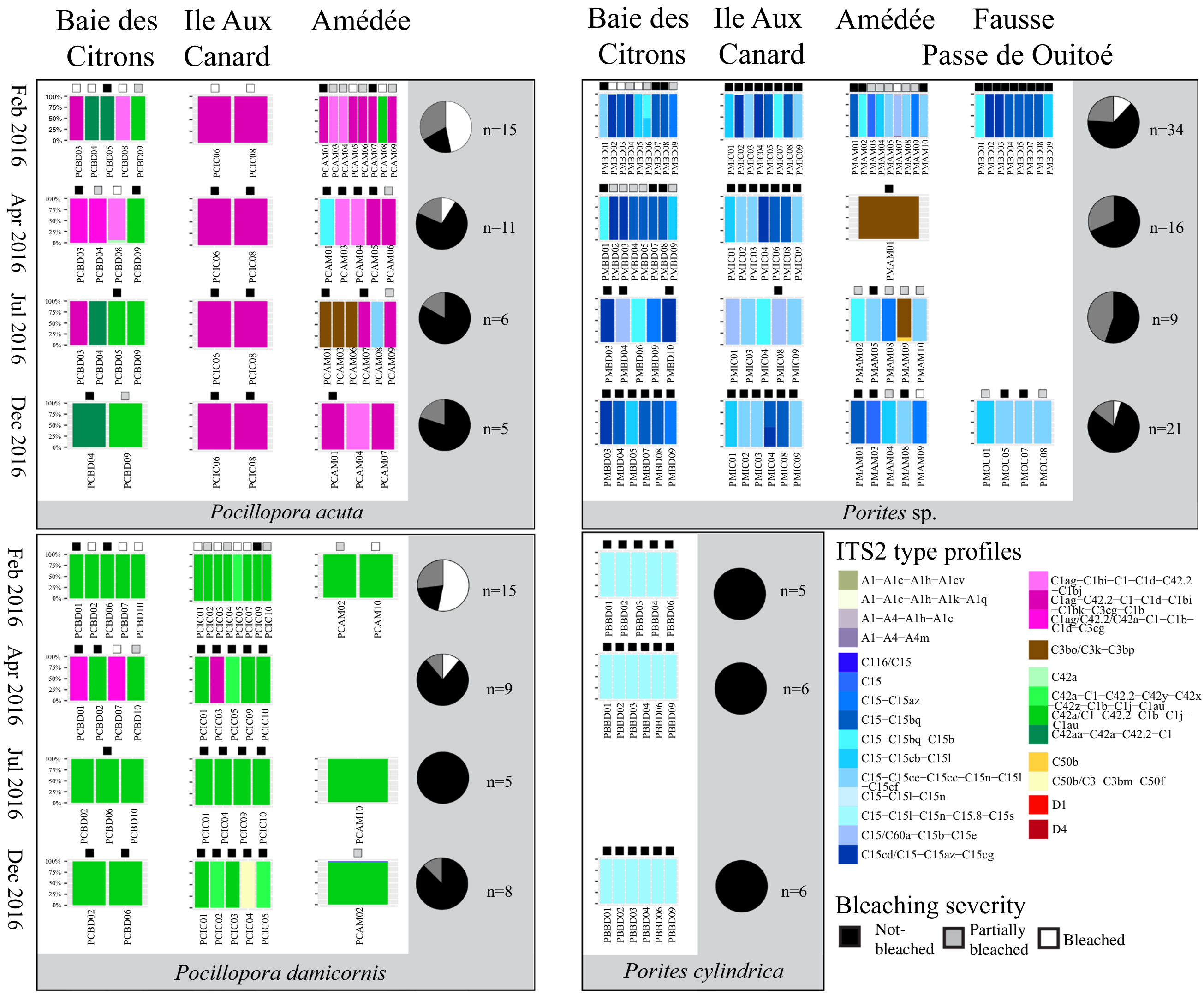

Fig. 2 Symbiodiniaceae ITS2 type profiles per species in time. Symbiodiniaceae ITS2 type profiles associated with *Poc. acuta*, *Poc. damicornis*, *Por. cylindrica*, and *Por.* sp. at four times during 2016 (February, April, July, December). Each stacked horizontal bar represents a single coral colony

comprising New Caledonia (Turham et al. 2021). In our work, at all sites and times *Poc. damicornis* was mainly associated with one type profile belonging to the C42 radiation. The finding of ITS2 sequences C42 and C1d, and related variants, at all sites and times from colonies of *Pocillopora* is diagnostic of recently described *Cladocopium* co-evolved with these hosts (Turnham et al. 2021). While the ITS2 marker region is widely used to discriminate among close related Symbiodiniaceae lineages, the inclusion of additional single-copy markers would have complemented the NGS rDNA information and ultimately informed the species assignation for the current study (Sampayo et al. 2009; Turnham et al. 2021; LaJeunesse et al. 2022). For example, this could have helped discriminate whether the different ITS2 type profiles retrieved in *Poc. acuta* represent different Symbiodiniaceae species from the symbionts associated to *Poc. damicornis*.

Porites has also been shown to predominantly associate with *Cladocopium* in the Pacific, comprising New Caledonia (Camp et al. 2020). In our study, *Porites* mainly associated with taxa in the C15 radiation, in agreement with previous studies where closely related C15 taxa were found with *Porites* across a wide range of environments (e.g., LaJeunesse et al. 2003; Fitt et al. 2009; Camp et al. 2020; Hoadley et al. 2021). Our results showed that *Por. cylindrica* did not show any signs of bleaching and presented a unique C15-related ITS2 type profile at all times, supporting the notion that corals exhibiting C15 taxa maintain efficient photosynthetic activity when exposed to thermal anomalies (Fisher et al. 2012; Fitt et al. 2009).

Table 1 PERMANOVA results for host genus (*Pocillopora, Porites*), host species (*Poc. acuta*, *Poc. damicornis*, *Por. cylindrica*, *Por.* sp.), sampling site (inshore sites, mid-shelf island, outer barrier), and sampling time during 2016 (February, April, July, December) for the variable Symbiodiniaceae ITS2 type profiles

Predictor	Df	Res	Pseudo-F	*P*-value	CAP (%)
Host genus	1	188	24.623	**0.001**	97.36
Host species	3	186	26.516	**0.001**	93.68
Cross-shelf gradient	2	187	4.8293	**0.001**	75.78
Sampling time	3	186	1.259	0.142	24.84

Significant *P*-values in bold

Df Degrees of freedom, *Res* Residual degree of freedom, *CAP* Cross validation PERMANOVA

The collected *Por.* sp. showed higher symbiont diversity, which might relate to the fact that multiple massive *Porites* species may have been sampled. Hoadley et al. (2021) confirmed the presence of species- and site-specific Symbiodiniaceae lineages in *Por. rus* and *Por. cylindrica* across reefs in Palau, documenting the physiological distinction of closely related lineages within the C15 radiation, and proving they are pivotal in species ability to cope with thermal stress. To conclude, they showed how high temperature boosted symbiont carbon assimilation and delivery in inshore *Por. cylindrica*, which might align with the scenario we recovered at Baie des Citrons.

The ITS2 type profiles correlated with coral host identity and displayed significant across-shelf structuring (Table 1). Yet, no significant temporal variation was found. However, the total numbers of colonies tracked from February 2016 to December 2016 was less compared to the initial number of tracked colonies (Online Resource 7), so we cannot confirm this was the case for all colonies.

In conclusion, the Symbiodiniaceae hosted in the investigated corals in New Caledonia showed species- and site-specific partitioning, which appeared stable under warming pressure in time. As symbiotic algae genotypes might play a crucial role in coral thermal tolerance, our results encourage further exploration of these relationships to unravel the adaptation potential of Symbiodiniaceae to environmental disturbances and its impact on coral health.

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Data availability Sequence data have been submitted at https://www.ncbi.nlm.nih.gov/sra under BioProject ID: PRJNA856438.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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