RESEARCH ARTICLE

Effects of temperature and UVR on organic matter fluxes and the metabolic activity of Acropora muricata

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ABSTRACT
Coral bleaching events are predicted to occur more frequently in the coming decades with global warming. The susceptibility of corals to bleaching during thermal stress episodes depends on many factors, including the magnitude of thermal stress and irradiance. The interactions among these two factors, and in particular with ultraviolet radiation (UVR), the most harmful component of light, are more complex than assumed, and are not yet well understood. This paper explores the individual and combined effects of temperature and UVR on the metabolism of Acropora muricata, one of the most abundant coral species worldwide. Particulate and dissolved organic matter (POM/DOM) fluxes and organic matter (OM) degradation by the mucus-associated bacteria were also monitored in all conditions. The results show that UVR exposure exacerbated the temperature-induced bleaching, but did not affect OM fluxes, which were only altered by seawater warming. Temperature increase induced a shift from POM release and DOM uptake in healthy corals to POM uptake and DOM release in stressed ones. POM uptake was linked to a significant grazing of pico- and nanoplanckton particles during the incubation, to fulfil the energetic requirements of A. muricata in the absence of autotrophy. Finally, OM degradation by mucus-associated bacterial activity was unaffected by UVR exposure, but significantly increased under high temperature. Altogether, our results demonstrate that seawater warming and UVR not only affect coral physiology, but also the way corals interact with the surrounding seawater, with potential consequences for coral reef biogeochemical cycles and food webs.

KEY WORDS: Acropora muricata, Thermal stress, UV radiation, Climate change, Organic matter fluxes, Microbial loop

INTRODUCTION
Tropical marine ecosystems, including coral reefs, harbor more than 30% of the marine biodiversity (Doney et al., 2012), and provide goods and services to almost one billion people every year (Moberg and Folke, 1999; Wilkinson et al., 1999). However, they are currently threatened by climate change-induced increase in sea surface temperature (Nicholls et al., 2007), and in the incident flux of ultra-violet radiation (UVR, 280-400 nm) (Häder et al., 2007). This later increase is due to the effects of global warming on the stratospheric circulation and to a greater water stratification (Watanabe et al., 2011), leading to a deeper penetration of UVR in the water column (Vodacek et al., 1997).

The effects of rising sea surface temperature on coral physiology have already been well studied. Since most corals live at or near their threshold of temperature tolerance (Hoegh-Guldberg, 1999), thermal stress induces coral bleaching (i.e. loss of photosynthetic symbionts and/or chlorophyll content) and reduces coral photosynthesis and calcification (Hoegh-Guldberg, 1999). The coral response is, however, species specific, depending on the symbiont clade associated to the coral species (Wham et al., 2017), or the energetic reserves of the host tissue (i.e. lipid and protein content) (Fitt et al., 2009). It is also influenced by a myriad of environmental factors, including the level of UVR received by corals. Although UVR is highly mutagenic and enhances cell oxidative state, especially under elevated temperatures (Häder et al., 2007; Sharma et al., 2012), the combined effects of UVR and temperature on coral physiology remain poorly understood because of the complexity of the interactions between these two factors (Courtial et al., 2017; D’Croz and Maté, 2002; D’Croz et al., 2001; Ferrier-Pagès et al., 2007; Fitt and Warner, 1995; Lesser and Farrell, 2004; Lesser et al., 1990). Indeed, while no change was observed on the photosynthetic/autotrophic capacities of Porites lobata or Turbinaria reniformis under the combined stressors (Courtial et al., 2017; D’Croz et al., 2001), these capacities were strongly affected in Montastrea annularis and Pocillopora damicornis (Courtial et al., 2017; D’Croz and Maté, 2002; Fitt and Warner, 1995). The scarcity of experimental studies in this field does not allow good predictions of the combined effects of UVR and temperature on coral physiology. More studies are thus needed to better understand the species-specific response to these factors, and the mechanisms underlying coral susceptibility to thermal stress.

Two other underestimated aspects of thermal and UVR stress on coral biology concern the changes in organic matter (OM) fluxes (uptake and/or release of OM by corals) and recycling by the associated bacteria. Under healthy conditions, corals can release half of the photosynthetically fixed carbon and nitrogen into the surrounding reef waters in the form of mucus, i.e. dissolved and particulate carbon (DOC and POC, respectively) and nitrogen (DON and PON, respectively) (Crossland et al., 1980; Davies, 1984). OM is then degraded by prokaryotes through their extracellular enzyme activity (EAA), and is used for bacterial growth (Cunha et al., 2010), or it enters into the recycling pathways of carbon and nitrogen (Wild et al., 2004). OM therefore supports pelagic and benthic production, and plays a major role in the
nutrient cycles and trophic structure of the whole reef ecosystem (Bythell and Wild, 2011). Elevated temperature, UVR and other stressors can, however, indirectly alter the quality and quantity of OM released by corals (Niggl et al., 2008; Tremblay et al., 2012; Wooldridge, 2009), and change the associated bacterial diversity (Ainsworth and Hoegh-Guldberg, 2009), likely affecting OM degradation rates. Although few studies have investigated OM fluxes in healthy and thermally stressed corals (Fonville et al., 2015; Grottioli et al., 2006; Levas et al., 2015; Niggl et al., 2008; Tremblay et al., 2012; Wooldridge, 2009), the effects of UVR on these fluxes remain unknown. As far as we know, the impact of elevated temperature and/or UVR on the enzymatic activities of mucus-associated bacteria has also never been investigated in tropical corals. The only knowledge on this subject comes from studies performed on water column bacteria from temperate and cold systems (reviewed in Cunha et al., 2010). They showed that bacterial enzymatic activities can be enhanced by temperature and repressed by UVR because of direct enzyme photolysis. Understanding how thermal and UVR stresses alter microbial degradation of coral OM and microbial growth will improve our understanding on future changes of the reef biochemical cycling, remineralization pathway and reef trophic structure.

The purpose of this study was to address some existing knowledge gaps regarding the effects of thermal stress, UVR and their combination on the quality, quantity and bacterial degradation of OM produced by a scleractinian coral, and to link these changes to coral metabolism. A. muricata was chosen because it belongs to one of the 10 most abundant genera in New Caledonia (Fenner and Muir, 2008) and worldwide (Veron, 2000), and is likely to be one of the major contributors affecting the reef biochemical processes. We hypothesize that UVR will exacerbate the effect of thermal stress on coral bleaching and overall metabolism. We also hypothesize that each stressor, alone or in combination, will alter organic carbon and nitrogen fluxes, both in terms of quantity and quality, which will likely change bacterial enzymatic activity in the released mucus. These changes will have a cascading effect on the whole pattern of reef nutrient recycling under global warming scenario.

RESULTS
Effects of temperature and UVR on coral physiology
Four conditions were tested: 26°C without UVR (LT0UV), 26°C with UVR (LTUV), 30°C without UVR (HT0UV) and 30°C with UVR (HTUV) (see Materials and Methods). After 2 weeks at 26°C, exposure to UVR (LTUV) had no significant effect on coral physiology, except for the protein concentration, which was significantly lower in UV treatment (Figs 1 and 2; Table S1). Conversely, exposure to elevated temperature alone (HT0UV) impaired the symbiont density, the chlorophyll a (chl a) and protein content, and the maximum relative electron transport rate \( r\text{ETR}_{\text{max}} \) (Fig. 1; Table S1). The combination of both stressors had an interactive (protein and \( r\text{ETR}_{\text{max}} \)) or synergistic (symbiont density and chl a) impact on coral physiology (HTUV; Table S1). Two weeks of thermal stress alone induced a 30% and 40% decrease in symbiont density and chl a, respectively, and this decline reached 70% and 60%, respectively, when thermal stress was combined with UVR exposure (Fig. 1A,B; Table S1). Net photosynthesis (Pn) normalized per symbiont cell stayed constant (26°C−2 s\(^{-1}\)) (Tables S1 and S2). UVR exposure had no significant effect on this activity.

Enzymatic activity and organic matter degradation
At 26°C, glucosidase maximum extracellular enzyme activity \( \text{EEM}_{\text{max}} \) was significantly higher in nubbins shaded from UVR (5.4±1.3 ng h\(^{-1}\) cm\(^{-2}\); Fig. 4A). High temperatures significantly increased glucosidase \( \text{EEM}_{\text{max}} \), which reached 15.2±3.0 ng h\(^{-1}\) cm\(^{-2}\) (Fig. 4A; Table S2), without any effect of UVR (Table S2). Aminopeptidase \( \text{EEM}_{\text{max}} \) presented the same trends as the glucosidase \( \text{EEM}_{\text{max}} \), with low rates at 26°C (Fig. 4B, 2.3±2.3 ng h\(^{-1}\) cm\(^{-2}\)) and a significant increase at 30°C (16.1±2.5 ng h\(^{-1}\) cm\(^{-2}\)) (Table S2). UVR exposure had no significant effect on this activity.
At low temperature, only a small fraction of the total OM released was degraded (0.03% and 1% of the total carbon and nitrogen released, respectively). However, at high temperature, 0.7% and 8% for the total carbon and nitrogen released were degraded, respectively (Fig. 4C,D; Table S2).

**DISCUSSION**

By simultaneously quantifying covariation in coral photosynthesis, calcification, tissue composition, OM fluxes and degradation by mucus-associated bacteria, this study allows deeper understanding of how two major environmental factors, elevated temperature and UVR, alone or in combination, impact the metabolism and close surrounding environment of *A. muricata*, a dominant coral reef species (Fenner and Muir, 2008). Specifically, our results demonstrate that elevated temperature was the main factor to affect the overall metabolism of *A. muricata*, as well as OM fluxes and bacterial activity. The results, however, highlight a significant combined effect of UVR and temperature on the bleaching susceptibility and photosynthetic efficiency of this coral species, as well as on the decrease in protein reserves over time. This study also reveals, for the first time, that the shift from auto- to heterotrophy that occurred in the short-term bleached *Acropora* nubbins led to a change in both the quality of the OM released and the population dynamics of the associated microorganisms. Finally, OM degradation by mucus-associated bacterial activity was unaffected by UVR exposure, but significantly increased under high temperature. Altogether, our results demonstrate that seawater warming not only affects coral physiology, but also the way corals interact with their nearest environment, with potential consequences for coral reef biogeochemical cycles and food webs.

*A. muricata* nubbins did not present any change in their physiology when they were experimentally shaded from UVR and maintained under their normal growth temperature. This lack of UVR effect was likely due to the acclimation to UVR of the colonies used in this experiment, which grew at 2-3 m depth and were therefore likely protected by mycosporine-like amino acids (MAAs), synthesized in most shallow water corals (Shick et al., 1995). This protection was, however, suppressed or reduced under...
thermal stress (Fitt and Warner, 1995), lowering the coral’s capacity to cope with the accumulation of reactive oxygen species and oxidative stress (Lesser et al., 1990). Temperature presented an additive and synergistic effect with UVR on symbiont density and chl a content, respectively. Corals, therefore, bleached and lost 35% of their symbionts under thermal stress alone, and up to 68% under the combined stress, consistent with previous laboratory and field studies which showed greater effects of double than single stress in diverse coral species (Courtial et al., 2017; D’Croz and Maté, 2002; Ferrier-Pagès et al., 2007; Fitt and Warner, 1995). Bleaching was amplified with the stress duration as only 5% of the symbionts remained in nubbins kept for 4 weeks at high temperature under UVR. These results suggest that corals naturally exposed to low UVR could better resist long thermal stress events than UVR-exposed corals.

In addition to studying the effects of thermal and UVR stress on coral physiology, we also expanded our measurements to assess the coral-induced changes in seawater biogeochemistry (via mucus release and degradation) with thermal and/or UVR stress. Coral mucus (i.e. dissolved and particulate organic carbon and nitrogen) has several functions, both for corals (defense against external stressors and food source (Brown and Bythell, 2005; Levás et al., 2016) and for the reef organisms (energy carrier and particle trap) (Wild et al., 2004); however, changes in mucus quality and quantity under different environmental conditions are still poorly understood (Niggl et al., 2008; Tremblay et al., 2012), because few studies have investigated both carbon and nitrogen fluxes, in dissolved or particulate forms, in healthy and stressed coral species (Bednarz et al., 2012; Naumann et al., 2010), preventing a comprehensive overview of OM fluxes in corals. Our results first show constant release rates of total organic carbon (TOC) and total organic nitrogen (TON) by *A. muricata*, irrespective of the stress state. The high TOC/TON ratio (13 to 15) of the released OM, already observed for several coral species of the Red Sea (Naumann et al., 2010), indicates a higher degree of nitrogen retention in coral tissue compared to carbon. Although *A. muricata* also presents 10 times higher TOC release rates than other species of the Red Sea or the Caribbean (Levás et al., 2016; Naumann et al., 2010), these rates are...
in the range of previously reported values in several *Acropora* species from Malaysia and Jordan (Nakajima et al., 2009, 2010; Naumann et al., 2010). Overall, *Acropora* species tend to mainly be a source of energy-rich carbon compounds to the reef food chain. In New Caledonia, this production can partly explain the exceptionally high rates of N2 fixation in the water column (Camps et al., 2016) compared to other reef systems (Bednarz et al., 2017), since diazotrophs need large amounts of energy-rich photosynthates to perform N2 fixation (Bednarz et al., 2017).

The analysis of the DOM and POM forms shows that the quality of the OM (i.e. particulate or dissolved matter) changes with the environmental conditions under which corals are thriving. *A. muricata* released DOM and POM and took up DOM under normal growth conditions, while the reverse was observed in bleached colonies. Although most previous studies show a release of DOC by healthy corals (Crossland, 1987; Wild et al., 2010a,b, 2004a,b, 2005, 2008; Houblôbreque et al., 2004; Tanaka et al., 2008, 2009; Haas et al., 2010; Naumann et al., 2010; Levas et al., 2015), some studies show the contrary (Houblôbreque et al., 2004; Naumann et al., 2010; Niggl et al., 2008). Observations of OM fluxes in bleached or thermally-stressed corals evidenced the same contrasted results: while *Porites divaricata*, *Porites astreoides* and *Orbicella faveolata*, were shown to take up DOC (Grottoli et al., 2006, 2014; Levas et al., 2013, 2016), *Acropora* sp., *Porites* spp. and *Stylophora pistillata* released it (Haas et al., 2010; Niggl et al., 2008; Tremblay et al., 2012). Overall, no common pattern can be deduced from these previous observations. Our measurements, which took into account the OM as well as the pico- and nanoplanктon concentrations, however, suggest that the changes in POM and DOM fluxes in *A. muricata* are linked to its heterotrophic activity. DOM includes both nonliving material and living particles such as bacteria and small autotrophs linked to its heterotrophic activity. POM includes both nonliving (i.e. wax esters, triglycerides, fatty acids) contained in the mucus, to contribute to the important nutrient recycling pathways observed in the reef bottoms, where it will sustain bacterial growth, and will poorly degraded by prokaryotes. POM will thus rapidly sediment to the reef bottoms, where it will sustain bacterial growth, and will contribute to the important nutrient recycling pathways observed in reefs (Muscatine and Porter, 1977; Richter et al., 2001; Wild et al., 2004). During bleaching, *A. muricata* will release labile DOM, which is more likely to stay in the water column and therefore promote the development of free-living-bacteria (Ferrier-Pagès et al., 2000; Wild et al., 2004), including pathogenic communities (Haas et al., 2013; Nelson et al., 2013). Unless bacteria enter the microbial loop and higher trophic levels, such stimulation may lead to the “microbialization” of the reef (Haas et al., 2016) with negative consequences for coral health such as the promotion of opportunistic pathogen invasion (Barott and Rohwer, 2012). Our study also emphasizes the importance of considering UVR exposure when predicting long-term coral bleaching. As UVR impact on coral physiology is increased with the stress duration, the effects measured during this short-term experiment could be underestimated on a longer term.

**MATERIALS AND METHODS**

**Coral collection and experimental setup**

Eighty 2-3 cm long *A. muricata* nubbins were collected between 2 and 3 m depth from 10 parent colonies on the reef of...
and growth rates and then frozen at 20°C for symbiont, chl a, protein content and surface measurements. In the meantime, five additional nubbins per condition were used for OM fluxes and bacterial activity measurements (as described below) before being frozen at −20°C. Twelve days later (28 days of stress), the physiological parameters (chl a, symbiont density, protein and rETRmax) were re-assessed on the remaining nubbins (five per condition and for all conditions).

For all incubations, temperature and light were maintained constant and identical to the experimental conditions. All data were normalized to the surface area of the corals, measured using the wax technique (Stimson and Kinzie, 1991), or per symbiont cell (determined as described below).

### Physiological measurements

Five nubbins per condition were incubated in the dark for 10 min before the relative electron transport rate (rETR) versus irradiance, or rapid light curves, were generated with a Pulse Amplitude Modulation (PAM) fluorometer (Diving-PAM, Walz, Effeltrich, Germany) according to Ralph and Gademann (2005). For this purpose, nubbins were illuminated for 10 s with seven different light intensities (from 0 to 900 µmol quanta m$^{-2}$ s$^{-1}$) and the rETR$_{\text{max}}$ were deduced from the curves.

The same nubbins were then used to measure rates of photosynthesis, respiration and calcification. They were thus incubated in individual 100 ml beakers filled with 0.45 µm filtered seawater, continuously stirred with stirring bars and hermetically closed using transparent plastic film to avoid any oxygen exchange with the ambient air. Each beaker was equipped with an oxygen sensor spot (SP-PSt6-NAU, PreSens, Regensburg, Germany) and oxygen concentration was measured with a polymer optical fiber and Fibox 4 (PreSens) at the beginning and at the end of the incubations. Changes in oxygen production were measured during 1 h incubation in the dark for the determination of the respiration rate ($R$) and 30 min at the optimal photosynthetic light intensity (600 µmol photons m$^{-2}$ s$^{-1}$, Aquablue plus neon, Blue-white, 15,000 K, Giesemann, Nettetal, Germany) to assess net photosynthesis (Pn). This optimal irradiance was deduced from the rapid light curves and from preliminary Pn-irradiance curves (Fig. S1). Pn and R were estimated from the difference between the final and the initial oxygen concentrations. After the incubations,
nubbins were frozen at −20°C for the subsequent determination of tissue parameters as described below. Data were expressed in µmol O₂ h⁻¹ cm⁻² d⁻¹ and corrected against a blank (filtrated seawater incubated for the same period without nubbin).

The incubation seawater of each beaker was filtered through 0.2 µm filters and stored at 4°C for the subsequent determination of the calcification rates using the total alkalinity anomaly method (Smith and Key, 1975). The measurement was performed using a TIM865 titration manager (TitraLab, Hach, Loveland, USA). Titration error was verified using AT standards provided by A.G. Dickson (University of California, San Diego, USA; batch 142). Data were expressed in µmol CaCO₃ cm⁻² d⁻¹ and corrected against a blank (filtrated seawater incubated for the same period without nubbin).

To calculate the total daily CZAR, oxygen fluxes were converted to carbon equivalent using respiratory (RQ) and photosynthetic (PQ) quotients equal to 0.8 and 1.1, respectively (Gattuso and Jaubert, 1990; Muscatine et al., 1981). We considered that coral colonies photosynthesize during 12 h (light period) and respire during 24 h. CZAR (%) was calculated as

\[
CZAR = \left( \frac{(\mu molO_2 \, produced \times 12}{(\mu molO_2 \, consumed \times 24 \times RQ)} \right) \times 100
\]

Here, we considered the respiration of the whole coral holobiont (i.e. host, symbionts and microbiome), not only the animal, to take into account all respiratory needs.

**Symbiont, chl a and protein content**

Nubbin tissue was removed from the skeleton using an air pick and homogenized with a Potter tissue grinder. A sub-sample was used to assess the protein content according to Hoogenboom et al. (1998). In brief, growth rates in the control beakers (kc) and in the presence of coral nubbins (kn) were computed as:

\[
k = ln(Cf/C0)/(T_f - T_0)
\]

with C₀ and Cᵢ representing the microorganism concentrations (cell ml⁻¹) at time T₀ and Tᵢ, respectively, expressed per hour. These growth rates were then used to calculate g, the grazing coefficient (h⁻¹).

\[
g = kc - kn
\]

They were also used to calculate F, the filtration rate (ml h⁻¹ cm⁻²)

\[
F = V \times g/S
\]

where V is the incubation volume (ml), S the coral surface (cm²) and g (h⁻¹) the grazing coefficient. The ingestion rate I (ingested cell h⁻¹ cm⁻²) was finally calculated as

\[
I = F \times C
\]

where F (ml h⁻¹ cm⁻²) is the filtration rate and C (cell ml⁻¹) is the average prey concentration equal to

\[
C = C_0[1-(k-g) \times (T_f - T_0) - 1]/(k - g) \times (T_f - T_0)
\]

with C₀ the prey concentration at T₀. Because of the heterogeneity in the carbon content of the different autotrophs present in seawater, we could not quantify the equivalent carbon ingested by the coral using these data. However, this contribution was estimated using the \(CHAR_{POC}\) above.
Extracellular enzymatic activities
EEAs were monitored using fluorescent substrate analogs according to standard protocols (Hoppe, 1983). L-Leucine-7-amido-4-methylcoumarin hydrochloride (MCA) and 4-methylumbelliferyl-α-D-glucopyranoside (αMUF) were therefore used to assess aminopeptidase and alpha-glucosidase activities, respectively. These two compounds emit a fluorescent signal after cleavage by the enzymes. Correspondence between fluorescence value and the quantity of substrate hydrolyzed was obtained using amino 4-methylcoumarin (MCA) and 4-methylumbelliferone (MUF). Three replicates of the incubation water were sampled at the end of the 4 h incubation and added to the substrates to a final concentration of 250 µM. Samples were incubated in the dark for up to 16 h in a thermostated shaking bath at the experimental temperatures (26°C or 30°C). EEAs were measured every 24 h using a spectrofluorometer (Synergy-H1, BioTek, Bad Friedrichshall, Germany). For this purpose, 96-well plates (300 µl volume) were filled up with 240 µl sample and 60 µl of 10.8 Tris-HCl buffer was added to adjust pH to obtain maximal fluorescence intensity (Fonvielle et al., 2015).

Carbon degradation was calculated with the following equation:

\[
\% C_{\text{degraded}} = \frac{EEMax \times 100}{TOC_{\text{coral}}} 
\]

with EEMax the α-glucosidase maximal enzymatic activity (nmol l\(^{-1}\) h\(^{-1}\)) of the mucus-associated bacteria and TOC (nmol l\(^{-1}\) h\(^{-1}\)) the quantity of organic carbon contained in the mucus, calculated as

\[
TOC = TOC_{\text{coral}} - TOC_{\text{blk}}
\]

TOC\(_{\text{coral}}\) and TOC\(_{\text{blk}}\) (nmol l\(^{-1}\) h\(^{-1}\)) are the TOC concentrations in seawater after 4 h of incubation with or without nubbins, respectively.

Similarly, nitrogen degradation was calculated using the following equation:

\[
\% N_{\text{degraded}} = \frac{EEMax \times 100}{TON_{\text{coral}}} 
\]

with EEMax the aminopeptidase maximal enzymatic activity (nmol l\(^{-1}\) h\(^{-1}\)) of the mucus-associated bacteria and TON (nmol l\(^{-1}\) h\(^{-1}\)) the quantity of total organic nitrogen contained in the mucus, calculated as

\[
TON = TON_{\text{coral}} - TON_{\text{blk}}
\]

with TON\(_{\text{coral}}\) and TON\(_{\text{blk}}\) (nmol l\(^{-1}\) h\(^{-1}\)) the TON concentrations in seawater after 4 h of incubation with or without nubbins, respectively.

**Statistical analysis**
The effects of UVR and high temperature on the parameters measured after 16 days of thermal stress were assessed with two-way ANOVAs using UVR (presence, absence) and temperature (26°C and 30°C) as factors. To test the effects of high temperature and UVR over time, three-way ANOVAs using time (after 16 and 28 days), UVR and temperature as factors were performed on symbiont density, chl a, protein content and ETR\(_{\text{max}}\). For all tests, normality of the residuals and variance homoscedasticity were tested using Shapiro and Bartlett tests, respectively. When needed, data were log transformed in order to fulfill those criteria. A Tukey’s post hoc test was performed when results of the ANOVAs were significant.

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**Competing interests**
The authors declare no competing or financial interests.

**Author contributions**

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**Supplementary information**
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