Coral Bleaching Induced Mortality Transforms Local and Global Carbon Cycles: A Positive Feedback Loop That May Accelerate Reef Decline

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Abstract. Increases in atmospheric carbon have led to widespread, frequent, and severe coral bleaching, resulting in global coral reef decline. Here, we show that bleaching corals severely impact the local carbon cycle by releasing significant amounts of dissolved organic carbon (DOC), which further stresses the local reef community and may trigger coral mortality. During a severe bleaching event in Mo'orea, French
20   Polynesia, we measured DOC concentrations 37% greater than Total Organic Carbon (DOC and Particulate Carbon combined), compared to non-bleaching conditions. In addition, this DOC was highest immediately adjacent to the reef, indicating that the corals were the source of this carbon. Further, when exposed to bleaching-derived DOC-rich exudate (~2mM DOC), otherwise healthy corals experienced bleaching, tissue loss, and mortality within 48 hours. While this is an extreme amount of DOC to be found

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25 on a reef *in situ*, it identifies a potential mechanistic impacts of coral-derived DOC on healthy corals. By extending our findings to regional scales, we estimate that large scale bleaching events can significantly alter the marine carbon cycle. For example, a single bleaching event on the Great Barrier Reef could have released an estimated 150 Gmol C as DOC alone. Our research identifies a previously unrecognized mechanism of coral mortality during bleaching events, in which biogeochemical shifts across the
30 reefscape that may result in a positive feedback loop that accelerates coral reef loss.dui.

1. Introduction:

Coral reefs are among the most valuable ecosystems on Earth, ecologically and economically. Tropical reefs are estimated to harbor more than one million species (Fisher et al., 2015), contribute a minimum of 36 billion US dollars annually to the global economy (Cesar et al., 2003), and are epicenters of
35 biogeochemical cycling (Haas et al., 2011; Nelson et al., 2013). Despite the recognized global importance, coral reefs are threatened due to warming oceans and local stressors, which independently or synergistically lead to coral bleaching (Donovan et al., 2021), the mass loss of algal symbionts (family Symbiodiniaceae) from coral hosts. If the underlying stress causing coral bleaching is not rapidly ameliorated, it can lead to coral mortality and overall reef decline. Bleaching events are increasing in their
40 frequency and severity, often shifting reef ecosystems from coral to macroalgal-dominated stable states (Hughes et al., 2018; Pandolfi et al., 2003; Hughes et al., 2017). Although thermal stress from ocean warming is recognized as an underlying cause of coral bleaching, the mechanisms that lead to coral mortality during and after bleaching events remain poorly understood (Hughes et al., 2018).

Coral reefs turn otherwise oligotrophic marine systems into highly productive coastal habitats. This is
45 accomplished through shifting the flow of carbon in their surrounding environment, particularly through the release of dissolved organic carbon (DOC). Under non-bleaching conditions, coral reefs release between 8-57 µmol C $dm^{-2} d^{-1}$ of DOC to the reefscape (Haas et al., 2013). These compounds are taken up rapidly by heterotrophic microorganisms, resulting in a water column that is depleted in DOC over reefs (Nelson et al., 2013, 2011; McCliment et al., 2012). The coral reefs (here, defined as reef-building

50   corals, associated microbial communities, and adjacent sand patches) of our study site are recognized as net sinks for DOC (Nelson et al., 2011) .

Reef biogeochemistry can be shifted by alterations in the type, concentration, and source of key nutrients in the system, often resulting in significant impacts to reef function and the weakening of coral holobionts (Sandin et al., 2008; Haas et al., 2016; Barott and Rohwer, 2012). During times of stress, corals increase

55   their release of exudates, potentially as a defense mechanism, and release exudates that differ in composition from those released under ambient conditions (Palmer et al., 2010; Wild et al., 2004; Nguyen-Kim et al., 2015, 2014; Han et al., 2019; Lampert et al., 2006; Shnit-Orland and Kushmaro, 2009). For example, corals under experimental thermal stress produced twice as much organic matter and released mucus with a higher lipid and protein content than non-stressed corals (Niggl and Wild, 2010;

60   Wright et al., 2019). The type and amount of DOC on the reef is an increasingly recognized component of reef health. In fact, in some of the first investigations of the impact of DOC on corals, Kline et al. (2006) found detrimental shifts in coral microbiomes in response to DOC stress, concluding that increasing DOC levels are a threat to reef health and should be routinely monitored. As the efflux of DOC per surface area tends to be significantly lower for non-stressed corals than other benthic species such as

65   fleshy and/or turf algae (Haas et al., 2011), to date our understanding of DOC stress on reefs is largely centered on results from macroalgal invasion.

The impact of macroalgal DOC on a reefscape is well highlighted by the DDAM (DOC, disease, algae, microorganisms) model, wherein algal invasion (often from overfishing or eutrophication) increases reef DOC concentrations leading to cascading effects across the reefscape and promoting coral demise (Haas

70   et al., 2016). In this model, the increased efflux of DOC by algae, coupled with the highly labile nature of macroalgal DOC, promotes the growth of copiotrophs and radically shifts the reef microbial community, increasing pathogenicity, virulence, and oxygen drawdown across the reef. Once a phase-shift to an algal dominated reefscape has occurred, the highly heterotrophic reef microbial community depletes DOC levels (often to concentrations below those of non-impacted reefs) but the reef cannot

75   recover due to both physical and pathogenic barriers to settlement and success (Barott and Rohwer, 2012).

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Although we increasingly understand how local stressors (i.e. algal overgrowth from eutrophication or pollution) trigger biogeochemical phase shifts, the potential interplay of global stressors (e.g., thermal bleaching) with reef biogeochemistry has heretofore eluded us. In early 2019, we recorded a severe bleaching event that occurred on the island of Mo'orea, French Polynesia (Burgess et al., 2021; Donovan

80   et al., 2021). During this event, temperatures on the forereef remained above 29.2°C for 8 weeks, a temperature considered the thermal threshold for Mo'orea (Adjeroud et al., 2009), and in April 2019 exceeded 30°C for the first time since 1981 when high resolution, continuous, in situ sea surface temperature records were first initiated. This led to a cumulative heat stress of 17 degree heating days (DHD) at this location; DHD is a metric of heat stress that is proposed to be the most ecologically relevant

85   to coral species (Burgess et al., 2021). By April of 2019, >89% of the island's forereef corals were moderately bleached, and 67% were severely bleached (SI Methods). When sites were revisited in August of 2019, the majority (60%) of the previously bleached corals had died and were overgrown by algae (Fig S1).

Here, through a combined approach of field observation and lab experimentation, we quantify the *in situ*

90   impact of the 2019 bleaching event on long term patterns of carbon distribution, and experimentally demonstrate that DOC released by bleaching can induce mortality in corals. This research elucidates a previously unrecognized and potential driver of coral reef demise, in which bleaching-induced DOC release drives a bleaching cascade across the reefscape, exacerbating reef decline and impacting the function and resilience of the reef ecosystem at large. Further, we use our results to evidence how DOC

95   from corals may alter global carbon cycles during mass bleaching events.

2. Methods

2.1 General overview

Samples were collected on the island of Mo'orea in French Polynesia (-17.475, -149.837) at the Mo'orea Coral Reef Long-Term Ecological Research (MCR LTER). At a 10m deep forereef location that has been

100   sampled for over a decade as part of the LTER station time series sampling (LTER-1), water was collected

just above the reef (10m depth), at midwater level (5m depth), and just below the surface (1m depth). Complementing this long term dataset, water was collected within this LTER legacy site during the initial onset of the bleaching event on April 1, 2019, before temperatures peaked, and then again following the temperature peak (April 28 - May 15, 2019). Samples were taken at three points along a transect that ran

105   parallel to the reef, separated by 15m. Near-reef (~300m and ~600m perpendicular from the reef crest) and off-reef (1 km from reef crest) water samples were collected at 1m and 10m depths. The off-reef site historically has an 'offshore' signature similar to that found at the 5km distance from reef crest site used for MCR-LTER collections (SI Figure 1; Nelson et al 2011). 2019 samples were collected in sterile WhirlPak bags by either divers on SCUBA or with the deployment of niskin bottles. Samples were stored

110   on ice until they were filtered through a combusted glass fiber filter into acid-leached, MilliQ flushed, sample rinsed 60 mL polyethylene bottles which were stored at -20ºC until analysis. DOC samples were sent to the Nutrient Analytical Services at the Chesapeake Biological Laboratory of the University of Maryland Center for Environmental Science (UMCES). In all cases, our DOC values were much greater than minimum reproducible and reportable values from UMCES, which at the time of analysis was 13.3

115   μmol C/ L and all of our values were >60 μmol C/ L. Contour plots of DOC concentrations were made in Ocean data viewer (v.5.1.7; 36) using the DIVA-gridding algorithm and interpolating to a 30x30 scale-length grid.

Images of the Mo'orea fore reef that included scale bars were annotated using ImageJ as either bleached (completely white), partially bleached (contained some pigment but had clear areas of bleaching), or

120   unlikely to be bleaching (no visible white spots beyond normal for the species). The surface area of each was quantified through tracing the exterior of individual corals and summing across the plots which were between 46 and 93m^2 apiece with three areas of the forereef measured, corresponding to MCR LTER sites 0, 1, and 2. The resolution of the images was such that individual species could be easily identified.

2.2 Mesocosm Experiment:

125   Along with the *in situ* reef measurements, we ran mesocosm experiments on land to test the impact of various abiotic and biotic stressors on coral health and survivorship. All exposure experiments used coral

fragments from a single coral head, replicated on 3 coral genets (i.e. different coral colonies) for 2 genera of coral (*A. hyacinthus* and *Pocillopora spp.).* The *Pocillipora* spp. sampled form a morphologically indistinguishable species complex in Mo'orea although they have previously been called *Pocillopora*

130 *verrucosa* at this location (Burgess et al., 2021). We refer to it as *Pocillopora* spp. even though all colonies belonged to the same morphotype. Coral colonies were collected at 5m depth on the forereef, via diver, transported in a cooler to the research station, fragmented into ca. 2cm x 2cm fragments, and acclimated for 24 hours in a running seawater table in partial shade.

After acclimation, corals were placed in individual closed systems ('mesocosms') which consisted of

135 1.5L of 0.2um filtered seawater (FSW) spread between a 500ml glass jar (PTFE lined lid) and a 1.0 L mylar bag. Water was constantly circulated with a peristaltic pump creating a 1.5L water volume which was large enough to avoid nighttime hypoxia in control corals. Since the corals were in a glass jar it allowed a natural cycle of photosynthesis by coral symbionts which oxygenated the water.

Corals were exposed to 3 treatments: no modification, +3°C temperature increase (manipulated by tank

140 heaters and quantified by Onset Hobo temperature loggers), and coral bleaching exudate. The coral exudate was created by bleaching coral fragments (from the same colony that was used for a given replicate) via exposure to temperature and light stress for 24 hours in sterile containers filled with 0.2 micron filtered seawater. To collect the exudate released from a bleaching coral, the water surrounding a bleaching coral was passed through a coarse, non-quantitative filter to remove particulates (nominally,

145 0.6 μm filter). Filtrate was diluted resulting in exudate treatments having DOC concentrations of 2.2±0.6 mM; subsamples of the filtrate were preserved at the initiation of the experiment to measure the realized DOC manipulation, although quantification of DOC was not possible in the field. We acknowledge that this is a significant amount of DOC added, however it is less than 1cm^2 of coral release during bleaching into a L of seawater (quantified below). Further, while potentially an overestimate, may represent the

150 microenvironment a coral experiences during bleaching which may be drastically different compared to water 1 m above the coral head. Each time point and replicate was run in parallel and sacrificed at the specific time intervals (6, 12, 24, 48 hours). At time zero, three fragments of the coral were haphazardly chosen as time-zeros and the FSW used in the mesocosms was sampled for water chemistry. DOC samples

were collected along with coral health variables including symbiont density, chlorophyll a concentration,

155 and a visual health index (see Supplemental Material for detailed methods). Holobiont health was assessed

based on photosynthetic efficiency (Fv/Fm). Symbiodiniaceae genetic diversity characterized based on

the Internal Transcribed Spacer-2 region of ribosomal DNA (see Supplementary Material).

2.3 Global DOC flux estimates:

To parameterize the impact of coral bleaching on regional and global carbon cycles, we quantified the

160 amount of DOC released by a bleaching coral and scaled that to global distribution of corals and

bleaching. To determine total DOC release by bleaching and non-bleaching corals, we experimentally

bleached *Pocillopora* spp., *Pocillopora eydouxi*, and *Porites lobata.* In contrast to other studies that

measure DOC flux on *in situ* corals, our goal was to quantify the total DOC released as a coral bleaches.

We acknowledge that corals bleach over much more than 24 hours in the wild, however our goal was not

165 the natural state of healthy coral (as best done in the field; *sensu* Haas et al. 2011; Haas et al. 2014) but

instead the net DOC released when they do bleach. While we used *A. hyacinthus* in the mesocosm

experiments that were carried out 6 months prior to the bleaching event, we did not include this species

in the bleaching assay. The bleaching assay was conducted during the bleaching event and there were not

enough live or healthy *A. hyacinthus* colonies on the reef to justify experimentation. Coral reef global

170 surface area estimates were taken from Costanza et al., (2014) for current coverage (280,000 km^2). To

calculate the DOC flux from non-bleaching corals, we averaged DOC flux values from literature

(Naumann et al., 2012; Haas et al., 2013, 2011) and applied that to coral coverage estimates (Table S3

and S4; Equation S1). To provide a conservative estimate, we calculated that during a global bleaching

event, only 10% of the corals on the reef bleach and applied our experimental bleaching DOC release

175 values (Table S2 and S4; Equation S2).

We further aimed to quantify the potential regional impact of a bleaching event based on the well

quantified 2016-2017 bleaching of the Great Barrier Reef (GBR). Areal extent of GBR Near Surface

Reefs of the region that underwent bleaching quantification is 20,678 km^2 (Harris et al., 2013). We then

applied the percent of the reef that bleached during the 2016-17 event (Hughes et al., 2017). We calculated

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180 the amount bleached separately for each area based on the total surface area of the region covered by coral

and the percent bleached in that region, in all cases using the lower percentage of bleaching within each

of the bins to result in a conservative estimate (Table S5; Hughes et al., 2017). We then applied the DOC

release measured from our experiments to the calculated percent surface area that bleached (Equation S3).

3. Results

185 **3.1 DOC enrichment during bleaching event**

During the 2019 bleaching event, we measured a shift in the reef from a carbon sink to a carbon source.

Time series data from the MCR LTER and our own measurements in April 2019 show that prior to this

bleaching event, Mo'orea's coral reefs maintained its consistent pattern of on-reef Organic Carbon

concentration less than offshore, supporting that the reef itself is a sink for DOC. Total Organic Carbon

190 (TOC) has remained a 10% lower onshore compared to off-shore since 2007 and the on-reef value had a

mean of 70.8 ± 1.4 µmol TOC (Figs 1a, S2, S3; offshore and off-reef typically have similar TOC

concentrations, see methods for more detail; Broad et al., 2018). At the onset (April 1) of the 2019

bleaching event, the concentration of DOC on the reef was 82.5 ± 1.4 µmol DOC (n=3), an increase to

this long term mean TOC values. Note that in early April cumulative heat stress at this site was already 4

195 DHD and the bleaching threshold for the island had been surpassed by the end of March (Burgess et al.

2021). We also note that we measured DOC, rather than TOC, and at this location 95-96% of TOC is

DOC (Nelson et al. 2011). During the onset of bleaching, the reef remained an apparent DOC sink as

indicated by the relative distribution of DOC, where reef DOC values were 24% less than off-reef values

(Figs 1c, S2, S3). However, as bleaching intensified, on-reef waters became further enriched in DOC,

200 with on-reef DOC values averaging 8% greater than off-reef concentrations. This shift in the on-reef/off-

reef DOC balance was 18% greater than pre-bleaching TOC conditions in the time series data and 32%

greater DOC than pre-mass bleaching and mortality conditions from our own data. During this period of

on-reef DOC enrichment, values reached 97.0 ± 6.7 µmol DOC, 37% greater than pre-bleaching TOC

values from the time series data. Such a dramatic shift in DOC across the reefscape during the most

205 intense period of the bleaching event indicates that the reef changed from a sink to a source of elevated

DOC. We also note that all of our values are well within the analytical range of the facility and approach used to measure DOC.

3.2 DOC release by bleaching coral fragments

Based on mesocosm experiments, we also found that exposure to DOC-rich coral exudates from bleaching
210 and coral mortality causes apparently healthy corals to bleach, often leading to rapid coral mortality (Figs 2, S4, S5). When *A. hyacinthus* and *Pocillopora* spp. fragments were exposed to coral exudates (~2 mM DOC; see methods) the corals showed initial signs of bleaching within 6 hours and moderate to severe tissue sloughing and/or mortality within 48 hours (Figs 2). Temperature stress (+3°C above control) produced less severe bleaching in fragments of the same individuals from both coral species and, when
215 bleaching did occur, it coincided with the release of DOC, at concentrations up to 6.1 mmol C/ (coral cm)^2 (Fig 2). Aside from a single outlier control fragment that bleached, all other control fragments (which were from the same coral colonies exposed to stress treatments) remained healthy throughout the experiment and exhibited no signs of bleaching. Corals were kept in 1500mL of filtered seawater that was constantly recirculated to provide conditions that consistently avoided nighttime oxygen hypoxia. It is of
220 note that in all instances of coral bleaching in the experiment, including the control coral fragment that unexpectedly bleached, we saw a concomitant peak in DOC release (Fig 2b).

Observed peaks in DOC in the coral exudate treatments were coupled with oxygen drawdown and a decrease in the photosynthetic efficiency (Fv/Fm, a metric for photosystem II health) of the dinoflagellate endosymbionts of corals (Family Symbiodiniaceae; Fig 2). The corals in the exudate treatments, which
225 were hypoxic after 6 hours, had a persistent and continued decrease in Fv/Fm indicative of observed bleaching and tissue sloughing (Table S1). Fv/Fm decreased by 86 and 61% in *A. hyacinthus* and *Pocillopora* spp., respectively. This decrease in Fv/Fm in corals exposed to the exudate coincided with a decrease in coral health as quantified through a visual health scale, with the exudate having obvious and significant impact 12 hours after the beginning of the experiment (Figure S4; Table S1). Coral fragments
230 exposed to increased Temperature and Control treatments did not significantly decrease in coral health over time (Table S1). Density of Symbiodiniaceae and Cholorophyll *a* in all treatments had high among

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replicate variance, leading to no significant differences among treatments even though the exudate treatments had a clear and lower, albeit non-significant, value at the 48hour time point for both metrics (Figure S4; Table S1). The genetic identity of the Symbiodiniaceae in each coral fragment was consistent

235 among time points, treatments, and replicates, although it differed between host species (Figs S6, S7). The *Cladocopium* symbionts in two bleached *Pocillopora* fragments at the 48-hour time point could not be fully resolved with the sequence data available (Fig S6).

3.3 Implications for global carbon budgets

Experimentally forced bleaching and mortality of *Pocillopora* spp., *Pocillopora eydouxi*, and *Porites*
240 *lobata* revealed that DOC fluxes were, on average, 7.4-fold higher in bleaching corals, as compared to controls in our experiments (2.3 ± 0.3 mmol C/cm^2, 0.31 ± 0.07 mmol C/cm^2, respectively; Table S2). Based on multiple on-reef incubation studies (Haas et al., 2013; Naumann et al., 2012; Haas et al., 2011), and global coral cover estimates, corals release an average of 8.4×10^{11} mmol C as DOC daily under non-bleaching conditions (Table S3 and 4). In contrast to these studies, we specifically quantified how much
245 DOC is released when they did bleach, and while bleaching normally occurs over days to weeks these short term assays were aimed to estimate the total DOC released during a bleaching event. Applying our quantified DOC release during a global event in which 10% of corals bleach, we estimate that 6.4×10^{14} mmol C would be released or over 760x the daily DOC flux from all corals globally during non-bleaching conditions. Or viewed another way, during a bleaching event a coral will release the equivalent of 760
250 days of normal DOC flux over the relatively short period of a bleaching event (days to weeks) that the corals undergo bleaching. We note that for this calculation, we are comparing *in situ* flux data to laboratory data in which corals were forced to bleach and in some cases died. This is intentional as *in situ* data are the best representation of steady state conditions and our forced lab experiments provide an end point to the amount of carbon released by the coral. This also represents what a coral would release
255 if bleached whether in the laboratory or the ocean. In contrast, comparison of our bleaching data to our controls, which reflect the conditions of corals in a laboratory setting with reduced applicability to *in situ* quantification, still identified a 7.4x increase as a result of bleaching and bleaching induced mortality, all of which occur during wide scale bleaching events. Another way to illustrate the impact of these flux

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data, is through applying our estimates to the major and well-characterized 2016-2017 bleaching event

260 on the Great Barrier Reef where the extent of bleaching was accurately quantified. In this case, a minimum

of 1.5×10^{11} mol C as DOC was released into the marine system over the duration of this event. Bleaching

events, especially when coral mortality occurs, represents a significant transition from carbon stored in

the coral tissues into the pelagic environment of the reefscape.

4.0 Discussion

265 Corals play an important role in the overall flow of energy on reef habitats, as evidenced by the

quantification of carbon released from bleaching corals in this study. Increased mucus production is a

known stress response of corals and mucus is an important source of Particulate Organic Carbon (POC)

as it facilitates nutrient retention on lagoonal reef systems, both trapping particulate as well as stimulating

carbon processing in sandy and other reef habitats (Wild et al., 2004). Seasonal increases in temperature

270 can result in a doubling of the total release of DOC from corals (Roth et al., 2021) and nutrient stress has

also been shown to increase the overall release of DOM from corals (Quinlan et al., 2018). Changes in

the concentration and composition of DOC on reefs has been associated with declines in reef health, yet

this damaging impact of DOC has been associated primarily with algal-related DOC release (Haas et al.,

2016) but not for corals themselves, in part because corals are often sinks rather than sources of DOC

275 (Wild et al. 2010; Nelson et al. 2011). On the forereef of Mo'orea, there was low coverage of both macro-

and turf algae ($1.2 \pm 0.5\%$ and $10.0 \pm 1.5\%$ cover, respectively) and high coral cover ($80\pm2.6\%$ cover)

prior to the bleaching event (Sloan et al., 2019). Considering this, and the quantified DOC flux from the

experimentally bleached coral fragments, we interpret the blanket DOC covering the corals during the

bleaching event to be derived from the bleaching and dying corals themselves rather than from algae.

280 While previous important work have shown how corals are key components of the carbon flux across a

reef as a result coral exudate that then dissolves (Wild et al. 2004; Wild et al. 2010) and identified how

this area of research is critical to understand in the context of climate change (Bythell and Wild 2011),

our work represents the first quantification of a coral-induced DOC perturbation on reefs during a

bleaching event.

4.1 Ecosystem Feedbacks of Coral-Induced DOC Perturbation

Our combined *in situ* reef and experimental mesocosm data together provide a mechanism where coral bleaching and mortality events can trigger shifts in the carbon balance of a reef ecosystem and lead to a DOC-induced cascade; this cascade may further the extent and severity of coral bleaching and mortality, transforming both the function and the composition of a reefscape (Fig 3). In this positive feedback mechanism of coral mortality, we hypothesize that, as corals begin bleaching in response to a stressor, they significantly increase DOC concentrations leading to: (1) increased microbial growth in the coral and the surrounding water column, (2) increased oxygen drawdown, (3) reduced coral health, and (4) mortality (Kline et al., 2006; Kuntz et al., 2005; Haas et al., 2016; Cárdenas et al., 2018; Nguyen-Kim et al., 2015, 2014). Potential feedbacks from this DOC-driven mechanism include the rapid consumption of oxygen in bleaching derived-DOC areas; in turn, this results in local hypoxic conditions, an increase in the DIC pool, and increased pathogenicity.

Exudates from stressed corals are highly labile and are known to enhance net heterotrophy in reef systems (Wright et al., 2019; Kline et al., 2006; Kuntz et al., 2005; Altieri et al., 2017; Nelson and Altieri, 2019). Additionally, pelagic microbial communities are known to rapidly oxidize coral-released DOC, a process that would be hastened by the warm waters that induced bleaching in Mo'orea. This rapid degradation of bleaching coral-released DOC was measured in our mesocosm experiments (Figure 2). While this was extremely obvious in our coral exudate treatment, even pulses of DOC release in response to bleaching in other experimental treatments were followed by a rapid drawdown in oxygen and coral mortality, and this was in the absence of temperature stress (Fig 2). Further, rapid respiration of DOC was apparent on the reef of Mo'orea in May 2019 with the lowest DOC concentrations recorded from near-reef waters (57.1 ± 4.3 µmol DOC; Fig 1d) where a pelagic microbial community was likely consuming the high DOC measured along the bleaching reef. This resulting drawdown of oxygen has been shown to be a driving factor in bleaching events (Altieri et al., 2017; Nelson and Altieri, 2019) and has been empirically demonstrated to lead to coral mortality in the absence of temperature stress (Altieri et al., 2017). Certain coral taxa, in particular members of the *Acropora* genus, can be highly sensitive to oxygen stress even under moderate hypoxia (Haas et al., 2014). While we observed very low oxygen in our DOC treatments,

this was likely an underestimation of oxygen-stress on the coral host as biologically relevant oxygen measurements are difficult considering the microniches present within coral tissues. Highly active heterotrophic microorganisms in the surface mucus layer could result in extreme hypoxia for the coral host even if water column oxygen levels remain within normoxic values. It is debatable whether our significant addition of DOC to the corals are experienced during in situ bleaching events, however it provides impetus for research to focus on the role of DOC during bleaching at the spatial scale of the coral surface.

This enhanced local respiration would have likely released additional dissolved inorganic carbon (DIC) into already carbon saturated waters, potentially leading to increased ocean acidification conditions that are known to impact calcification rates and lead to the dissolution of carbonate coralline structures (Leggat et al., 2019). Following the 2016-2017 mass bleaching of the GBR, coral skeletons became covered with a microbial biofilm and there was marked degradation of the calcium carbonate corallite structure (Leggat et al., 2019). In subsequent experimental analyses the authors found that decalcification rates were significant (5 times higher than rates in extreme pCO_2 conditions), did not shift in light vs. dark scenarios, and continued after the removal of external biofilms. High rates of respiration and CO_2 release were observed, with a potential source given as the breakdown of DOC from dead coral tissue by heterotrophic bacteria.

Notably, the exposure of healthy corals to organic carbon compounds alone (excluding the viruses or pathogens that coral exudates may contain) has been shown to cause coral mortality through pathologies consistent with band disease (Nguyen-Kim et al., 2015; Kline et al., 2006; Kuntz et al., 2005). The pathologies observed in these experiments would often follow similar patterns to that observed in our study, with rapid mortality following tissue sloughing. In this mechanism, coral exudates may spread disease by both enriching DOC that stimulates microbial growth within coral tissue and the surrounding water column, and by directly ejecting viruses and other pathogens from their surface mucus layer into the surrounding environment, increasing transmission rates (Kuntz et al., 2005; Kline et al., 2006; Thurber et al., 2017; Nguyen-Kim et al., 2015).

4.2 Contributions to Global Carbon Budgets

A feedback loop (Fig 3) driven by coral bleaching that fundamentally shifts the biogeochemistry of local
340   reefscapes and, when extrapolated to recent mass bleaching events, is substantial enough to elucidate a
novel aspect of how a warming ocean impacts the marine carbon cycle. The worst bleaching events on
reefs throughout the world, from the Gulf of Mexico to the Great Barrier Reef, continue to occur with
more regularity and severity, with greater than 60% of reefs around the globe bleaching in recent years
(Johnston et al., 2019; Hughes et al., 2018; Cressey, 2016; Hughes et al., 2017). Our estimates of the
345   carbon released from a widespread global event (10% global reefs bleach; 6.44×10^{11} mol C DOC) or
single region (2016-2017 GBR bleaching event; 1.5×10^{11} mol C DOC) constitute a large and
unrecognized perturbation to the carbon cycle. To place these flux estimates in context, 2.5×10^{13} mol C
was unaccounted for in the 2017 global carbon budget (Le Quéré et al., 2018). Our estimated carbon
release from the 2017-2016 GBR bleaching event thus accounts for 0.6% of this global carbon
350   discrepancy, even though our estimate is constrained to a region that covers only 0.004% of the globe.
This represents a footprint on the global carbon discrepancy that is 150x larger than the physical footprint
of coral reefs. In addition, the extent of these bleaching events far surpasses the conservative parameters
invoked above, and thus our calculation of total carbon released during mass bleaching events is a severe
underestimate. The release of such a quantity of carbon during a singular and spatially restricted area has
355   a multitude of implications for these ecosystems. Our initial quantification of carbon released from
bleaching reefs provides another example of how warming oceans cause unexpected consequences. In
this case, bleaching-induced carbon release disrupts tropical ecosystems and adds to our atmospheric
carbon footprint. These impacts on the marine system will continue to cause future bleaching events if
international resolutions to reduce carbon production are not met.

360   **5. Conclusions**

The worst bleaching events on reefs throughout the world, from the Gulf of Mexico to the GBR, have
been observed in recent years (Johnston et al. 2019; Hughes et al. 2018; Hughes et al. 2017; Cressey
2016). While we often focus on the stressors that initiate coral bleaching and coral loss, our results here

365 indicate a potential unrealized mechanism in coral decline, wherein coral exudates released during bleaching lead to increased mortality of local corals. We show a drastic shift in the carbon balance of a reef system in response to a major bleaching event and posit a detrimental impacts to coral survival from this increased DOC.

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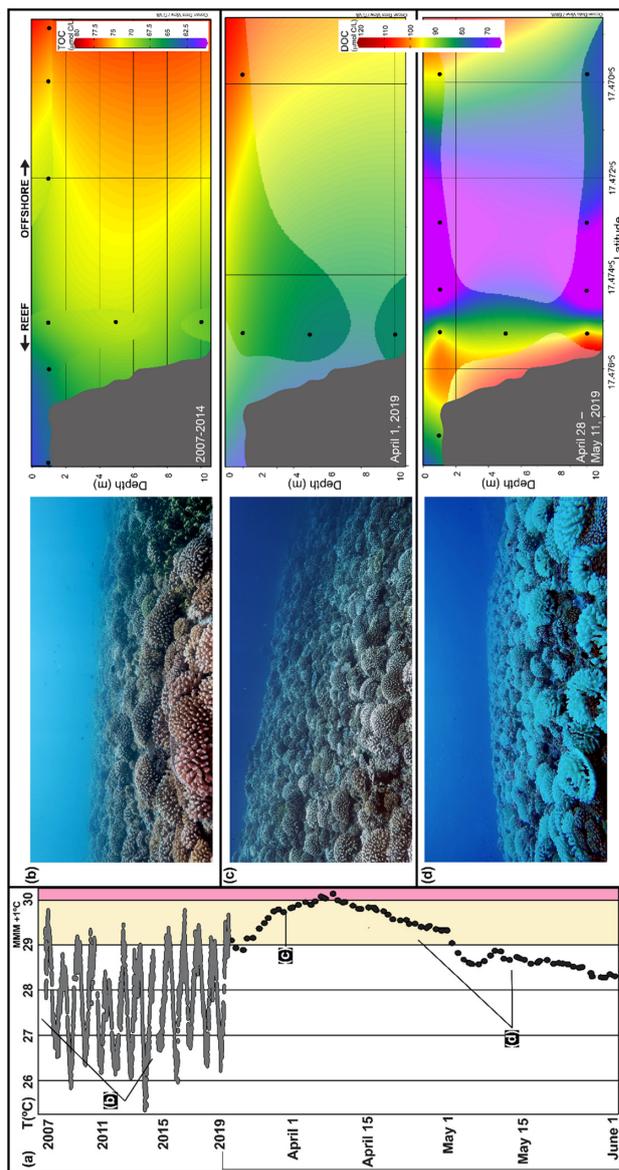
Fig. 1 Reef conditions, representative pictures, and organic carbon distributions before and during the 2019 bleaching event. (A) Temperature values at 10m depth at the forereef site, 'LTER 1' between 2007 and 2019. Temperature values highlighted in yellow and red are >29°C and >30°C, respectively. (B) Representative picture of the forereef and the distribution of total organic carbon (TOC) during normal, non-bleaching, conditions. TOC is composed of 95-97% dissolved organic carbon (DOC) on this reef. (C-D) Representative pictures and the distribution of DOC at the onset of the bleaching event and the peak of the bleaching event, respectively. Grey shading on the contour plots indicates the seafloor.
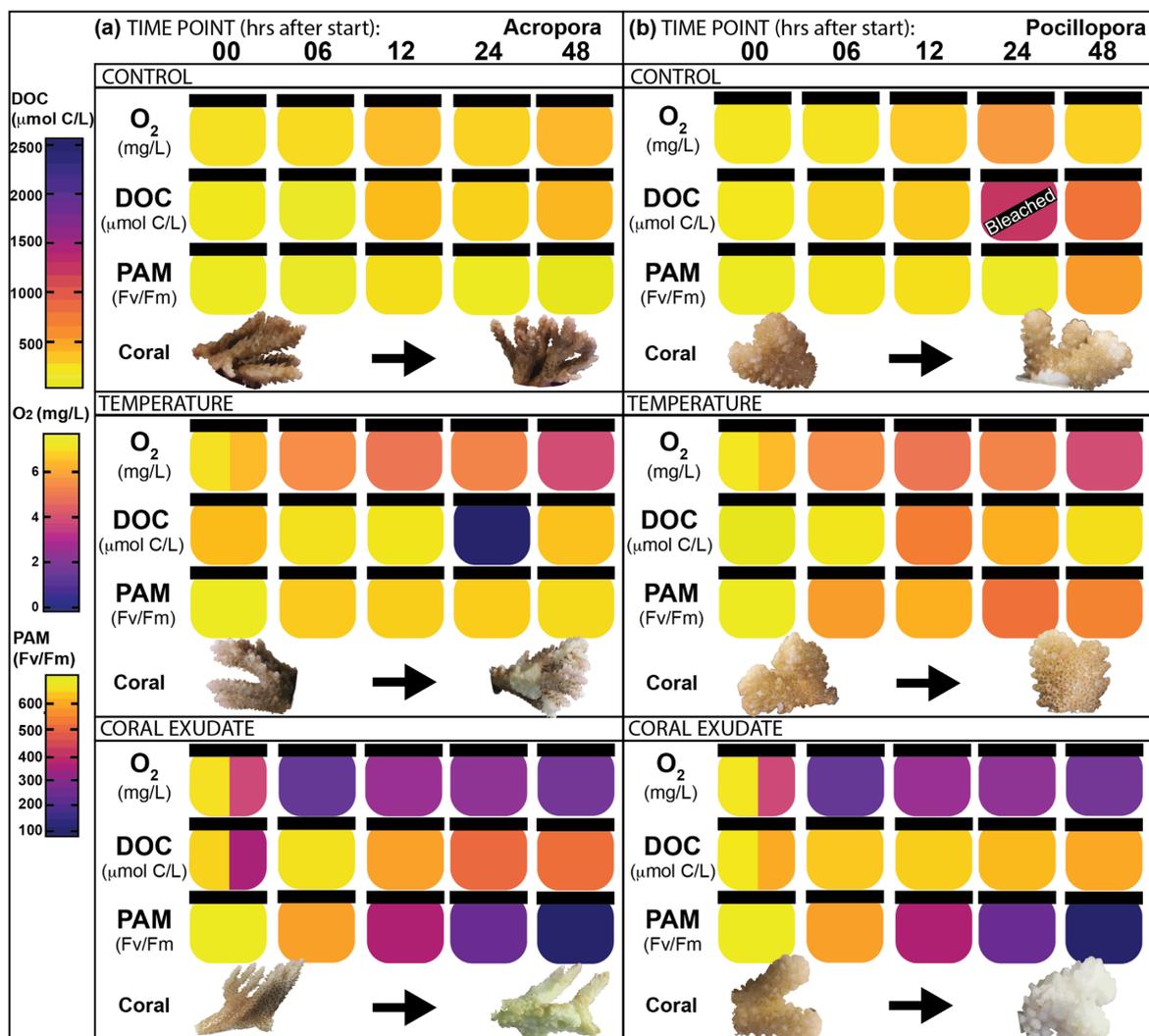
21

Fig 2: Heatmap values plotted as jar symbols indicate dissolved organic carbon (DOC; µmol C) and oxygen (mg/L) concentrations, as well as Pulse-Amplitude Modulation Fluorometry (Fv/Fm) values, averaged per coral species (n=3 per species) for each time point throughout the mesocosm experiment in temperature, coral exudate, and control treatments. At time point 0 (T0; start of the experiment), the 'jars' are split in some instances to show pre- and post-treatment effects on DOC and oxygen values. Images of

representative coral fragments pre- and post-treatment show changes in their visual appearance from the start of the experiment (T0) to the end of the experiment (T48). In one instance within the control treatment for *Pocillopora* spp., a fragment bleached, causing an increase in DOC concentrations for the

535   24hr time point. This is indicated with 'bleached' written over the 'jar'. This outcome was not observed in the other control replicates.
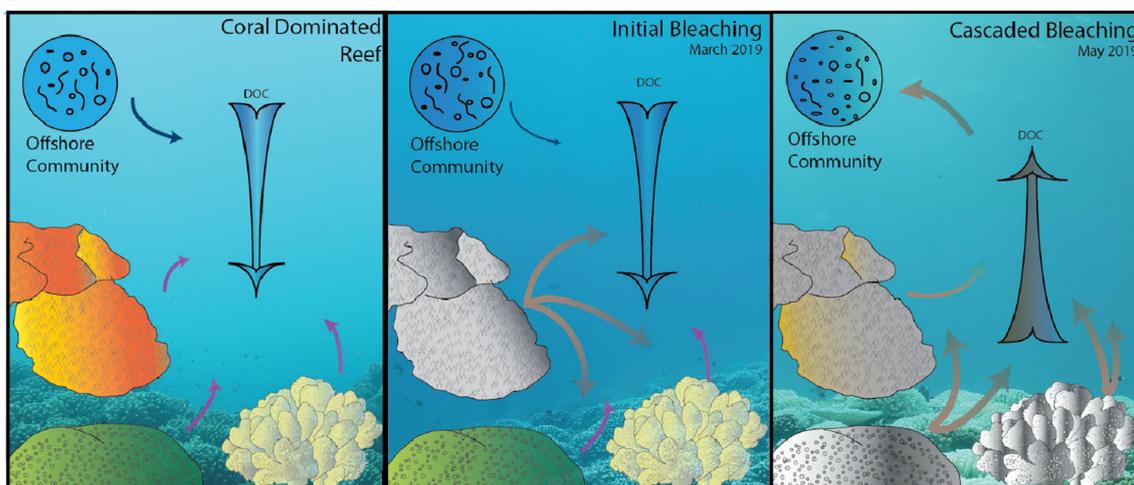

Fig 3: Proposed mechanism of expedited reef decline. **Coral-Dominated Reef** (Left): Under non-bleaching conditions, corals release minimal DOC (0.008-0.056 mmol m^{-2} day^{-1}), which is rapidly broken

540   down. Corals under normal conditions also facilitate the degradation of oceanic sources of DOC (*16*), making the integrated activity of corals and the reef microbial communities a sink for DOC (*3*). The average DOC depletion on-reef is 10% that of corresponding offshore values, based on measurements spanning 10 years. **Initial Bleaching** (Center): When more susceptible corals begin bleaching, they release DOC and mucus exudates that interact with adjacent, non-bleaching corals. The additional DOC

545   released by these initially bleaching corals increases the total uptake of DOC by heterotrophic microorganisms by 10%. This DOC, through a variety of potential mechanistic pathways including localized acidification, facilitation of pathogens, and oxygen stress, exacerbates bleaching impacts in adjacent corals. **Widespread Bleaching** (right): Following widespread bleaching of the reef, the local

microbial community is no longer able to oxidize the DOC released by nearby corals, leading to a

550 bleaching event carbon flux that is 7,000x greater than the daily non-bleaching state. Arrows indicate net

flux of carbon with color indicating source (Blue = pelagic; purple = non-bleached coral; brown =

bleaching coral DOC). The images that the diagram is overlain on are from each of the DOC states

quantified and time points indicated (including in Fig.1).