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Organic carbon fluxes mediated by corals at elevated pCO_2 and temperature

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ABSTRACT: Increasing ocean acidification (OA) and seawater temperatures pose significant threats to coral reefs globally. While the combined impacts of OA and seawater temperature on coral biology and calcification in corals have received significant study, research to date has largely neglected the individual and combined effects of OA and seawater temperature on coral-mediated organic carbon (OC) fluxes. This is of particular concern as dissolved and particulate OC (DOC and POC, respectively) represent large pools of fixed OC on coral reefs. In the present study, coral-mediated POC and DOC, and the sum of these coral-mediated flux rates (total OC, TOC = DOC + POC) as well as the relative contributions of each to coral metabolic demand were determined for 2 species of coral, *Acropora millepora* and *Turbinaria reniformis*, at 2 levels of pCO_2 (382 and 741 µatm) and seawater temperatures (26.5 and 31.0°C). Independent of temperature, DOC fluxes decreased significantly with increases in pCO_2 in both species, resulting in more DOC being retained by the corals and only representing between 19 and 6% of TOC fluxes for *A. millepora* and *T. reniformis*. At the same time, POC and TOC fluxes were unaffected by elevated temperature and/or pCO_2. These findings add to a growing body of evidence that certain species of coral may be less at risk to the impacts of OA and temperature than previously thought.

KEY WORDS: Ocean acidification · Carbon dioxide · Ocean warming · *Acropora* · *Turbinaria* · Calcification · Climate change

INTRODUCTION

Coral reefs are threatened globally due to a combination of direct and indirect human perturbations to ocean waters (e.g. Hoegh-Guldberg et al. 2007). Rising atmospheric carbon dioxide (CO_2) concentrations have contributed to increases in global seawater temperatures and an overall decrease in ocean pH (i.e. increase in ocean acidification, OA; Sabine et al. 2004, IPCC 2013). As hypercalcifying organisms that

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live close to their thermal temperature limit, corals are severely threatened by both increasing temperatures and OA (Hoegh-Guldberg et al. 2007, Wild et al. 2011).

OA is the direct result of roughly half of anthropogenic CO_2 emissions being taken up by the world's oceans (Caldeira & Wickett 2003, Sabine et al. 2004). CO_2 reacts with water to form carbonic acid, which, through the production of protons (H^+) and bicarbonate ions (HCO_3^-), subsequently lowers pH, carbonate ion (CO_3^{2-}) concentration, and the calcium carbonate saturation state (Ω) of seawater (Orr 2011). Globally, surface seawater pH has declined by an average of 0.1 units since the start of the industrial revolution (Caldeira & Wickett 2003) and is projected to decrease another 0.3 to 0.4 units by the end of this century (Orr 2011). Increasing OA is predicted to result in a decrease in coral calcification between 15 and 40% by the end of the century (Kleypas et al. 1999, 2011, Langdon et al. 2000). Under experimental OA conditions, coral calcification rates either decrease (e.g. Marubini & Atkinson 1999, Langdon & Atkinson 2005, Edmunds et al. 2012, Comeau et al. 2013b, Schoepf et al. 2013) or remain unchanged (Reynaud et al. 2003, Edmunds et al. 2012, Houlbrèque et al. 2012, Comeau et al. 2013b, Schoepf et al. 2013). In addition to calcification, OA has been shown to result in decreased tissue biomass, chlorophyll *a* (chl *a*) concentrations, and increased susceptibility to bleaching (i.e. loss of endosymbionts) in some coral species (Anthony et al. 2008, Edmunds et al. 2012, Comeau et al. 2013a), but to have limited or no effect on coral energy reserves, biomass, or chl *a* in other species (Schoepf et al. 2013).

Increased seawater temperature has also been associated with declines in coral calcification rates, tissue biomass, and energy reserves (i.e. lipids, protein, and carbohydrates) (Jokiel & Coles 1977a, Fitt et al. 1993, Edmunds et al. 2003, Marshall & Clode 2004, Grottoli et al. 2006, Rodrigues & Grottoli 2006, 2007, Cantin et al. 2010, Levas et al. 2013). When both seawater temperature and pCO_2 are simultaneously elevated, calcification either decreases (Reynaud et al. 2003, Anthony et al. 2008, Rodolfo-Metalpa et al. 2011) or remains unchanged (Langdon & Atkinson 2005, Rodolfo-Metalpa et al. 2010, Edmunds 2011, Schoepf et al. 2013). In the case of the 2 species used in the present study (*Acropora millepora* and *Turbinaria reniformis*), calcification rates do not change, energy reserves do not decline, and photosynthesis and/or algal density decline or do not change when both seawater temperature and pCO_2 are simultaneously elevated (Schoepf et al. 2013). However, despite the implications for coral physiology and coral reef biogeochemical carbon (C) cycling, no studies to date have assessed the individual or interactive effects of elevated temperatures and pCO_2 on coral-mediated organic matter fluxes. This is of particular concern, as corals play an important role in coral reef biogeochemical cycles and fauna–microbe interactions through the production of mucus (Wild et al. 2004a,b, 2005a,b, 2008, 2009) and its subsequent degradation into particulate and dissolved organic matter (Brown & Bythell 2005, Bythell & Wild 2011).

Coral-mediated particulate and dissolved organic matter may have unique ecological functions in coral reef ecosystems. In healthy coral reefs, corals secrete particulate organic matter in the form of mucus that acts as a trap for organic and inorganic matter which they can ingest or slough off, where it may be deposited to the seafloor, where roughly 90% of coral-mediated particulate organic C (POC) is degraded by benthic microbial consumers (Wild et al. 2004a). Meanwhile, coral-mediated production of dissolved organic C (DOC) is rapidly utilized and supports heterotrophic microbes in the water column (Nelson et al. 2013). In addition to producing POC and DOC, corals have been shown to take up DOC and POC under normal and elevated temperature conditions, presumably as a source of fixed C (Ferrier-Pagès et al. 1998, Anthony 2000, Haas et al. 2010, Naumann et al. 2010, Tremblay et al. 2012, Levas et al. 2013), which may serve as a supplemental nutritional resource under stressful conditions and be associated with coral resilience. Under elevated temperatures, coral bleaching results in decreases in the acquisition of photosynthetically fixed C and often results in the depletion of energy reserves (Fitt et al. 1993, Edmunds et al. 2003, Grottoli et al. 2006, Rodrigues & Grottoli 2007). At the same time, OA potentially makes calcification more energetically costly (Cohen & Holcomb 2009, Erez et al. 2011, Pandolfi et al. 2011). Therefore, under stressful environmental conditions such as elevated temperatures and OA, coral fixed C budgets could be dramatically strained. Thus, we hypothesize that some corals may alter their DOC and POC fluxes in order to conserve organic carbon (OC) as a mechanism to tolerate the stress and/or promote recovery. This has implications for coral reef biogeochemical cycles and host–microbe interactions through the production of mucus, which supports a diverse microbial community (Wild et al. 2004a,b, 2005a,b, 2008, 2009), its subsequent degradation into POC and DOC (Brown &

Bythell 2005, Bythell & Wild 2011), and ensuing fueling of the reef microbial loop.

In the present study, we evaluated the individual and interactive effects of seawater pCO_2 and temperature on coral-mediated POC and DOC fluxes, total OC (TOC = DOC + POC) fluxes, and the relative contributions of each flux to coral metabolic demand in 2 species of Pacific coral. Collectively, these measurements were used to evaluate how coral-mediated OC fluxes may change with the predicted increases in baseline seawater temperature and seawater pCO_2 forecasted for the end of this century.

MATERIALS AND METHODS

Experimental design

Coral collection, acclimation, experimental design, and procedures used in the present study and the seawater chemical parameters (Table 1) have been described previously by Schoepf et al. (2013). Briefly, 6 parent colonies each of *Acropora millepora* and *Turbinaria reniformis* were collected at 3 to 10 m depth in northwest Fiji (17° 29' 19" S, 177° 23' 39" E) in April 2011 and transported to Reef Systems Coral Farm in New Albany, Ohio, USA. Four coral fragments were collected from each parent colony (total of 24 fragments per species), mounted onto prelabeled tiles, and allowed to acclimate in a holding tank with natural light for 2.5 mo.

In July 2011, all 48 fragments were transferred to experimental recirculating indoor aquaria with custom-made artificial seawater (ESV Aquarium Products), which was designed to mimic the chemical composition and alkalinity of natural reef seawater. Fragments were then allowed to acclimate for another 10 d at ambient seawater temperature and pCO_2 (26.5°C and pCO_2 of 382 µatm) and light (275 µmol quanta m^{-2} s^{-1} on a 9:15 h light:dark cycle) prior to exposure to the experimental conditions. Four experimental treatments were used: 26.5°C with 382 µatm pCO_2, 26.5°C with 741 µatm pCO_2, 31.0°C with 382 µatm pCO_2, and 31.0°C with 741 µatm pCO_2. The 2 pCO_2 levels used (382 and 741 µatm) were designed to represent present-day pCO_2 and the average pCO_2 level expected by the second half of the 21st century (IPCC 2013). The control temperature (26.5°C) represents the current average annual temperatures in Fiji (www.ospo.noaa.gov/Products/ocean/index.html). Temperatures in the elevated seawater temperature treatments were increased gradually over the course of the study in order to avoid shocking the corals (Fig. 1). Each seawater temperature–pCO_2 combination consisted of a separate recirculating tank system with one 905 l sump and 6 aquaria of 57 l each. One fragment from each parent colony per species was placed in 1 of the 6 aquaria in each system such that each parent colony of each species was represented in each system. The experiment lasted for 24 d. Throughout the experiment, corals were fed every 3 d with 48 h old brine shrimp nauplii. Each fragment was also buoy-

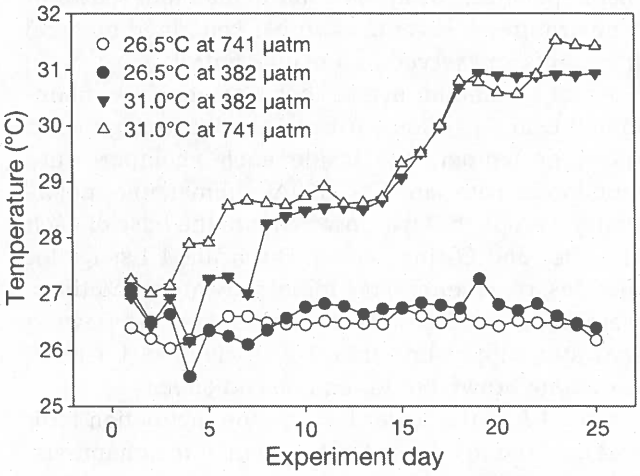

Fig. 1. Mean ± SE daily temperature for each treatment throughout the study. Errors are sometimes very small, making the error bars smaller than the symbol and not visible

Table 1. Mean ± SE seawater conditions for each treatment representing 2 pCO_2 levels and 2 temperature regimes as reported by Schoepf et al. (2013). Temp.: temperature; T: total scale; TA: total alkalinity; Ω_{arag}: saturation state of aragonite

Variable	Ambient pCO_2		Elevated pCO_2	
	Ambient temp.	Elevated temp.	Ambient temp.	Elevated temp.
Temperature (°C)	26.45 ± 0.01	29.31 ± 0.02	26.61 ± 0.01	28.93 ± 0.02
pH_T	8.07 ± 0.01	8.04 ± 0.01	7.83 ± 0.01	7.81 ± 0.01
pCO_2 (µatm)	364.31 ± 9.69	400.62 ± 16.83	732.04 ± 22.37	749.63 ± 26.21
TA (µmol kg^{-1})	2269.9 ± 10.84	2270.1 ± 11.15	2306.3 ± 10.64	2304.5 ± 9.081
Ω_{arag}	3.69 ± 0.07	3.79 ± 0.09	2.40 ± 0.06	2.52 ± 0.06

antly weighed on Days 1, 12, and 24 of the experiment, and calcification rates per cm^2 were determined for the first and the second half of the experiment as reported by Schoepf et al. (2013).

POC, DOC, and TOC fluxes

To assess coral-mediated organic matter fluxes, individual coral fragments were incubated in circular 1.25 l UV-transparent acrylic chambers (15.3 cm tall × 10.7 cm diameter). Since these incubations were only conducted during the day, calculated values reflect daytime fluxes. Six coral fragments of the same species and treatment were cleaned of any epizootic organisms and detritus and their tiles thoroughly cleaned of encrusting organisms and algae. Each fragment was transferred to an individual chamber freshly filled with treatment-specific seawater, with air exposure limited to ~1 s. A lid was securely placed on top of the chamber, making sure to eliminate all air bubbles, and the chamber was fully submerged in a large tank supplied with treatment-specific flowing seawater to maintain seawater temperature. A seventh chamber contained no coral fragments and served as a blank control.

Water circulation inside each chamber was maintained using a Teflon stir-bar. Dissolved oxygen and seawater temperature inside each chamber were monitored with an YSI 550A submersible polargraphic probe that was inserted into the base of each chamber and O-ring sealed. Duplicate 1 l seawater samples, representing the initial seawater conditions, were collected from the treatment-specific flowing seawater supply line into 2 acid-cleaned 1 l polycarbonate brown bottles and placed on ice.

After 1.5 h, the water level in the incubation tank was lowered to expose the top 3 cm of the chambers. All coral fragments were then removed and placed back in the respective treatment aquaria, and the seawater from each chamber was collected into an individual acid-cleaned 1 l brown bottle and placed on ice. The incubations were limited to 1.5 h to ensure that dissolved oxygen did not reach supersaturation, which can be a potential stressor. Each 1 l sample was then filtered onto a pre-combusted (500°C for 4 h) GF/F filter (0.7 µm nominal pore size) and stored at –20°C for POC analysis. A 30 ml subsample of the filtrate was collected in an acid-cleaned polycarbonate bottle, acidified to a pH ≤2 using ultra high purity HCl, and stored at –20°C for DOC analysis. Duplicate GF/F filters and 30 ml aliquots were also collected from the blank chamber for POC and DOC analysis, respectively. Two sets of incubations on separate fragments were performed per day (one starting at 10:00 h and the other starting at 14:00 h), and all incubations were completed over the course of the last 4 d of the experiment. To facilitate comparisons among treatments within a species, *A. millepora* incubations were always conducted from 10:00 to 11:30 h and *T. reniformis* incubations were always conducted from 14:00 to 15:30 h. Chambers were cleaned and thoroughly rinsed with treatment-appropriate seawater prior to each incubation.

DOC concentrations were determined using high-temperature catalytic oxidation using a Shimadzu model 5050 TOC analyzer. After thawing, samples were sparged 2 min with ultra-high purity air, and then 250 µl of sample were injected into the instrument. A standard consisting of 1000 µM glucose was used to establish a 4-point calibration curve. A regular quality control check consisting of glucose was also injected after every 5 samples. The standard deviation of replicate measurements of the glucose standard was ±4%.

For POC analyses, GF/F filters were dried for 24 h at 60°C and then acidified in a clean glass desiccator using concentrated fuming HCl for 24 h to remove inorganic C. POC was determined using a Costech Elemental Analyzer (EA). An acetanilide standard was used to establish a 4-point calibration curve and as a quality control standard spaced throughout each EA sample run. The standard deviation of the replicate measurements of the standard was ±1.8%.

For each coral incubation, the DOC and POC concentrations were corrected for potential microheterotrophic and microautotrophic biases by subtracting the POC and DOC concentrations of their blank chamber from their respective values. Since microbially mediated DOC degradation is not observed in the first 2 h (Nakajima et al. 2009), a short incubation time combined with the use of a blank correction minimizes any interference of bacterial degradation in the signal. Fluxes (i.e. release or uptake; µmol C h^{-1} cm^{-2}) were calculated as the difference between the blank-corrected OC concentration (µmol) of the coral fragment and the initial seawater concentration, and standardized to the incubation duration (1.5 h) and fragment surface area (FSA; cm^2) as determined by the foil technique (Marsh 1970) using the following equation:

$$\text{Daytime OC flux} = \frac{(OC_{coral} - OC_{blank}) - OC_{Initia}}{1.5 \times FSA} \quad (1)$$

Negative fluxes indicate a net uptake by coral fragments, and positive fluxes indicate a net release from

coral fragments. TOC flux was calculated as the sum of the individual POC and DOC fluxes.

Proportionate contribution of POC, DOC, and TOC to coral respiration

The proportionate contribution of heterotrophically derived OC to the coral daytime C budget was calculated relative to respiration, which is termed the percent contribution of heterotrophy to animal respiration (CHAR; Grottoli et al. 2006). Here, CHAR for POC ($CHAR_{POC}$), DOC ($CHAR_{DOC}$), and TOC ($CHAR_{TOC}$) were determined as follows.

Respiration was measured on each coral fragment individually during the last 4 d of the experiment using previously described methods (Fitt & Warner 1995). For a given fragment, respiration incubations were conducted 1 d before the POC and DOC incubations in order to minimize any potential stress to the corals and to ensure that both sets of measurements were contemporaneous. In brief, coral fragments were individually placed in 350 ml water-tight UV-transparent acrylic chambers filled with their respective treatment seawater and a stir bar, and dissolved gaseous oxygen was lowered to 80% by bubbling with ultra high purity nitrogen gas. Chambers were then placed into a 20 l Plexiglas tank filled with fresh water, which was temperature controlled by a heater/chiller unit and set to 26.5°C or 31.0°C, depending on the treatment. The incubation tank was then covered by black plastic, and dissolved oxygen was measured for approximately 15 min. Respiration was then determined by calculating the slope of the oxygen concentration recorded during the last 10 min of each run.

Daytime $CHAR_{POC}$ and $CHAR_{DOC}$ for each fragment were calculated as the daytime flux of POC or DOC in µg C standardized to grams ash-free dry weight h^{-1} (POC_f and DOC_f, respectively), divided by the µg C lost via daytime respiration h^{-1} (R_c), assuming a mole-to-mole relationship of O_2 consumed to CO_2 produced during respiration. Thus, daytime $CHAR_{POC}$ and $CHAR_{DOC}$ were calculated as:

$$CHAR_{POC} = \frac{POC_f}{R_c} \times 100\% \quad (2)$$

$$CHAR_{DOC} = \frac{DOC_f}{R_c} \times 100\% \quad (3)$$

Therefore here, $CHAR_{POC}$ and $CHAR_{DOC}$ are the percentage of a coral's respiration that can be met or lost through OC uptake or released during the day. $CHAR_{TOC}$ for each fragment was calculated as the sum of $CHAR_{POC}$ and $CHAR_{DOC}$. Negative CHAR values indicate a net loss of OC relative to respiratory demand, and positive CHAR values indicate a net gain of OC relative to respiratory demand. We recognize that POC and DOC fluxes (S. Levas unpubl. data) and respiration (Rodrigues & Grottoli 2007) vary between day and night. Since we only have daytime measurements for all 3 variables, our interpretation is limited to daytime fluxes.

Statistical analysis

Three-way mixed-model ANOVA was run for each species separately and tested the effects of temperature, pCO_2, and genotype on POC fluxes, DOC fluxes, TOC fluxes, daytime respiration, $CHAR_{POC}$, $CHAR_{DOC}$, and $CHAR_{TOC}$. Temperature and pCO_2 were fixed and fully crossed, whereas genotype was a random factor. The purpose of including the genotype in the ANOVA model was to determine whether any single genotype was systematically different from all others for a given variable. In cases where significant genotype effects were detected, Tukey tests revealed that all average values overlapped among genotypes. As such, we concluded that the selected colonies represented the natural variation in the population, and no single or group of colonies was consistently different from the others. Thus, interaction terms involving genotype were not included in the ANOVAs. All data were deemed to be normally distributed using Shapiro-Wilk normality tests. All data sets met the assumptions of homogeneity of variances as determined with plots of expected versus residual value. Tukey post hoc tests were performed when main effects were significant ($p \leq 0.05$). *A posteriori* slice tests (e.g. tests of simple effects, Winer 1971) determined whether low (382 µatm) and high (741 µatm) pCO_2 treatment averages significantly differed within each temperature treatment. Bonferroni corrections were not applied due to increased likelihood of false negatives (Quinn & Keough 2002, Moran 2003). To explore possible relationships between a suite of published variables on these same corals and the data in this study, Pearson correlation analyses were run between calcification rates and total energy reserve data from Schoepf et al. (2013) and POC, DOC, and TOC fluxes here. Statistical analyses were performed using SAS software, Version 9.3 of the SAS System for Windows.

RESULTS

POC, DOC, TOC fluxes, and daytime respiration

In *Acropora millepora*, POC flux rates were unaffected by both temperature and pCO_2 (Fig. 2A, Table 2). However, DOC fluxes averaged 59% lower in the elevated pCO_2 treatments (741 µatm) than in ambient pCO_2 treatments (382 µatm; Fig. 2B, Table 2). This pCO_2 effect was most pronounced at ambient temperature (Fig. 2B). No significant temperature or pCO_2 effect was detected for *A. millepora* TOC fluxes (Fig. 2C, Table 2), while daytime respiration rates were 39% lower in elevated pCO_2 treatments than in ambient conditions irrespective of temperature (Fig. 2D, Table 2). Overall, DOC fluxes constituted about 45% of the TOC flux at ambient pCO_2 and 19% at elevated pCO_2 (Fig. 2). *Turbinaria reniformis* POC fluxes were unaffected by both temperature and pCO_2, while DOC fluxes decreased by an average of 100% under elevated pCO_2, independent of temperature (Fig. 2E,F, Table 2). Despite significant declines in DOC fluxes at elevated pCO_2,

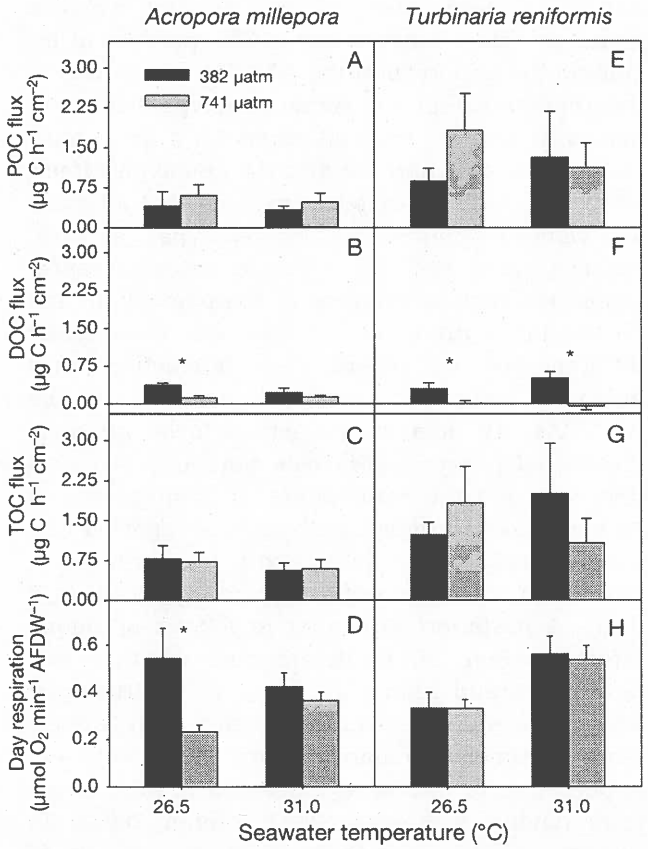

Fig. 2. Mean ± SE daytime particulate, dissolved, and total organic carbon (POC, DOC, and TOC, respectively) fluxes and daytime respiration for (A–D) *Acropora millepora* and (E–H) *Turbinaria reniformis*. Within each panel, asterisks indicate significant differences between 382 and 741 µatm averages within a specific temperature (determined by *a posteriori* slice tests). Positive rates indicate release/loss, whereas negative rates indicate uptake. Sample sizes ranged between 5 and 6 coral fragments in each treatment

Table 2. Results of 3-way ANOVAs for *Acropora millepora* and *Turbinaria reniformis* particulate organic carbon (POC), dissolved organic carbon (DOC), and total organic carbon (TOC) fluxes, and daytime respiration at 2 temperatures (26.5°C and 31.0°C) and 2 pCO_2 levels (382 and 741 µatm). Effects of temperature (T) and pCO_2 were fixed and fully crossed. Genotype (G) was a random effect. Significant effects are shown in **bold**

Variable	Effect	df	F	p
A. millepora				
POC	Model	8,22	0.78	0.6308
	T	1	0.28	0.6035
	pCO_2	1	0.85	0.3708
	G	5	1.04	0.4339
	$T \times pCO_2$	1	0.01	0.9375
DOC	Model	8,21	3.10	**0.0343**
	T	1	1.33	0.2961
	pCO_2	1	10.62	**0.0062**
	G	5	1.64	0.2194
	$T \times pCO_2$	1	2.60	0.1311
TOC	Model	8,22	1.11	0.4145
	T	1	0.97	0.3426
	pCO_2	1	0.00	0.9958
	G	5	1.57	0.2308
	$T \times pCO_2$	1	0.08	0.7805
Daytime respiration	Model	8,22	1.78	0.1655
	T	1	0.01	0.9338
	pCO_2	1	5.86	**0.0297**
	G	5	1.03	0.4381
	$T \times pCO_2$	1	2.69	0.1231
T. reniformis				
POC	Model	8,23	0.72	0.6709
	T	1	0.04	0.8397
	pCO_2	1	0.38	0.5474
	G	5	0. 90	0.5034
	$T \times pCO_2$	1	0.83	0.3774
DOC	Model	8,21	3.68	**0.0185**
	T	1	0.72	0.4119
	pCO_2	1	21.21	**0.0005**
	G	5	1.17	0.3749
	$T \times pCO_2$	1	2.16	0.1656
TOC	Model	8,21	0.61	0.7586
	T	1	0.00	0.9904
	pCO_2	1	0.02	0.8997
	G	5	0.68	0.6445
	$T \times pCO_2$	1	1.30	0.2747
Daytime respiration	Model	8,21	1.42	0.2643
	T	1	10.09	**0.0063**
	pCO_2	1	0.04	0.8506
	G	5	0.25	0.9346
	$T \times pCO_2$	1	0.03	0.8730

there were no overall temperature or pCO_2 effects on *T. reniformis* TOC fluxes (Fig. 2G, Table 2). However, *T. reniformis* daytime respiration rates were 40% greater at elevated temperatures but unaffected by elevated pCO_2 (Fig. 2H, Table 2). Overall, DOC fluxes constituted about 30% of the TOC flux at ambient pCO_2 and 6% at elevated pCO_2 (Fig. 2).

Proportionate contribution of POC, DOC, and TOC to coral respiration

A. millepora $CHAR_{POC}$, $CHAR_{DOC}$, and $CHAR_{TOC}$ as well as *T. reniformis* $CHAR_{POC}$ and $CHAR_{TOC}$ were unaffected by temperature and pCO_2 (Fig. 3A–D, F, Table 3). However, in *T. reniformis*, $CHAR_{DOC}$ was more negative at ambient compared to elevated pCO_2 levels, and positive at elevated temperature (Fig. 3E, Table 3). Overall, $CHAR_{DOC}$ constituted 31% and 25% of the $CHAR_{TOC}$ at ambient and elevated pCO_2 for *A. millepora*, respectively, and 26% and −1% of the $CHAR_{TOC}$ at ambient and elevated pCO_2 for *T. reniformis*, respectively (Fig. 3).

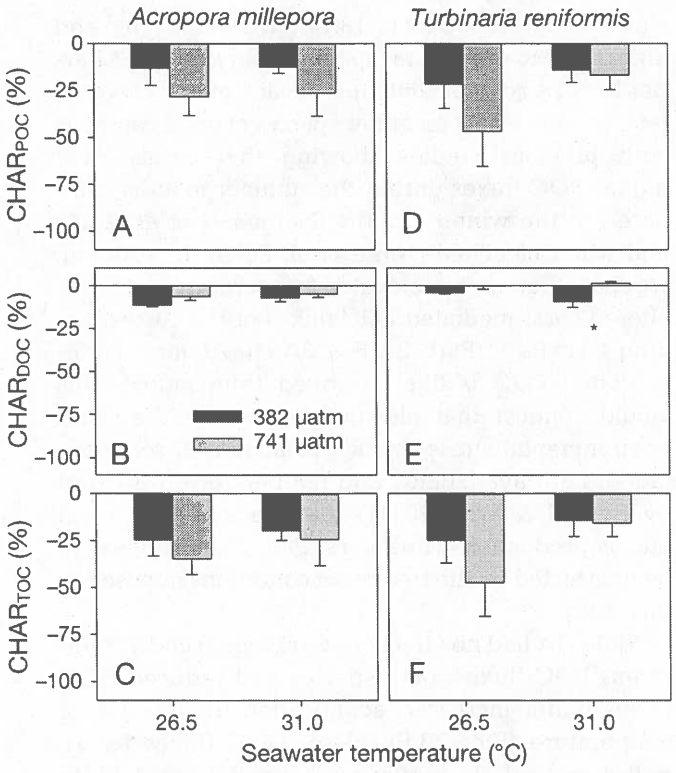

Fig. 3. Mean ± SE daytime percent contribution of heterotrophically derived particulate, dissolved, and total organic carbon (POC, DOC, and TOC, respectively) to animal respiration ($CHAR_{POC}$, $CHAR_{DOC}$, and $CHAR_{TOC}$, respectively) for (A–C) *Acropora millepora* and (D–F) *Turbinaria reniformis* in each treatment. Within each panel, asterisks indicate significant differences between 382 and 741 µatm averages within a specific temperature (determined by *a posteriori* slice tests). Negative values indicate carbon losses. Sample sizes ranged between 5 and 6 individual coral fragments in each treatment

Relationship of POC, DOC, and TOC to calcification and energy reserves

A. millepora POC and TOC fluxes were not significantly correlated with respiration, calcification rates, or total energy reserves (Table 4). Only *A. millepora*

Table 3. Results of 3-way ANOVAs for *Acropora millepora* and *Turbinaria reniformis*, daytime percent contribution of heterotrophically derived particulate, dissolved, and total organic carbon (POC, DOC, and TOC, respectively) to animal respiration ($CHAR_{POC}$, $CHAR_{DOC}$, and $CHAR_{TOC}$, respectively) at 2 temperatures (26.5°C and 31.0°C) and 2 pCO_2 levels (382 and 741 µatm). Effects of temperature (T) and pCO_2 were fixed and fully crossed. Genotype (G) was a random effect. Significant effects are shown in **bold**

Variable	Effect	df	F	p
A. millepora				
$CHAR_{POC}$	Model	8, 2	1.62	0.2062
	T	1	0.09	0.7732
	pCO_2	1	3.34	0.0889
	G	5	2.00	0.1403
	$T \times pCO_2$	1	0.01	0.9412
$CHAR_{DOC}$	Model	8, 22	1.65	0.2040
	T	1	1.87	0.1943
	pCO_2	1	2.87	0.1140
	G	5	1.27	0.3332
	$T \times pCO_2$	1	0.90	0.3609
$CHAR_{TOC}$	Model	8, 21	1.76	0.1760
	T	1	0.89	0.3639
	pCO_2	1	1.40	0.2579
	G	5	2.43	0.0916
	$T \times pCO_2$	1	0.00	0.9609
T. reniformis				
$CHAR_{POC}$	Model	8, 21	0.92	0.5286
	T	1	1.67	0.2174
	pCO_2	1	1.47	0.2457
	G	5	0.63	0.6792
	$T \times pCO_2$	1	1.02	0.3303
$CHAR_{DOC}$	Model	8, 21	1.96	**0.0298**
	T	1	1.27	0.2810
	pCO_2	1	17.0	**0.0012**
	G	5	1.28	0.3305
	$T \times pCO_2$	1	3.61	0.0800
$CHAR_{TOC}$	Model	8, 20	0.71	0.6768
	T	1	1.24	0.2857
	pCO_2	1	0.45	0.5155
	G	5	0.51	0.7645
	$T \times pCO_2$	1	1.45	0.2495

Table 4. Pearson's correlation analyses for *Acropora millepora* and *Turbinaria reniformis*. POC: particulate organic carbon flux (μmol C h^{-1} cm^{-2}); DOC: dissolved organic carbon flux (μmol C h^{-1} cm^{-2}); TOC: total organic carbon flux (DOC + POC; μmol C h^{-1} cm^{-2}); Day *R*: daytime respiration (μmol C h^{-1} cm^{-2}); Calc.1: calcification during the first 12 d of the experiment (mg d^{-1} cm^{-2}); Calc.2: calcification during the last 12 d of the experiment (mg d^{-1} cm^{-2}); E. reserves: sum of protein + carbohydrate + lipid concentrations (mg g^{-1} ash-free dry weight). Calcification and E. reserve data from Schoepf et al. (2013). Significant correlations are shown in **bold**

Variable		*A. millepora*				*T. reniformis*			
		Day *R*	Calc.1	Calc.2	E. reserves	Day *R*	Calc.1	Calc.2	E. reserves
POC	r	0.096	0.143	−0.039	−0.150	0.152	0.194	0.201	0.201
	p	0.65	0.51	0.86	0.49	0.47	0.36	0.34	0.34
	N	23	23	22	23	24	24	24	24
DOC	r	−0.369	0.055	**0.537**	−0.395	−0.269	−0.007	−0.072	−0.350
	p	0.09	0.81	**0.01**	0.06	0.22	0.97	0.74	0.10
	N	22	21	**21**	22	22	22	22	22
TOC	r	−0.017	0.185	0.166	−0.275	0.158	0.272	0.238	0.145
	p	0.93	040	0.45	0.20	0.48	0.22	0.28	0.51
	N	23	23	22	23	22	22	22	22

DOC fluxes were positively correlated with calcification rates during the second half of the experiment (Table 4). *T. reniformis* POC, DOC, and TOC fluxes were not significantly correlated with respiration, calcification rates, or total energy reserves (Table 4).

DISCUSSION

Previous studies have investigated OC fluxes by corals and coral reef organisms under ambient (Crossland et al. 1980, Crossland 1987, Tanaka et al. 2008, 2009, Haas et al. 2010, Naumann et al. 2010) and varying environmental conditions such as eutrophication (Tanaka et al. 2007), elevated temperature (Haas et al. 2010, Levas et al. 2013), and during different seasons (Naumann et al. 2010). However, this study is the first to assess the combined impacts of elevated pCO_2 and temperature on coral-mediated OC fluxes.

POC, DOC, and TOC fluxes

Both coral species had positive POC fluxes (i.e. released POC) irrespective of pCO_2 or temperature treatments (Fig. 2A,E). Average POC fluxes for *Acropora millepora* of 3.36 to 6.08 mg POC m^{-2} h^{-1} were within the range of those reported for *Acropora* corals from Japan and the Red Sea of 1.0 to 7.1 mg POC m^{-2} h^{-1} (Tanaka et al. 2008, 2009, Naumann et al. 2010). *Turbinaria reniformis* POC fluxes in this study varied from 8.80 to 18.24 mg POC m^{-2} h^{-1} and are similar to other coral species from the Great Barrier Reef (Wild et al. 2005b). The lack of any elevated temperature effect on either species of coral contrasts with previous studies showing that corals have higher POC fluxes during the summer months compared to the winter months (Naumann et al. 2010) and when bleached (Niggl et al. 2008). In addition, we show that neither elevated temperature nor pCO_2 altered coral-mediated POC fluxes or the corresponding $CHAR_{POC}$ (Figs. 2A,E & 3A,D). As most coral-mediated POC is likely derived from mucus, this would suggest that elevated pCO_2—unlike other environmental stressors such as increased sedimentation, light availability, and temperature (reviewed by Bythell & Wild 2011)—has no effect on coral mucus production. Thus, coral POC fluxes appear to be unaffected by the treatment conditions imposed in this study.

While OA had no effect on *A. millepora* and *T. reniformis* POC fluxes, both species had reduced DOC fluxes under increased acidification irrespective of temperature (Fig. 2B,F). Here, DOC fluxes for *A. millepora* and *T. reniformis* ranged from 1.17 to 3.72 mg DOC m^{-2} h^{-1} and −0.53 to 5.09 mg DOC m^{-2} h^{-1}, respectively. This is within the range of DOC flux measurements reported for healthy *Acropora* ranging from 1.9 mg DOC m^{-2} h^{-1} (Tanaka et al. 2008) to 30.7 mg DOC m^{-2} h^{-1} (Naumann et al. 2010). The lack of any significant temperature effect on DOC fluxes is consistent with previous findings for *A. millepora* and *T. reniformis* (Niggl et al. 2008). However, previous measurements on temperature stres-

sed *Porites* corals showed an increase in DOC flux rates (Haas et al. 2010), which suggests that there may be location- or population-specific responses with the same species. We hypothesize as to the mechanisms driving the retention or release of DOC under elevated pCO_2 below, but further study is needed to fully test these ideas.

Interestingly, despite the decrease in DOC fluxes for all *A. millepora* under elevated pCO_2, there was no corresponding decrease in $CHAR_{DOC}$ because respiration decreased under all conditions (Figs. 2D & 3B). At the same time, *A. millepora* maintained energy reserves while calcification declined (Schoepf et al. 2013). Together, these findings suggest that this coral species either modifies its DOC losses or is incapable of maintaining its DOC fluxes. Either way, limiting the loss of organic C via DOC fluxes does not prevent calcification from declining under pCO_2 stress conditions (Schoepf et al. 2013). Decreases in DOC fluxes at elevated pCO_2 were even more pronounced in *T. reniformis* (Fig. 2E), with dramatic decreases in $CHAR_{DOC}$ when both pCO_2 and temperature were elevated (Fig. 3E). At the same time, *T. reniformis* maintained energy reserves and calcification rates (Schoepf et al. 2013). Together these findings show that this coral species is also capable of modifying its DOC losses, and suggests that DOC modification may play a role in optimizing the coral's C-budget and maintaining calcification under OA and elevated temperature conditions.

Net TOC fluxes (POC flux + DOC flux) were always positive (i.e. corals released TOC) and did not significantly vary with temperature and/or $pCO2$ (Fig. 2C, G). TOC fluxes ranged from 5.5 to 7.8 mg C m^{-2} h^{-1} for *A. millepora* and from 10.8 to 20.0 mg C m^{-2} h^{-1} for *T. reniformis* (Fig. 2C,G). These values are up to 9 times higher than net TOC fluxes by control and temperature-stressed *Stylophora pistillata* (Tremblay et al. 2012). Thus, TOC fluxes appear to vary widely among species. In addition, $CHAR_{TOC}$ was not significantly affected by elevated temperature and/or pCO_2 (Fig. 3C,F), despite the significant decline in $CHAR_{DOC}$ in *T. reniformis*. This is because TOC is predominantly composed of POC, which was not affected by the treatment conditions. Furthermore, C lost as TOC accounted for 14 to 47% of coral metabolic demand (Fig. 3C,F). This is in contrast to *S. pistillata*, which has positive $CHAR_{TOC}$ when healthy and only small OC losses (i.e. $CHAR_{TOC}$ losses of 3 to 6%) when temperature stressed (Tremblay et al. 2012). This would suggest that OC uptake and/or production is highly species and health-status specific.

Model for coral OC loss under normal and elevated pCO_2

Corals release POC in the form of mucus that coats the outer epidermal surface of the animal and as DOC exudates (Fig. 4, adapted from Brown & Bythell

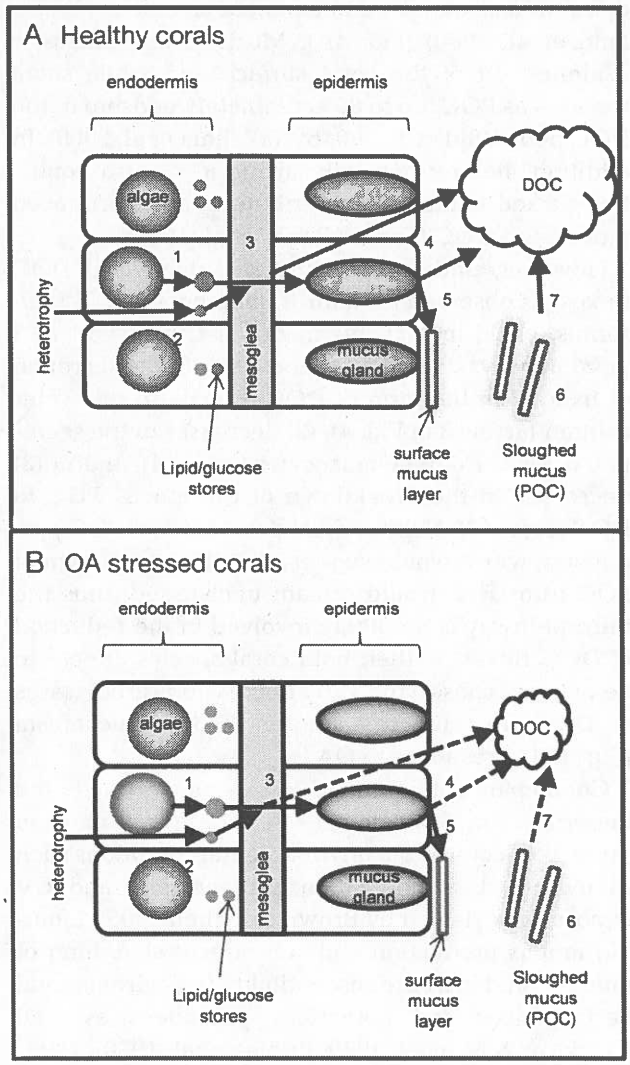

Fig. 4. Model of coral mucus as particulate organic carbon (POC) and dissolved organic carbon (DOC) release in (A) healthy and (B) ocean acidification (OA) stressed corals. In healthy corals, carbon translocation associated with POC and DOC production is as follows (solid arrows in A). (1) Endosymbiotic algae (algae) photosynthetically fix carbon and translocate it to the coral host. (2) Fixed carbon can also be acquired from heterotrophic consumption of plankton. (3) Fixed carbon is either secreted as DOC to the water column or is translocated to mucus glands. (4) Mucus glands secrete DOC and (5) mucus. (6) The sloughed mucus constitutes the coral holobiont-mediated POC, which can also (7) dissolve or be bacterially degraded to form DOC (adapted from Brown & Bythell 2005). In OA stressed corals, pathways 3, 4, and 7 are diminished (dashed lines)

2005). In healthy corals, endosymbionts translocate excess photosynthetically fixed C to the host (Muscatine 1967, 1990, Patton et al. 1977, Harland et al. 1991). While some of this fixed C is stored as energy reserves (Battey & Patton 1984, Edmunds & Spencer Davies 1986), any excess is either released directly to the water column as DOC or transferred to the mucocytes (mucus glands) and excreted as mucus (Crossland et al. 1980) (Fig. 4A). Much of this mucus is sloughed off of the coral surface and while some remains as POC, up to 80% ultimately ends up in the DOC pool (Wild et al. 2004b, Nakajima et al. 2009). In addition, heterotrophically acquired C also contributes fixed C that can contribute to coral-produced mucus and DOC (Ferrier-Pagès et al. 1998).

However, under OA conditions, decreased DOC fluxes, as observed for both *A. millepora* and *T. reniformis*, could impact this model of C-transport in 3 possible ways (Fig. 4B): (1) decreases in the secretion of fixed C in the form of DOC directly to the water column (arrow 3 in Fig. 4), (2) decreases in the secretion of DOC from the mucocytes (arrow 4), and/or (3) decreases in the breakdown of the mucus POC to DOC (arrow 7). Neither coral decreased its POC production, which would suggest that the breakdown of POC into DOC would remain unchanged, thus the third pathway is not likely involved in the reduction of DOC fluxes. Rather, both coral species appear to be actively conserving C by decreasing direct losses of DOC from the first and/or second mechanism (Fig. 4B) in response to OA.

Corals may not limit POC loss as mucus due to the important physio-chemical role that mucus plays in protecting corals from environmental conditions such as increased sedimentation, temperature, and UV exposure (reviewed by Brown & Bythell 2005). Limiting mucus production and subsequent sloughing of mucus could increase susceptibility to environmental perturbations and potentially pathogens as well (Ducklow & Mitchell 1979, Rublee et al. 1980). However, a large fraction of DOC is comprised of lipid (Crossland 1987) which represents a potential energy source. Thus, while POC fluxes are not altered, limiting the loss of DOC through mechanisms (1) and (2) therefore has the potential to limit the amount of lipids lost in the form of DOC. This hypothesis is consistent with recent findings showing that lipid concentrations did not decrease in either species when exposed to elevated pCO_2 (Schoepf et al. 2013). It also indicates that corals can be flexible in their organic matter fluxes and respiration rates in such a way that maintains overall TOC irrespective of OA and/or temperature stress.

Implications

Our findings indicate that coral organic matter fluxes are highly variable and largely species-specific in their responses to elevated pCO_2 and temperature. Decreases in DOC fluxes were accompanied by decreases in respiration resulting in stable $CHAR_{TOC}$. In addition, retaining DOC has the potential to help sustain energy reserves. This is consistent with previous findings showing that biomass and energy reserves are maintained in both *A. millepora* and *T. reniformis* (Schoepf et al. 2013). It is also consistent with emerging findings that increased pCO_2 does not cause significant additional energetic demand on calcification (Edmunds 2011, 2012, McCulloch et al. 2012, Schoepf et al. 2013). However, since DOC represents a significant source of reduced C for planktonic bacteria (Ducklow & Mitchell 1979), decreases in coral-mediated DOC released to the water column could negatively impact reef microbial communities. Overall, these findings add to a growing body of evidence that certain species of corals may be less at risk to the impacts of OA and temperature than previously thought (Edmunds 2012, McCulloch et al. 2012, Schoepf et al. 2013).

It is imperative to keep in mind that these results are based on a short-term (24 d) exposure to elevated temperature and pCO_2. As described by Comeau et al. (2014), it is ideal for experiments testing the impacts of OA to last months to years in order to allow the organisms to acclimate. Clearly, further studies are needed to assess how coral DOC and POC fluxes respond to elevated temperature and $pCO2$ in other species, and over longer periods of time. Longer studies are essential to determine whether changes in coral DOC and POC production ultimately affect coral C budgets and calcification in the long term. In addition, further research is needed to explore how microbial community composition and density might change under future global change scenarios and how that might influence coral OC fluxes.

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