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Marine biology

High pCO_2 promotes coral primary production

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While research on ocean acidification (OA) impacts on coral reefs has focused on calcification, relatively little is known about effects on coral photosynthesis and respiration, despite these being among the most plastic metabolic processes corals may use to acclimatize to adverse conditions. Here, we present data collected between 2016 and 2018 at three natural CO_2 seeps in Papua New Guinea where we measured the metabolic flexibility (i.e. *in hospite* photosynthesis and dark respiration) of 12 coral species. Despite some species-specific variability, metabolic rates as measured by net oxygen flux tended to be higher at high pCO_2 (*ca* 1200 µatm), with increases in photosynthesis exceeding those of respiration, suggesting greater productivity of Symbiodiniaceae photosynthesis *in hospite*, and indicating the potential for metabolic flexibility that may enable these species to thrive in environments with high pCO_2. However, laboratory and field observations of coral mortality under high CO_2 conditions associated with coral bleaching suggests that this metabolic subsidy does not result in coral higher resistance to extreme thermal stress. Therefore, the combined effects of OA and global warming may lead to a strong decrease in coral diversity despite the stimulating effect on coral productivity of OA alone.

1. Introduction

The ongoing increase in atmospheric carbon dioxide (CO_2) decreases ocean pH and modifies the carbonate chemistry of seawater, a process known as ocean acidification (OA). While OA generally leads to reduced net calcification rate for a range of marine calcifiers [1], it may also result in increased photosynthetic rates in some aquatic photoautotrophs such as seagrasses and fleshy macroalgae (e.g. [2]). For symbiotic corals, little is known about the impacts of OA on the productivity of dinoflagellates (i.e. Symbiodiniaceae) since they are located within the host [3], complicating exchanges between the algae, the host and the external medium. Studies measuring the photosynthetic rates of the coral holobiont exposed to high pCO_2 have revealed variable effects on Symbiodiniaceae photosynthesis *in hospite*, ranging from a 47% enhancement to total inhibition. Aerobic respiration has been suggested to increase under OA conditions to balance the increased cost of calcification [4], yet experimental manipulations have shown high variability in coral response to OA (reviewed in [5]). These responses varied between coral species [3,5–8] but also among Symbiodiniaceae types [9–11], suggesting differential host carbon acquisition pathways and strain-specific tolerance to OA. Furthermore, treatment conditions and temporal scales differed among studies, with relatively few coral species tested. These discrepancies make it difficult to perform a synthetic

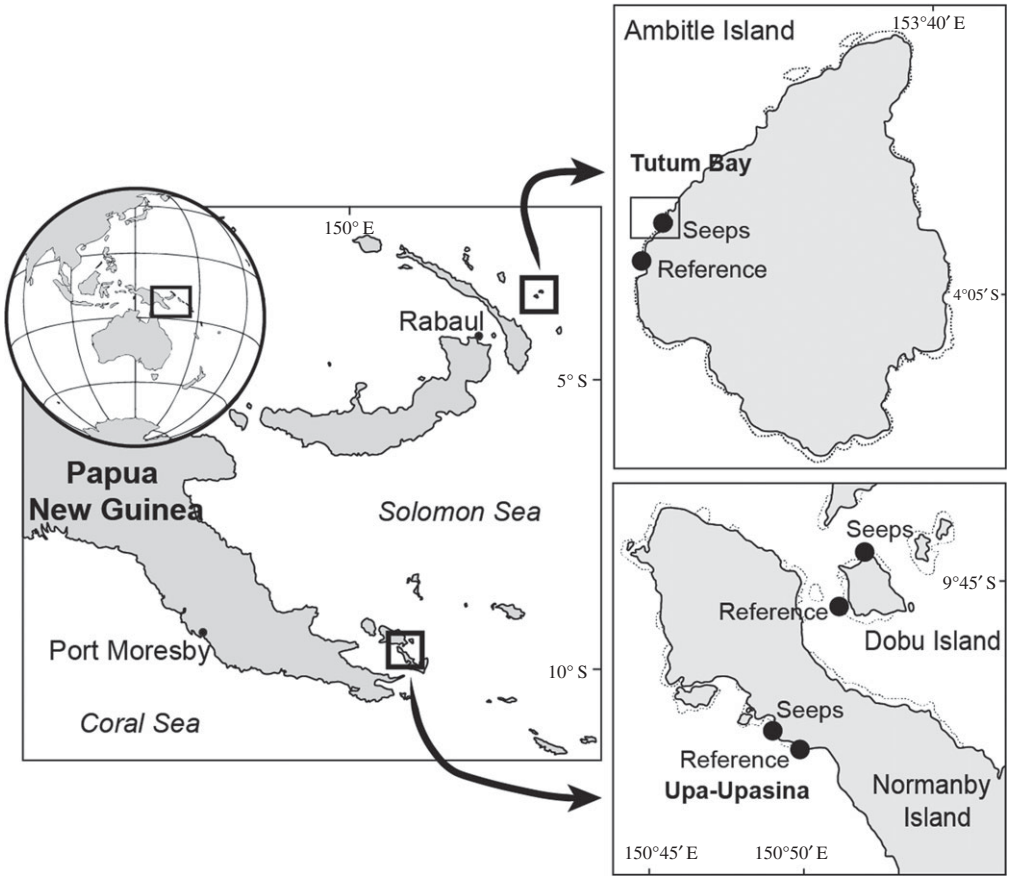

Figure 1. The three study locations in Ambitle and Normanby Islands.

analysis on the effect of OA on coral productivity. Here, we investigated the impact of OA on the photosynthesis and respiration rates of 12 coral species collected at volcanic CO_2 seeps in Papua New Guinea (PNG). Volcanic CO_2 seeps provide natural analogues of future conditions [12,13] and despite some well-known limitations, they are still one of the most ecologically realistic tools for examining responses of marine organisms to OA. Following Comeau *et al*. [5], we hypothesized that both the photosynthetic and respiration rates of corals would not be affected by high pCO_2, that this would result in no net difference in metabolic rates, and that there would be no change in density of Symbiodiniaceae density or chlorophyll content.

2. Material and methods

During four cruises between September 2016 and June 2018, we visited three locations with CO_2 seep sites (figure 1): Upa-Upasina, Dobu and Tutum Bay. The range of ambient pCO_2 conditions and carbonate chemistry of these locations, characterized by previous studies [12,14], and monitored during our fieldwork, provide insight into the generality of OA effects in a naturally heterogeneous environment. Fragments of corals (see the electronic supplementary materials) occurring at both CO_2 seeps (high pCO_2) and nearby (0.5–1 km distant) reference reefs (ambient pCO_2) were collected from different parent colonies at each location; 12 species were collected in total, but only four were common at more than one location.

Net photosynthesis (P_n) and dark respiration (R) rates of each coral fragment was measured on board the research vessel under controlled conditions (constant at 29°C and pH_T 7.73–7.75 and 8.02–8.13) using seawater collected at their sampling sites (table 1). A saturating light intensity of 250 ± 10 µmol photons $m^{-2}\,s^{-1}$ was used during 40 min followed by a 30 min dark period. At the end of each incubation, fragments were frozen for future analyses to determine their Symbiodiniaceae and total chlorophyll contents. Methods are described in further detail in the electronic supplementary materials.

The ratio of gross photosynthesis ($P_g = P_n + R$) to R ($P_g : R$) was analysed first as a generalized mixed model (GLMER, see the electronic supplementary material). Strong site effects varying with location, and therefore species, were further investigated using separate Wilcoxon tests to compare P_g, R and $P_g : R$ between reference and seep sites; the same process was used to analyse differences in Symbiodiniaceae and chlorophyll contents. The overall effect of site upon the above combined metabolic and symbiotic responses in different suites of corals at the different locations was also analysed using a nested PERMANOVA. Multivariate effects were visualized using nMDS of centroids of species by site for each location. Univariate statistical analyses were performed in R v. 3.2.5, multivariate in PRIMER v. 6.

3. Results

(a) Gross photosynthesis, respiration and $P_g : R$ ratio

Respiration and P_g rates covaried strongly across locations (glmer, $p < 0.001$; electronic supplementary material, table S1) and seep sites overall had higher P_g: R ratios than reference sites ($p < 0.001$; figure 2). There was, however, heterogeneity of response to sites between locations ($p < 0.01$) and strong species-specificity of response ($p < 0.001$).

Gross photosynthesis (P_g) of 14 of 18 sets of corals (e.g. *P. damicornis* from Tutum Bay and from Dobu = 2 sets) were significantly higher at seep compared with those at reference sites (Wilcoxon, $p < 0.05$; table 2), which corresponds to 11 of 12 species. No significant differences in P_g rates between

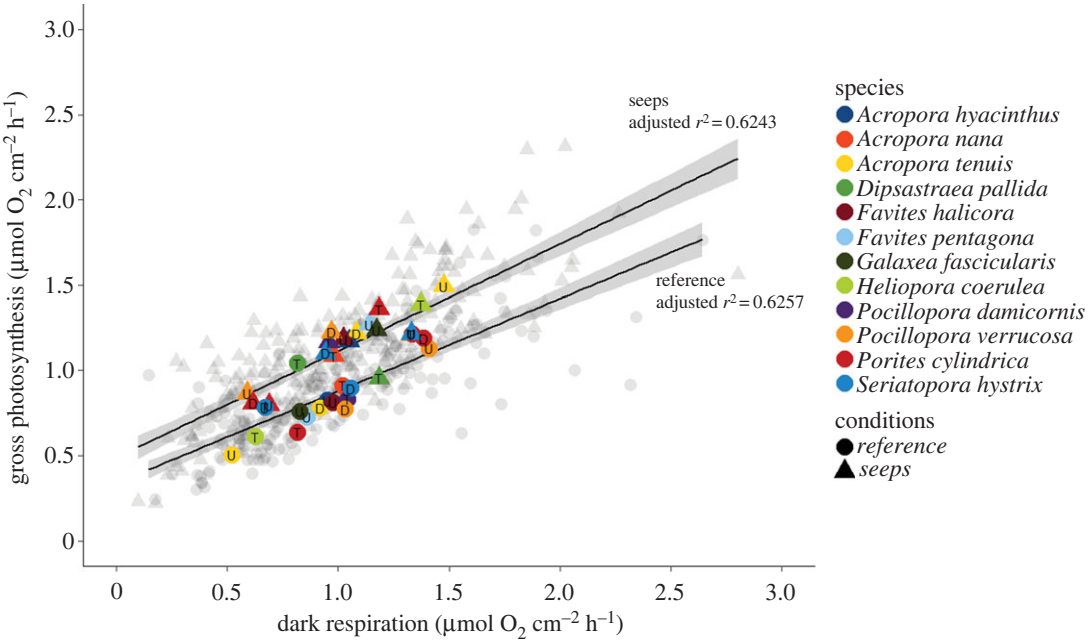

Figure 2. Linear regression of the gross photosynthesis (O_2 production) against dark respiration (O_2 consumption) measured on corals from reference (circle) and seep (triangle) sites. Coloured markers show the average P_g : R ratio of each species at each site and location with T, U and D referring to Tutum Bay, Upa-Upasina and Dobu, respectively.

Table 1. Mean (±s.d. in brackets) seawater conditions measured at the study sites (see electronic supplementary materials for details).

location/site (no. of replicates)	*T* (°C)	pH_T	pCO_2 µatm	CO_2 µmol kg^{-1}	HCO_3^- µmol kg^{-1}	CO_3^{2-} µmol kg^{-1}	Ω_{arag}
Tutum Bay							
reference (18)	29.09	8.12	436	11	1667	203	4.95
	(0.89)	(0.07)	(97)	(2)	(59)	(24)	(0.6)
seep (70)	28.93	7.75	1179	30	1927	99	2.41
	(0.9)	(0.06)	(166)	(5)	(31)	(12)	(0.3)
Upa-Upasina							
reference (24)	29.70	8.02	573	15	1777	175	4.28
	(0.46)	(0.02)	(25)	(1)	(14)	(6)	(0.1)
seep (87)	29.30	7.75	1197	31	1960	102	2.48
	(0.53)	(0.05)	(156)	(4)	(30)	(12)	(0.3)
Dobu							
reference (60)	28.48	8.13	443	12	1766	214	5.22
	(0.25)	(0.03)	(37)	(1)	(29)	(12)	(0.3)
seep (12)	29.38	7.73	1283	33	2043	102	2.50
	(0.51)	(0.01)	(42)	(1)	(7)	(3)	(0.1)

seep and reference sites were found for *D. pallida* from Tutum Bay and *P. verrucosa* from Upa-Upasina, while P_g rates of *P. cylindrica* from Dobu and Upa-Upasina were lowest at the seeps ($p < 0.001$).

Respiration rates of nine sets of corals were significantly higher at seep than at reference sites (Wilcoxon, $p < 0.05$; table 2), which corresponds to eight of 12 species; six sets were not significant, while three were significantly lower at seeps ($p < 0.001$).

P_g : R ratio was overall higher for corals at seeps compared to those at reference sites (figure 2), which was significant for 12 of 18 sets of corals (Wilcoxon, $p < 0.05$; table 2) which corresponds to nine of 12 species. By contrast, *D. pallida* and *P. verrucosa* both from Tutum Bay showed a higher P_g : R ratio at the reference site ($p < 0.05$). Interestingly, the two species found across locations, *P. verrucosa* and *P. cylindrica*, were significantly higher at two of three seeps and at three of three seeps, respectively.

(b) Symbiodiniaceae and chlorophyll contents

Symbiodiniaceae content did not differ significantly between seeps and reference sites; only random effects of species were significant in the linear model. Six sets of corals showed significant pair-wise differences; two were lower and

Table 2. Mean (±s.d. in brackets) gross photosynthesis (P_g) and dark respiration (R), P_g : R ratio and statistical significances (Wilcoxon test) of the coral species at each location (Upa-Upasina: U, Tutum Bay: T and Dobu: D) and site (see table 1 for the water chemistry conditions during incubation). All $n = 15$ with exception of instances marked '7' (e.g. U^7 where $n = 7$). n.s. = not significant, *<0.05, **<0.01, ***<0.001.

		gross photosynthesis (μmol O_2 production cm^{-2} h^{-1})			respiration (μmol O_2 consumption cm^{-2} h^{-1})			P_g : R		
species	Loc.	ref.	seep	*p*	ref.	seep	*p*	ref.	seep	*p*
Acropora hyacinthus	U^7	0.52	0.74	***	0.21	0.23	n.s.	2.50	3.22	*
		(0.06)	(0.11)		(0.01)	(0.03)		(0.32)	(0.37)	
Acropora nana	T	1.36	1.65	***	0.64	0.62	n.s.	2.16	2.93	***
		(0.13)	(0.24)		(0.09)	(0.21)		(0.25)	(0.87)	
Acropora tenuis	D	0.94	1.47	***	0.56	0.72	*	1.72	2.07	**
		(0.27)	(0.42)		(0.19)	(0.20)		(0.33)	(0.39)	
	U	0.57	1.68	***	0.27	0.84	***	2.13	2.01	n.s.
		(0.5)	(0.44)		(0.07)	(0.23)		(0.45)	(0.30)	
Dipsastraea pallida	T	0.98	0.90	n.s.	0.55	0.80	*	1.95	1.14	***
		(0.23)	(0.2)		(0.22)	(0.20)		(0.47)	(0.11)	
Favites halicora	U^7	0.40	0.58	*	0.26	0.27	n.s.	1.57	2.22	**
		(0.11)	(0.06)		(0.08)	(0.06)		(0.23)	(0.36)	
Favites pentagona	U^7	0.27	0.47	***	0.19	0.26	**	1.41	1.75	*
		(0.05)	(0.10)		(0.03)	(0.04)		(0.22)	(0.18)	
Galaxea fascicularis	U^7	0.36	0.59	**	0.19	0.27	*	1.93	2.21	n.s.
		(0.09)	(0.10)		(0.06)	(0.05)		(0.32)	(0.36)	
Heliopora coerulea	T	0.63	1.44	***	0.34	0.75	***	2.01	2.05	n.s.
		(0.23)	(0.20)		(0.18)	(0.22)		(0.49)	(0.46)	
Pocillopora damicornis	T	1.13	1.59	**	0.66	0.61	n.s.	1.77	2.63	***
		(0.31)	(0.44)		(0.23)	(0.17)		(0.36)	(0.48)	
Pocillopora verrucosa	D	1.51	2.43	**	1.01	0.95	n.s.	1.63	2.87	***
		(0.56)	(0.95)		(0.46)	(0.51)		(0.37)	(0.90)	
	T	(0.15)	1.42	***	0.32	0.63	***	3.13	2.30	*
			(0.14)		(0.10)	(0.13)		(0.93)	(0.30)	
	U	1.76	1.35	n.s.	1.21	0.60	***	1.47	2.55	***
		(0.56)	(0.55)		(0.41)	(0.33)		(0.14)	(1.03)	
Porites cylindrica	D	1.41	0.96	***	0.93	0.41	***	1.54	2.55	***
		(0.30)	(0.35)		(0.22)	(0.22)		(0.20)	(0.72)	
	T	0.97	2.08	***	0.47	0.82	**	2.10	2.75	*
		(0.21)	(0.34)		(0.07)	(0.30)		(0.40)	(0.64)	
	U	0.93	0.61	***	0.49	0.25	***	1.92	2.67	**
		(0.25)	(0.32)		(0.12)	(0.15)		(0.32)	(0.87)	
Seriatopora hystrix	D	1.05	1.29	*	0.50	0.49	n.s.	2.19	2.89	*
		(0.24)	(0.22)		(0.15)	(0.16)		(0.40)	(0.95)	
	U	1.01	1.56	***	0.28	0.53	***	4.01	3.10	n.s.
		(0.24)	(0.37)		(0.11)	(0.16)		(1.58)	(0.84)	

four higher at the seep sites, respectively (Wilcoxon, $p < 0.05$; electronic supplementary material, table S2).

Chlorophyll content differed significantly across sites (glmer, $p < 0.001$; electronic supplementary material, table S3) but this was highly dependent upon location and species. Seven sets of corals showed no significant difference between sites (Wilcoxon, $p > 0.05$; electronic supplementary material, table S2), seven had significantly higher chlorophyll content at seep sites ($p < 0.05$), and four a higher content at reference sites ($p < 0.05$).

PERMANOVA indicated significant effects of site ($p < 0.05$) and location ($p < 0.05$) upon the overall data, with coral species responding idiosyncratically to site effects depending upon location ($p < 0.001$) (electronic supplementary material, figure S1; and table S4).

4. Discussion

This study encompassed 217 incubations with 12 coral species that endured consistently high pCO_2 in their environment. To

the best of our knowledge, this is the most exhaustive study on the long-term effect of OA conditions on the metabolic flexibility through photosynthetic and respiration changes of tropical corals. Omnibus tests using multivariate approaches suggested that overall physiological effects of exposure to acidified conditions are consistently present but idiosyncratic and species-specific in magnitude.

High pCO_2 stimulated the P_g rate of 11 of the 12 coral species, suggesting either that Symbiodiniaceae were CO_2-limited at ambient pCO_2 or that high pCO_2 acted as fertilizer [11]. Consequently, we reject our initial null hypothesis and conclude that high pCO_2 affects coral metabolism. We suggest that the variability in responses of symbiotic scleractinian corals to high pCO_2 as reported in earlier studies ([5] and references therein) might be attributed to the short duration of acclimation to high pCO_2 ranging from a few hours to several months. Indeed, our findings are consistent with previous results on soft and hard coral species that were fully acclimatized to high pCO_2 environments at CO_2 seeps [15,16]. Our study provides additional support for the notion that most symbiotic corals are able to acclimatize to high pCO_2 environments and potentially benefit from these conditions.

High coral productivity could not be attributed to changes in Symbiodiniaceae or chlorophyll content, because symbiont content was similar between corals at seep and reference sites and differences in the chlorophyll concentration were inconsistent, with three different coral species containing either high or low chlorophyll concentrations at the seep sites, one species (i.e. *P. cylindrica*) containing both, while the remaining seven were not significantly different (electronic supplementary material, table S2). Moreover, a previous study found that no change occurs in Symbiodiniaceae types at seeps [17]. Therefore, flexibility of the coral metabolism may be driven by enhanced uptake of dissolved inorganic carbon (DIC), or increased host membrane diffusivity. Indeed, the identification of numerous pathways in corals that supply Symbiodiniaceae with HCO_3^- [18,19] suggests the role of the latter as the stimulating DIC source for coral photosynthesis and calcification. Another potential pathway of energetic stimulation on corals exposed to OA conditions is the coral-mediated dissolved organic carbon (DOC) flux. As an example, an increase in the DOC retained by corals was found for two species exposed for 24 days to 741 µatm pCO_2 [8]. High DOC could therefore result in sustained coral energy reserves and thereby help the coral resist effects of OA.

The observed high P_g could also be supported by the higher respiration rates of the corals from the seep sites, since this brings extra metabolic CO_2 to Symbiodiniaceae. However, this cannot be the only explanatory factor since the respiration rates were variable among species and pCO_2 conditions (table 2). Eight species had higher respiration rates at seeps, probably to counter the increased cost of functioning at elevated pCO_2, such as the debated cost of calcification [4,20], or perhaps simply because higher productivity might help corals to boost metabolic processes such as lipid storage, reproduction and protein synthesis. This energetic benefit from CO_2 enrichment was also shown by the increased $P_g : R$ at CO_2 seeps, suggesting an increase in the energetic balance that may actually enable these species to thrive in high pCO_2 [12].

Finally, we observed that a substantial mortality of coral reefs around Upa-Upasina had occurred between January 2017 and June 2018, with most coral species found dead. According to previous reports [12,21], heat induced coral bleaching has occurred frequently in the area of Upa-Upasina during the last decade. Unfortunately, although we noted the massive mortality, during our last cruise in 2018 dead colonies were already covered by algae and were indistinguishable from previously dead ones; we were therefore unable to reliably quantify the recent mortality. Although the intensity of thermal stress was unknown, these observations seem to confirm what Noonan & Fabricius [21] experimentally demonstrated during a moderate thermal stress: benefits of OA had little effect on coral survival after thermal stress because of bleaching. Therefore, the combined effects of OA and global warming may lead to a strong decrease in coral diversity despite the stimulating effect of OA alone on coral productivity [12]. With atmospheric CO_2 driving both OA and global warming, there is urgent need for research studying their interactive effects to better predict the future of coral reefs under climate change.

Ethics. Experiments were realized in agreement with PNG governmental institutions and local communities. Coral sampling was allowed by CITES (permits no. 016232 and 017027).

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d6q7jq2 [22].

Authors' contributions. T.B., M.Z., A.L., S.J., F.H. and R.R.-M. performed the experiments; T.B., R.R.-M., M.Z. and S.J. participated in the data analysis; T.B. and A.F. performed statistical analyses; T.B. and R.R.-M. wrote the paper. All authors helped draft the manuscript and gave final approval for publication. All authors are also agreed to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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