Coral Reefs (2021) 40:1–7
https://doi.org/10.1007/s00338-020-02021-6

NOTE

# Biogeochemical variability and trophic status of reef water column following a coral bleaching event

**Veronica Z. Radice**[1,2,4] · **Brian Fry**[3] · **Sophie G. Dove**[1,2] · **Ove Hoegh-Guldberg**[1,2]

Received: 9 April 2020 / Accepted: 19 October 2020 / Published online: 30 October 2020

**Abstract** Although resource availability is important for coral reef nutrient cycling and trophic ecology, it is poorly understood how particulate resources may change following an oceanic heat stress event. Here, carbon and nitrogen concentrations and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of particulate organic matter (POM; 10 and 30 m) were compared from before and after the 2016 mass coral bleaching event in the Maldives, Indian Ocean. To characterize the trophic status of the post-bleaching water column, dissolved inorganic nutrients across shallow to mesophotic coral reefs (10–50 m) and plankton $\delta^{13}C$ and $\delta^{15}N$ were measured. Eight months after the mass bleaching, an oligotrophic water column with decreased particulate organic nitrogen and variable yet increased mean $\delta^{13}C$ of POM was observed. Elemental and isotopic data of particulate resources from pre- and post-bleaching revealed three oceanographic regimes related to ocean mixing. This study highlights the importance of characterizing water column biogeochemistry to understand nutrient cycling in coral reef ecosystems especially post-disturbance.

**Keywords** Biogeochemistry · Coral reef · Coral bleaching · Mesophotic · Nutrients · Particulate organic matter · Stable isotopes

## Introduction

The dynamic nature of nutrient availability is integral to understanding coral reef ecology. Regional and reef scale processes influence dissolved nutrient availability while the coastal environment and marine productivity comprise primary drivers of particulate availability across reefs (Wyatt et al. 2013; Lowe and Falter 2015). Particulate resource availability is a critical component of fish productivity (Morais and Bellwood 2019), and marine primary production is a driver of heterotrophic feeding patterns in corals (Fox et al. 2018). For example, particulate feeding by some corals can positively affect coral growth parameters (Fabricius 2005) and help to meet the daily energy requirements under normal and anomalous ocean temperatures that cause coral bleaching (Grottoli et al. 2006; Houlbrèque and Ferrier-Pagès 2009). Therefore, changes in reef trophodynamics may have consequences for organisms that are dependent on particulate resources.

As heat stress events can increase the death and decay of reef organisms (Leggat et al. 2019), an invigorated detrital cycle may increase the availability of POM as a major source of carbon for consumers in degraded reefs (Morillo-Velarde et al. 2018). Increased levels of ultraviolet radiation, often associated with thermal stress induced coral bleaching, can cause corals to release organic matter that is depleted in nitrogen (Courtial et al. 2018). Although the

Topic Editor Stuart Sandin

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00338-020-02021-6) contains supplementary material, which is available to authorized users.

✉ Veronica Z. Radice
vradice@odu.edu

[1] Australian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, St. Lucia, QLD, Australia

[2] School of Biological Sciences, The University of Queensland, St. Lucia, QLD, Australia

[3] Australian Rivers Institute, Griffith University, Nathan, QLD, Australia

[4] Present Address: Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA

regeneration of mucus-derived organic matter by bacteria in the reef environment may increase organic nitrogen, it is possible that nitrogen availability may be depleted during this process (Coles and Strathmann 1973; Courtial et al. 2018). Reef macroalgae are also known to release POM (Haas et al. 2010), while sponges play an important role in cycling coral-derived and algal-derived organic matter and releasing it as detrital POM (Rix et al. 2017, 2018). Considering the importance of particulate resources for many reef organisms especially during and following disturbance events such as coral bleaching, it is critical to characterize resource availability in the reef water column.

This study investigated particulate organic availability and isotopic composition following a mass coral bleaching event in the Maldives, Indian Ocean. Carbon and nitrogen concentrations and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of POM were compared across shallow (10 m) and mesophotic (30 m) reefs one year before and eight months after the 2016 mass coral bleaching event. Further, a surface pump allowed for the deeper sampling (50 m) of POM and comparison of two sampling methods (diver versus pump) post-bleaching. Because plankton are also a food source for corals and fish, plankton $\delta^{13}C$ and $\delta^{15}N$ values were measured after the bleaching event. Inorganic nutrients, including a subset of samples for nitrogen and oxygen stable isotope analysis ($\delta^{15}N$-nitrate and $\delta^{18}O$-nitrate), were measured to investigate post-bleaching nutrient availability and trophic status of the shallow to mesophotic (10–50 m) water column (Casciotti 2016).

## Materials and methods

### Field collection

Pre-bleaching (2015) sampling of POM occurred in the boreal spring (intermonsoon) in the Maldives and is further detailed in Radice et al. (2019) while post-bleaching sampling occurred during the same season in 2017 (Supplementary Material Table S1, Fig. S1). To survey shallow (10 ± 2 m) and mesophotic depths (30 ± 3 m; 47 ± 3 m) along oceanic reef slopes ('fore reef'), seawater was collected by divers (10 and 30 m) and via a surface pump (all depths) paired with a Sensus Ultra depth recorder (ReefNet) (Fig. S2). Given that optimal mesophotic photosynthetically active radiation (PAR) is 7.5% of the surface (Tamir et al. 2019), 30 m depth in these Maldives reefs is mesophotic since only 4% of surface PAR is available (Radice et al. 2019). Sampling of the 50 m mesophotic depth target required repositioning the boat an average of 600 m from shallow reefs. Seawater (min. 3L, mean 7L) was filtered, and frozen (− 20°C): (1) stored in HDPE bottles prior to inorganic nutrient analysis (0.22 µm polyethersulfone, Millex-GP, Merck), and (2) filtered for isotopic analysis of POM (nominal 0.4 µm glass fiber filters [Machery-Nagel], pre-combusted for 5 h at 450°C). Plankton were collected at dusk by towing mesh nets (53 and 250 µm) submerged below the surface for 10 min at a speed of ~ 2 knots. Daily wind data were obtained from the Maldives Meteorological Service (Maldives Meteorological Service 2018).

### Inorganic nutrient and isotopic analyses

Inorganic nutrients (nitrate [$NO_3^-$], ammonium [$NH_4^+$], phosphate [$PO_4^{3-}$]) (mean ± SD) were measured by flow injection analysis at the Advanced Water Management Centre, University of Queensland. Nitrite was undetectable for the majority of samples, and phosphate was undetectable for two samples. Potential nutrient limitation was evaluated using the Redfield ratio of dissolved nutrients (($[NO_3^-] + [NH_4^+])/[PO_4^{3-}]$) (mean ± SD), with values deviating from the 16:1 ratio providing evidence of either nitrogen or phosphorous limitation (Redfield 1958). A subset of samples ($n = 21$, 7 samples/depth) were analyzed for nitrogen and oxygen stable isotope values ($\delta^{15}N$ and $\delta^{18}O$) of nitrate via a bacterial denitrification assay at the Woods Hole Oceanographic Institution (Sigman et al. 2001; Casciotti et al. 2002). Repeated measurements of three references resulted in analytical precision of 0.5‰ for $\delta^{15}N$ and 1.6‰ for $\delta^{18}O$. Stable isotope values are reported in the delta (δ) notation (mean ± SD) expressed in per mil (‰): for example, $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$ where R is the heavy to light isotope ratio ($^{15}N/^{14}N$).

Glass fiber filters were briefly treated with HCl to remove any carbonates, neutralized with Milli-Q water, and oven-dried. Carbon and nitrogen concentrations and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of POM ($n = 112$) were analyzed with an Elementar Vario EL Cube elemental analyzer and with a PDZ Europa ANCA-GSL for plankton ($n = 30$), with analyzers interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon) at the University of California Davis. Repeated measurements of laboratory reference materials (G-6: Nylon 6, G-13: Bovine liver, G-20: Glutamic acid, G-21: Enriched alanine) resulted in analytical precision of < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. Due to analytical detection limits, samples with very low nitrogen (< 10 µg; $n = 21$) were removed from analyses. For elemental C and N, blank corrections were applied by subtracting the average of five samples with the lowest C or N contents (Figs. S3 and S4). Particulate organic nitrogen (PON) and carbon (POC) concentrations were calculated as N or C (µg), respectively, per liter of seawater.

### Statistical analyses

Statistical analyses and visualization were conducted using the R computing environment (Wickham 2016; Wilke 2019; R Core Team 2020). Two oceanographic regimes were identified during back-to-back sampling in the 2015 cruise, with Cyanobacterial bloom and Upwelling regimes characterized by different POM $\delta^{15}$N (Radice et al. 2019). The monsoon climate dominates the oceanography in the Maldives, with upwelling occurring the majority of the year. Initial evaluation of post-bleaching (2017) POM data showed that low $\delta^{15}$N values, characteristic of cyanobacteria, were absent. Therefore, post-bleaching POM data (Oligotrophic regime) were compared to the pre-bleaching Upwelling regime data. POM $\delta^{13}$C, $\delta^{15}$N, POC, and PON were analyzed using linear mixed effects models (‘nlme’) with year (pre- and post-bleaching) and depth (10 and 30 m) as fixed interactive effects and site as the random effect (Pinheiro et al. 2020). Following model selection based on Akaike information criteria (AIC), depth was removed only in the POM $\delta^{15}$N model. The pre- versus post-bleaching POM analysis only considered data collected by the same method (diver).

Inorganic nutrient data ($NO_3^-$, $NH_4^+$, $PO_4^{3-}$), collected only in 2017, were analyzed using linear mixed effects models with sampling method (diver and pump) and depth (10, 30, 47 m) as fixed effects and site as the random effect. Following model selection based on AIC, sampling method was removed from the model investigating nitrate and phosphate while depth was removed from the model investigating ammonium. The effect of size fraction (53, 250 μm) on plankton $\delta^{13}$C and $\delta^{15}$N values was analyzed using linear mixed effects models with site as the random effect. The $\delta^{13}$C and $\delta^{15}$N values of post-bleaching POM were analyzed using linear mixed effects models with sampling method (diver and pump) and depth (10, 30, 47 m) as fixed effects and site as the random effect. Following model selection based on AIC, depth was removed from the $\delta^{15}$N model. Post-hoc (Tukey) tests of significant main effects by least-squares means were performed (‘emmeans’) (Lenth 2020).

## Results and discussion

Oceanographic regimes in the Maldives were defined a posteriori considering biogeochemical characteristics: cyanobacterial bloom (2015; low $\delta^{15}$N), upwelling (2015; $\delta^{15}$N $\sim$ 5‰), and oligotrophic (2017; low PON) (Fig. 1). POM $\delta^{13}$C values increased in both shallow (10 m) and

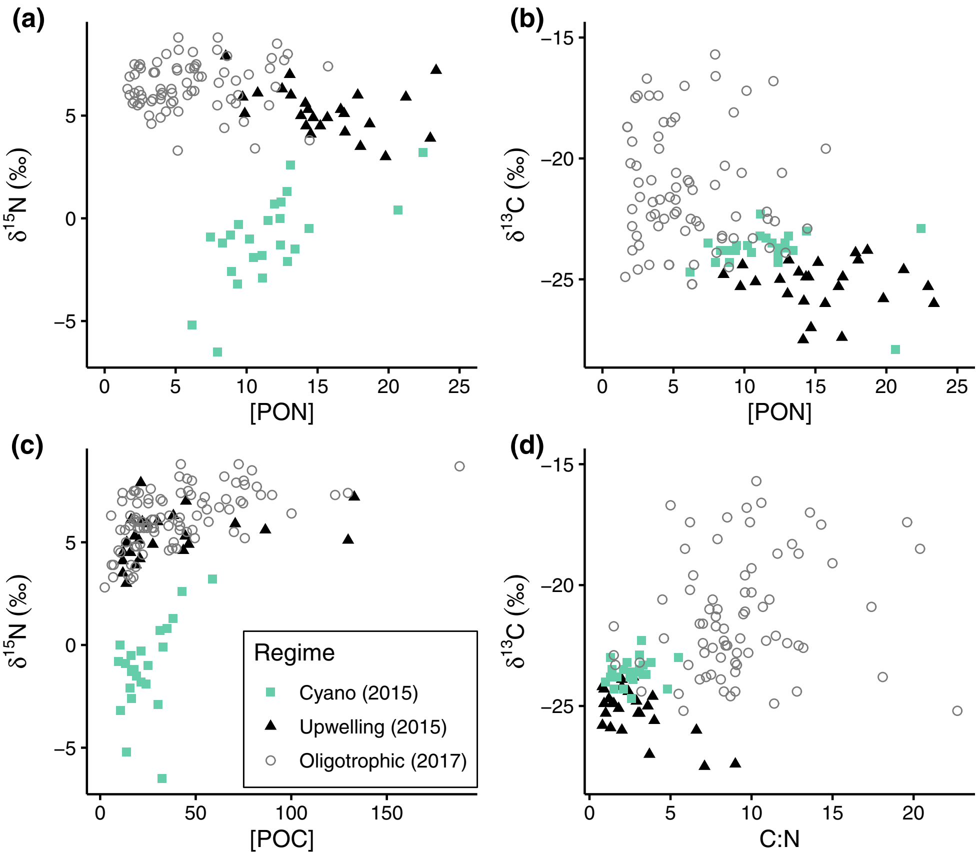

**Fig. 1** Coral reef water column biogeochemistry and elemental ratios show three oceanographic regimes in the Maldives archipelago. Filled symbols depict pre-bleaching POM samples and open symbols depict post-bleaching POM samples in relation to the 2016 mass coral bleaching event. Particulate organic nitrogen (PON) is shown in relation to **a** nitrogen ($\delta^{15}$N) and **b** carbon stable isotope values ($\delta^{13}$C) of particulate organic matter (POM), **c** particulate organic carbon (POC) is shown in relation to POM $\delta^{15}$N values, and **d** molar C:N ratios are shown in relation to POM $\delta^{13}$C values

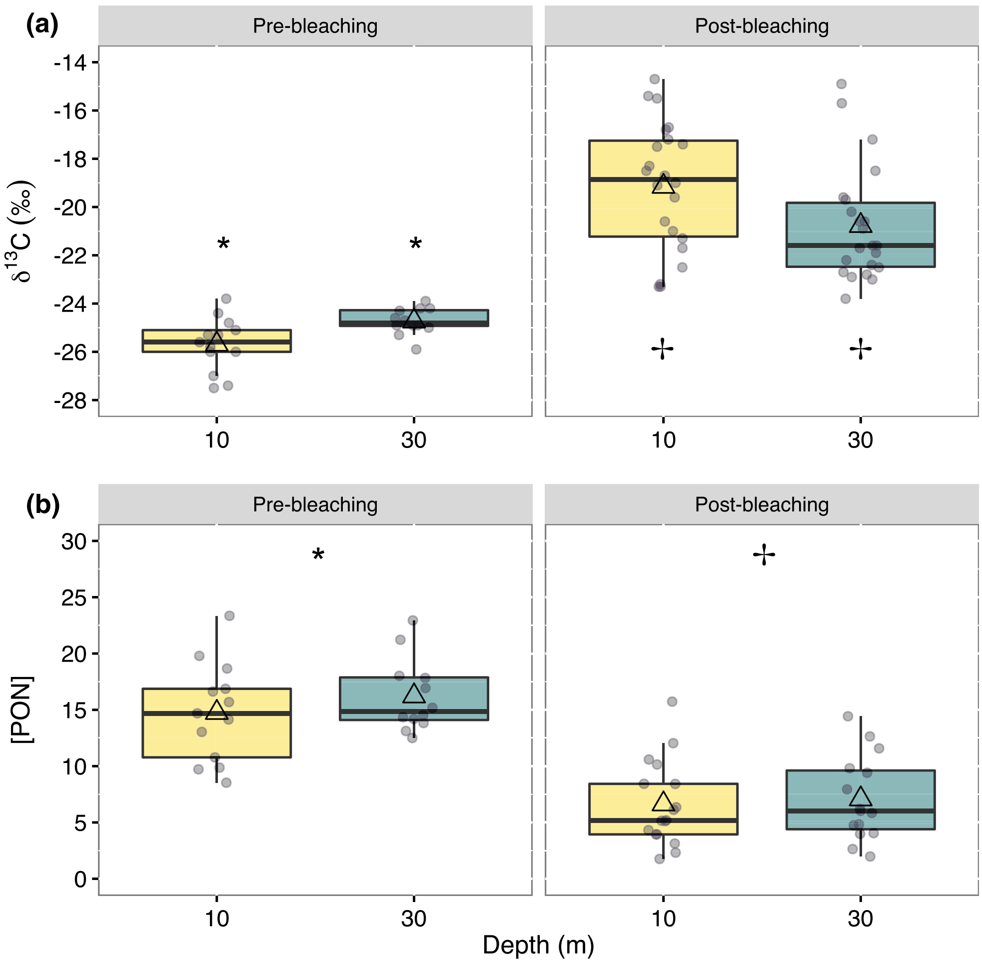

**Fig. 2** A comparison of particulate organic matter biogeochemistry from shallow (10 m) and mesophotic (30 m) coral reefs before and after the 2016 mass coral bleaching in the Maldives. **a** Carbon stable isotope values ($\delta^{13}C$) of POM. Symbols show the differences between years at each depth, but no differences were found between depths. **b** Particulate organic nitrogen (PON) concentrations, with symbols showing differences pre- versus post-bleaching. The box and whiskers plots display the median and first and third quartiles while the triangle symbols represent the mean values

**Table 1** Particulate organic matter carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values, carbon (POC) and nitrogen (PON) concentrations, and molar C:N ratios (mean ± SD) from coral reefs across the central Maldives one year before (2015) and after (2017) the oceanic heat stress event that caused mass coral bleaching in 2016

| Bleaching | Regime | Sampling method | n | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | POC | PON | C:N |
|---|---|---|---|---|---|---|---|---|
| Before | Cyano bloom | Diver | 25 | − 23.8 ± 1.0 | − 1.2 ± 2.3 | 24.0 ± 12.2 | 11.7 ± 3.7 | 2.6 ± 1.1 |
| Before | Upwelling | Diver | 25 | − 25.2 ± 1.0 | 5.3 ± 1.2 | 37.4 ± 33.8 | 15.5 ± 3.9 | 2.8 ± 2.1 |
| After | Oligotrophic | Diver | 44 | − 20.0 ± 2.6 | 5.6 ± 1.4 | 40.8 ± 36.2 | 6.8 ± 3.7 | 8.2 ± 4.3 |
| After | Oligotrophic | Pump | 51 | − 21.6 ± 2.8 | 6.6 ± 1.2 | 39.2 ± 24.7 | 5.4 ± 3.2 | 10.0 ± 3.6 |

mesophotic (30 m) reefs in the post-bleaching oligotrophic regime (post-hoc $p < 0.001$ and $p < 0.001$, respectively), but did not differ between depths in either year (Fig. 2a; Tables 1 and S2). Increased mean $\delta^{13}C$ of POM post-bleaching could be due to: (1) an input of isotopically heavier, carbon-rich sources (e.g., reef-derived POM such as mucus or detritus), (2) a reduction in oceanic POM, or (3) changes in POM community composition, with the latter considered the most likely (Tanaka et al. 2008; Kolasinski et al. 2011; Karati et al. 2017). In a nutrient-depleted oligotrophic water column, small nutrient inputs can affect the POM signal; indeed, highly variable $\delta^{13}C$ values were observed post-bleaching (mean − 20.9 ± 2.9‰; range: − 25.3 to − 13.4‰). The wide range in post-bleaching POM $\delta^{13}C$ values suggests there is greater diversity in community composition, such as *Trichodesmium* (high $\delta^{13}C$) and small cyanobacteria and/or eukaryotes (low $\delta^{13}C$), while uniformity in $\delta^{15}N$ provides evidence of tight recycling of nitrogen across a variety of species (Tchernov and Lipschultz 2008). Post-bleaching,

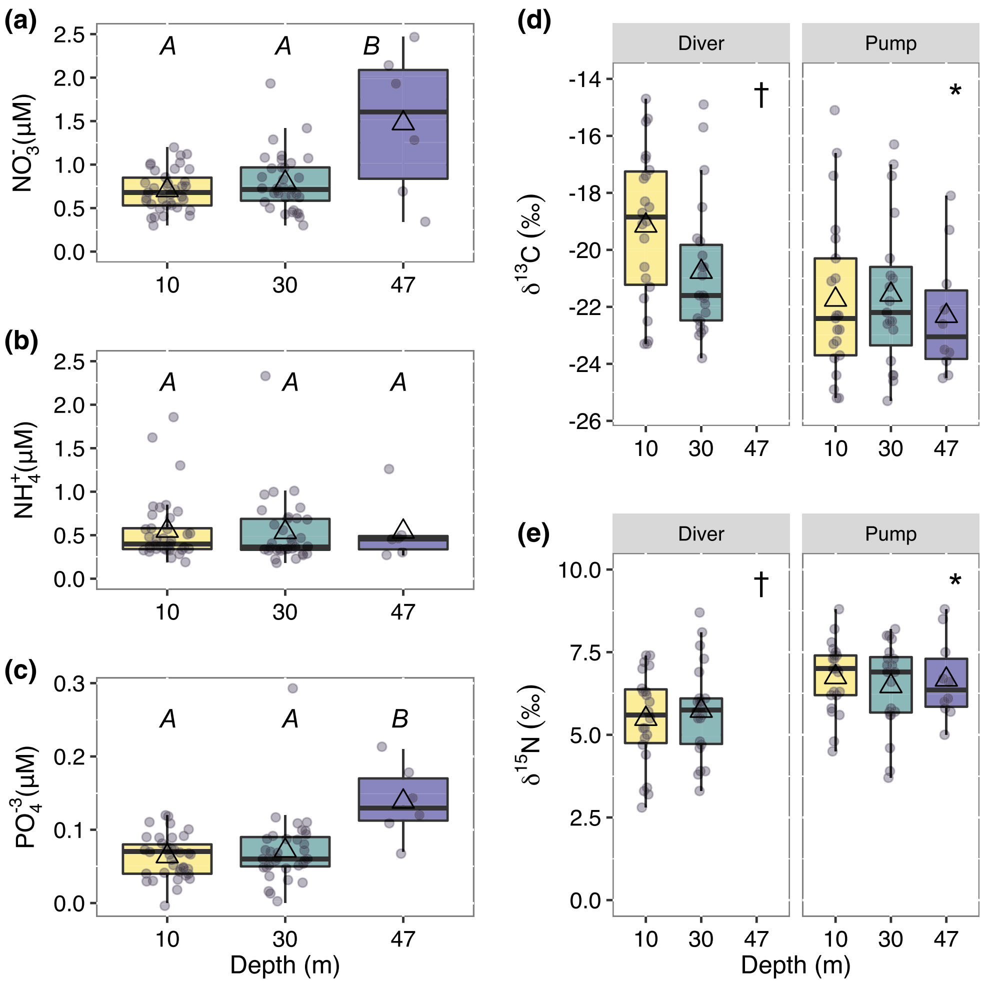

**Fig. 3** Post-bleaching water column nutrient chemistry across shallow (10 m) and mesophotic (30 and 47 m) coral reefs in the Maldives (2017 only). Dissolved inorganic nutrient concentrations from shallow and mesophotic coral reefs include: **a** nitrate ($NO_3^-$), **b** ammonium ($NH_4^+$), and **c** phosphate ($PO_4^{-3}$), with italic letters showing differences between depths. Post-bleaching particulate organic matter **d** carbon ($\delta^{13}C$) and **e** nitrogen stable isotope values ($\delta^{15}N$) are shown in relation to depth and sampling method, with symbols denoting differences between sampling methods. The box and whiskers plots display the median and first and third quartiles while the triangle symbols represent the mean values

the large range in C:N indicates many unique combinations of production and recycling while low C:N pre-bleaching reflects cyanobacteria but also possible nitrate storage in phytoplankton (Bode et al. 1997; Liu et al. 2019).

POM $\delta^{15}N$ did not differ between pre-bleaching (upwelling) and post-bleaching (oligotrophic) regimes across shallow or mesophotic reefs (Table S2). Nitrogen loss due to recycling may lead to higher $\delta^{15}N$ while some nitrogen fixation counterbalances with lower $\delta^{15}N$ inputs, leading to the relatively more consistent $\delta^{15}N$ values (mean 6.2 ± 1.4‰; range: 2.8 to 8.8‰) but variable $\delta^{13}C$ post-bleaching. Similar $\delta^{15}N$ values of POM (as above) and plankton (mean 6.4 ± 0.8‰) indicate tight coupling between primary and secondary production, revealing low fractionation between these groups and providing further evidence of an oligotrophic environment (Fig. S5). Plankton $\delta^{15}N$ (as above) and $\delta^{13}C$ (mean – 21.5 ± 0.4‰) did not differ between the size fractions (Tables S3 and S4). Despite the lack of historic temporal data on POM dynamics and isotopes in the region, the POM data presented effectively characterizes the regional oceanographic regimes that are dependent on upper ocean mixing dynamics (Garcia et al. 2018).

The decreased PON concentrations post-bleaching coincided with reduced wind speed and duration that may have affected wind-driven upwelling in the months preceding the sampling (Fig. 2b, Table S5). In addition to low concentrations of PON and phosphate, the oligotrophic water column was also characterized by: (1) the persistence of high residual $\delta^{18}O–NO_3^-$ values due to low nutrient concentrations, (2) high Redfield ratios (21.8 ± 13.0), and (3) $\delta^{15}N–NO_3^-$ values reflecting potential fractionation due to phytoplankton uptake (Table S6). Overall, there was substantial variability in both $\delta^{15}N–NO_3^-$ and $\delta^{18}O–NO_3^-$ values. Isotopic values indicate that nitrate was derived from a combination of marine and atmospheric sources, with the latter enriched in $\delta^{18}O$ (Fig. S6) (Kendall et al. 2008). High Redfield ratios suggest phosphate limitation, which could allow atmospheric nitrate (enriched $\delta^{18}O$) to accumulate in surface waters during periods of anthropogenic aerosol loading such as the northeast monsoon season (Ramana and Ramanathan 2006; Das et al. 2011). The signature of marine-derived nitrate ($\delta^{15}N$ ~ 5–6‰) is also evident in POM from the upwelling and oligotrophic regimes as well as plankton. Given a fractionation factor of ~ 5‰, the mean $\delta^{15}$N–$NO_3^-$ value (9.2 ± 4.9‰) likely reflects phytoplankton assimilation of a deep-water nitrate source of approximately 5‰ (Altabet 2001). Previous work has shown that $\delta^{15}$N values of reef-building corals are consistent with deep-water nitrate $\delta^{15}$N (~ 5‰), which indicates coral dependence on inorganic nutrients and particulates from the dominant upwelling regime (Radice et al. 2019).

Some inorganic nutrient concentrations were affected by reef depth, with higher nitrate and phosphate at 47 m compared to 10 and 30 m depths ($p < 0.001$ and $p \leq 0.001$, respectively) (Fig. 3a-c, Tables S3 and S7). The higher concentration of inorganic nutrients at the deepest sampling depth (47 m) aligns with expectations of increased nutrient concentrations at greater depths (Leichter et al. 2007). While there were differences of 1.6‰ and 1.0‰ in POM mean $\delta^{13}$C and $\delta^{15}$N, respectively, between the sampling methods used in 2017, no effect of depth was observed (Fig. 3d-e, Tables 1 and S3). The discrepancy in the $\delta^{13}$C and $\delta^{15}$N values of POM sampled by divers on the reef versus pump (mean 600 m offshore from shallow reef) may be due to the relative proportion of reef-derived versus offshore (pelagic) organic matter, the phytoplankton community composition, and/or oceanographic forcing of inorganic nutrient supply (Wyatt et al. 2013; Karati et al. 2017). Despite the importance of upwelling ecosystems, our understanding of the dynamics of benthic-pelagic nutrient cycling is often hindered by a lack of measurements of nutrient sources in the tropics in particular (MacKenzie et al. 2019), including the understudied central Indian Ocean. Because of the interactive oceanic-atmospheric processes affecting upwelling (Alory and Meyers 2009), it is important to consider how climate change may affect such regional processes that supply essential nutrients to marine ecosystems. For coral reefs ecosystems in particular, it is critical to consider how the supply and cycling of nutrients may change at local scales in relation to oceanic heat stress events and the consequent impact on reef trophic ecology.

**Acknowledgements** We thank Kristen Brown, Dominic Bryant, Mary Bryant, Pete Dalton, Susie Green, Christopher Hoegh-Guldberg, the XL Catlin Seaview Survey team, the Maldives Marine Research Institute (formerly Centre), especially Shiham Adam, Nizam Ibrahim and Mohamed Shimal, the Maldives Ministry of Fisheries and Agriculture, the Maldives Environmental Protection Agency, and the crew and dive guides of the MV Emperor Atoll for their invaluable field support. We thank Scott Wankel, Jen Karolewski, Joy Matthews, and Beatrice Keller-Lehmann for analytical sample analysis, and Martin Wynne, Alexa Grutter, Sarah Pausina, and Frank Coman for discussions & equipment for plankton sampling. This study was accomplished as part of the XL Catlin Seaview Survey, designed and undertaken by the Global Change Institute and funded by XL Catlin in partnership with Underwater Earth, The Ocean Agency, and The University of Queensland. This study was supported by the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies (OHG, SD), an ARC Laureate Fellowship (OHG), and The University of Queensland Research Training Scholarship (VZR).

### Compliance with ethical standards

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

## References

Alory G, Meyers G (2009) Warming of the upper equatorial Indian Ocean and changes in the heat budget (1960–99). J Clim 22:93–113

Altabet MA (2001) Nitrogen isotopic evidence for micronutrient control of fractional $NO_3^-$ utilization in the equatorial Pacific. Limnol Oceanogr 46:368–380

Bode A, Botas JA, Fernández E (1997) Nitrate storage by phytoplankton in a coastal upwelling environment. Mar Biol 129:399–406

Casciotti KL (2016) Nitrogen and oxygen isotopic studies of the marine nitrogen cycle. Ann Rev Mar Sci 8:379–407

Casciotti KL, Sigman DM, Hastings MG, Böhlke JK, Hilkert A (2002) Measurement of the oxygen isotopic composition of nitrate in seawater and freshwater using the denitrifier method. Anal Chem 74:4905–4912

Coles SL, Strathmann R (1973) Observations on coral mucus “flocs” and their potential trophic significance. Limnol Oceanogr 18:673–678

Courtial L, Planas Bielsa V, Houlbrèque F, Ferrier-Pagès C (2018) Effects of ultraviolet radiation and nutrient level on the physiological response and organic matter release of the scleractinian coral *Pocillopora damicornis* following thermal stress. PLoS ONE 13:e0205261

Das R, Granat L, Leck C, Praveen PS, Rodhe H (2011) Chemical composition of rainwater at Maldives Climate Observatory at Hanimaadhoo (MCOH). Atmos Chem Phys 11:3743–3755

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146

Fox MD, Williams GJ, Johnson MD, Radice VZ, Zgliczynski BJ, Kelly ELA, Rohwer FL, Sandin SA, Smith JE (2018) Gradients in primary production predict trophic strategies of mixotrophic corals across spatial scales. Curr Biol 28:3355-3363.e4

Garcia CA, Baer SE, Garcia NS, Rauschenberg S, Twining BS, Lomas MW, Martiny AC (2018) Nutrient supply controls particulate elemental concentrations and ratios in the low latitude eastern Indian Ocean. Nat Commun 9:4868

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Haas AF, Naumann MS, Struck U, Mayr C, el-Zibdah M, Wild C (2010) Organic matter release by coral reef associated benthic algae in the Northern Red Sea. J Exp Mar Bio Ecol 389:53–60

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev Camb Philos Soc 84:1–17

Karati KK, Vineetha G, Madhu NV, Anil P, Dayana M, Shihab BK, Muhsin AI, Riyas C, Raveendran TV (2017) Variability in the phytoplankton community of Kavaratti reef ecosystem (northern Indian Ocean) during peak and waning periods of El Niño 2016. Environ Monit Assess 189:653

Kendall C, Elliott EM, Wankel SD (2008) Tracing anthropogenic inputs of nitrogen to ecosystems. Stable isotopes in ecology and environmental science. Blackwell Publishing, Oxford, pp 375–449

Kolasinski J, Rogers K, Cuet P, Barry B, Frouin P (2011) Sources of particulate organic matter at the ecosystem scale: a stable isotope and trace element study in a tropical coral reef. Mar Ecol Prog Ser 443:77–93

Leggat WP, Camp EF, Suggett DJ, Heron SF, Fordyce AJ, Gardner S, Deakin L, Turner M, Beeching LJ, Kuzhiumparambil U, Eakin CM, Ainsworth TD (2019) Rapid coral decay is associated with marine heatwave mortality events on reefs. Curr Biol 29:2723-2730.e4

Leichter JJ, Paytan A, Wankel S, Hanson K, Miller S, Altabet MA (2007) Nitrogen and oxygen isotopic signatures of subsurface nitrate seaward of the Florida Keys reef tract. Limnol Oceanogr 52:1258–1267

Lenth R (2020) emmeans: estimated marginal means, aka Least-Squares Means (R 1.4.6)

Liu Q, Kandasamy S, Wang H, Wang L, Lin B, Gao A, Chen CTA (2019) Impact of hydrological conditions on the biogeochemical dynamics of suspended particulate organic matter in the upper mixed layer of the Southern East China Sea. J Geophys Res Ocean 124:6120–6140

Lowe RJ, Falter JL (2015) Oceanic forcing of coral reefs. Ann Rev Mar Sci 7:43–66

MacKenzie KM, Robertson DR, Adams JN, Altieri AH, Turner BL (2019) Structure and nutrient transfer in a tropical pelagic upwelling food web: from isoscapes to the whole ecosystem. Prog Oceanogr 178:102145

Maldives Meteorological Service (2018) Daily wind data for Hulhule (Kaafu Atoll). www.meteorology.gov.mv/

Morais RA, Bellwood DR (2019) Pelagic subsidies underpin fish productivity on a degraded coral reef. Curr Biol 29:1521-1527.e6

Morillo-Velarde PS, Briones-Fourzán P, Álvarez-Filip L, Aguíñiga-García S, Sánchez-González A, Lozano-Álvarez E (2018) Habitat degradation alters trophic pathways but not food chain length on shallow Caribbean coral reefs. Sci Rep 8:4109

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) nlme: Linear and Nonlinear Mixed Effects Models (R 3.1–147)

R Core Team (2020) R: a language and environment for statistical computing

Radice VZ, Hoegh-Guldberg O, Fry B, Fox MD, Dove SG (2019) Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. Funct Ecol 1365–2435:13314

Ramana MV, Ramanathan V (2006) Abrupt transition from natural to anthropogenic aerosol radiative forcing: Observations at the ABC-Maldives Climate Observatory. J Geophys Res 111:D20207

Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205–221

Rix L, de Goeij JM, van Oevelen D, Struck U, Al-Horani F, Wild C, Naumann M (2018) Reef sponges facilitate the transfer of coral-derived organic matter to their associated fauna via the sponge loop. Mar Ecol Prog Ser 589:85–96

Rix L, de Goeij JM, van Oevelen D, Struck U, Al-Horani FA, Wild C, Naumann MS (2017) Differential recycling of coral and algal dissolved organic matter via the sponge loop. Funct Ecol 31:778–789

Sigman DM, Casciotti KL, Andreani M, Barford C, Galanter M, Böhlke JK (2001) A bacterial method for the nitrogen isotopic analysis of nitrate in seawater and freshwater. Anal Chem 73:4145–4153

Tamir R, Eyal G, Kramer N, Laverick JH, Loya Y (2019) Light environment drives the shallow-to-mesophotic coral community transition. Ecosphere 10:e02839

Tanaka Y, Miyajima T, Koike I, Hayashibara T, Ogawa H (2008) Production of dissolved and particulate organic matter by the reef-building corals *Porites cylindrica* and *Acropora pulchra*. Bull Mar Sci 82:237–245

Tchernov D, Lipschultz F (2008) Carbon isotopic composition of *Trichodesmium* spp. colonies off Bermuda: effects of colony mass and season. J Plankton Res 30:21–31

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York

Wilke CO (2019) cowplot: streamlined plot theme and plot annotations for “ggplot2” (R 1.0.0)

Wyatt ASJ, Lowe RJ, Humphries S, Waite AM (2013) Particulate nutrient fluxes over a fringing coral reef: Source-sink dynamics inferred from carbon to nitrogen ratios and stable isotopes. Limnol Oceanogr 58:409–427