

## RESEARCH ARTICLE

# Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system

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## Abstract

1. Oceanographic processes shape coral reefs worldwide by redistributing inorganic nutrients and particulate resources over depth. Deep-water upwelling occurs frequently in coral reef ecosystems, but its impact on coral nutrition remains unclear.
2. This study investigated the influence of upwelling on the trophic ecology of three common reef-building corals (*Galaxea fascicularis*, *Pachyseris speciosa* and *Pocillopora verrucosa*) from different reef depths (shallow reef, 10 m, vs. deep reef, 30 m) and reef exposures (oceanic rim vs. Inner Sea) across > 250 km of the Maldives archipelago, Indian Ocean. Carbon and nitrogen stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of coral hosts, their symbionts and particulate organic matter (POM) were used to characterize coral trophic strategies.
3. Across the Maldives, consistent mean  $\delta^{15}\text{N}$  values were recorded in hosts (5.5‰) and symbionts (5.2‰) of the three coral species from shallow and deep reefs of oceanic and Inner Sea reef exposures. Coral hosts, symbionts and POM from both depths had  $\delta^{15}\text{N}$  values that were consistent with the isotopic signature of a deep-water nitrate source transported to surface waters via upwelling.
4. In contrast, a wide range of  $\delta^{13}\text{C}$  values (~10‰) revealed different trophic strategies and isotopic niches among the coral species. Different mean  $\delta^{13}\text{C}$  values of *G. fascicularis* indicated greater symbiont autotrophy in corals from shallow (-15.5‰) compared to deep reefs (-17.6‰). Conversely, the mean  $\delta^{13}\text{C}$  values of *P. speciosa* (-15.1‰) and *P. verrucosa* (-17.7‰) were not affected by reef depth. These corals maintained consistent trophic strategies over depth, with *P. speciosa* relying more on autotrophy compared to *P. verrucosa*.
5. Despite different reef exposure to oceanic waters, coral host and POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values did not differ between oceanic and Inner Sea reef exposures. Nutritional resources appear to be homogenous in the central Maldives due to atoll-wide water circulation. However, species-specific trophic strategies resulted in diverse patterns of  $\delta^{13}\text{C}$  values over depth. Because heterotrophic feeding has been linked to coral host survival through coral bleaching events, understanding the trophic ecology of corals within the reef assemblage can provide insight into species resilience under ocean warming conditions. As a member of the typically

competitive Pocilloporidae family, the dependence of *P. verrucosa* on heterotrophy may help this coral be a future “winner” under sustained ocean warming.

#### KEYWORDS

coral reef exposure, coral trophic strategy, Indian Ocean, Island Mass Effect, isotopic niche ecology, Maldives, particulate organic matter, upwelling

## 1 | INTRODUCTION

The function of coral reef ecosystems depends on the complex nutrient dynamics of ocean and reef processes (Lowe & Falter, 2015), with resource availability across environmental gradients playing an important role in shaping the physiological niches of corals (Anthony & Connolly, 2004). Nutrient fluxes in reef ecosystems have important implications for coral community structure and function (Roder et al., 2011; Schmidt et al., 2012). Deep-water upwelling and internal waves generate fluxes of inorganic nutrients that increase reef-wide primary productivity and the availability of particulate resources, which can be an important factor for the growth of corals, especially in deep reefs (Leichter & Genovese, 2006; Leichter, Shellenbarger, Genovese, & Wing, 1998; Stuhldreier et al., 2015). Variation in nutrient and particulate concentrations can influence the trophic strategies of symbiotic corals, which obtain nutrients (carbon and nitrogen) from their photosynthetic algal endosymbionts (herein “symbionts”; autotrophy) and from coral host feeding (heterotrophy) on organic resources such as particulate organic matter (POM; Porter, 1976). While heterotrophic feeding provides an important input of carbon and nitrogen for corals (Goreau, Goreau, & Yonge, 1971; Fanny Houlbrèque & Ferrier-Pagès, 2009), feeding rates are species-specific and are influenced by local environmental conditions (Palardy, Grottoli, & Matthews, 2005; Sebens, Vandersall, Savina, & Graham, 1996). For example, spatial variation in the deep-water delivery of nutrients and particulate resources can structure coral trophic strategies across regions and over depth within a single reef system (Fox et al., 2018; Williams et al., 2018). However, there is a limited understanding of how upwelling affects the trophic strategies of corals within different reef depths (shallow vs. low-light deep reefs) and reef exposures (oceanic rim vs. Inner Sea) in an oceanic atoll system.

Stable isotopes are commonly used to study nutrient dynamics in ecology given that isotope ratios (e.g.,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) provide insight into the source and relative abundance of assimilated nutrients (Peterson & Fry, 1987) and are used to trace sources of carbon and nitrogen in symbiotic corals (reviewed in Maier, Weinbauer, & Pätzold, 2010). There are distinct isotopic signatures of primary sources of new nitrogen such as that derived from nitrogen fixation ( $\delta^{15}\text{N}$  -2 to 0‰) versus deep-water nitrate ( $\delta^{15}\text{N}$  +5 to 6‰; Sigman, Altabet, McCorkle, Francois, & Fischer, 2000; Montoya, Carpenter, & Capone, 2002). Because of the slow turnover (>300 days) of nitrogen in coral tissue (Tanaka, Suzuki, & Sakai, 2018), diverse  $\delta^{15}\text{N}$  values of corals reflect regional primary nitrogen sources. For example, nitrogen fixation is an important source of nitrogen in the

oligotrophic Red Sea (e.g., low  $\delta^{15}\text{N}$  values; Kürten et al., 2014) while higher  $\delta^{15}\text{N}$  values (e.g., >10‰) can result from incomplete nitrate uptake by phytoplankton and/or water-column denitrification (Altabet, 2001; Wang et al., 2016). Reef-building corals acquire new nitrogen primarily by feeding on particulates and also through the uptake of dissolved inorganic nitrogen (DIN; Grover, Maguer, Allemand, & Ferrier-Pagès, 2003; Houlbrèque, Tambutté, Richard, & Ferrier-Pagès, 2004; Houlbrèque & Ferrier-Pagès, 2009). In regard to sources of dissolved nitrogen, DIN can provide up to 75% of the daily coral nitrogen budget compared to dissolved organic nitrogen (DON); at high concentrations, DON sources such as dissolved free amino acids can contribute only up to 11%–21% of the daily nitrogen budget (Grover, Maguer, Allemand, & Ferrier-Pagès, 2008; Hoegh-Guldberg & Williamson, 1999). Overall, dissolved organic matter is typically less bioavailable than POM (Lønborg, Álvarez-Salgado, Duggan, & Carreira, 2018) and is found in lower concentrations in oceanic seawater compared to shallow lagoons (Tanaka, Ogawa, & Miyajima, 2011). Therefore, our study focuses on POM and DIN as the major potential sources of nitrogen for corals in an oceanic reef system (Wyatt, Falter, Lowe, Humphries, & Waite, 2012).

Corals from turbid reef environments, where photosynthesis may be impeded, have a greater ability to ingest POM compared to conspecifics from less turbid reefs (Anthony, 2000). To acclimate to different light environments, structural modifications by coral hosts and symbionts can modulate the light available to symbionts (Kaniewska et al., 2011) while symbionts can increase light capture efficiency (Iglesias-Prieto & Trench, 1994). Overall, the variation in  $\delta^{13}\text{C}$  values among individual colonies of a given species is attributed to environmental conditions including light and water flow (Maier et al., 2010; Roder et al., 2010). The principal carbon source for autotrophy (symbiont photosynthesis) is seawater-derived dissolved inorganic carbon (DIC,  $\delta^{13}\text{C}$  ~ +1‰) and dissolved  $\text{CO}_2$  ( $\delta^{13}\text{C}$  ~ -7‰), with host-respired  $\text{CO}_2$  directed towards calcification (Furla, Galgani, Durand, & Allemand, 2000). The apparent use of distinct DIC pools for calcification and photosynthesis by coral hosts and symbionts implies that a shift towards more negative  $\delta^{13}\text{C}$  in symbionts is driven by reductions in the rate of photosynthesis (Alamaru, Loya, Brokovich, Yam, & Shemesh, 2009). Generally, less negative  $\delta^{13}\text{C}$  values (e.g., -11‰) of symbionts reflect a carbon limitation in shallow reefs (i.e., high rates of photosynthesis maintain the discrimination against  $^{13}\text{C}$ ) compared to more negative  $\delta^{13}\text{C}$  of symbionts in deeper reefs where light is limited (Farquhar, Ehleringer, & Hubick, 1989; Muscatine, Porter, & Kaplan, 1989). As photosynthesis rates decline in some coral species in deep reefs, increased heterotrophic

feeding can result in decreased  $\delta^{13}\text{C}$  values that approach those of particulate sources such as POM (e.g.,  $-21$  to  $-26\%$ ; Muscatine et al., 1989; Einbinder et al., 2009; Soares et al., 2015). If coral population density is maintained across environmental gradients, then a reduction in one mechanism for acquiring energy would be presumably matched by an increase in another strategy. Because an organism's ecological niche is linked with resource availability and feeding strategies, the isotopic niche is used as a proxy for the ecological niche with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values revealing the isotopic niche position in  $\delta$ -space (Newsome, Martinez del Rio, Bearhop, & Phillips, 2007). In order to evaluate species-specific trophic strategies and baseline resources, our study considers both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values that comprise the isotopic niche. A large isotopic niche would indicate the use of a wide variety of resources (more mixotrophic) while a small isotopic niche would indicate a more restricted use of resources.

The interaction between island/atoll topography and circulation that causes localized upwelling is referred to as the Island Mass Effect (Doty & Oguri, 1956). Although the Island Mass Effect is prominent across the Pacific Ocean (Gove et al., 2016), its influence on coral reef atolls/islands in the central Indian Ocean remains to be characterized (Sasamal, 2006). In the remote archipelago of the Maldives located along the Laccadive–Chagos ridge, upwelling is generated by seasonally reversing winds driven by the South Asian Monsoon climate (Preu & Engelbrecht, 1991). With upwelling occurring the majority of the year, marine primary productivity associated with the monsoon seasons drives the shifting distribution of chlorophyll (Kumar, Prakash, Ravichandran, & Narayana, 2016). There are high concentrations of surface chlorophyll during the monsoon seasons while chlorophyll concentrations are reduced during the brief inter-monsoon transition periods (de Vos, Pattiaratchi, & Wijeratne, 2014). The Maldives atolls, which are subject to strong currents (Owen, Kruijssen, Turner, & Wright, 2011; Preu & Engelbrecht, 1991), are dominated by the input of deep-water nutrients via upwelling while land-derived eutrophication is considered negligible (Jaleel, 2013). DON is not considered a major source of nitrogen because macroalgal cover is generally very low in Maldives reefs, and there is no evidence of macroalgal blooms that would create unfavourable conditions for coral growth (Brown, Bender-Champ, Bryant, Dove, & Hoegh-Guldberg, 2017). The monsoonal climate controls the spatial variation in resource delivery throughout the year (i.e., west vs. east). The east-west shifting phytoplankton blooms affect seasonal manta ray distribution (Anderson, Adam, & Goes, 2011), but the extent of the availability and use of upwelling resources by benthic reef-building corals across different reef exposures are unknown.

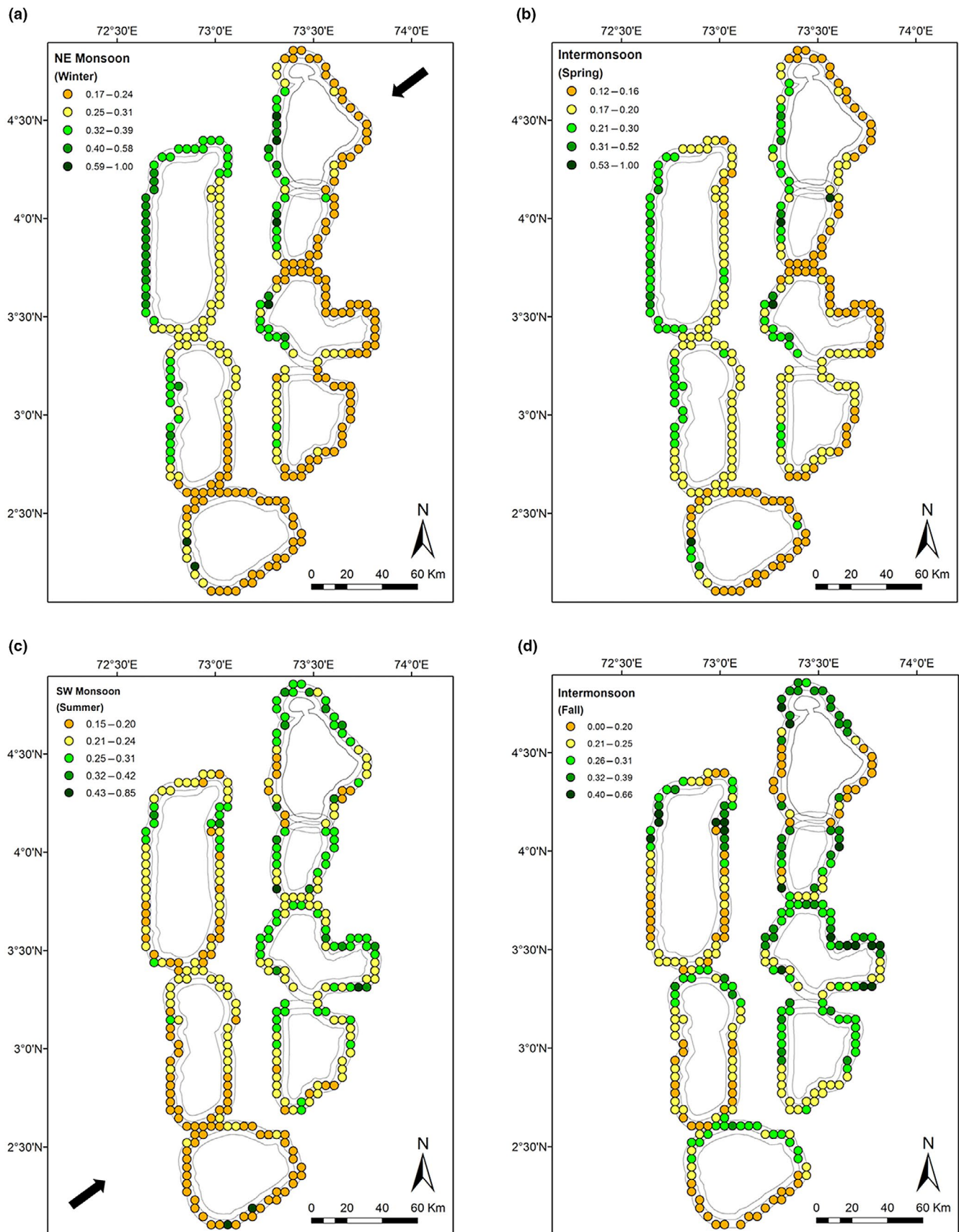
There is great interest in the effects of upwelling on coral trophic strategies because coral heterotrophic feeding is typically considered facultative with species-specific patterns evident over small changes in depth (Palardy et al., 2005). Because the distribution of coral is largely affected by life-history traits and resource use (Jackson, 1991), this study focuses on three species of coral with diverse life-history strategies: the “competitive” species *Pocillopora verrucosa*, the “generalist” species *Pachyseris speciosa*, and the “stress-tolerant” species *Galaxea fascicularis* (Darling, Alvarez-Filip,

Oliver, McClanahan, & Côté, 2012; Madin et al., 2016). This study investigates how trophic strategies of reef-building corals vary across gradients of light and resource availability (reef depth and reef exposure) in the Maldives by analysing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of POM (particulate food source) and coral host and symbiont tissue from three morphologically distinct coral species (*G. fascicularis*, *P. speciosa* and *P. verrucosa*) that are present between 10 and 30 m depth (Pichon & Benzoni, 2007). To determine whether coral and POM  $\delta^{15}\text{N}$  values reflect different sources of nitrogen across reef depth and reef exposure, corals and POM from reefs of the oceanic rim (facing the Indian Ocean; drop-offs to 2,000 m) were compared to reefs in the shallower Inner Sea ( $\leq 550$  m) of the central Maldives (Betzler et al., 2013). Further, relative coral colony abundance was estimated across reef depths and exposures and remotely sensed measurements of surface chlorophyll-*a* concentrations (chl-*a*) and in situ temperature sensors were used to investigate potential differences in species distribution and resource availability associated with upwelling. It was hypothesized that deep reef corals would have  $\delta^{15}\text{N}$  values close to the isotopic signature of deep-water nitrate (expected for both hosts and symbionts) and more negative  $\delta^{13}\text{C}$  values indicative of greater heterotrophy reflecting greater access to POM and deep-water nitrate via upwelling. It was expected that corals from exposed oceanic reefs would have  $\delta^{15}\text{N}$  values that reflect greater access to deep-water nitrate and POM than reefs from the shallower Inner Sea (Sawall, Khokiattiwong, Jompa, & Richter, 2014). Conversely, it was expected that corals would be more abundant in shallow reefs and have higher  $\delta^{13}\text{C}$  values consistent with greater reliance on carbon from symbiont photosynthesis.

## 2 | MATERIALS AND METHODS

### 2.1 | Measurement of environmental variables

Variability in nearshore primary production (as a proxy for upwelling) was characterized in the central Maldives to examine seasonal shifts in primary production associated with the monsoon climate. Climatological means of surface chl-*a* concentrations were used as proxies for primary production in the central Maldives over the long term (2004–2015) as well as the timeframe of the study in 2015 (Gove et al., 2013; see Appendix S1 in Supporting Information). Temperature data were obtained from the oceanic reef environment by deploying loggers (HOBO Pendant, Onset, U.S.A.; 5-min recording interval) in shallow (10 m) and deep (30 m) reefs at three sites (31 March to 20 April 2015) to monitor for cold-water pulses associated with upwelling and quantify patterns of temperature variability over depth. Concurrent deployments of light loggers, Odyssey PAR (Dataflow Systems, New Zealand; 10-s recording interval) and DEFI-L (JFE Advantech Co., Japan; 15-min recording interval; greater depth rating) were used to measure irradiance in shallow and deep reefs, respectively. Odyssey PAR loggers were calibrated using DEFI-L calibration. The highest astronomical tide recorded in the Maldives (Malé) is 0.64 m (Owen et al., 2011).



**FIGURE 1** Mean surface chlorophyll-*a* concentrations (2004–2015;  $\text{mg}/\text{m}^3$ ) during the (a) north-east (NE; winter) and (c) south-west (SW; summer) monsoon seasons and the (b) spring and (d) fall inter-monsoon periods show shifts in primary productivity in the central Maldives. Maps are shown in chronological order, with arrows indicating monsoon wind direction

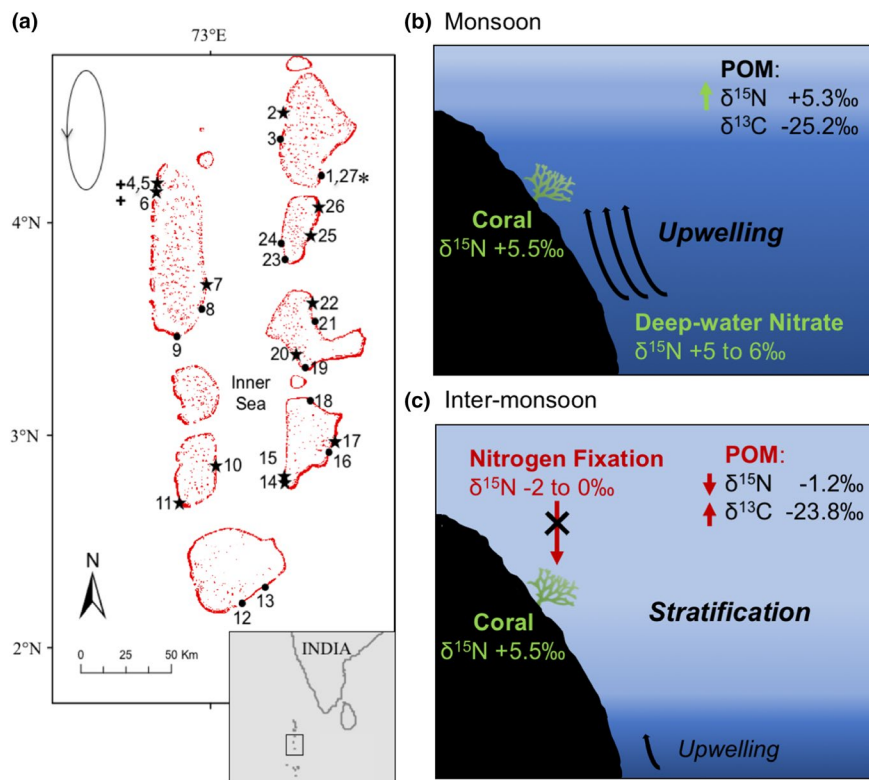
## 2.2 | Sample collection and processing

In March–April 2015 (spring inter-monsoon), fragments of corals *G. fascicularis*, *P. speciosa* and *P. verrucosa* were collected by divers from shallow (10 m) and deep (30 m) fore reefs throughout the central Maldives (Figure 2a–c, Supporting Information Tables S1 and S2), rinsed with filtered seawater and frozen ( $-20^{\circ}\text{C}$  shipboard then transferred to  $-80^{\circ}\text{C}$ ). Equal effort (time investment) was applied to the sampling of corals at each site and depth (target of nine colonies per species per depth at five oceanic reef sites and five Inner Sea reef sites), such that the number of sampled colonies can be used as a proxy for visible colony abundance. To examine the role of POM as a possible source of nutrition, seawater (10 L) was collected from each depth at all sites (except site 5) and filtered through pre-combusted ( $450^{\circ}\text{C}$ , 5 hr)  $0.4\ \mu\text{m}$  nominal pore size glass fibre filters ( $n = 50$ ; Macherey-Nagel). Tissue was removed from coral skeletons using a pressurized airbrush with  $0.22\ \mu\text{m}$  filtered seawater, with symbionts ( $n = 155$ ) being separated from coral host tissue ( $n = 161$ ) by centrifugation (minimum four times each at  $3,000 \times g$  and subsequently resuspended in filtered seawater) (Reynaud et al., 2002). Coral host tissue, symbiont tissue and glass fibre filters were

acidified briefly with 1 N HCl to remove any remaining carbonates, rinsed with Milli-Q water and freeze-dried prior to isotopic analysis. There were fewer symbiont samples analysed due to insufficient dry weight of some samples.

## 2.3 | Isotopic analysis and isotopic niche estimates

Coral host and symbiont tissue samples were analysed ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , shown as mean  $\pm$  SD) with a PDZ Europa ANCA-GSL elemental analyser and glass fibre filters (POM) were analysed ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) with an Elementar Vario EL Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany), each interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.), at the University of California Davis, U.S.A. Stable isotope ratios are reported in the delta ( $\delta$ ) notation, which is expressed in per mil (‰):  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ , where R represents the ratio of the heavy to light isotope (i.e.,  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ). A subset of samples ( $n = 40$ ) were measured in duplicate or triplicate and resulted in isotope values typically differing by  $\leq 0.2\%$ . Repeated measurements of six internal standards (G-7: peach leaves, G-13: bovine liver, G-17:



**FIGURE 2** (a) Map of the central Maldives atolls with sampling sites shown in chronological order of the survey (sampling: • = particulate organic matter (POM) only, ★ = POM and corals; + = temperature and light loggers). Site 1/27, which is noted by an asterisk (\*), represents the start and end of the survey with the arrow on the oval (top left) showing survey direction. The Maldives climate is characterized by (b) monsoon seasons and (c) brief inter-monsoon periods, with POM carbon ( $\delta^{13}\text{C}$ ) and nitrogen isotope values ( $\delta^{15}\text{N}$ ) reflecting the dominant sources available ( $\delta^{15}\text{N}$  isotopic signatures for nitrogen fixation and deep-water nitrate obtained from the literature cited within the Introduction). POM and coral isotope ratios are results from this study. Nitrogen fixation is not depicted during the (b) monsoon season due to the strong upwelling and water-column mixing while nitrogen fixation represents a potential nitrogen source during the (c) brief inter-monsoon when water stratification occurs. However, a potential nitrogen source derived from nitrogen fixation appears insignificant for overall coral nutrition due to predominant upwelling of deep-water nitrate in this reef system

USGS-41 glutamic acid, G-18: nylon 5, G-20: glutamic acid, and G-21: enriched alanine) resulted in precision of  $\leq 0.13\%$  for  $\delta^{13}\text{C}$  and  $\leq 0.15\%$  for  $\delta^{15}\text{N}$ . To compare isotopic niche position among coral species (Newsome et al., 2007), maximum-likelihood standard ellipses were fitted to  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data. Species-specific coral host and symbiont standard ellipse areas ( $\%{}^2$ ), representing individual isotopic niche size, were estimated by Bayesian modelling ( $2 \times 10^6$  posterior draws with  $10^4$  burn-in) using the "SIBER" package in R (Stable Isotope Bayesian Ellipses in R; Jackson, Inger, Parnell, & Bearhop, 2011; R Core Team, 2017). Credibility intervals of model solutions are presented in probability density distribution plots.

## 2.4 | Statistical analysis

A linear mixed effects model was used to examine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of coral hosts and symbionts in regard to the factors coral host species (*G. fascicularis*, *P. speciosa* and *P. verrucosa*), reef depth (shallow vs. deep) and reef exposure (oceanic vs. Inner Sea) with individual coral colony and site treated as random effects. Because a major change in POM  $\delta^{15}\text{N}$  values was observed between two consecutive time periods of the survey (Period 1: sites 1–14, 29 March to 8 April 2015 and Period 2: sites 15–27, 8–16 April 2015), the effect of sampling period was considered in the analysis of POM isotopic data. We used a linear mixed effects model, with POM sample (individual glass fibre filter) and site included as random effects, to assess the effect of reef depth (shallow vs. deep), reef exposure (oceanic vs. Inner Sea) and sampling period (Period 1 vs. Period 2) on POM  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. The linear mixed effects model was fit using the function "lme" from the "nlme" package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018). Data met assumptions of normality (QQ-plots and residual plots) and homogeneity of variance (Levene's test). Statistical significance was determined with an alpha value of 0.05.

## 3 | RESULTS

### 3.1 | Variability of environmental parameters across sites in the Maldives

Climatological maps of chl-*a* (12-year mean) from the central atolls show seasonal east-west shifts in the concentration of chl-*a* (Figure 1). Increased chl-*a* concentrations occur downwind in the west during the NE monsoon when winds are from the east, whereas plumes develop downwind in the east during the SW monsoon when winds are from the west. At monthly intervals, for example the year (2015) when the study took place, chl-*a* concentrations reflected changes in the monsoon seasons with elevated chl-*a* downwind as a consistent upwelling signal (Figure 2b,c and Supporting Information Figure S1). During the study period, wind direction switched abruptly with the change in monsoon season (Supporting Information Figure S2).

Temperature and light were measured in shallow and deep reefs during the expedition (Supporting Information Figure S3).

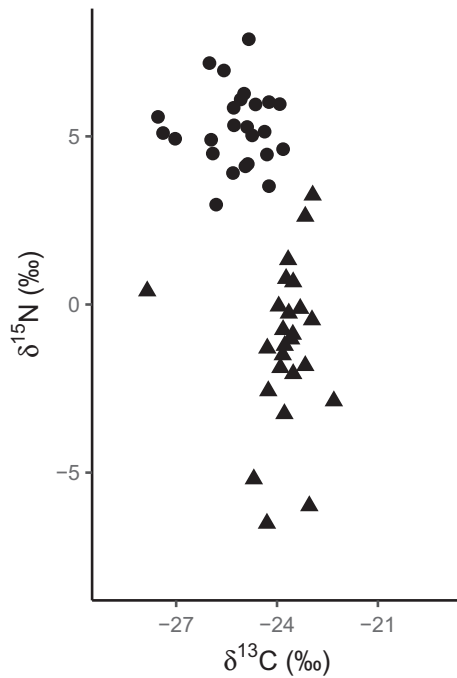
Temperature records from the 3-week period during the inter-monsoon revealed fluxes of cooler water (minimum 26.68°C) in deep (30 m) but not shallow (10 m) reefs (Supporting Information Figure S3a–c). Over this period, the daily average seawater temperature was 29.77 and 29.47°C in shallow and deep reefs, respectively. In the third week, daily seawater temperatures increased and exceeded the long-term maximum monthly mean temperature in both shallow and deep reefs, but this was then followed by a temperature decline (Supporting Information Figure S3d). Light loggers recorded an average day-time (600–1800 hr) irradiance of 160.43  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  in shallow reefs and 60.44  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  in deep reefs. Surface light averaged about 1,500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , so light levels in shallow and deep reefs were about 10% and 4%, respectively.

### 3.2 | Isotope ratios of particulate organic matter, coral hosts and symbionts

POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were measured to estimate potential differences in nitrogen and carbon sources between shallow and deep reefs and between oceanic and Inner Sea reefs, with the major available nitrogen source for corals inferred from POM  $\delta^{15}\text{N}$  values. POM isotope ratios did not differ by reef depth (Supporting Information Table S3). POM  $\delta^{15}\text{N}$  values significantly decreased from  $5.3 \pm 1.1\%$  in Period 1 to  $-1.2 \pm 2.4\%$  in Period 2 (Figure 3 and Supporting Information Figure S4; Supporting Information Table S3). There was also a shift in POM  $\delta^{13}\text{C}$  values between Period 1 ( $-25.2 \pm 1.0\%$ ) and Period 2 ( $-23.8 \pm 1.0\%$ ) although the change was not significant (Supporting Information Table S3). The magnitude of the shift between Period 1 and Period 2 was smaller for  $\delta^{13}\text{C}$  (1.4%) than for  $\delta^{15}\text{N}$  (6.5%; Figure 3 and Supporting Information Figure S4). There were large changes in POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values at the same site sampled at the start and end of the survey (Supporting Information Figure S4). The shift in POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values between Period 1 and Period 2 supports the existence of two different water masses sampled during the survey (Figure 3 and Supporting Information Figure S4).

Despite extensive plumes of chl-*a* moving westward in the months preceding the survey (Supporting Information Figure S1), coral host  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values did not differ between oceanic and Inner Sea reefs (Table 1, Figure 4). There was a narrow range of  $\delta^{15}\text{N}$  values (means of 5.2–5.8%) of all three coral host species from both depths (Supporting Information Table S4). The significant interaction between coral species and depth explained the variability among coral host  $\delta^{13}\text{C}$  values (Table 1 and Supporting Information Table S4). Mean  $\delta^{13}\text{C}$  values of host *G. fascicularis* differed significantly between shallow ( $-15.5 \pm 1.2\%$ ) and deep reefs ( $-17.6 \pm 0.8\%$ ), resulting in the widest isotopic range observed among the coral species. Irrespective of depth, host *P. speciosa* had significantly higher mean  $\delta^{13}\text{C}$  values (shallow  $-15.2 \pm 1.4\%$ , deep  $-15.1 \pm 1.0\%$ ) than host *P. verrucosa* (shallow  $-17.4 \pm 1.1\%$ , deep  $-18.0 \pm 0.8\%$ ) and deep host *G. fascicularis* ( $-17.6 \pm 0.8\%$ ).

The variation in symbiont  $\delta^{13}\text{C}$  values was due to the interaction among the factors coral host species, reef depth and reef



**FIGURE 3** Particulate organic matter (POM) from coral reef waters shows changes in nitrogen isotope ratios ( $\delta^{15}\text{N}$ ) but not carbon isotope ratios ( $\delta^{13}\text{C}$ ) during the brief inter-monsoon period in the Maldives. POM samples are grouped by (consecutive) sampling periods: Period 1 (circle) represents POM from the first part of the survey (29 March to 8 April 2015), and Period 2 (triangle) shows POM from the second part of the survey (8–16 April 2015). Data are shown from both shallow and deep reefs because reef depth did not affect POM isotopic ratios

exposure (Table 1). The interaction was driven by lower  $\delta^{13}\text{C}$  values of *P. speciosa* symbionts from shallow oceanic reefs ( $-15.4 \pm 1.5\%$ ) compared to shallow Inner Sea reefs ( $-13.4 \pm 2.1\%$ ) and deep oceanic reefs ( $-13.7 \pm 2.0\%$ ) (Figure 5). *Pachyseris speciosa* (shallow  $-14.0 \pm 2.1\%$ , deep  $14.1 \pm 1.6\%$ ) and *P. verrucosa* (shallow  $-16.3 \pm 1.3\%$ , deep  $-17.0 \pm 0.9\%$ ) symbionts each had similar mean  $\delta^{13}\text{C}$  values between depths, reflecting patterns of the coral host. *Galaxea fascicularis* symbiont  $\delta^{13}\text{C}$  values were significantly lower in deep reefs ( $-17.2 \pm 1.0\%$ ) compared to its symbionts from shallow reefs ( $-15.0 \pm 1.3\%$ ; Table 1). Mean  $\delta^{15}\text{N}$  values of each species' symbionts were also within a narrow range (4.3–5.7‰; Supporting Information Table S4). Coral species and reef depth had an effect on symbiont  $\delta^{15}\text{N}$  values, with significantly lower mean  $\delta^{15}\text{N}$  values of *G. fascicularis* symbionts in shallow reefs ( $4.3 \pm 0.5\%$ ) compared to deep reefs ( $4.9 \pm 0.7\%$ ), with *G. fascicularis* symbionts from both depths differing from shallow *P. verrucosa* symbionts ( $5.4 \pm 0.6\%$ ) (Table 1). Overall, *G. fascicularis* symbionts ( $4.6 \pm 0.7\%$ ) had lower mean  $\delta^{15}\text{N}$  values compared to those of *P. speciosa* ( $5.5 \pm 0.6\%$ ). There was a significant effect of reef exposure, which was attributed to the lower  $\delta^{15}\text{N}$  values of *G. fascicularis* symbionts compared to the symbionts of the other coral species (e.g., Inner Sea *G. fascicularis*  $4.8 \pm 0.6\%$  vs. Inner Sea *P. speciosa*  $5.7 \pm 0.6\%$ ) (Figure 5).

### 3.3 | Coral colony abundance between shallow and deep reefs

The number of colonies of each species collected with equal sampling effort revealed differences in species abundance between shallow and deep reefs (Supporting Information Table S4). There was a significant effect of coral species and depth on coral colony abundance (ANOVA,  $F_{2,48} = 10.453$ ,  $p < 0.001$ ) but no effect of reef exposure. *Pachyseris speciosa* was significantly less abundant in shallow compared to deep reefs (Tukey  $p = 0.009$ ), while *G. fascicularis* was significantly more abundant than *P. speciosa* in shallow reefs (Tukey  $p = 0.012$ ).

### 3.4 | Coral isotopic niches

The isotopic niches of three species of coral hosts from shallow and deep reefs revealed distinct species-specific patterns (Figure 6a). The shallow isotopic niche ( $1.6\%$ ) of coral host *G. fascicularis* was more than twice the size of its deep isotopic niche ( $0.7\%$ ), with no overlap between the two niches (Figure 6a and Supporting Information Figure S5, Supporting Information Table S4). The shallow ( $1.7\%$ ) and deep ( $1.8\%$ ) isotopic niches of host *P. speciosa* were similar in size and position while the smaller isotopic niches (shallow  $1.0\%$ , deep  $0.8\%$ ) of host *P. verrucosa* had marginal overlap. The isotopic niche of shallow host *G. fascicularis* overlapped with the niches of shallow and deep host *P. speciosa* while the niche of deep host *G. fascicularis* overlapped with those of shallow and deep host *P. verrucosa*. The symbionts of shallow *G. fascicularis* showed the most distinct isotopic niche among all species due to lower  $\delta^{15}\text{N}$  values (Figure 6b). In contrast, symbionts of deep *G. fascicularis* had similar isotopic niches to *P. verrucosa* symbionts across both depths but remained distinct from *P. speciosa* symbionts. The isotopic niche sizes of symbionts were generally larger than those of their coral hosts (Supporting Information Table S4, Supporting Information Figures S5 and S6).

## 4 | DISCUSSION

### 4.1 | Nitrogen isotope ratios indicate importance of deep-water nitrate and water-column mixing

In the Maldives, prevailing wind-driven upwelling associated with the monsoon seasons (~10 months of the year) has a greater impact on nutrient and particulate availability than the short inter-monsoon transition periods (~2 months) (Figure 2b,c). Despite fluxes of cooler seawater recorded in deep (30 m) but not shallow (10 m) reefs, reef depth did not affect the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of POM. Nutrients are likely distributed across the double atoll chain of the central Maldives via strong currents within and between the atolls (Owen et al., 2011; Preu & Engelbrecht, 1991). The results showed that POM and coral hosts from both oceanic and Inner Sea reef exposures had similar  $\delta^{15}\text{N}$  values. Similar mean  $\delta^{15}\text{N}$  values of three species of coral hosts (range between 5.2 and

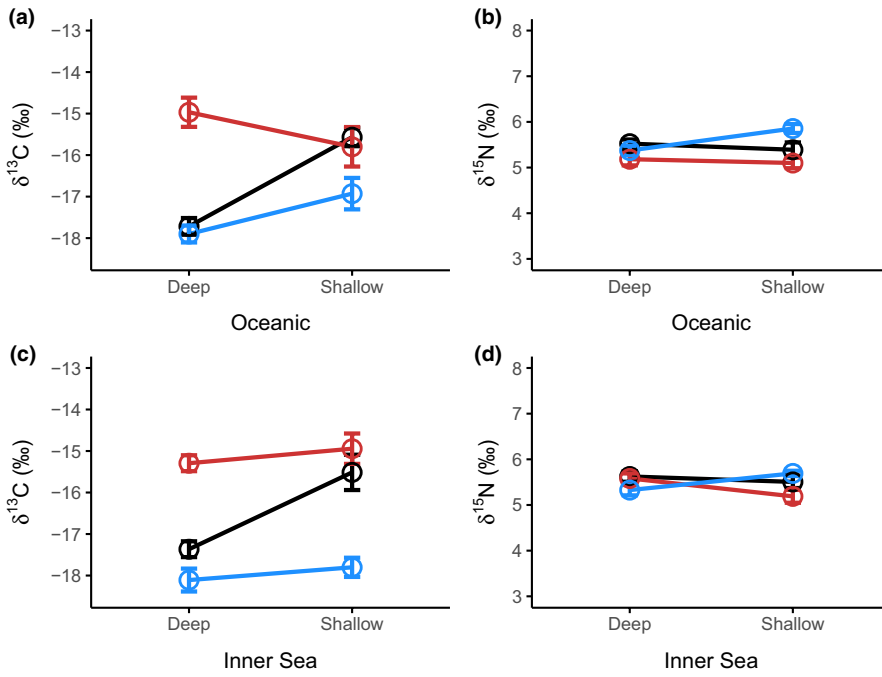
**TABLE 1** A linear mixed effects model was used to test the variables coral species (*Galaxea fascicularis*, *Pachyseris speciosa* and *Pocillopora verrucosa*), reef depth (shallow or deep) and reef exposure (oceanic or Inner Sea) on coral host and symbiont carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios (*df*: degrees of freedom; *SE*: standard error; bold font indicates significance as per alpha value)

Variable	$\delta^{13}\text{C}$					$\delta^{15}\text{N}$				
	<i>df</i>	Estimate	<i>SE</i>	<i>t</i> -value	<i>p</i> -value	<i>df</i>	Estimate	<i>SE</i>	<i>t</i> -value	<i>p</i> -value
Coral Host										
(Intercept)	149	-17.4	0.3	-54.62	<0.001	149	5.6	0.1	43.04	<0.001
Oceanic		-0.4	0.4	-0.87	0.385		-0.1	0.2	-0.61	0.545
Pachyseris		2.1	0.4	4.95	<0.001		0.0	0.2	-0.25	0.802
Pocillopora		-0.7	0.4	-1.69	0.094		-0.3	0.2	-1.65	0.102
Shallow		1.9	0.4	4.42	<0.001		-0.1	0.2	-0.69	0.490
Oceanic: Pachyseris		0.7	0.6	1.22	0.226		-0.3	0.2	-1.30	0.196
Oceanic:Pocillopora		0.6	0.6	0.96	0.339		0.1	0.2	0.62	0.539
Oceanic: Shallow		0.3	0.6	0.54	0.591		0.0	0.2	-0.06	0.949
Pachyseris: Shallow		-1.5	0.6	-2.66	0.009		-0.3	0.2	-1.18	0.242
Pocillopora: Shallow		-1.5	0.6	-2.57	0.011		0.5	0.2	1.96	0.052
Oceanic: Pachyseris:Shallow		-1.5	0.8	-1.76	0.081		0.3	0.3	0.94	0.351
Oceanic: Pocillopora:Shallow		0.4	0.8	0.45	0.655		0.1	0.3	0.39	0.698
Symbiont										
(Intercept)	142	-16.9	0.4	-41.59	<0.001	143	5.2	0.2	30.35	<0.001
Oceanic		-0.5	0.5	-1.06	0.291		-0.5	0.2	-2.34	0.021
Pachyseris		2.4	0.5	4.44	<0.001		0.8	0.2	3.50	0.001
Pocillopora		-0.1	0.6	-0.26	0.796		0.0	0.2	0.02	0.987
Shallow		2.0	0.5	3.65	<0.001		-0.7	0.2	-3.09	0.002
Oceanic: Pachyseris		1.4	0.7	1.92	0.057		-0.1	0.3	-0.49	0.626
Oceanic: Pocillopora		0.7	0.8	0.89	0.376		0.6	0.3	1.82	0.071
Oceanic: Shallow		0.4	0.7	0.56	0.575		0.2	0.3	0.50	0.617
Pachyseris: Shallow		-0.9	0.7	-1.19	0.236		0.1	0.3	0.34	0.736
Pocillopora: Shallow		-1.9	0.8	-2.42	0.017		0.7	0.3	2.21	0.029
Oceanic: Pachyseris:Shallow		-3.3	1.1	-2.97	0.003		0.3	0.5	0.66	0.513
Oceanic: Pocillopora:Shallow		0.6	1.1	0.60	0.551		0.2	0.5	0.48	0.632

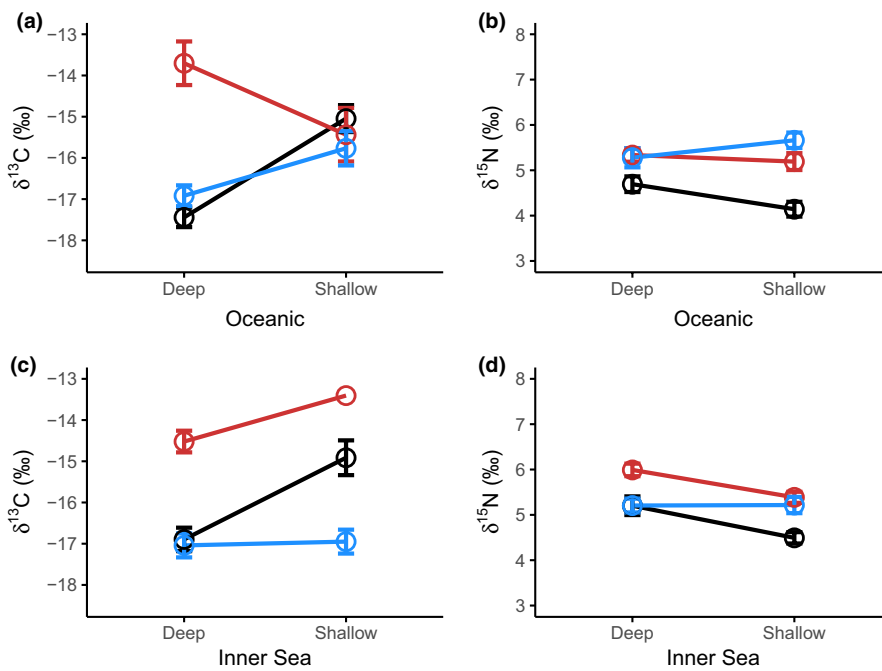
5.8‰), their symbionts (range between 4.3 and 5.7‰) and POM (5.3‰, Period 1) from both shallow and deep reefs are consistent with a well-mixed water column supplied with deep-water nitrate as the major nitrogen source. Previous records of bulk coral (combined host and symbiont tissue of *Porites lobata*) from the Maldives showed similar mean  $\delta^{15}\text{N}$  values (5.8‰), with the exception of coral collected from sites potentially affected by sewage disposal (Risk, Dunn, Allison, & Horrill, 1993). The long-term retention and recycling of nitrogen between coral hosts and symbionts indicate that Maldives coral  $\delta^{15}\text{N}$  values of ~5–6‰ reflect a time-integrated signal of nitrogen principally derived from a deep-water nitrate source (Tanaka et al., 2018; Tremblay, Maguer, Grover, & Ferrier-Pagès, 2015). In other regions subject to upwelling of deep-water nitrate, such as the Florida Keys reef tract, regional oceanography also appears to influence coral  $\delta^{15}\text{N}$  values (Leichter et al., 2007; Swart, Saied, & Lamb, 2005).

Although the  $\delta^{15}\text{N}$  values of corals in the Maldives indicate community- and reef-wide reliance on an upwelled nitrate source, nitrogen fixation can provide an important source of new nitrogen for some coral species and reef ecosystems (Cardini et al., 2015). Despite consistent  $\delta^{15}\text{N}$  values among the majority of the coral host species (5.5‰) and symbionts (5.3‰) from Maldives reefs, the symbionts of *G. fascicularis* from shallow reefs (4.3‰) occupied a unique isotopic niche due to lower  $\delta^{15}\text{N}$  values (Figure 6). Because symbionts, rather than the host, preferentially use nitrogen derived from nitrogen fixation (Lesser et al., 2007), the lower  $\delta^{15}\text{N}$  values of shallow *G. fascicularis* symbionts could be due to a small proportion of nitrogen derived from nitrogen-fixing bacteria (Rädecker, Pogoreutz, Voolstra, Wiedenmann, & Wild, 2015). Further investigation into the potential role of nitrogen-fixing bacteria and its association with symbionts of *G. fascicularis* is required (Li et al., 2013). However, based on the  $\delta^{15}\text{N}$  values from





**FIGURE 4** Coral host carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios by coral species, reef depth (shallow vs. deep) and reef exposure (oceanic vs. Inner Sea). The three species of reef-building corals (*Galaxea fascicularis*—black, *Pachyseris speciosa*—red, *Pocillopora verrucosa*—blue) were collected from shallow (10 m) and deep (30 m) reefs in the central Maldives. Coral host  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  SE) are grouped by oceanic reef exposure (a and b, respectively) and by Inner Sea reef exposure (c and d, respectively)

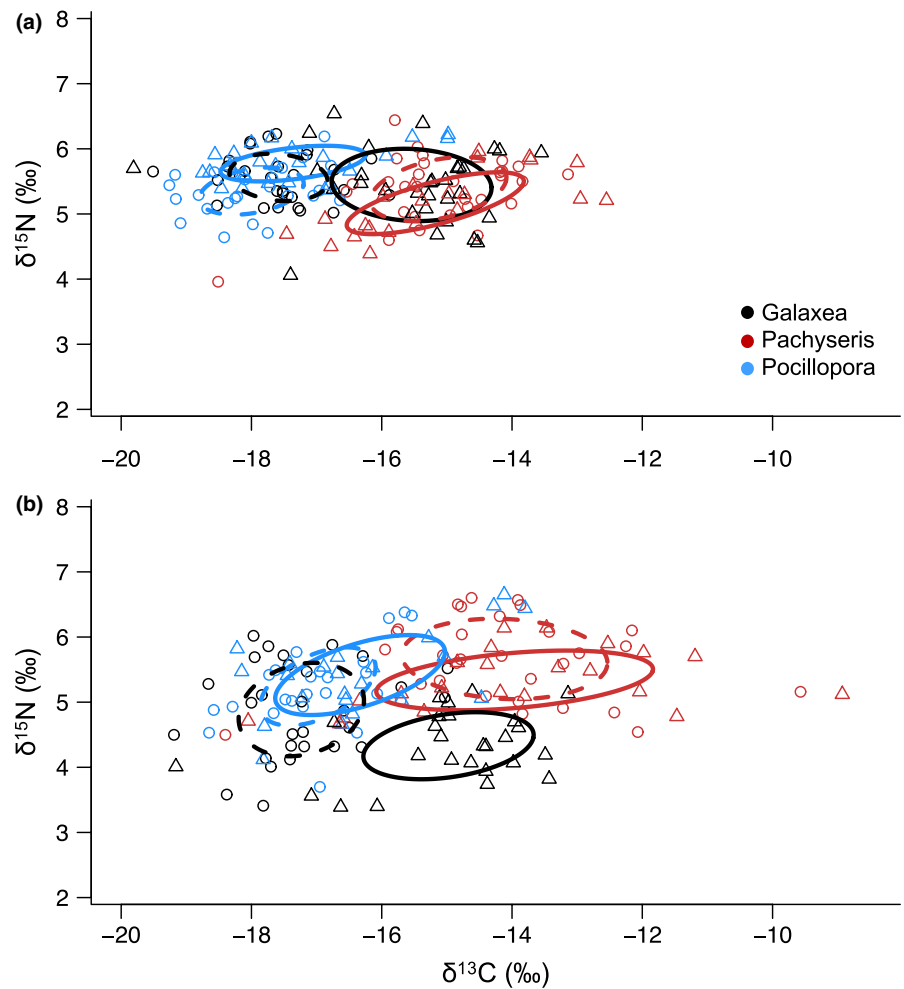


**FIGURE 5** The effect of coral host species, reef depth and reef exposure on symbiont carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios. Symbionts were isolated from three species of reef-building corals (*Galaxea fascicularis*—black, *Pachyseris speciosa*—red, *Pocillopora verrucosa*—blue) collected from shallow (10 m) and deep (30 m) reefs in the central Maldives. Symbiont  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  SE) are grouped by oceanic reef exposure (a and b, respectively) and by Inner Sea reef exposure (c and d, respectively)

the Maldives, the potential input of nitrogen derived from nitrogen fixation would be minimal. *Galaxea fascicularis* host and symbionts from the Maldives did not have particularly low  $\delta^{15}\text{N}$  values as corals from other regions, which have  $\delta^{15}\text{N}$  values reflecting the distinct isotopic signature of nitrogen fixation (Alamaru et al., 2009; Lesser et al., 2007).

Spatiotemporal sampling during our survey revealed a significant shift in mean  $\delta^{15}\text{N}$  values of POM between the consecutive Period 1 (5.3‰) and Period 2 (−1.2‰). This change in isotopic ratios of POM likely reflected the variation in the primary nitrogen source during the shift from the dominant upwelling system (deep-water nitrate) to a

stratified water column (nitrogen fixation) during the brief inter-monsoon transition period (Figures 2 and 3, Supporting Information Figure S4; Qasim, 1970). The slight increase in  $\delta^{13}\text{C}$  values of POM in Period 2 (from −25.2‰ to −23.8‰) possibly reflects an increase in the abundance of *Trichodesmium* (higher  $\delta^{13}\text{C}$ ) and/or  $^{13}\text{C}$ -rich diatoms within the phytoplankton community, which can contain cyanobacteria (Carpenter et al., 1999; Fry & Wainright, 1991; Tchernov & Lipschultz, 2008). During the inter-monsoon period in the Maldives, lower concentrations of chl-*a* and blooms of nitrogen-fixing *Trichodesmium* provide support for the hypothesis that POM from Period 2 reflected increased nitrogen fixation in the water column (Gower & King, 2011;



**FIGURE 6** Isotopic niches of shallow (solid line,  $\Delta$ ) and deep (dash line,  $\circ$ ) reef-building corals from the central Maldives. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios of (a) coral hosts *Galaxea fascicularis*, *Pachyseris speciosa* and *Pocillopora verrucosa* and (b) their symbionts are shown with maximum-likelihood standard ellipses representing isotopic niches

Kumar et al., 2016). Alternatively, a decrease in  $\delta^{15}\text{N}$  values (e.g., POM) can result from fractionation under high (e.g.,  $>15\ \mu\text{M}$ ) nitrate concentrations (Montoya, 2008). However, the latter is unlikely given that seawater temperatures increased and satellite maps showed relatively low concentrations of surface chl-*a* (a proxy for low upwelling), all of which are consistent with low-nutrient, stratified waters as winds subsided and shifted direction during the inter-monsoon period (Supporting Information Figures S1–S4). Changes in POM  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from the same site sampled at the start and end of the survey indicate that the isotopic differences reflected temporal shifts in water mass rather than regional east-west differences (Figure 3 and Supporting Information Figure S4). In regions where the Island Mass Effect or oceanographic processes generate localized upwelling, deep-water nitrate can have a greater role than nitrogen fixation in supplying nitrogen to the reef and can support an increased abundance of plankton that can be beneficial for coral heterotrophic feeding (Gove et al., 2016; Yamazaki et al., 2011).

#### 4.2 | Species-specific trophic strategies reveal distinct isotopic niches across shallow to deep reefs

Despite similar particulate resources over depth (e.g., POM  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and water-column mixing supporting consistent coral

host  $\delta^{15}\text{N}$  values, host  $\delta^{13}\text{C}$  values reflected differentiation in the physiology of the coral host species and their symbionts. Different  $\delta^{13}\text{C}$  values resulting in distinct shallow and deep isotopic niches of host *G. fascicularis* indicate a difference in carbon resources due to decreased photosynthesis and/or greater heterotrophic feeding with increasing depth (Muscatine et al., 1989). Although *G. fascicularis* has been shown to have a lower feeding rate and requirement for heterotrophic carbon relative to other species when grown in aquaria (Hoogenboom, Rottier, Sikorski, & Ferrier-Pagès, 2015; van Os et al., 2012), the external digestion of particulate prey via mesenterial filaments is a mechanism by which *G. fascicularis* can obtain carbon and nitrogen (Wijgerde, Diantari, Lewaru, Verreth, & Osinga, 2011). While the feeding rate of *G. fascicularis* does not appear to be affected by light availability (Hii, Soo, & Liew, 2009), changes in *G. fascicularis* skeleton structure may help to optimize photosynthesis in shallow reefs where light is not limiting (Crabbe & Smith, 2006). Indeed, skeletal growth of *G. fascicularis* is greatest at high irradiance (Schutter et al., 2008). As corals can depend more on heterotrophy in regions of high primary productivity (Fox et al., 2018), the twofold difference in the isotopic niche size of shallow versus deep *G. fascicularis* from a well-mixed water column is likely due to changes in symbiont autotrophy over depth. Because symbiont physiology and irradiance can affect carbon acquisition (Ezzat, Fine, Maguer, Grover,

& Ferrier-Pagès, 2017), future work could examine carbon isotope fractionation in relation to DIC fluxes in symbionts especially since *G. fascicularis* can associate with two symbiont clades (Dong, Huang, Huang, & Li, 2009; Hoins et al., 2016; Maier et al., 2010).

Coral host *P. speciosa* showed consistent  $\delta^{13}\text{C}$  values over depth, resulting in an overlap of both its isotopic niches with that of host *G. fascicularis* from shallow reefs. Although the isotopic niche size and position of shallow and deep *P. speciosa* did not differ with depth, *P. speciosa* colony abundance was greater in deep reefs. The 2-dimensional plating morphology of this coral species and symbiont photobiological acclimation to reduced irradiance due to increasing depth and/or turbidity help to explain the apparent cryptic nature of *P. speciosa* in shallow reefs and its greater abundance in reef cavities and lower-light upper mesophotic reefs of the Maldives (4% of surface irradiance at 30 m; Ciarapica & Passeri, 1993; Cooper et al., 2011; Browne, Smithers, & Perry, 2012). Indeed, *P. speciosa* symbionts are efficient autotrophs over large depth ranges (i.e., 0–60 m), with the coral host showing a consistent association with one clade of symbionts across shallow to deep mesophotic reefs in different oceans (Bongaerts et al., 2011; Cooper et al., 2011; Ziegler, Roder, Büchel, & Voolstra, 2015a). In addition to our findings from the Maldives, a previous study also observed a decreased abundance of *P. speciosa* colonies in shallow reefs compared to deep reefs of the upper mesophotic zone (Ziegler, Roder, Büchel, & Voolstra, 2015b). Therefore, the similar, more positive values of  $\delta^{13}\text{C}$  of *P. speciosa* from shallow and deep reefs are likely related to a dependence on symbiont autotrophy over depth. The heterotrophic feeding capacity of *P. speciosa* is possibly limited to fine organic matter due to an absence of tentacles although it has mesenterial filaments that could be used for feeding (Goreau et al., 1971).

Compared to other more oligotrophic reef systems, the relatively high primary productivity in the Maldives is tightly coupled with coral heterotrophy especially for *P. verrucosa* (Fox et al., 2018). Colonies of the typically competitive branching coral *P. verrucosa* showed similar abundance and consistent  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in shallow and deep reefs, which indicates that *P. verrucosa* maintains the same trophic strategy independent of reef depth. Within the Pocilloporidae family, the focal species *P. verrucosa* is known to be an effective heterotroph with high phenotypic plasticity (Séré, Massé, Perissinotto, & Schleyer, 2010; Ziegler et al., 2015b) while its congener *Pocillopora meandrina* is also dependent on heterotrophy (Fox et al., 2018; Roder et al., 2010). The more negative  $\delta^{13}\text{C}$  values of *P. verrucosa* recorded in this study provide evidence for its dependence on heterotrophy in both shallow and deep reefs in the Maldives. The ability to obtain nutrients through coral host heterotrophy likely supports the lower levels of coral bleaching and coral loss observed for Pocilloporid corals, including *P. verrucosa* (Grottoli, Rodrigues, & Palardy, 2006; Hughes et al., 2018; Muir, Marshall, Abdulla, & Aguirre, 2017). However, if a coral bleaching event would occur during an inter-monsoon period when water-column mixing is reduced, then coral feeding capacity and survival rates may be affected (Palardy, Rodrigues, & Grottoli, 2008). Further work defining the trophic niches of individual coral species is needed to understand coral community and reef ecosystem function, especially because coral reef assemblages are

changing due to the increased frequency of climate-driven oceanic thermal stress conditions.

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## AUTHORS' CONTRIBUTIONS

V.Z.R., S.D., B.F. and O.H.G. conceived the ideas and designed methodology; V.Z.R. and M.D.F. collected the data; V.Z.R., S.D., M.D.F., B.F. and O.H.G. analysed the data; and V.Z.R., S.D. and B.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Isotopic data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.270600g> (Radice, Hoegh-Guldberg, Fry, Fox, & Dove, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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