

High rates of carbon and dinitrogen fixation suggest a critical role of benthic pioneer communities in the energy and nutrient dynamics of coral reefs

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Abstract

1. Following coral mortality in tropical reefs, pioneer communities dominated by filamentous and crustose algae efficiently colonize substrates previously occupied by coral tissue. This phenomenon is particularly common after mass coral mortality following prolonged bleaching events associated with marine heatwaves.
2. Pioneer communities play an important role for the biological succession and reorganization of reefs after disturbance. However, their significance for critical ecosystem functions previously mediated by corals, such as the efficient cycling of carbon (C) and nitrogen (N) within the reef, remains uncertain.
3. We used 96 carbonate tiles to simulate the occurrence of bare substrates after disturbance in a coral reef of the central Red Sea. We measured rates of C and dinitrogen (N₂) fixation of pioneer communities on these tiles monthly over an entire year. Coupled with elemental and stable isotope analyses, these measurements provide insights into macronutrient acquisition, export and the influence of seasonality.
4. Pioneer communities exhibited high rates of C and N₂ fixation within 4–8 weeks after the introduction of experimental bare substrates. Ranging from 13 to 25 μmol C cm⁻² day⁻¹ and 8 to 54 nmol N cm⁻² day⁻¹, respectively, C and N₂ fixation rates were comparable to reported values for established Red Sea coral reefs. This similarity indicates that pioneer communities may quickly compensate for the loss of benthic productivity by corals. Notably, between 40% and 85% of fixed

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organic C was exported into the environment, constituting a vital source of energy for the coral reef food web.

- Our findings suggest that benthic pioneer communities may play a crucial, yet overlooked role in the C and N dynamics of oligotrophic coral reefs by contributing to the input of new C and N after coral mortality. While not substituting other critical ecosystem functions provided by corals (e.g. structural habitat complexity and coastal protection), pioneer communities likely contribute to maintaining coral reef nutrient cycling through the accumulation of biomass and import of macronutrients following coral loss.

KEYWORDS

biogeochemical cycling, carbon and nitrogen stable isotopes, carbon budget, community succession, diazotrophy, photosynthesis, productivity

1 | INTRODUCTION

Coral reefs display some of the highest rates of gross primary production (GPP) in the marine environment, despite a low ambient nutrient availability and little sustained exogenous nutrient inputs (Hatcher, 1990). The high rates of productivity are primarily attributed to the efficient retention and recycling of nutrients and substantial trophic transfer of energy by coral reef communities (De Goeij et al., 2013; Muscatine & Porter, 1977; Odum & Odum, 1955; Wild et al., 2004). In addition, diazotrophy, the metabolic ability to fix atmospheric dinitrogen (N_2) into a biologically useful form (i.e. ammonia), plays an essential role in replenishing the nitrogen (N) pool and sustaining net ecosystem production and growth (Cardini, Bednarz, Foster, & Wild, 2014; O'Neil & Capone, 2008).

In healthy coral reefs, scleractinian corals comprise a major component of the benthic 'nutrient capacity', mediating the fluxes of carbon (C) and N between benthic and pelagic compartments of the ecosystem (Allgeier, Burkpile, & Layman, 2017; Wild et al., 2004, 2011). In fact, corals contribute 41%–76% to benthic GPP budgets, and 10%–14% to benthic N inputs by N_2 fixation during nutrient-depleted conditions, suggesting a strong biogeochemical coupling between diazotrophy and the reef C cycle (Cardini et al., 2016). Thereby, the efficient transfer of energy and nutrients is facilitated by corals mainly via the production, release and subsequent remineralization of coral mucus to other reef organisms and trophic levels (Coffroth, 1990; Wild et al., 2004, 2005) but also through corallivory (reviewed in Rotjan & Lewis, 2008), or decay.

Particularly, recurrent bleaching, as a recent phenomenon mainly triggered by global warming, can inflict a widespread and rapid loss of live coral cover (Hughes, Anderson, et al., 2018; Hughes et al., 2017; Hughes, Kerry, et al., 2018; McClanahan et al., 2019). The sudden change in the benthic community structure arising from bleaching-induced coral mortality implies the loss of critical ecosystem functions conveyed by corals, including nutrient provisioning and regeneration (Holmes & Johnstone, 2010; Morillo-Velarde et al., 2018; Wild et al., 2011). Hence, if the loss of these functions

is not compensated for by other organisms within the ecosystem, coral mortality may have downstream effects on the productivity and trophodynamics of the reef during reef succession.

Whether coral mortality occurs naturally on a small scale or in the form of mass mortality events after severe (anthropogenic) stress, the surface area of bare hard-bottom substrates, that is, the carbonate structures and skeletons from dead corals, is available for (re)-colonization. These substrates are quickly covered with biofilms and colonized by diverse benthic organisms, including heterogeneous assemblages of filamentous algae, crustose coralline algae (CCA), but also sessile invertebrates and coral larvae (reviewed in Norström, Nyström, Lokrantz, & Folke, 2009). Constant disturbances and small-scale differences in environmental conditions result in a mosaic of community stages at varying stages of succession. Consequently, coral reef community composition can be highly heterogeneous resulting in the co-occurrence of pioneers as well as mature coral communities but their relative abundance may change as a result of coral mortality and colonization. Thus, the existing literature mainly focuses on recruitment and succession patterns of these 'pioneer communities' to predict trajectories of recovery (or shifts to alternate states; e.g. Burt, Bartholomew, Bauman, Saif, & Sale, 2009; Humanes & Bastidas, 2015; Jessen, Voolstra, & Wild, 2014; Roth, Stuhldreier, Sánchez-Noguera, Morales-Ramírez, & Wild, 2015; Stuhldreier, Bastian, Schöning, & Wild, 2015). Yet, a study by Davey, Holmes, and Johnstone (2008) indicates that skeletons of artificially bleached corals were also active sites of N_2 fixation. While these laboratory experiments indicate an important role of diazotrophs on apparently 'bare' substrates after coral mortality, in-depth investigations targeting the significance of pioneer communities in their natural environment on the C and N dynamics of a reef are still lacking.

Here we investigate C and N dynamics during the succession of pioneer communities in a coral reef in the central Red Sea. For this, rough carbonate tiles were deployed to simulate the occurrence of bare substrates after disturbance events. Primary productivity and N_2 fixation of the colonizer communities were measured

monthly over 1 year. C and N elemental, as well as stable isotope analyses complemented community-wide flux measurements to (a) quantify rates of primary production and N_2 fixation of benthic pioneer communities, (b) investigate the effects of temporal variability of key environmental variables and (c) gain insights into element acquisition (storage in biomass) and regeneration (export or supply to the environment) of pioneer communities in coral reefs after disturbance.

2 | MATERIALS AND METHODS

2.1 | Study site and environmental conditions

The experiments were carried out at Abu Shosha reef located in the central Red Sea on the west coast of Saudi Arabia (22°18'16.3"N; 39°02'57.7"E). All experiments described below were repeated monthly from January 2017 until December 2017 (duration = 52 weeks).

Prior to the start of the experiments, the relative benthic cover was assessed by line-point-intercept surveys along three consecutively placed 25 m line transects, with a 5-m inter-transect distance (Hill & Wilkinson, 2004). The benthic composition was determined at 50 cm intervals for a total of 50 data points per transect. The relative benthic cover of the main functional groups was as follows (mean \pm SE): Filamentous turf algae = $36.8 \pm 4.8\%$; hard corals = $28.7 \pm 6.6\%$; coral rubble = $10.2 \pm 3.1\%$; biogenic rock = $8.7 \pm 3.3\%$; soft corals = $8.5 \pm 0.2\%$; reef sediments = $6.0 \pm 2.4\%$; *Tridacna* sp. = $0.7 \pm 0.3\%$; and macroalgae $0.4 \pm 0.1\%$. Reef rugosity (as a measure of the structural complexity) was assessed by the chain method (Frost, Burrows, Johnson, Hanley, & Hawkins, 2005) of the same transects described above and averaged 1.90 ± 0.26 . Abu Shosha reef shows a high standing biomass of herbivorous fish (>150 g/m²), as surveyed by Roth et al. (2018). We performed additional fish surveys around experimental aluminium frames to explore whether the introduced structures attracted fish to the area. No differences in both the abundance and community structure were observed around experimental frames as compared to fish surveys in the wider reef (see Table S1).

The area is characterized by strong seasonal fluctuations of environmental variables throughout the year. Key environmental variables were routinely monitored at the sampling site. Water temperature (T) was measured continuously (logging interval = 30 min) for 1 year with data loggers (Onset HOB0 Water Temperature Pro v2 Data Logger-U22-001; accuracy: $\pm 0.21^\circ\text{C}$). Light availability was measured continuously (logging interval = 1 min) for three full days per month with a data logger (Onset HOB0 Pendant UA-002-64; spectral detection range 150–1200 nm). Light readings in lux were converted to photosynthetically active radiation (PAR; $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$; 400–700 nm wavelengths) using the following approximation: $1 \mu\text{mol quanta m}^{-2} \text{s}^{-1} = 51.8$ lux. This conversion factor was obtained by inter-calibrating the lux readings with data obtained from a

parallel deployment of a PAR sensor (LI-COR LI-192S quantum sensor) for 4 hr of daylight. Both readings showed a linear correlation ($r^2 = 0.92$), and the obtained conversion factor of 51.8 was similar to 52.0 reported by Valiela (1984). Salinity was measured during each day of sampling with a conductivity measuring cell (TetraCon[®], 925, WTW, accuracy: $\pm 0.5\%$ of value).

Seawater samples for the determination of dissolved nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{3-}) were taken in triplicates each month from 1 m above the reef substrate with 60 ml syringes. On the boat, samples were filtered immediately through syringe filters (Isopore[™] membrane filters, 0.2 μm GTTP) into acid-washed 15 ml centrifuge tubes and stored dark and cool for transportation. In the laboratory, samples were stored frozen at -50°C until analysed. From the remaining water in the syringes, 5 ml subsamples for ammonium (NH_4^+) measurements were filtered separately into acid-washed 15 ml centrifuge tubes, and 1.2 ml orthophthaldialdehyde-solution (OPA) was added (Holmes, Aminot, Kerouel, Hooker, & Peterson, 1999). NH_4^+ was determined fluorimetrically within 8 hr after sampling (Trilogy[®] Laboratory Fluorometer) after >4 hr incubation with OPA in the dark (limit of quantification [LOQ] = $0.094 \mu\text{mol NH}_4^+ \text{L}^{-1}$). NO_3^- , NO_2^- and PO_4^{3-} concentrations were determined using a continuous flow analyzer (AA3 HR, SEAL) following the designated colorimetric methods (Wangersky, 1978; LOQ = $0.084 \mu\text{mol NO}_3^- \text{L}^{-1}$, $0.011 \mu\text{mol NO}_2^- \text{L}^{-1}$ and $0.043 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$). NH_4^+ , NO_3^- and NO_2^- are collectively termed 'dissolved inorganic nitrogen' (DIN) hereafter. Monthly data of environmental variables are presented in Table S2.

2.2 | Experimental design

Eight anodized aluminium frames (50 \times 50 cm) were haphazardly deployed onto the reef at a depth of 5 m (Figure 1a). The frames were secured to the substrate with weights, keeping a distance of 1.5–2.5 m between frames. Each of the frames was equipped with 12 rough, untreated, carbonate tiles. Each tile was about 8 \times 8 cm and had a mean (\pm SE) planar surface area of 64 ± 0.8 cm². Rough carbonate tiles were used, as their surface mimics coral rock and enhances natural species richness and biomass compared to other artificial substrates (Kennedy, Ordonez, Lewis, & Diaz-Pulido, 2017; Mallela, Milne, & Martinez-Escobar, 2017). In addition, previous studies assessed whether artificial substrates affect the abundance and composition of recruits on tiles as compared to natural reef substrata. As spatial patterns of variation and the relative abundance of organisms on artificial and natural substrata do not significantly vary when using rock-like tiles (e.g. Penin et al., 2010) such as the ones used in the present experiments, we conclude that the use of carbonate settlement tiles did not bias the results presented here. Tiles were installed at a 45-degree angle relative to the substrate on a tough plastic net fixed between the vertical poles to reduce excess sedimentation. Monthly, randomly selected settlement tiles were collected from each frame for further analysis. In total, 96 settlement tiles were analysed.

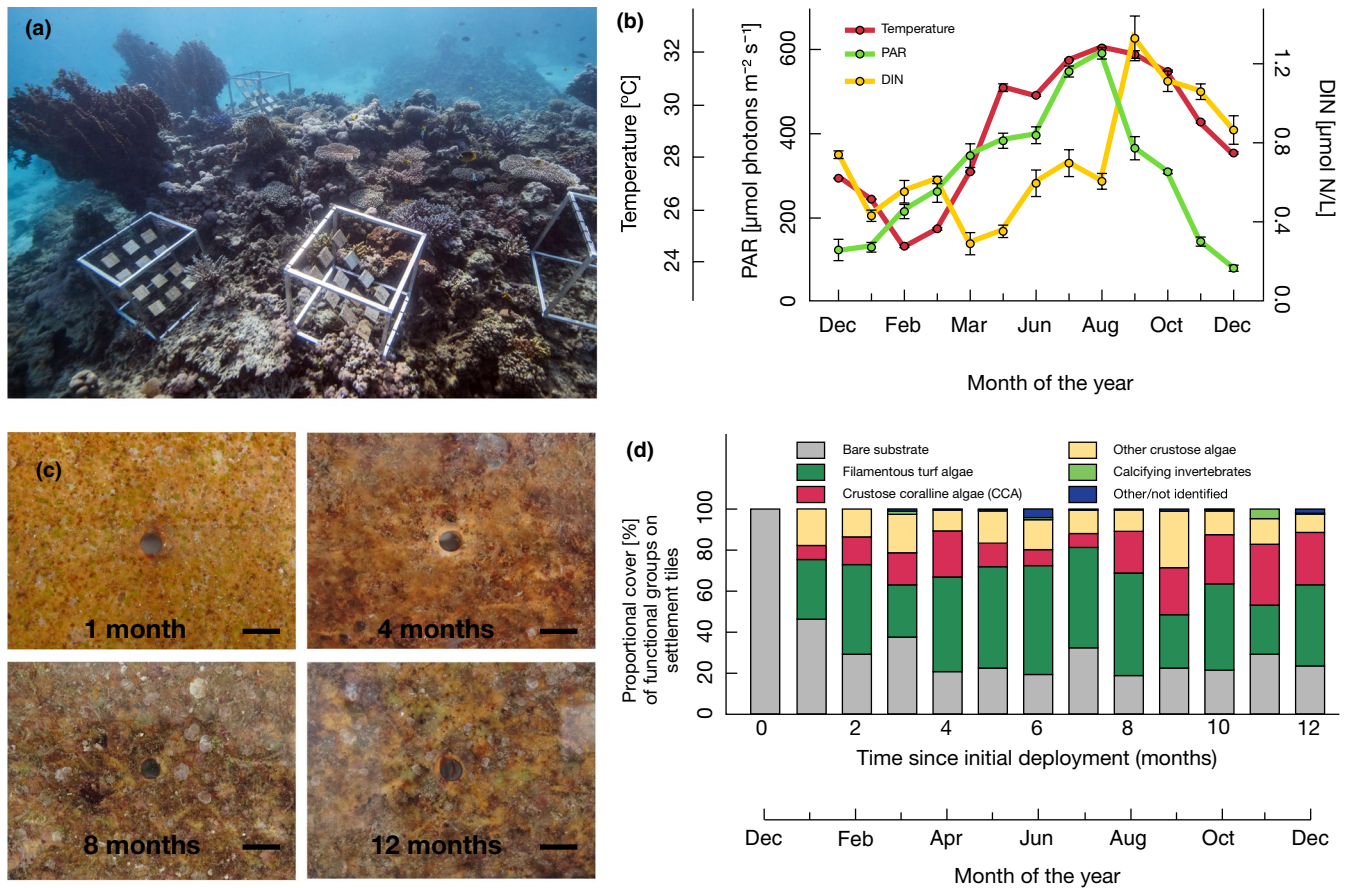


FIGURE 1 Experimental setup at Abu Shosha reef (a), environmental background variables during the study period (b), exemplary pictures of the settlement tiles 1, 4, 8 and 12 months after deployment (c) and the respective proportional cover of functional groups on settlement tiles (d). Aluminium frames with settlement tiles were haphazardly deployed directly onto the reef at 5 m water depth (a). Communities developing on settlement tiles showed a gradual development from filamentous turf algae towards more encrusting algae and sessile invertebrates (details in c and d). In (b), photosynthetically active radiation (PAR, in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) values are presented as daytime averages of three separate days per month \pm SE. Dissolved inorganic nitrogen (DIN, in $\mu\text{mol/L}$) values are averages calculated from three discrete water samples per month \pm SE. Seawater temperature was measured continuously, and values represent the monthly mean \pm SE. Lines in (b) connect the means. Abbreviations: mo, months. Picture in (a) adapted from Roth et al. (2018). Scalebar in (c) = 0.5 cm

2.3 | Quantification of primary production and N_2 fixation

Every month, eight settlement tiles were incubated with surrounding seawater to quantify rates of net primary production (NPP), dark respiration (R) and N_2 fixation under natural water and light conditions. Incubations for NPP and R took place immediately after collection inside separate 1,000 ml gas-tight glass jars that were placed on the seafloor in the direct vicinity to the sampling location. Incubations always started at 10:30 a.m. One additional incubation jar containing only seawater served as a control for planktonic background activity. Another jar was closed with the others and immediately brought to the surface to measure the initial concentration of dissolved oxygen (DO) using an optical DO probe (FDO[®], 925, WTW, temperature and salinity corrected; accuracy: $\pm 0.5\%$ of value). The incubation jars for R were covered with thick aluminium foil to measure O_2 fluxes in the absence of photosynthesis. After 60–70 min incubation time, all glass chambers were transported to the boat, and the concentration of DO was measured in the incubation medium of each chamber. Readings

were recorded after gently stirring the seawater to ensure homogeneous DO distribution. After DO measurements, tiles were left in the jars and transported to the laboratory, where they were kept in an incubator at in situ temperature and light conditions until the beginning of the acetylene (C_2H_2) reduction assay (ARA) starting in the evening of the same day.

Acetylene reduction assay was used to measure the activity of the unspecific N-fixing enzyme nitrogenase (Stewart, Fitzgerald, & Burris, 1967) to approximate N_2 fixation rates (Capone, Taylor, & Taylor, 1977; Shashar, Feldstein, Cohen, & Loya, 1994). For the assay, the eight settlement tiles (i.e. originating from the NPP and R incubations in the field) were transferred to 1 L gas-tight glass chambers for subsequent incubations. In addition, duplicate seawater control chambers were incubated to correct for planktonic N_2 fixation. Each chamber contained 720 ml of seawater collected from the field on the same day and 80 ml of C_2H_2 -enriched seawater. Of the 200 ml air headspace, 10% was replaced with C_2H_2 gas. About 2.5 ml gas samples were collected at the beginning from the gas headspace with a glass syringe and injected into vacuum glass tubes (COVIDEN, Monoject

Blood collection tubes). Subsequently, glass chambers were placed on inductive drive stirrers (500 rpm) in laboratory incubators set to in situ temperature and light conditions. Conditions in the incubators followed a 12 hr light/dark cycle. Additional gas samples were drawn after 12 hr to quantify ethylene (C_2H_4) production during night-time and after 24 hr, for the full 24 hr period respectively. C_2H_4 concentrations in the gas samples were determined using a gas chromatograph with flame ionization detector (Agilent Technologies 7890A) and a GS-GasPro column (Agilent J&W GC Columns, length 30 m, diam. 0.320 mm, Agilent Technologies) with an LOQ = 7.41 ppm.

2.4 | C and N elemental and stable isotope analysis

After the incubation experiments, all tiles were rinsed with freshwater to remove mobile invertebrates, sediments and salt. All sessile organisms were scraped off with razor blades and collected on pre-combusted, pre-weighed tinfoil. Tinfoil packages with content were dried at 40°C for 48 hr and subsequently weighed again to derive the total dry mass of material from each settlement tile. Dried samples were homogenized with an agate mortar and pestle. Subsamples were weighed and transferred into tin capsules for bulk C and N isotope analysis. For $^{13}C_{org}$ analysis, dried subsamples were weighed into silver capsules and decalcified by dripping hydrochloric acid (2N HCl) directly onto the sample. After completion of the decalcification process, samples were re-dried at 40°C for 24 hr. Isotopic ratios for $^{13}C_{org}/^{12}C_{org}$ and $^{15}N/^{14}N$ signatures, and total C_{org} and N contents were measured using an elemental analyser (Thermo Flash EA 1112) coupled to a stable isotope mass spectrometer (IRMS, DELTA V Advantage). C_{org} and total N contents (given in weight %) from the subsamples were scaled back up to the entire tile by multiplying the percentage to the total dry mass of all the material on the tile. Afterwards, values were converted from grams to moles and normalized to the surface area of each tile (i.e. expressed as $\mu\text{mol C}/\text{cm}^2$ and $\mu\text{mol N}/\text{cm}^2$) to achieve standardization with the C and N_2 fixation measurements. C and N stable isotope ratios were expressed by the delta (δ) notation in units per mil (‰) and calculated as: $\delta^{13}C$ or $\delta^{15}N = (R_{\text{sample}}/R_{\text{ref}} - 1) \times 1,000$, where R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample, and R_{ref} is the heavy/light isotope ratio of the reference material ($C/R_{\text{ref}} = 0.01118$, Vienna Pee Dee Belemnite; $N/R_{\text{ref}} = 0.00368$, atmospheric N_2 (Mariotti, 1983). The standard deviation for repeated measurements of laboratory standard material (peptone) was <0.15‰ for N and C respectively. Standard deviations of concentration measurements of replicates of the laboratory standard were <3% of the concentration analysed.

2.5 | Data exploration and analyses

Daytime averages were calculated for seawater temperature and light availability from continuous measurements. NPP and R for each incubated tile were derived from DO concentration differences in the incubation medium calculated by subtracting the start from the end concentration. Results were corrected for DO concentration

differences measured in controls and incubation water volume, and normalized to incubation time and 2D surface area of the settlement tile. GPP was calculated by adding positive R rates to their corresponding NPP rates ($GPP = NPP + |R|$). The biological C fixation was calculated by the amount of oxygen released/taken up during photosynthesis/respiration as a proportion of the volume of carbon dioxide (CO_2) used in that process with a photosynthetic quotient of 1.04 and respiratory quotient of 0.96, as previously established for turf algae and coral rock (Carpenter & Williams, 2007). Hourly rates from each incubation were extrapolated to daily rates (12 hr for NPP, 24 hr for R , and $GPP = NPP + |R|$), resulting in daily NPP, R and GPP rates in $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$. We acknowledge a small overestimation of NPP for the first and last months of the experiment and a small underestimation during the middle part of it by not incorporating the seasonal change of the day length. However, N_2 fixation experiments were run in the laboratory in incubators set to 12:12 hr (dark:light) throughout the study. Thus, N_2 fixation rates cannot be re-calculated. For a better comparability between the two processes (C and N fixation) and the subsequent calculation of the photo-metabolic nitrogen demand (PND; see details further below), we refrain from only adjusting the C fluxes.

We explored the relationships of GPP and N_2 fixation with environmental variables. Details for the model selection process are in the Appendices S1 and S2; Figures S1–S5; Tables S3–S6.

The photosynthetic C assimilation is known to vary with environmental temperature due to the temperature-dependent activation and deactivation of the carbon-fixing enzyme Rubisco (Farquar, Von Caemmerer, & Berry, 1980). We, therefore, used a modified Arrhenius equation (Leuning, 2002) to fit the measured temperature dependence of GPP.

$$GPP(T) = f \times \frac{\left(1 + e^{\left(\frac{S_v T_{\text{ref}} - H_d}{RT_{\text{ref}}}\right)}\right) \times e^{\left(\frac{H_a}{RT} \times \left(1 - \frac{T_{\text{ref}}}{T}\right)\right)}}{1 + e^{\left(\frac{S_v T - H_d}{RT}\right)}}, \quad (1)$$

where H_a represents the activation energy, H_d is the energy for deactivation, S_v is a constant related to entropy, T is the ambient temperature, T_{ref} is a reference temperature of 27°C, R is the gas constant, and f is a scaling factor to convert to units of $\mu\text{mol cm}^{-2} \text{ day}^{-1}$. For parameter values see Table S5.

N_2 fixation rates were calculated based on C_2H_4 concentration differences in the headspace between the start and endpoint of the incubation. The amount of C_2H_4 absorbed in the incubation water was accounted for by Bunsen gas solubility coefficients of 0.072–0.082 of ethylene, depending on the temperature and salinity during the incubations (Breitbarth, Mills, Friedrichs, & LaRoche, 2004). To convert the temporal evolution of C_2H_4 to N_2 fixation rates, a conservative theoretical ratio of 4:1 ($C_2H_4:N_2$) was used, which assumes that 4 mol of C_2H_4 are reduced per 1 mol of N_2 (Mulholland, Bronk, & Capone, 2004; Stal, 1988). As appropriate conversion factor may differ depending on substrate and environmental conditions (Capone, 1988; Capone et al., 2005; Graham, Hamilton, & Campbell, 1980; Larkum, Kennedy, & Muller, 1988), we applied a conservative theoretical ratio to allow direct comparisons to other studies in similar environments

(Bednarz et al., 2018; Cardini et al., 2016). All N_2 fixation rates were corrected for the respective seawater controls and normalized to incubation time and 2D surface area of the settlement tile, and are expressed as $\text{nmol N cm}^{-2} \text{ day}^{-1}$.

We estimated the importance of N_2 fixation derived N to the PND (Bednarz et al., 2018; Cardini et al., 2014; Cardini, van Hoytema, Bednarz, Al-Rshaidat, & Wild, 2018). PND is a function of the atomic C_{org}/N ratio in phototrophs, reflecting the amount of N assimilated relative to C_{org} fixed (e.g. Raven, Handley, & Andrews, 2004). Thus, we calculated PND using the C_{org}/N ratios from the C and N elemental analyses of the scraped off material from settlement tiles, as:

$$\text{PND} = \frac{\text{NCP}}{C_{\text{org}}/N}, \quad (2)$$

with PND = the theoretical amount of N required to supplement fixed carbon from net photosynthesis for the incorporation into biomass (in $\mu\text{mol N cm}^{-2} \text{ day}^{-1}$); NCP = net community production (in $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$); and C_{org}/N = the atomic ratio of organic carbon to nitrogen in the biomass on settlement tiles. As seasonal variations resulted in corresponding variations in C_{org}/N ratios, the PND was calculated for each month and tile individually. By considering the actual biomass elemental properties of the communities on our settlement tiles, we avoided using theoretical C_{org}/N ratios (such as the Redfield ratio of 106 $C_{\text{org}}:16 \text{ N}$) that can vary in time, space and among species (Redfield, 1958). Subsequently, we calculated the contribution (in %) of N_2 fixation derived N to the PND of each tile and timepoint, as:

$$\text{PND met by } N_2 \text{ fix [\%]} = \frac{N_2 \text{ fix}}{\text{PND}} \times 100, \quad (3)$$

where $N_2 \text{ fix}$ is the amount of N fixed (in $\mu\text{mol N cm}^{-2} \text{ day}^{-1}$) by diazotrophy on settlement tiles.

Finally, we explored how much of the C_{org} fixed by NCP was exported/lost from the settlement tiles to the environment. This export can be due to, among other processes, grazing (Fong & Paul, 2011), organic matter exudates (Haas et al., 2010; Quinlan et al., 2018) or by the decay of biomass (Duarte & Cebrián, 1996). As we did not measure these 'losses' directly and as individual processes, we subtracted the absolute gains of C_{org} from one month to the next (i.e. calculated as the differences between C_{org} contents of tiles between two consecutive months) from the theoretical gains of C_{org} that could have been accumulated by NCP in the respective timeframe (i.e. if all C_{org} fixed by NCP would have remained on the settlement tiles). We accounted for the losses of C by respiration using only daytime NCP rates, and subtracting night-time R . The calculation can be summarized as:

$$\text{Export/loss of } C_{\text{org}} = ((\text{NCP} \times 12) - (R \times 12)) - \frac{(C_{\text{org}(b)} - C_{\text{org}(a)})}{d}, \quad (4)$$

with NCP = hourly net community production ($\mu\text{mol C cm}^{-2} \text{ hr}^{-1}$); R = hourly respiration (in $\mu\text{mol C cm}^{-2} \text{ hr}^{-1}$); d = the number of days from one to the following sampling event; and $C_{\text{org}(a)}$ and $C_{\text{org}(b)}$ are the

organic carbon contents of biomass of one month (i.e. a) and the following month (i.e. b) respectively.

Since the activity of the nitrogen fixing enzyme nitrogenase is inhibited by the presence of NO_3^- (Holl & Montoya, 2005; Meeks, Wycoff, Chapman, & Enderlin, 1983), we fit an inverse Michaelis-Menten equation to describe the relation between daily N_2 fixation and NO_3^- concentration (Equation 5),

$$N_2 \text{ fixation} = V_{\text{max}} \times \left(1 - \frac{\text{NO}_3^-}{\text{NO}_3^- + K_i} \right), \quad (5)$$

where V_{max} is the maximal rate of dinitrogen fixation and K_i is the half-saturation concentration for the inhibition by NO_3^- . For parameter values see Table S6.

In addition, we explored whether the cover of benthic functional groups influenced GPP or N_2 fixation rates using multiple regression analysis with GPP or N_2 fixation as the response variables, respectively, and the % cover of all functional groups on settlement tiles individually as predictor variables.

Statistical analyses were conducted in R v3.2.2 (R Development Core Team, 2015) and JMP[®] Pro14 (SAS Institute) statistic software. Models for GPP and N_2 fixation were programmed in Python, with details on packages and algorithms in the Supporting Information.

3 | RESULTS

3.1 | Environmental conditions

All monitored environmental variables exhibited a strong temporal variability (details in Table S2; Figure 1b). Mean monthly water temperature ranged from $24.6 \pm 0.1^\circ\text{C}$ in February to a maximum of $32.2 \pm 0.1^\circ\text{C}$ in August. DIN was lowest in April ($0.29 \pm 0.01 \mu\text{mol N/L}$) and highest in September ($1.35 \pm 0.12 \mu\text{mol N/L}$), while PO_4^{3-} was lowest in January and highest in July (0.02 ± 0.01 and $0.18 \pm 0.02 \mu\text{mol PO}_4^{3-} \text{ L}^{-1}$ respectively).

3.2 | Succession of benthic pioneer communities on settlement tiles

Bare tiles were gradually inhabited by various benthic organisms (Figure 1d). Within 4 weeks, over 50% of the tile surfaces were covered by filamentous turf algae (29%), green and brown crustose algae (18%), as well as CCA (7%). Filamentous turf algae proliferated for the following 2–4 months, covering more than 50% of each tile, while other biotic functional groups did not increase in their occurrence. After 4–6 months from the beginning of the experiment, the availability of bare space on the settlement tiles halved and remained at 20%, while crustose algae and CCA progressively replaced filamentous turf algae. In addition, calcifying invertebrates (1%–5%), such as barnacles, polychaetes, but also coral spats and recruits were observed more frequently. Representative pictures of the settlement tiles 1, 4, 8 and 12 months after deployment are shown in Figure 1c.

3.3 | Biomass accumulation of C and N

Total C_{org} and N accumulated gradually on settlement tiles plateauing after 6–8 months (Figure 2a,b). Total C_{org} increased by 32% monthly, reaching a maximum of $52.4 \pm 8.1 \mu\text{mol C/cm}^2$ in September. Likewise, total N increased by 30% per month, until reaching a maximum of $4.0 \pm 0.7 \mu\text{mol N/cm}^2$ in August. The concomitant increase in elemental C_{org} and N resulted in stable C_{org}/N ratios of biomass (11.6 ± 0.4) throughout the study period. A slight but significant drop of the C_{org}/N ratio to 7.7 ± 0.5 was observed in June (Figure 2c).

3.4 | Primary production and N_2 fixation activity

Within 4–8 weeks after deployment, benthic pioneer communities reached a state in which they exhibited high rates of C and N_2 fixation, with strong temporal variations (Figure 3a,b).

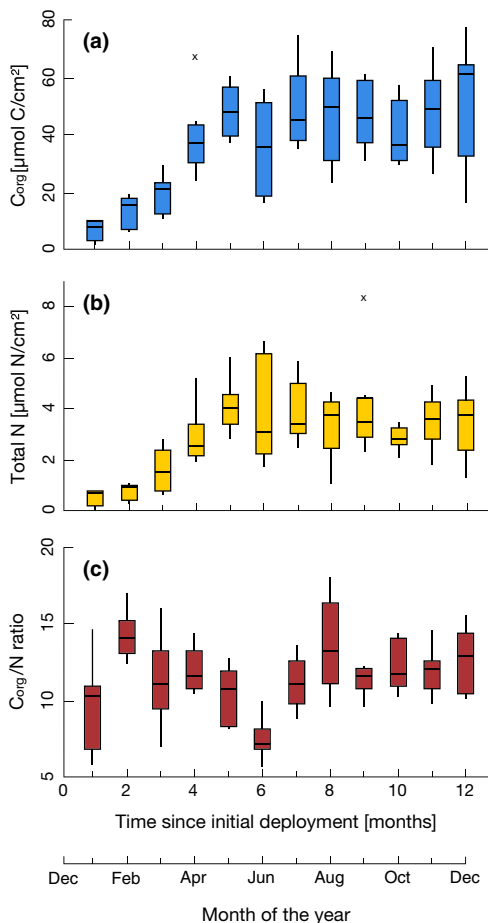


FIGURE 2 Accumulation of organic carbon (a), total nitrogen (b), and the respective C_{org}/N ratio of biomass (c) by benthic pioneer communities over the study period of 12 months. Boxplots show the median (line across a box), quartiles (upper and lower bounds of each box) and extremes (upper and lower whisker). The ends of the whisker are set at $1.5 \times$ interquartile range (IQR) above the third quartile (Q3) and $1.5 \times$ IQR below the first quartile (Q1). Stars in (a) and (b) represent outliers

Gross primary production averaged $17.6 \pm 0.5 \mu\text{mol C cm}^{-2} \text{ day}^{-1}$, with highest rates in June and lowest rates in February (24.7 ± 0.9 and $12.9 \pm 2.1 \mu\text{mol C cm}^{-2} \text{ day}^{-1}$, respectively). Overall, productivity was driven by NPP; daily community R contributed 20%–30% to GPP only, resulting in a stable GPP/ R ratio of 3.9 ± 0.2 throughout the study period. GPP was temperature-dependent and increased with increasing temperature until it reached an optimum temperature at 30.5°C . Above 30.5°C , GPP declined with rising temperature (Figure 4a). Multiple regression analysis revealed a slight correlation between the cover of functional groups on settlement tiles and GPP ($r^2 = 0.15$ and $p = 0.0485$). However, this significant correlation was only attributed to the relative contribution of bare substrates on tiles ($p = 0.0176$), while the per cent cover of all other functional groups were no significant predictors of GPP (Table S7).

N_2 fixation rates were highly variable, ranging from 8 to $54 \text{ nmol N cm}^{-2} \text{ day}^{-1}$ (Figure 3b). NO_3^- concentration had a strong inhibitory effect on the rates of N_2 fixation (Figure 4b) resulting in highest N_2 fixation rates under nutrient-depleted conditions and lowest rates under high NO_3^- concentrations. Multiple regression analysis revealed no association of the cover of functional groups on settlement tiles and N_2 fixation rates ($r^2 = 0.08$; $p = 0.3342$), with none of the functional groups significantly contributing to predicting N_2 fixation (Table S8).

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures of biomass on settlement tiles followed the seasonal patterns of GPP and N_2 fixation respectively (Figure 3c,d). $\delta^{13}\text{C}$ ranged from $-14.08 \pm 0.37\text{‰}$ to $-9.04 \pm 0.36\text{‰}$, being significantly enriched during summer. Linear regression indicated a positive relationship between $\delta^{13}\text{C}$ and GPP ($r^2 = 0.22$, $p = 0.008$). $\delta^{15}\text{N}$ of biomass ranged from $-0.13 \pm 0.09\text{‰}$ to $3.14 \pm 0.23\text{‰}$ and correlated negatively with N_2 fixation ($r^2 = 0.34$, $p < 0.001$) and positively with DIN ($r^2 = 0.23$, $p < 0.001$). $\delta^{15}\text{N}$ was significantly depleted ($-0.12 \pm 0.11\text{‰}$) in April and May, when DIN concentrations were lowest, and N_2 fixation was highest.

3.5 | Estimating regeneration rates of carbon from benthic pioneer communities

The export of C_{org} (C_{org} produced, but not consumed or incorporated by the community itself) from the settlement tiles was derived by subtracting the C_{org} acquisition rates (elemental analysis) by the C fixation rates (incubations) by primary production. On an average, $10.2 \pm 0.5 \mu\text{mol C cm}^{-2} \text{ day}^{-1}$, comprising almost 60% of the photosynthetically fixed C, was not incorporated into biomass of the communities, implying that it was released into the seawater or consumed by higher trophic levels outside these pioneer communities. The rates of this export/loss to outside of the pioneer communities fluctuated between months (Figure 5). Interestingly, however, already at the first measurement 4 weeks after deployment, 57% ($8.0 \pm 0.9 \mu\text{mol C cm}^{-2} \text{ day}^{-1}$) of the fixed C was exported/lost into the environment, hence, only limited biomass accumulation took place even during the initial settlement phase.

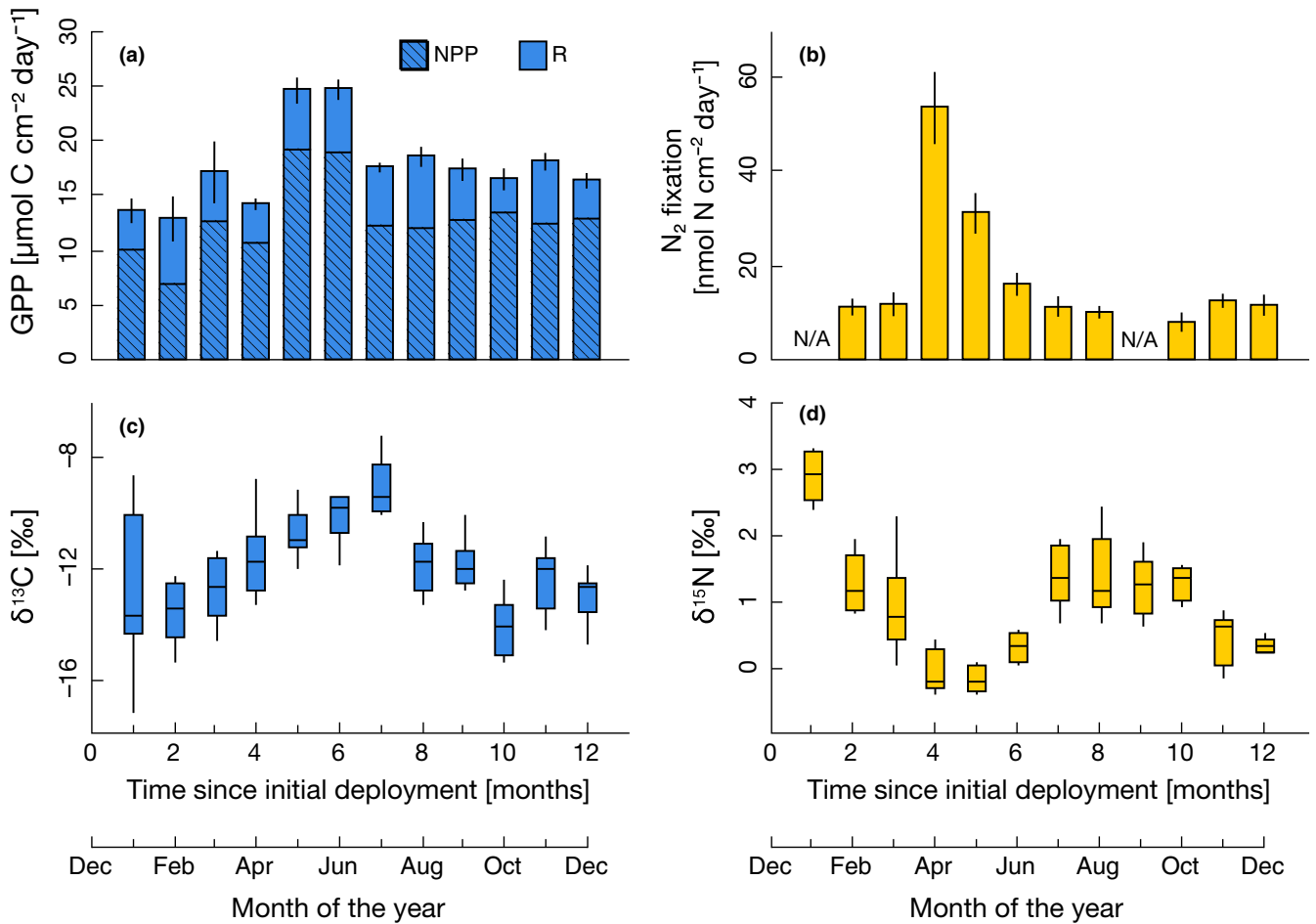


FIGURE 3 Monthly rates of gross primary production (GPP; a) and dinitrogen fixation (b) of benthic pioneer communities, along with their respective carbon (c) and nitrogen (d) stable isotope signature of biomass. GPP is divided into net primary production (NPP) and respiration (R), where $NPP + |R| = GPP$. Dinitrogen (N_2) fixation rates were indirectly derived from acetylene reduction assays. Bar charts show the mean \pm SE. Boxplots in (c) and (d) show the median (line across a box), quartiles (upper and lower bounds of each box) and extremes (upper and lower whisker). The ends of the whisker are set at $1.5 \times$ interquartile range (IQR) above the third quartile (Q3) and $1.5 \times$ IQR below the first quartile (Q1). N/A, no data available on these dates [Correction added on 8 August 2020, after first online publication: unit “‰” added to y-axis labels in Figures 3c and 3d.]

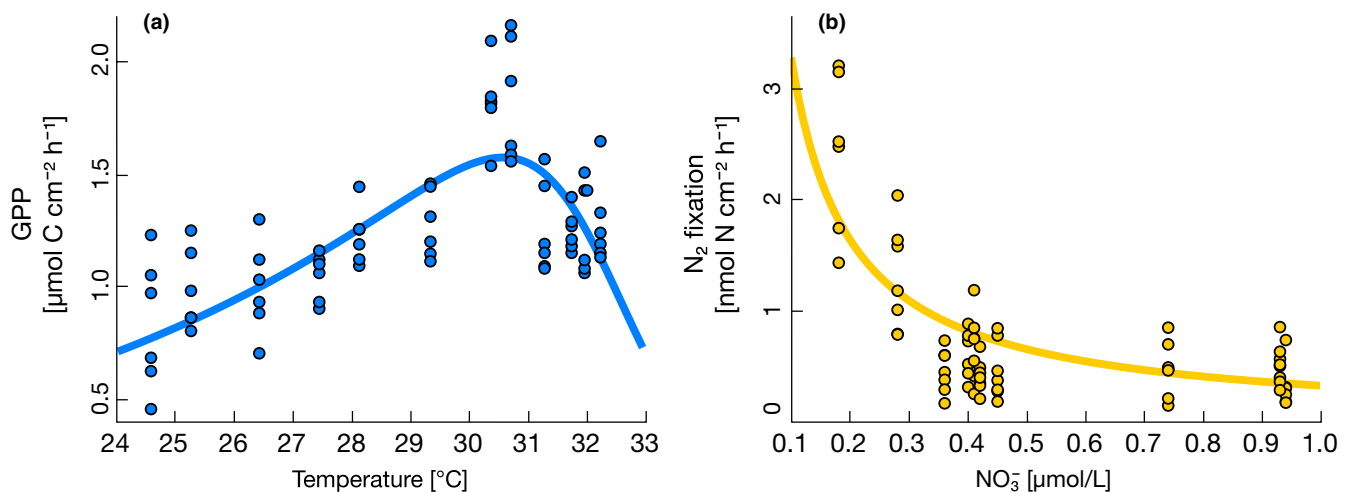


FIGURE 4 Nonlinear relationships of gross primary production (GPP) with temperature (a), and dinitrogen fixation with environmental nitrate concentrations (b). The temperature dependence of GPP is simulated with a modified Arrhenius curve (Equation 1) for the activation and inactivation of the carbon assimilating enzyme Rubisco (Farquar et al., 1980; Leuning, 2002). The nitrate dependence of N_2 fixation is simulated with an inverse Michaelis–Menten equation (Equation 5)

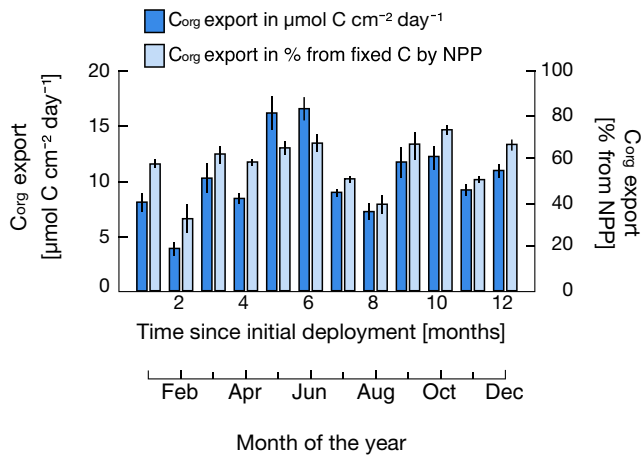


FIGURE 5 Export of organic carbon from pioneer communities. The export was calculated by subtracting the organic carbon (C_{org}) acquisition rates (i.e. the differences between C_{org} contents between two consecutive months) from the maximum amount of carbon that could have been accumulated by primary production in the respective time frame. Losses of carbon by respiration were accounted for by using daytime net primary production rates only, and subtracting night-time respiration. Bar charts show the mean \pm SE

4 | DISCUSSION

The data presented here demonstrate that benthic pioneer communities play a critical role as a trophodynamic component of coral reefs. Organisms establishing on bare substrates can produce considerable quantities of C_{org} and N within only weeks after the initial settlement. While the biomass accumulation of pioneer communities is limited, the export of organic material to the ecosystem is substantial and consistent over time, despite significant variations in the rates of assimilation that are influenced by environmental conditions. Ultimately, pioneer communities may serve as an important source of C and N through which the wider coral reef ecosystem may acquire (limiting) elements. Under conditions where pioneer communities colonize available space previously occupied by corals (e.g. after mass coral mortality following prolonged bleaching events), C and N by pioneer communities may help during ecosystem reorganization and recovery.

4.1 | High rates of primary productivity and N_2 fixation in benthic pioneer communities

Pioneering functional groups on settlement tiles were, as commonly observed, mainly short (<2 mm) filamentous turf algae, crustose algae and CCA (e.g. Adjeroud et al., 2009; Jessen et al., 2014; Mellin, Aaron Macneil, Cheal, Emslie, & Julian Caley, 2016). Usually, these consortia of epibenthic algae belong to the most productive functional groups of benthic producers (Hatcher, 1988). Already 4 weeks after the introduction of bare substrates, epilithic autotrophs on settlement tiles displayed high rates of GPP. Rates of GPP by pioneer communities were slightly

higher than those of common coral reef framework substrates, such as 'biogenic coral rock' (i.e. 13–25 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in this study, compared to 4–9 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in van Hoytema et al., 2016) and CCA (i.e. 515 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008), and lower than GPP rates reported for dense turf algae (i.e. >30 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in Adey & Goertemiller, 1987 and Rix et al., 2015). The cover of individual functional groups (i.e. the 'makeup' of the community) was not a significant predictor of GPP, further demonstrating the taxonomic heterogeneity of pioneer communities on settlement tiles. Importantly, GPP of pioneer communities was similar to community-wide budgets for coral reefs in the Northern Red Sea (i.e. 13–25 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in this study, compared to 22–26 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in Cardini et al., 2016, or 20–30 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$ in van Hoytema et al., 2016) and elsewhere (Eidens et al., 2014; Hatcher, 1988).

N_2 fixation of pioneer communities slightly exceeded rates of coral-dominated communities shortly after colonization (Cardini et al., 2016; Shashar, Cohen, Loya, & Sar, 1994). Thus, our study corroborates the importance of pioneer communities for coral reef nitrogen budgets and highlights the ubiquity of diazotrophs in benthic reef environments (Cardini et al., 2014).

4.2 | Temporal variability and contribution of N_2 fixation to primary productivity

Both primary productivity and N_2 fixation displayed a temporal variability in relation to changing environmental conditions.

The observed fluctuations in primary production throughout the year were, primarily, attributed to temperature (Figure 4a) rather than the successional stage or 'makeup' of the pioneer communities on settlement tiles (Table S7) or other environmental variables (Figure S1). As a temperature-sensitive process (Yamori, Hikosaka, & Way, 2014), primary production followed a typical combination of two Arrhenius curves (Equation 1) for the activation and deactivation of the carbon assimilating processes (Farquar et al., 1980; Leuning, 2002) that exhibits a maximum at 30.5°C. While primary production maxima are typically observed during summer at many reef locations world-wide, photosynthesis was highest in spring (i.e. May), indicating that summer temperatures can exceed the metabolic optima for some reef organisms in the central Red Sea (Roik, Roder, Röthig, & Voolstra, 2016; Sawall et al., 2015). Temperature-coded scatterplots of productivity versus light availability (Figure S3) helped to identify the dominance of the effect of temperature over that of light on photosynthesis in the current experiment (details in Appendix S1). Interestingly, high rates of photosynthesis were sustained throughout the study period, despite low inorganic nutrient availability during some months. This suggests that either primary production was not N limited or that additional nutrient sources contributed to supporting photosynthesis.

Concomitantly, N_2 fixation rates were mainly influenced by seawater NO_3^- concentrations (Figure 4b). This NO_3^- dependence

closely fitted a classic saturation curve for the NO_3^- -inhibition of the N-fixing enzyme nitrogenase (Holl & Montoya, 2005; Meeks et al., 1983), which corresponds to the inverse of a Michaelis–Menten model (Equation 5). Despite the higher energetic costs of N_2 fixation compared to N assimilation (Gallon, 2001), N_2 fixation was likely a seasonally relevant process to compensate the scarcity of N. We estimated that N_2 fixation supplied up to 13% of the PND during nutrient-depleted conditions, as was previously indicated by a positive relationship between the productivity and N_2 fixation for both turf algae and coral rock (Rix et al., 2015) and other reef substrates (Bednarz et al., 2015; Cardini et al., 2015; Tilstra et al., 2017). At the same time, N_2 fixation still occurred even when NO_3^- concentrations were high, suggesting that productivity remained N limited throughout the year. The higher rates of N_2 fixation were also reflected in a depleted $\delta^{15}\text{N}$ isotopic signature of biomass that approximated atmospheric N_2 ($\sim 0\%$) during periods of high N_2 fixation activity (Ryabenko, 2013; Stuyck, 1902). As an important source of N supply for photosynthesis, N_2 fixation likely also supported the stable $\text{C}_{\text{org}}/\text{N}$ ratios of biomass throughout the year.

4.3 | Accumulation and regeneration of C and N by pioneer communities

We observed low rates of biomass accumulation, despite high rates of NPP and little community-wide R . The relative constancy of biomass (i.e. limited net accumulation) after the first succession of pioneer communities suggests a tight coupling between production and loss on settlement tiles. Thereby, the export/loss of C_{org} to the environment from the settlement tiles comprised on average 60% (at times >80%) of the photosynthetically fixed C that was not lost through metabolic activity by the community (R by algae, heterotrophs and decomposers). In absolute numbers, C_{org} exports from pioneer communities (ranging from 2–15 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$) were higher compared to those of corals from the Northern Red Sea (2.5 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$, annual mean; Naumann et al., 2012) or the Pacific Ocean (5 $\mu\text{mol C cm}^{-2} \text{ day}^{-1}$, Hata, Kudo, Yamano, Kurano, & Kayanne, 2002). Particularly grazing keeps epilithic algae in a cropped, early successional, and highly productive state in which they contribute most to the efficient transfer of energy to higher trophic levels (Fong & Paul, 2011). Concordantly, a high standing biomass of herbivorous fish (>150 g/m^2) in the studied reef likely maintained a substantial top-down control over organisms settling on bare substrates (Roth et al., 2018). In addition, C and N from benthic autotrophs are also released as dissolved organic matter exudates (Haas et al., 2010; Quinlan et al., 2018) or by the decay of biomass (Duarte & Cebrián, 1996), constituting energy and nutrient sources for other trophic levels.

4.4 | Ecological implications

Based on the processes outlined above, pioneer communities demonstrate features that indicate their critical role as a trophodynamic component of coral reefs, a role that is substantially enhanced after

extensive coral mortality. These features are as follows: (a) pioneer communities are naturally abundant on coral reefs, even in coral-dominated states. Following coral mortality, pioneer communities develop rapidly, often colonizing all available space previously occupied by corals; (b) pioneer communities show high assimilation rates of C and N. These rates are in the same order of magnitude as observed in coral-dominated communities. Likewise, there is a strong coupling between the fixation of C and N, as indicated by the seasonal changes and (c) there is a high trophodynamic connectivity with higher trophic levels. A large fraction of the accumulated C and N may be exported to higher trophic levels in the ecosystem via the release of organic matter or grazing, normally similar or even exceeding that of coral-dominated communities.

Thus, independent of whether pioneer communities coexist within a healthy reef (e.g. after loss of individual coral colonies) or increase in abundance after widespread coral mortality events, the high associated turnover of organic material from pioneer communities may temporarily serve as an alternative and direct source of C and N to compensate for the loss of functions previously provided by corals. While these pioneer communities cannot substitute important ecosystem functions that characterize scleractinian corals as reef ecosystem engineers (Wild et al., 2011), our data highlight that pioneer communities play an important role in the functioning of coral reef ecosystems via maintaining the nutrient provisioning and regeneration, which, in turn, may trigger a cascade of subsequent processes. First, by providing an alternative source of C and nutrients following coral mortality, pioneer communities aid sustaining higher trophic level consumers and prevent a complete change in the food web architecture. Particulate or dissolved organic compounds released from pioneer communities may be consumed directly by grazers (Crossman, Choat, Clements, Hardy, & McConochie, 2001), plankton (Nakajima et al., 2017) or are quickly remineralized to inorganic forms via detrital and microbial pathways (Haas et al., 2013), helping to transfer energy and nutrients through multiple trophic levels. Fish directly graze on pioneer communities, thereby transferring the acquired energy efficiently to higher trophic levels (Bellwood et al., 2018). The extensive turnover can, thereby, sustain a larger abundance of consumers than would be predicted by their biomass (Russ, 2003).

Second, pioneer communities serve as trophic conduits in a much more direct (and efficient) way than coral production, which, locally, may attract herbivorous fish (Francini-Filho, Ferreira, Coni, De Moura, & Kaufman, 2010). In turn, a high grazing activity ensures the availability of suitable settlement substrates for pioneer communities that include CCA and coral larvae, and the consumption of organic material promotes the remobilization of energy and nutrients within and across the borders of the ecosystem via excretion and egestion (Allgeier et al., 2017; Allgeier, Layman, Mumby, & Rosemond, 2014; Burkepille et al., 2013). Lastly, in cases in which coral mortality is patchy and coexists with bleaching, the increased availability of nutrients and heterotrophic sources may support the recovery of bleached corals and the recruitment of new coral colonies, as it may enhance coral thermo-tolerance, growth and calcification

(Anthony, Hoogenboom, Maynard, Grottoli, & Middlebrook, 2009; Cox, 2007; Ferrier-Pagès, Witting, Tambutté, & Sebens, 2003; Fox et al., 2018; Hanafy, Amer, Habib, Rouphael, & Baird, 2010).

However, the successional development of benthic pioneer communities, and their impact on the C and N dynamics herein, directly depends on the initial habitat characteristics (Roth et al., 2018), rates of grazing (top-down control) and nutrient availability (bottom-up control) within the reef (e.g. Burkepile & Hay, 2006; Smith, Hunter, & Smith, 2010). Under conditions of limited habitat complexity, low grazing pressure or nutrient pollution, pioneer communities may shift to a dominance of dense turf and macroalgae that are considered less palatable, resistant to grazing, and/or allelopathic (Hixon & Brostoff, 1996; Smith et al., 2010). Counterintuitively, taller and denser algae are less productive, transfer less energy through the food web, can trap more sediment (Miller & Barimo, 2001), leak more labile dissolved organic carbon (DOC; Haas et al., 2013) and promote higher microbial loads (Haas et al., 2016)—all of which could negatively impact the trajectories of recovery within the reef system.

Early pioneer communities may, thus, only assist in the recovery of coral reefs as long as a healthy consumer structure is present and the water quality remains adequate (Barkley et al., 2018). Management and conservation efforts should, therefore, aim at preserving the structural integrity of a reef, reduce the fishing pressure on important functional groups (e.g. herbivores), and limit anthropogenic nutrient inputs. Under these conditions, pioneer communities may support the initial energy and nutrient demands of coral reef communities following coral mortality and large-scale disturbance events.

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AUTHORS' CONTRIBUTIONS

F.R., C.W., N.R. and S.C. conceptualized and designed research; F.R., D.B.K., F.S. and T.T. performed research; F.R., S.H., N.R., B.K. and U.S. analysed data; C.R.V. and B.H.J. contributed to research materials, logistics and to the draft manuscript; F.R. wrote original draft of the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gb5mkkwms> (Roth et al., 2020).

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REFERENCES

- Adey, W. H., & Goertemiller, T. (1987). Coral reef algal turfs: Master producers in nutrient poor seas. *Phycologia*, 26, 374–386. <https://doi.org/10.2216/i0031-8884-26-3-374.1>
- Adjeroud, M., Michonneau, F., Edmunds, P. J., Chancerelle, Y., de Loma, T. L., Penin, L., ... Galzin, R. (2009). Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs*, 28, 775–780. <https://doi.org/10.1007/s00338-009-0515-7>
- Allgeier, J. E., Burkepile, D. E., & Layman, C. A. (2017). Animal pee in the sea: Consumer-mediated nutrient dynamics in the world's changing oceans. *Global Change Biology*, 23(6), 2166–2178. <https://doi.org/10.1111/gcb.13625>
- Allgeier, J. E., Layman, C. A., Mumby, P. J., & Rosemond, A. D. (2014). Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology*, 20, 2459–2472. <https://doi.org/10.1111/gcb.12566>
- Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G., & Middlebrook, R. (2009). Energetics approach to predicting mortality risk from environmental stress: A case study of coral bleaching. *Functional Ecology*, 23, 539–550. <https://doi.org/10.1111/j.1365-2435.2008.01531.x>
- Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., & Hoegh-Guldberg, O. (2008). Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17442–17446. <https://doi.org/10.1073/pnas.0804478105>
- Barkley, H. C., Cohen, A. L., Mollica, N. R., Brainard, R. E., Rivera, H. E., DeCarlo, T. M., ... Luu, V. H. (2018). Repeat bleaching of a central Pacific coral reef over the past six decades (1960–2016). *Communications Biology*, 1, 1–10. <https://doi.org/10.1038/s42003-018-0183-7>
- Bednarz, V. N., Naumann, M. S., Cardini, U., Van Hoytema, N., Rix, L., Al-Rshaidat, M. M. D., & Wild, C. (2018). Contrasting seasonal responses in dinitrogen fixation between shallow and deep-water colonies of the model coral *Stylophora pistillata* in the northern Red Sea. *PLoS ONE*, 13, 1–13. <https://doi.org/10.1371/journal.pone.0199022>
- Bednarz, V. V. N., Van Hoytema, N., Cardini, U., Naumann, M. S. M., Al-Rshaidat, M. M. D. M., & Wild, C. (2015). Dinitrogen fixation and primary productivity by carbonate and silicate reef sand communities of the Northern Red Sea. *Marine Ecology Progress Series*, 527, 47–57. <https://doi.org/10.3354/meps11224>
- Bellwood, D. R., Tebbett, S. B., Bellwood, O., Mihalitsis, M., Morais, R. A., Streit, R. P., & Fulton, C. J. (2018). The role of the reef flat in coral reef trophodynamics: Past, present, and future. *Ecology and Evolution*, 8, 4108–4119. <https://doi.org/10.1002/ece3.3967>
- Breitbarth, E., Mills, M. M., Friedrichs, G., & LaRoche, J. (2004). The Bunsen gas solubility coefficient of ethylene as a function of temperature and salinity and its importance for nitrogen fixation assays. *Limnology and Oceanography: Methods*, 2, 282–288.
- Burkepile, D. E., Allgeier, J. E., Shantz, A. A., Pritchard, C. E., Lemoine, N. P., Bhatti, L. H., & Layman, C. A. (2013). Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports*, 3, 19–21. <https://doi.org/10.1038/srep01493>

- Burkpile, D. E., & Hay, M. E. (2006). Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. *Ecology*, *87*, 3128–3139.
- Burt, J., Bartholomew, A., Bauman, A., Saif, A., & Sale, P. F. (2009). Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *Journal of Experimental Marine Biology and Ecology*, *373*, 72–78. <https://doi.org/10.1016/j.jembe.2009.03.009>
- Capone, D. G. (1988). Benthic nitrogen fixation. In T. H. Blackburn & J. Sorensen (Eds.), *Nitrogen cycling in coastal marine environments* (pp. 85–123). Published on behalf of the Scientific Committee on Problems of the Environment (SCOPE) of the International Council of Scientific Unions (ICSU). Hoboken, NJ: Wiley. ISBN: 0471914045.
- Capone, D. G., Burns, J. A., Montoya, J. P., Subramaniam, A., Mahaffey, C., Gunderson, T., ... Carpenter, E. J. (2005). Nitrogen fixation by *Trichodesmium* spp.: An important source of new nitrogen to the tropical and subtropical North Atlantic Ocean. *Global Biogeochemical Cycles*, *19*, 1–17.
- Capone, D. G., Taylor, D. L., & Taylor, B. F. (1977). Nitrogen fixation (acetylene reduction) associated with macroalgae in a coral-reef community in the Bahamas. *Marine Biology*, *40*, 29–32. <https://doi.org/10.1007/BF00390624>
- Cardini, U., Bednarz, V. N., Foster, R. A., & Wild, C. (2014). Benthic N₂ fixation in coral reefs and the potential effects of human-induced environmental change. *Ecology and Evolution*, *4*, 1706–1727.
- Cardini, U., Bednarz, V. N., Naumann, M. S., van Hoytema, N., Rix, L., Foster, R. A., ... Wild, C. (2015). Functional significance of dinitrogen fixation in sustaining coral productivity under oligotrophic conditions. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20152257. <https://doi.org/10.1098/rspb.2015.2257>
- Cardini, U., Bednarz, V. N., van Hoytema, N., Rovere, A., Naumann, M. S., Al-Rshaidat, M. M. D., & Wild, C. (2016). Budget of primary production and dinitrogen fixation in a highly seasonal Red Sea coral reef. *Ecosystems*, *19*, 771–785. <https://doi.org/10.1007/s10021-016-9966-1>
- Cardini, U., van Hoytema, N., Bednarz, V. N., Al-Rshaidat, M. M. D., & Wild, C. (2018). N₂ fixation and primary productivity in a Red Sea *Halophila stipulacea* meadow exposed to seasonality. *Limnology and Oceanography*, *63*, 786–798.
- Carpenter, R. C., & Williams, S. L. (2007). Mass transfer limitation of photosynthesis of coral reef algal turfs. *Marine Biology*, *151*, 435–450. <https://doi.org/10.1007/s00227-006-0465-3>
- Coffroth, M. A. (1990). Mucous sheet formation on poritid corals: An evaluation of coral mucus as a nutrient source on reefs. *Marine Biology*, *105*, 39–49. <https://doi.org/10.1007/BF01344269>
- Cox, E. F. (2007). Continuation of sexual reproduction in *Montipora capitata* following bleaching. *Coral Reefs*, *26*, 721–724. <https://doi.org/10.1007/s00338-007-0251-9>
- Crossman, D. J., Choat, H. J., Clements, K. D., Hardy, T., & McConochie, J. (2001). Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography*, *46*, 1596–1605. <https://doi.org/10.4319/lo.2001.46.7.1596>
- Davey, M., Holmes, G., & Johnstone, R. (2008). High rates of nitrogen fixation (acetylene reduction) on coral skeletons following bleaching mortality. *Coral Reefs*, *27*, 227–236. <https://doi.org/10.1007/s00338-007-0316-9>
- De Goeij, J. M., Van Oevelen, D., Vermeij, M. J. A., Osinga, R., Middelburg, J. J., De Goeij, A. F. P. M., & Admiraal, W. (2013). Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science*, *342*, 108–110. <https://doi.org/10.1126/science.1241981>
- Duarte, C. M., & Cebrián, J. (1996). The fate of marine autotrophic production. *Limnology and Oceanography*, *41*, 1758–1766. <https://doi.org/10.4319/lo.1996.41.8.1758>
- Eidens, C., Bayraktarov, E., Hauffe, T., Pizarro, V., Wilke, T., & Wild, C. (2014). Benthic primary production in an upwelling-influenced coral reef, Colombian Caribbean. *PeerJ*, *2*, e554.
- Farquar, G. D., Von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 species. *Planta*, *149*, 78–90.
- Ferrier-Pagès, C., Witting, J., Tambutté, E., & Sebens, K. P. (2003). Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. *Coral Reefs*, *22*, 229–240. <https://doi.org/10.1007/s00338-003-0312-7>
- Fong, P., & Paul, V. J. (2011). Coral reef algae. In Z. Dubinsky & N. Stambler (Eds.), *Book: Coral reefs: An ecosystem in transition* (pp. 241–272). Dordrecht, The Netherlands: Springer. <https://doi.org/10.1007/978-94-007-0114-4>
- Fox, M. D., Williams, G. J., Johnson, M. D., Radice, V. Z., Zgliczynski, B. J., Kelly, E. L. A., ... Smith, J. E. (2018). Gradients in primary production predict trophic strategies of mixotrophic corals across spatial scales. *Current Biology*, *28*, 3355–3363.e4. <https://doi.org/10.1016/j.cub.2018.08.057>
- Francini-Filho, R. B., Ferreira, C. M., Coni, E. O. C., De Moura, R. L., & Kaufman, L. (2010). Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: Influence of resource availability and interference competition. *Journal of the Marine Biological Association of the United Kingdom*, *90*, 481–492. <https://doi.org/10.1017/S0025315409991147>
- Frost, N. J., Burrows, M. T., Johnson, M. P., Hanley, M. E., & Hawkins, S. J. (2005). Measuring surface complexity in ecological studies. *Limnology and Oceanography: Methods*, *3*, 203–210.
- Gallon, J. R. (2001). N₂ fixation in phototrophs: Adaptation to a specialized way of life. *Plant and Soil*, *230*, 39–48.
- Graham, B. M., Hamilton, R. D., & Campbell, N. E. R. (1980). Comparison of the nitrogen-15 uptake and acetylene reduction methods for estimating the rates of nitrogen fixation by freshwater blue-green algae. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 488–493. <https://doi.org/10.1139/f80-063>
- Haas, A. F., Fairoz, M. F. M., Kelly, L. W., Nelson, C. E., Dinsdale, E. A., Edwards, R. A., ... Rohwer, F. (2016). Global microbialization of coral reefs. *Nature Microbiology*, *1*(6), 16042. <https://doi.org/10.1038/nmicrobiol.2016.42>
- Haas, A. F., Naumann, M. S., Struck, U., Mayr, C., el-Zibdah, M., & Wild, C. (2010). Organic matter release by coral reef associated benthic algae in the Northern Red Sea. *Journal of Experimental Marine Biology and Ecology*, *389*, 53–60. <https://doi.org/10.1016/j.jembe.2010.03.018>
- Haas, A. F., Nelson, C. E., Rohwer, F., Wegley-Kelly, L., Quistad, S. D., Carlson, C. A., ... Smith, J. E. (2013). Influence of coral and algal exudates on microbially mediated reef metabolism. *PeerJ*, *1*, e108. <https://doi.org/10.7717/peerj.108>
- Hanafy, M. H., Aamer, M. A., Habib, M., Roupael, A. B., & Baird, A. H. (2010). Synchronous reproduction of corals in the Red Sea. *Coral Reefs*, *29*, 119–124. <https://doi.org/10.1007/s00338-009-0552-2>
- Hata, H., Kudo, S., Yamano, H., Kurano, N., & Kayanne, H. (2002). Organic carbon flux in Shiraho coral reef (Ishigaki Island, Japan). *Marine Ecology Progress Series*, *232*, 129–140. <https://doi.org/10.3354/meps232129>
- Hatcher, B. G. (1988). Coral reef primary productivity: A beggar's banquet. *Trends in Ecology & Evolution*, *3*, 106–111. [https://doi.org/10.1016/0169-5347\(88\)90117-6](https://doi.org/10.1016/0169-5347(88)90117-6)
- Hatcher, B. G. (1990). Coral-reef primary productivity – A hierarchy of pattern and process. *Trends in Ecology & Evolution*, *5*, 149–155. [https://doi.org/10.1016/0169-5347\(90\)90221-X](https://doi.org/10.1016/0169-5347(90)90221-X)
- Hill, J., & Wilkinson, C. (2004). *Methods for ecological monitoring of coral reefs*. The Australian Institute of Marine Science, Townsville. Report from <https://www.cbd.int/doc/case-studies/tttc/tttc-00197-en.pdf>
- Hixon, M. A., & Brostoff, W. N. (1996). Succession and herbivory: Effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs*, *66*, 67–90. <https://doi.org/10.2307/2963481>
- Holl, C. M., & Montoya, J. P. (2005). Interactions between nitrate uptake and nitrogen fixation in continuous cultures of the marine diazotroph *Trichodesmium* (Cyanobacteria). *Journal of Phycology*, *41*, 1178–1183.

- Holmes, G., & Johnstone, R. W. (2010). The role of coral mortality in nitrogen dynamics on coral reefs. *Journal of Experimental Marine Biology and Ecology*, 387, 1–8. <https://doi.org/10.1016/j.jembe.2010.03.006>
- Holmes, R. M., Aminot, A., Kerouel, R., Hooker, B. A., & Peterson, B. J. (1999). A simple and precise method for measuring ammonium in marine and freshwater ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 1801–1808. <https://doi.org/10.1139/f99-128>
- Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., ... Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 359, 80–83. <https://doi.org/10.1126/science.aan8048>
- Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., ... Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, 543, 373–377. <https://doi.org/10.1038/nature21707>
- Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., ... Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, 556, 492–496. <https://doi.org/10.1038/s41586-018-0041-2>
- Humanes, A., & Bastidas, C. (2015). In situ settlement rates and early survivorship of hard corals: A good year for a Caribbean reef. *Marine Ecology Progress Series*, 539, 139–151. <https://doi.org/10.3354/meps11501>
- Jessen, C., Voolstra, C. R., & Wild, C. (2014). In situ effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. *PeerJ*, 2, e339.
- Kennedy, E., Ordonez, A., Lewis, B., & Diaz-Pulido, G. (2017). Comparison of recruitment tile materials for monitoring coralline algae response to changing climate. *Marine Ecology Progress Series*, 569, 129–144.
- Larkum, A. W. D., Kennedy, I. R., & Muller, W. J. (1988). Nitrogen fixation on a coral reef. *Marine Biology*, 98, 143–155. <https://doi.org/10.1007/BF00392669>
- Leuning, R. (2002). Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell and Environment*, 25, 1205–1210. <https://doi.org/10.1046/j.1365-3040.2002.00898.x>
- Mallela, J., Milne, B. C., & Martinez-Escobar, D. (2017). A comparison of epibenthic reef communities settling on commonly used experimental substrates: PVC versus ceramic tiles. *Journal of Experimental Marine Biology and Ecology*, 486, 290–295. <https://doi.org/10.1016/j.jembe.2016.10.028>
- Mariotti, A. (1983). Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature*, 303, 685–687. <https://doi.org/10.1038/303685a0>
- McClanahan, T. R., Darling, E. S., Maina, J. M., Muthiga, N. A., D'agata, S., Jupiter, S. D., ... Leblond, J. (2019). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. *Nature Climate Change*, 9, 845–851. <https://doi.org/10.1038/s41558-019-0576-8>
- Meeks, J. C., Wycoff, K. L., Chapman, J. S., & Enderlin, C. S. (1983). Regulation of expression of nitrate and dinitrogen assimilation by anabaena species. *Applied and Environmental Microbiology*, 45, 1351–1359. <https://doi.org/10.1128/AEM.45.4.1351-1359.1983>
- Mellin, C., Aaron Macneil, M., Cheal, A. J., Emslie, M. J., & Julian Caley, M. (2016). Marine protected areas increase resilience among coral reef communities. *Ecology Letters*, 19, 629–637. <https://doi.org/10.1111/ele.12598>
- Miller, M. W., & Barimo, J. (2001). Assessment of juvenile coral populations at two reef restoration sites in the Florida Keys National Marine Sanctuary: Indicators of success? *Bulletin of Marine Science*, 69, 395–405.
- Morillo-Velarde, P. S., 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. *Scientific Reports*, 8, 1–12. <https://doi.org/10.1038/s41598-018-22463-x>
- Mulholland, M., Bronk, D., & Capone, D. (2004). Dinitrogen fixation and release of ammonium and dissolved organic nitrogen by *Trichodesmium* IMS101. *Aquatic Microbial Ecology*, 37, 85–94. <https://doi.org/10.3354/ame037085>
- Muscantine, L., & Porter, J. W. (1977). Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. *BioScience*, 27, 454–460. <https://doi.org/10.2307/1297526>
- Nakajima, R., Yamazaki, H., Lewis, L. S., Khen, A., Smith, J. E., Nakatomi, N., & Kurihara, H. (2017). Planktonic trophic structure in a coral reef ecosystem – Grazing versus microbial food webs and the production of mesozooplankton. *Progress in Oceanography*, 156, 104–120. <https://doi.org/10.1016/j.pocean.2017.06.007>
- Naumann, M. S., Richter, C., Mott, C., el-Zibdah, M., Manasrah, R., & Wild, C. (2012). Budget of coral-derived organic carbon in a fringing coral reef of the Gulf of Aqaba, Red Sea. *Journal of Marine Systems*, 105–108, 20–29. <https://doi.org/10.1016/j.jmarsys.2012.05.007>
- Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series*, 376, 293–306. <https://doi.org/10.3354/meps07815>
- O'Neil, J. M., & Capone, D. G. (2008). *Nitrogen in the marine environment* [D. G. Capone, D. A. Bronk, M. R. Mulholland, & E. J. Carpenter (Eds.)]. San Diego, CA: Elsevier, 2nd ed., pp. 949–989. ISBN: 978-0-12-372522-6. <https://doi.org/10.1016/B978-0-12-372522-6.00021-9>
- Odum, H. T., & Odum, E. P. (1955). Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs*, 25(3), 291–320. <https://doi.org/10.2307/1943285>
- Penin, L., Michonneau, F., Baird, A. H., Connolly, S. R., Pratchett, M. S., Kayal, M., & Adjeroud, M. (2010). Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology Progress Series*, 408, 55–64. <https://doi.org/10.3354/meps08554>
- Quinlan, Z. A., Remple, K., Fox, M. D., Silbiger, N. J., Oliver, T. A., Putnam, H. M., ... Nelson, C. E. (2018). Fluorescent organic exudates of corals and algae in tropical reefs are compositionally distinct and increase with nutrient enrichment. *Limnology and Oceanography Letters*, 3, 331–340. <https://doi.org/10.1002/lo2.10074>
- R Development Core Team. (2015). R. Vienna, Austria: University of Vienna.
- Raven, J. A., Handley, L. L., & Andrews, M. (2004). Global aspects of C/N interactions determining plant-environment interactions. *Journal of Experimental Botany*, 55, 11–25. <https://doi.org/10.1093/jxb/erh011>
- Redfield, A. C. (1958). The biological control of chemical factors in the environment. *American Scientist*, 46, 230A–221.
- Rix, L., Bednarz, V. N., Cardini, U., Van Hoytema, N., Al-Horani, F. A., Wild, C., & Naumann, M. S. (2015). Seasonality in dinitrogen fixation and primary productivity by coral reef framework substrates from the northern Red Sea. *Marine Ecology Progress Series*, 533, 79–92. <https://doi.org/10.3354/meps11383>
- Roik, A., Roder, C., Röthig, T., & Voolstra, C. R. (2016). Spatial and seasonal reef calcification in corals and calcareous crusts in the central Red Sea. *Coral Reefs*, 35, 681–693. <https://doi.org/10.1007/s00338-015-1383-y>
- Roth, F., Karcher, D. B., Rädicker, N., Hohn, S., Carvalho, S., Thomson, T., ... Wild, C. (2020). Data from: High rates of carbon and dinitrogen fixation suggest a critical role of benthic pioneer communities in the energy and nutrient dynamics of coral reefs. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.gb5mkkwms>
- Roth, F., Saalman, F., Thomson, T., Coker, D. J., Villalobos, R., Jones, B. H., ... Carvalho, S. (2018). Coral reef degradation affects the potential for reef recovery after disturbance. *Marine Environmental Research*, 142, 48–58. <https://doi.org/10.1016/j.marenvres.2018.09.022>
- Roth, F., Stuhldreier, I., Sánchez-Noguera, C., Morales-Ramírez, T., & Wild, C. (2015). Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral

- reef of Pacific Costa Rica. *Journal of Experimental Marine Biology and Ecology*, 468, 55–66. <https://doi.org/10.1016/j.jembe.2015.03.018>
- Rotjan, R., & Lewis, S. (2008). Impact of coral predators on tropical reefs. *Marine Ecology Progress Series*, 367, 73–91. <https://doi.org/10.3354/meps07531>
- Russ, G. R. (2003). Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs*, 22, 63–67. <https://doi.org/10.1007/s00338-003-0286-5>
- Ryabenko, E. (Ed.). (2013). Stable isotope methods for the study of the nitrogen cycle. In *Topics in oceanography*. IntechOpen. Retrieved from <https://www.intechopen.com/books/topics-in-oceanography/stable-isotope-methods-for-the-study-of-the-nitrogen-cycle>
- Sawall, Y., Al-Sofyani, A., Hohn, S., Banguera-Hinestroza, E., Voolstra, C. R., & Wahl, M. (2015). Extensive phenotypic plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential to warming. *Scientific Reports*, 5, 8940. <https://doi.org/10.1038/srep08940>
- Shashar, N., Cohen, Y., Loya, Y., & Sar, N. (1994). Nitrogen fixation (acetylene reduction) in stony corals: Evidence for coral–bacteria interactions. *Marine Ecology Progress Series*, 111, 259–264.
- Shashar, N., Feldstein, T., Cohen, Y., & Loya, Y. (1994). Nitrogen fixation (acetylene reduction) on a coral reef. *Coral Reefs*, 13, 171–174. <https://doi.org/10.1007/BF00301195>
- Smith, J. E., Hunter, C. L., & Smith, C. M. (2010). The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia*, 163, 497–507. <https://doi.org/10.1007/s00442-009-1546-z>
- Stal, L. (1988). Nitrogen fixation in cyanobacterial mats. *Methods in Enzymology*, 167, 474–484.
- Stewart, W. D. P., Fitzgerald, G. P., & Burris, R. H. (1967). In situ studies on N₂ fixation using the acetylene reduction technique. *Proceedings of the National Academy of Sciences of the United States of America*, 58, 2071–2078. <https://doi.org/10.1073/pnas.58.5.2071>
- Stuhldreier, I., Bastian, P., Schöning, E., & Wild, C. (2015). Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand. *Marine Pollution Bulletin*, 92, 35–44. <https://doi.org/10.1016/j.marpolbul.2015.01.007>
- Stuyck, J. (1902). La compatibilité de la loi belge avec le droit européen actuel. A la recherche d'un équilibre entre libre circulation et subsidiarité. Les pratiques du commerce. *L'information et la Protection du Consommateur*, 16, 273–329.
- Tilstra, A., Bednarz, V. N., Cardini, U., Van Hoytema, N., Al-Rshaidat, M. M. D., & Wild, C. (2017). Seasonality affects dinitrogen fixation associated with two common macroalgae from a coral reef in the northern Red Sea. *Marine Ecology Progress Series*, 575, 69–80. <https://doi.org/10.3354/meps12206>
- Valiela, I. (1984). *Marine ecological processes*. New York, NY: Springer. ISBN: 978-1-4757-1833-1. <https://doi.org/10.1007/978-1-4757-1833-1>
- van Hoytema, N., Bednarz, V. N., Cardini, U., Naumann, M. S., Al-Horani, F. A., & Wild, C. (2016). The influence of seasonality on benthic primary production in a Red Sea coral reef. *Marine Biology*, 163, 52. <https://doi.org/10.1007/s00227-015-2787-5>
- Wangersky, P. J. (1978). Methods of seawater analysis. *Marine Chemistry*, 7, 86–87. [https://doi.org/10.1016/0304-4203\(78\)90045-2](https://doi.org/10.1016/0304-4203(78)90045-2)
- Wild, C., Hoegh-Guldberg, O., Naumann, M. S., Colombo-Pallotta, M. F., Ateweberhan, M., Fitt, W. K., ... Van Woesik, R. (2011). Climate change impedes scleractinian corals as primary reef ecosystem engineers. *Marine and Freshwater Research*, 62, 205–215. <https://doi.org/10.1071/MF10254>
- Wild, C., Huettel, M., Klueber, A., Krems, S. G., Rasheed, M. Y. M., & Jørgensen, B. B. (2004). Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature*, 428, 66–70. <https://doi.org/10.1038/nature02344>
- Wild, C., Rasheed, M., Jantzen, C., Cook, P., Struck, U., Huettel, M., & Boetius, A. (2005). Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea. *Marine Ecology Progress Series*, 298, 69–78. <https://doi.org/10.3354/meps298069>
- Yamori, W., Hikosaka, K., & Way, D. A. (2014). Temperature response of photosynthesis in C3, C4, and CAM plants: Temperature acclimation and temperature adaptation. *Photosynthesis Research*, 119, 101–117. <https://doi.org/10.1007/s11120-013-9874-6>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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