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Seabird-derived nitrogen supply enhances photosynthetic activity in a reef-building coral

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ABSTRACT

Nutrient subsidies from seabirds (SDN) significantly impact coral reef ecosystems, but access to remote seabird nesting islands limits our understanding of how corals respond to this nutrient source. This study investigates the *in natura* effects of SDN on coral metabolism at Surprise Island in the southwestern Pacific. Specifically, we examine how the photobiology of the ubiquitous reef-building coral *Pocillopora damicornis* responds to SDN availability. On Surprise Island, seabird-derived nitrogen follows a well-defined gradient across the land–ocean continuum and significantly contributes to scleractinian coral nitrogen uptake. At stations exposed to SDN discharge, seawater exhibited an elevated N:P ratio due to high nitrate concentrations as phosphate and ammonium concentrations remained similar to those at the reference station. Corals exposed to SDN-enriched coastal waters displayed a 50 % increase in photosynthetic efficiency and a 40 % increase in photosynthetic rate, coupled with a 115 % increase in both symbiont density and chlorophyll concentrations. These findings demonstrate that nitrogen inputs from seabirds stimulate the photosynthetic activity of coral symbionts, highlighting the sensitivity of coral photophysiology to SDN. This underscores the critical link between seabird ecology and coral reefs functioning and emphasizes the need for integrated conservation efforts on coral islands.

1. Background

In coral reefs, the availability of inorganic nutrients determines the physiology of marine organisms and can have cascading effects at the ecosystem-scale (D'Angelo and Wiedenmann, 2014). Nutrient cycles are major determinants of reef ecosystems functioning (Elser et al., 2007) by shaping taxonomic and functional diversities (Savage et al., 2012; Wang et al., 2016), trophic foodwebs (Wang and Brose, 2018), as well as overall productivity (Isbell et al., 2013) and resilience to climate changes (DeAngelis, 1980). Responses of coral reef ecosystems to nutrient enrichment has mainly been studied in the context of human activities and coastal eutrophication, which can overwhelm and drastically alter coastal habitats (Thibault et al., 2020; Lapointe, 2019; Edinger et al., 2000). However, natural inputs linked to large-scale oceanographic processes such as upwelling, eddies, internal tides but also the movements of vertebrates (Fox et al., 2023; Johnson et al., 2020; Wang et al., 2007; Steibl et al., 2024) can deliver limiting nutrient to coral reef ecosystems. Recently, the contribution of seabird colonies to the functioning of tropical coral island ecosystem has captivated the attention of researchers from all horizons (Erler et al., 2024; Choisnard et al., 2024; Graham et al., 2018).

It has now been demonstrated that seabirds actively transfer and concentrate nutrients from the open ocean, where they feed, to their nesting grounds, as their faeces are enriched in nitrogen (N) and phosphorus (P) relative to other elements (Staunton Smith and Johnson, 1995; Anderson and Polis, 1999). In oligotrophic environments, seabird-derived nutrients (SDN) may locally dominate the nutrient fluxes with cascading effects on the surrounding coral reef ecosystems

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(Benkwitt et al., 2021; Lorrain et al., 2017). For instance, SDN boost reef productivity and ecosystem functions (Graham et al., 2018; Benkwitt et al., 2023; Dubinsky and Berman-Frank, 2001) and promote ecosystem recovery after a bleaching event (Benkwitt et al., 2019, 2023). Few *in natura* studies also revealed that SDN increase autotrophy in the coral *Pocillopora damicornis* (Thibault et al., 2022) and stimulates growth rate in the coral *Acropora* sp. (Savage, 2019; Dunn et al., 2024).

Yet, the response of coral physiology to changes in nutrient loading is not straightforward and varies with coral taxa, nitrogen species (ammonium vs. nitrate), enrichment source (natural vs. anthropogenic), and is modulated by the presence or absence of phosphate (Shantz and Burkepile, 2014; Nalley et al., 2023). This field of research is particularly relevant in the light of the ongoing global warming trend. Indeed, laboratory and field experiment suggest that excess nitrogen to corals increases bleaching susceptibility because of a variety of mechanisms (Wooldridge, 2009; Cunning and Baker, 2013; Wiedenmann et al., 2013). Latest studies however, indicate that nitrate enrichment would be detrimental to the coral holobiont, whereas ammonium could be beneficial (Ezzat et al., 2015; Burkepile et al., 2020). We build upon the knowledge acquired over the past decade on a permanent transect set on the reef flat of a seabird nesting island of the southwestern Pacific to characterize, *in natura* 1) the properties of the SDN discharged on the reef, and 2) to investigate its influence on the photobiology of the ubiquist, reef building coral *Pocillopora damicornis*.

2. Methods

2.1. Study site description

The D'Entrecasteaux reefs, located 223 km north to New Caledonia, belongs to the *Parc Naturel de la Mer de Corail* and is classified as a UNESCO heritage site with restricted access since 2018. Surprise Island lies on the eponymous atoll, within the D'Entrecasteaux reefs system, and is a major nesting site for a dozen species of larid, fregatid, sulid, and procellariid seabirds (Philippe-Lesaffre et al., 2023). Several expeditions led in 2015, 2016, 2017, 2019 and 2023 aimed at investigating the influence of SDN on coral physiology and reef functioning based on a permanent transect deployed on the leeward side of the island, across a 200 m-wide reef flat (Fig. 1). Over the past decade, this unique study site has permitted to shed light on various aspects of SDN dynamics and its influence on coral biology. In particular, it permitted 1) to evidence the uptake of SDN by the coral *Pocillopora damicornis* (Lorrain et al., 2017), 2) to highlight the importance of SDN in modulating *P. damicornis*' nutrition (Thibault et al., 2022) and 3) to elucidate the complex transfer pathways and transformation of SDN along the land-ocean *continuum* (Choisnard et al., 2024). Building on this permanent transect, we used the sampling scheme detailed below during the field expedition IGUANE 2019 aboard R/V Alis.

2.2. Seawater and coral sampling

Samples were collected by SCUBA diving in July 2019 at two stations on the island's coastal reef flat, 25 and 200 m away from the shore respectively, to explore the effect of coastal exposition to seabird-derived nutrients. These stations are hereafter referred to as 25 m and 200 m stations respectively. Apexes of ten parental strains of the branching coral *P. damicornis* were removed with cutting pliers at each sampling station. Each coral fragment was transported in individual ziplock bag in a cooler containing seawater (25 ± 0.2 °C at the time of the sampling). At the end of each diving, >20 L seawater was collected in

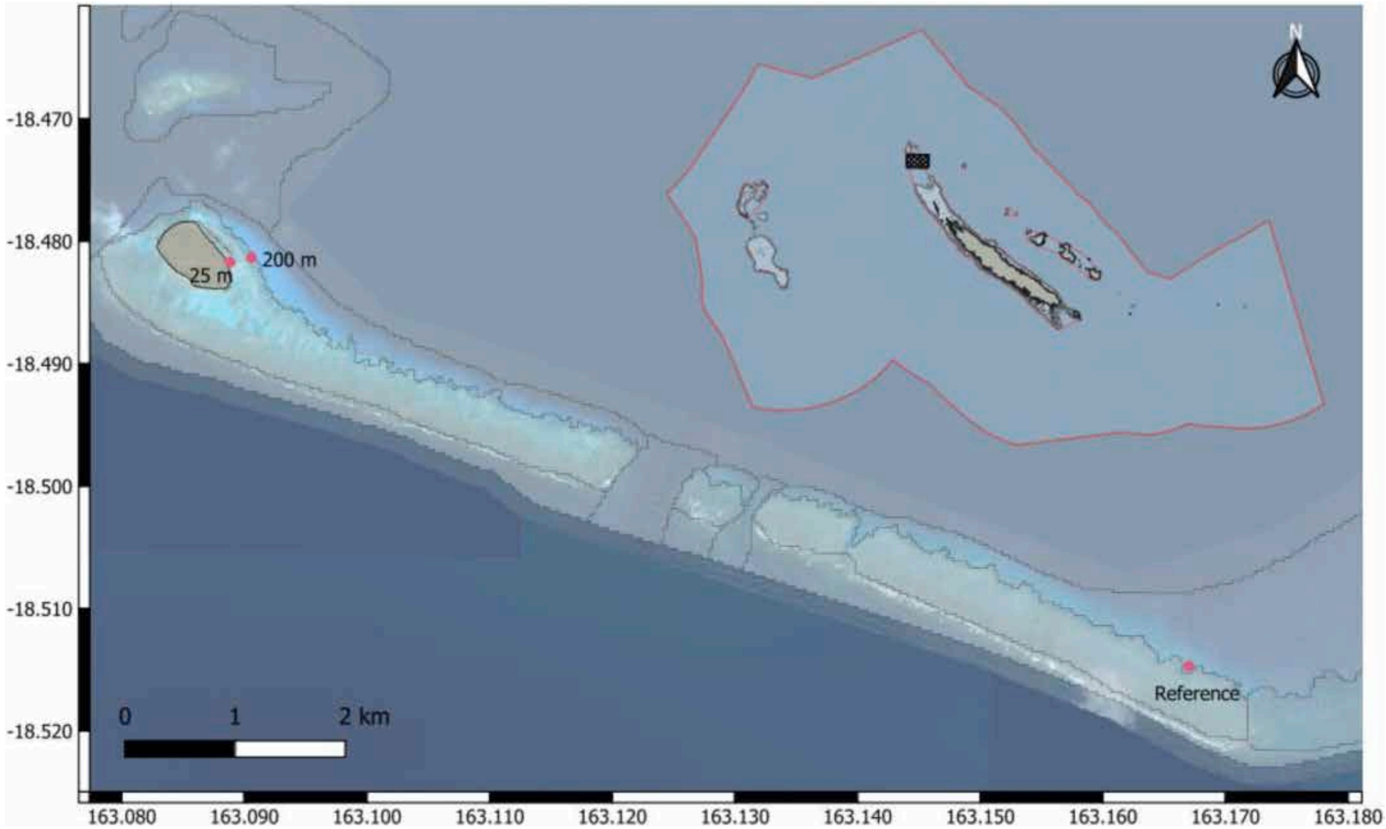

Fig. 1. Map of the sampling design, top-right incrustation represents New Caledonia archipelago delimited by its Economic Exclusive Zone (red polygon). D'Entrecasteaux reefs lie North the main island (black rectangle). The main map represents the southern part of Surprise atoll's reef. We sampled *P. damicornis* colonies on the inner reef flat (25 and 200 m offshore of Surprise island (left-hand side), and at a reference station. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

jerrycans and transported to R/V Alis within 15 min from collection, together with the coral fragments. Before incubation, fragments were allowed to recover for 2 h in two aquariums of 20 L supplied with seawater collected at the sampling site (26 ± 0.1 °C) and mixed using a submersible pump (Aquarium system, micro-jet MC 320, Mentor, OH, USA). Irradiance was controlled at 240 ± 5 μmol photons m^{-2} s^{-1} using four bulbs Aquablue plus (Blue-white, 15,000 K, Giesemann, Germany). Samples were stored frozen pending laboratory analyses. The same sampling protocol was replicated on a reference site located approx. nine kilometers away on the atoll rim (Fig. 1).

2.3. Photosynthetic efficiency measurements

Photosynthetic efficiency (Fv/Fm) and the relative Electron Transport Rate (rETR) of the photosystem II (PSII) of symbionts *in hospite* were measured on board the R/V on each coral fragment using a DIVING-PAM fluorometer (DIVING-PAM, Walz, Germany) (Schreiber et al., 1986). Before the measurements, these coral fragments were dark-adapted for 15mn (Hoegh-Guldberg and Jones, 1999). During measurements, the 8 mm-diameter optical fiber was maintained perpendicular to the fragments' surface using a black jacket maintained at a fixed distance of 5 mm, guaranteeing a correct distance from the coral. A weak-pulse red light (max. intensity <1 mol photons m^{-2} s^{-1}, width 3 μs, frequency 0.6 kHz) and a saturating pulse of actinic light (max. intensity 8000 μmol photons m^{-2} s^{-1}, pulse width 800 ms) were applied to the coral surface to measure the minimal (F_0) and maximal (F_m) Chlorophyll *a* fluorescence, respectively. Variable fluorescence (F_v) was calculated as F_m-F_0 (Biscéré et al., 2015). Fv/Fm represents the maximum quantum yield of the PSII. rETR were obtained through Rapid Light Curves (RLCs) (Ralph and Gademann, 2005). RLCs were collected by illuminating corals for 10-s periods with eight actinic light sequences from 0 to 1500 μmol photons m^{-2} s^{-1}. Consistency of natural exposition to Photosynthetically Active Radiations (PAR) was controlled *in situ* at 25 m (683 ± 52.3 μmol photons m^{-2} s^{-1}) and 200 m (688 ± 11.3 μmol photons m^{-2} s^{-1}) in a row during two dedicated transect dives. According to (Ralph and Gademann, 2005), RLC has three distinct regions: the light limited, the light-saturated and the photoinhibited region. The rise of the curve in the light-limiting region (α) is proportional to efficiency of light capture (effective quantum yield (Schreiber et al., 1986);). Minimum saturating irradiance (E_k) is determined by finding the interception of α with the maximum ETR_m. E_k is related to quenching, where photochemical quenching dominates below E_k, while non-photochemical quenching (NPQ) dominates the fluorescence quenching above E_k (Henley, 1993). Under moderate irradiance, the capacity of the electron transport chain limits photosynthesis and the curve reaches a plateau, where maximum photosynthetic capacity occurs ($rETR_{max}$ (Schreiber, 2004).

2.4. Photosynthetic rates

After the recovery period, measurements of net photosynthesis rates (P_n) of each coral fragment were assessed at 240 ± 5 μmoles photons m^{-2} s^{-1} (as described above). Five coral colonies from each station were placed in thermostatically controlled chambers at 26 ± 0.1 °C, filled with seawater collected at their sampling sites. Each chamber was equipped with a Unisense optode connected to a computer with Oxy-4 software (Chanel fiber-optic oxygen meter, PreSens, Regensburg, Germany). Optodes were calibrated against nitrogen-saturated and air-saturated seawater corresponding to 0 % and 100 % oxygen, respectively. Incubations lasted 60 min and P_n rates were estimated by regressing oxygen data against time. Data are expressed as μmol O_2 cm^{-2} h^{-1}. At the end of each incubation, fragments were frozen to determine their Symbiodiniaceae and total chlorophyll contents. Unfortunately, due to an optode malfunction, photosynthetic rates could not be measured at the reference station.

2.5. Symbiodiniaceae and chlorophyll *a* concentrations

Coral tissues were extracted from the skeleton using an air pick and homogenized with a Potter tissue grinder (Rodolfo-Metalpa et al., 2009). The symbiodiniaceae density was then quantified under light microscopy using a Neubauer's cell. To extract Chlorophyll *a*, 10 mL of homogenate was kept with 100 % acetone at 4 °C in the darkness for 24 h to insure total extraction. Extracts were then centrifuged at 10,000 g for 15 min and absorbance values were read at 630, 663, 750 nm. Chlorophyll *a* concentrations were calculated using the equations of Jeffrey et al. (Jeffrey and Humphrey, 1975). Symbiodiniaceae density, chlorophyll *a* concentrations and photosynthetic rates were normalized to the skeletal surface area (cm^2). These skeleton surfaces have been estimated using the wax-dipping method (Stimson and Kinzie, 1991).

2.6. Nutrient concentrations and nitrogen stable isotope ratios

Nitrite & nitrate concentration - Unfiltered samples of surface seawater (40 mL) were fixed with 20 μl saturated $HgCl_2$ and stored pending analysis at room temperature. NOx ($NO_2^- + NO_3^-$) concentrations were determined on a Bran-Luebbe III continuous flow autoanalyzer (Raimbault et al., 1990), at the Institute for Sustainable Development (IRD, Nouméa, New Caledonia, France).

Ammonium concentration – Samples of 40 mL unfiltered seawater stored in the dark (at room temperature) were processed and measured on board using a Trilogy Laboratory Fluorimeter (Turner Designs) between 6 and 18 h after 2 mL of OPA reagent (o-phthaldialdehyde) was added (Holmes et al., 1999).

Phosphate concentration – Unfiltered seawater samples were kept frozen (−20 °C) until PO_4 concentrations were measured with a SEAL Analytical QuAAtro39 Continuous Segmented Flow Analyzer at the Max Planck Institute for Chemistry (Mainz, Germany).

Nitrogen stable isotope ratios -After extraction and separation (see Thibault et al., 2022), coral tissues and symbiodiniaceae samples were dried at 60 °C before being encapsulated in tin cups for analysis at Union College (Schenectady, NY, United States). A Thermo Delta Advantage mass spectrometer, connected to a Costech Elemental Analyzer via ConFlo IV, was used for isotopic ratio analysis. Corrections for isotopic ratios and assignments to the appropriate isotopic scale were made using reference standards:IAEA-N-2 ammonium sulfate (δ15 N = 20.3 ± 0.2), IAEA-600 caffeine (δ13C = −27.771 ± 0.043, δ15 N = 1.0 ± 0.2), IAEACH-6 sucrose (δ13C = −10.449 h), and an in-house acetanilide standard (δ13C = −34.07, δ15 N = −0.96), with an analytical precision better than 0.1 ‰.

2.7. Statistical analysis

Site differences in each of the six parameters obtained at our three stations were tested with one-way ANOVA tests. Data normality and homoscedasticity conditions were controlled prior to analysis using Shapiro Wilk and Levene tests under "stats" and "car" packages respectively (Fox and Weisberg, 2018). Log transformation was applied to response variables when necessary (Boldina and Beninger, 2016). Post Hoc pairwise comparisons were then assessed with Tukey HSD tests. The efficiency of light capture (α), the minimum saturating irradiance (E_k) and the maximum photosynthetic capacity ($rETR_{max}$) were derived from fitted Rapid Light Curves at the sample resolution. We then used Generalized Additive Model (GAM) (Hastie and Tibshirani, 1990) to explore the effect of the distance to the islet source of nutrients on the rETR within corals symbionts. rETR was considered the quantitative response variable, on which we tested the effects of both the light intensity and the proximity to the islet. The effect of light intensity was considered interacting with the proximity factor with a k = 8 smoothing factor. The model was computed under the "mgcv" R Package (Wood, 2011), with a gaussian distribution and a Restricted Maximum Likelihood (REML) smoothing selector. Post Hoc pairwise comparisons with

Tukey p value corrections were computed with “emmeans” package (Lenth et al., 2023). All analyses were conducted in R v4.3.2 (R Core Team, 2023).

3. Results

The proximity to the island shore affected the N:P nutrient ratios in seawater (F(2,5) = 70.16, $p < 0.001$, Fig. 2A). This ratio was higher at

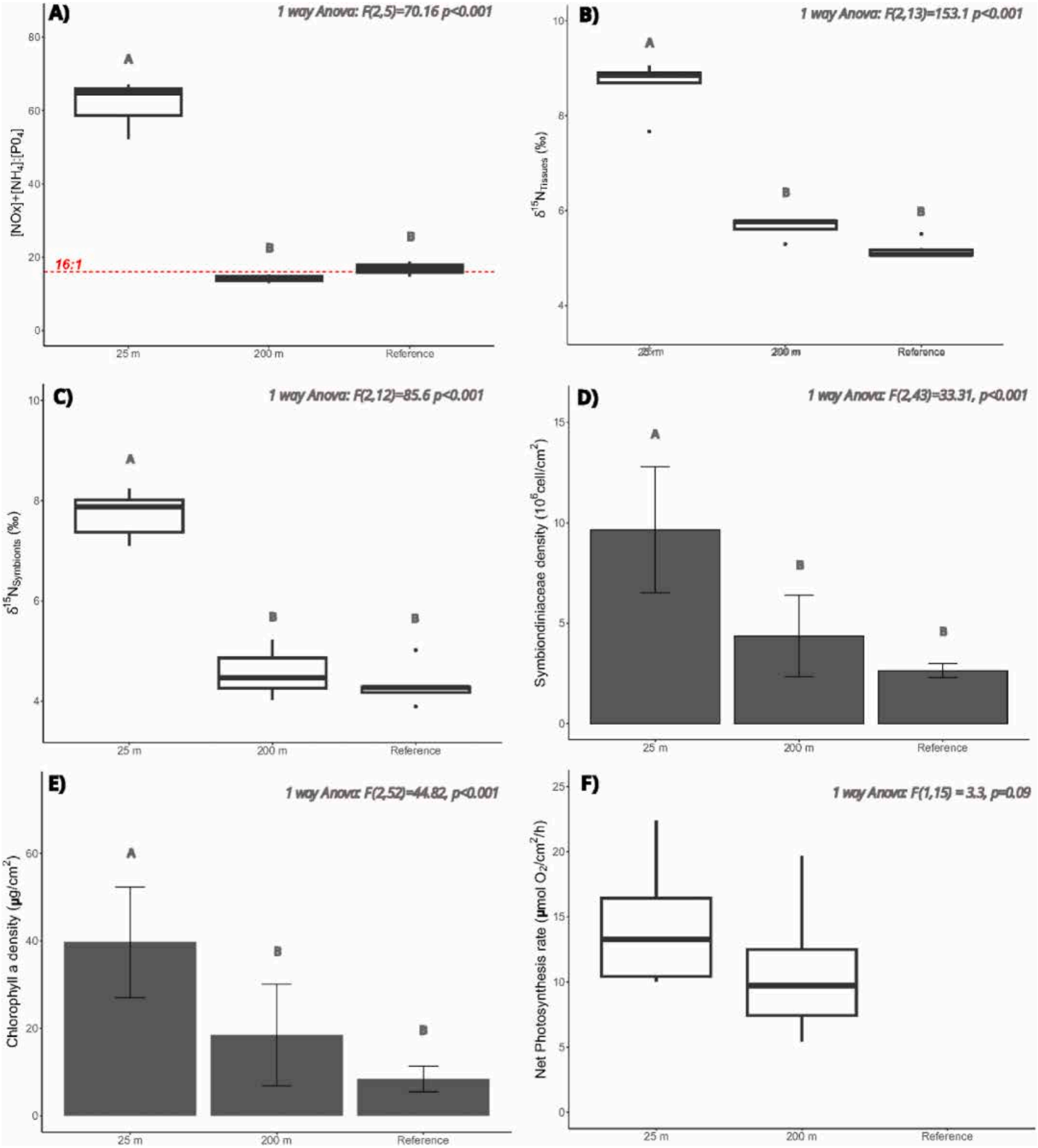

Fig. 2. Effect of the proximity to the islet source of SDN on: A) the availability of inorganic nutrients in seawater represented by the N:P ratio (the horizontal line represents the reference 16:1 ratio); B) $\delta^{15}N$ values measured in coral tissues; C) $\delta^{15}N$ values measured in coral symbionts; D) the Symbiodiniaceae density per unit surface skeleton (Symb. $\times 10^6$ cell cm^{-2}); E) the Chlorophyll *a* content per unit surface area of skeleton (µg cm^{-2}) and F) the rates of net photosynthesis per unit surface skeleton (µmol O_2 cm^{-2} h^{-1}) (mean ± SE, n = x). Significant differences are marked with group letters (A, B). Unfortunately, due to an optode malfunction, photosynthetic rates could not be measured at the reference station.

25 m (61.5 ± 8.02) off the island than at 200 m (14.1 ± 1.59, $p < 0.001$) and the reference station (16.8 ± 2.08, $p < 0.001$). The difference in N:P ratio measured 200 m off the island was similar to that of the reference station. Averages and standard deviations of NOx (nitrites were under detection limit), NH_4 and PO_4 as well as N:P ratios at the three locations are provided in Table 1. Changes observed in the N:P ratio were mainly a reflection of the increasing contribution of NOx, i.e. nitrates, at 25 m from shore since ammonium and phosphate concentrations remained stable along the transect (Table 1). The $\delta^{15}N$ values of coral tissues and symbionts were also statistically higher (by ~2.5 ‰, $p < 0.001$) at 25 m from the shore compared to 200 m and reference site (Fig. 2B and C).

A similar decreasing pattern with the distance to the island came out on the density of Symbiodiniaceae in sampled corals ($F(2,43) = 33.31$, $p < 0.001$, Fig. 2D). At station 25 m, Symbiodiniaceae density were higher as compared to both the station at 200 m (x2.14 ± 0.26, $p < 0.001$) and the reference one (x3.66 ± 0.82, $p < 0.001$). Once again, the difference between the 200 m and reference stations was not statistically significant (x1.71 ± 0.96, $p = 0.05$).

The proximity to the source of SDN also had a significant effect on the Chlorophyll *a* concentrations ($F(2,52) = 44.82$, $p < 0.001$). Chlorophyll *a* concentrations were higher in 25 m samples as compared to that of corals sampled at either the 200 m (x2.15 ± 0.27, $p < 0.001$) or the reference station (x4.74 ± 0.88, $p < 0.001$, Fig. 2E).

Finally, highest photosynthetic rates were measured in the samples located closest to the shore (14.5 $\mu mol\ O_2\ cm^{-2}\ h^{-1}$ at station 25 m) in comparison with the 200 m station (10.5 $\mu mol\ O_2\ cm^{-2}\ h^{-1}$). Yet, this difference was not statistically significant ($F(2,43) = 33.31$, $p = 0.09$, Fig. 2F).

At the closest location from the islet source of SDN (25 m), rETRm values were 30 % higher (92.3 ± 19.5) as compared to the reference station (59.5 ± 16.3) (Fig. 3). The α coefficient, proxy of the light capture efficiency was also higher at 25 m (0.19 ±. 0.002) and the minimum saturating irradiance was 20 % higher in corals collected close to the island as compared to further ones (Table 2).

4. Discussion

The permanent transect deployed at Surprise Island since 2015 provide a unique opportunity to disentangle the effects of seabird derived nutrients from physical parameters (*e.g.*, water mixing, depth, light) on coral biology (Choisnard et al., 2024). The transect stretches from the edge of the island, 200 m outward across a reef flat characterized by a constant depth (~1 m) and light intensity providing a homogeneous environment across the transect as well as at the reference site (Table 1). Within this experimental setting *in situ*, we found that SDN supply on the reef flat enhances the photobiology of the coral *P. damicornis*.

Table 1
Mean values and standard errors of seawater (NO_X, NH_4, PO_4 and N:P ratio), and coral parameters ($\delta^{15}N$ tissues, $\delta^{15}N$ symbionts, Symbiont Density, Chlorophyll *a* Density and net photosynthesis rate) for sample triplicates collected at the three stations.

	25 m	200 m	Reference
Seawater			
NO_X (μg/L)	1.27 ± 0.01	0.81 ± 0.02	0.51 ± 0.01
NH_4 (μM)	0.12 ± 0.04	0.15 ± 0.05	0.16 ± 0.01
PO_4 (μM)	0.02 ± 0.00	0.02 ± 0.05	0.04 ± 0.01
N: P	61.5 ± 8.02	14.1 ± 1.59	16.8 ± 2.08
PAR ($\mu M/m^2/s$)	683 ± 52.3	688 ± 11.3	–
P. damicornis			
$\delta^{15}N_{Tissues}$ (‰)	8.64 ± 0.56	5.65 ± 0.21	5.16 ± 0.18
$\delta^{15}N_{Symbionts}$ (‰)	7.72 ± 0.47	4.57 ± 0.48	4.33 ± 0.42
Symbionts Density (10^6 cell/ cm^2)	9.66 ± 3.15	4.51 ± 2.24	2.64 ± 0.34
Chlorophyll *a* Density ($\mu g/cm^2$)	39.7 ± 12.7	18.5 ± 11.6	8.38 ± 2.92
Net Photosynthesis Rate	14.5 ± 4.37	10.5 ± 4.59	–

Concentrations of nitrate, nitrite, ammonium and phosphate were measured to characterize the composition of the SDN discharge onto the reef. The main feature was a gradient of NOx concentration ranging from >1.3 μM at 25 m from shore, down to 0.5–0.8 μM at 200 m and at the reference site. This gradient is similar in amplitude with previous measurements made in 2017 (0.7–1.4 μM (Lorrain et al., 2017),), indicating that the NOx gradient is probably present most of the time and therefore exerts a strong influence on the coral community adjacent to the shore. Interestingly, SDN discharge does not have a noticeable footprint on the ammonium concentration on the reef flat. A similar observation has been reported from Lady Elliot Island, a seabird nesting island located in the Great Barrier Reef, where negligible ammonium concentration where found (Erler et al., 2024). This is likely explained by the fact that SDN transits through the groundwater lens before leaching onto the reef flat. In the process, ammonium is either volatilized (abiotic process) or oxidized into nitrate (bacteriological conversion) (Choisnard et al., 2024), leading to negligible, or no ammonium concentration in the groundwater discharged on the reef. The well buffered carbonate substrate making the bulk of the coral island mass promotes calcium phosphate (*i.e.*, guano) precipitation, that retains most of the phosphate derived from seabirds on land (Sims et al., 2020; Simmons, 1983; Simmons et al., 1985). This decoupling between the nitrogen and the phosphorus cycles is clearly expressed in the N:P ratio observed close to shore with values higher than 60 driven by changes in nitrate concentration, whereas the other sites displayed a more balanced (Redfield) stoichiometry (Table 1). High $\delta^{15}N$ values of coral tissues and symbionts at 25 m also confirmed seabird-derived nitrogen assimilation by corals as was already found in previous studies at this site for different years (Lorrain et al., 2017; Thibault et al., 2022). The SDN enrichment found at Surprise is interesting in that it is mostly driven by nitrate concentration, N species that is usually considered as less beneficial to photoautotrophs than ammonium due to an energetically costly reduction step (Ezzat et al., 2015; Patterson et al., 2010). Yet, the *P. damicornis* specimens exposed to higher NOx concentration and N:P ratio exhibited a typical response to nitrogen enrichment with a doubling of the symbiont density and chlorophyll-a content, paralleled with higher maximum photosynthetic capacity (ETR_{max} +50 %) and light capture efficiency (α +30 %) (Shantz and Burkepile, 2014; Nalley et al., 2023) suggesting that *P. damicornis* benefits from SDN inputs.

This positive response of the coral photobiology to nitrate enrichment should be interpreted cautiously since this pattern has been previously associated with impaired calcification, in particular under nitrate enrichment (Shantz and Burkepile, 2014; Nalley et al., 2023). However, Savage (2019) found an increase in the growth rate of another branching coral *Acropora formosa* when submitted to high guano inputs, suggesting that SDN also promotes calcification. Recent studies also showed that seabird guano contain trace elements (*e.g.*, Zn, Fe, Mn, Ni, Co) of which labile chemical forms are easily assimilated by marine organisms (De La Peña-Lastra et al., 2022) and may positively affect corals metabolism (Biscéré et al., 2015, 2017, 2018). However, very few studies assessing these metal fluxes and their influence are available, particularly in tropical areas. We would finally like to point out that ultimate benefits from SDN enrichment may not be equally distributed among coral species and that further studies on different species would be informative, such as *Acropora* sp., *Turbinaria* sp and the massive coral *Porites* sp that dominated the coral community at Surprise (pers. obs 2019) We would finally like to point out that ultimate benefits from SDN enrichment may not be equally distributed among coral species and that further studies on different species would be informative, such as *Acropora* sp., *Turbinaria* sp and the massive coral *Porites* sp that dominated the coral community at Surprise (pers. obs 2019).

Nevertheless, our study demonstrates the sensitivity of corals' photophysiology to SDN inputs and provides another proof of the tight linkage between seabird populations and coral reefs functioning in coral island ecosystems. These findings support the implementation of integrated conservation and restoration policies at the scale of the land-

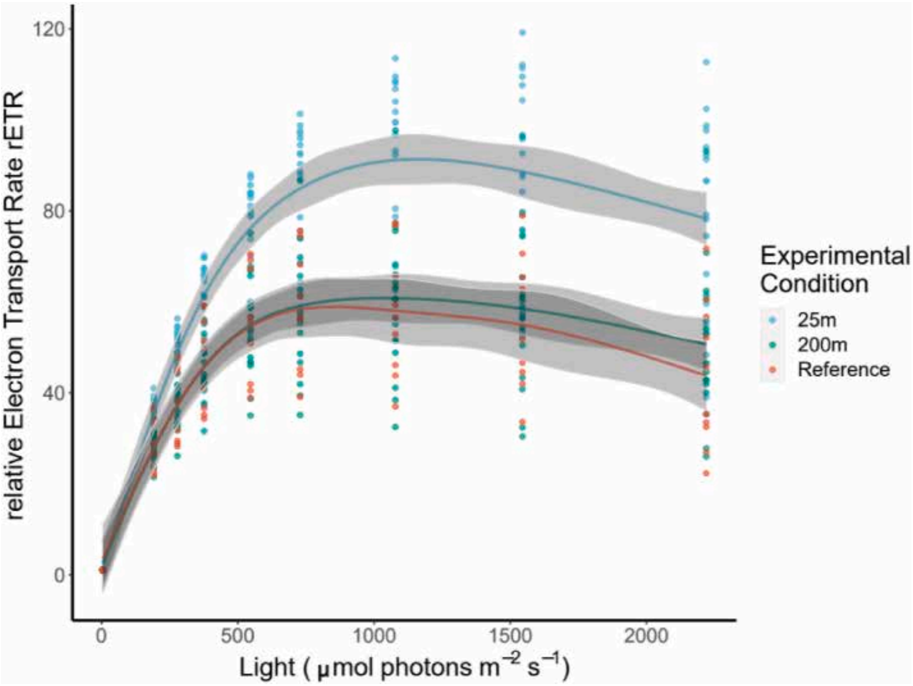

Fig. 3. Effect of proximity to the island source of SDN on the Electron Transport Rate (ETR) versus irradiance (PAR) of *P. damicornis*.

Table 2
Averaged (±s.d) maximum photosynthetic capacity (rETR$_{max}$), efficiency of light capture (α), and minimum saturating irradiance (E$_k$) derived from fitted Rapid Light Curves generated for coral samples collected at the three transect locations.

Transect	ETR$_{max}$	α	E$_k$
25 m	92.3 ± 19.5	0.19 ± 0.02	473 ± 73.9
200 m	61.9 ± 15.3	0.16 ± 0.02	389 ± 67.1
Reference	59.5 ± 14.2	0.16 ± 0.04	377 ± 68.1

ocean continuum on these remote islands.

CRediT authorship contribution statement

Martin Thibault: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anne Lorrain:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Nicolas N. Duprey:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Alfredo Martínez-García:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Fanny Houlbrèque:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

Ethics

Coral sampling was conducted under the sampling permit #2019–901/GNC granted by the Government of New Caledonia and The Parc naturel de la mer de Corail.

Data accessibility

All data are available in the main text and in the electronic supplementary material.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Anne Lorrain reports financial support was provided by Labex Mer et Corail. Anne Lorrain reports financial support was provided by LEFE EC2CO. Anne Lorrain reports financial support was provided by French Oceanographic Fleet. Alfredo Martinez-Garcia reports financial support was provided by Deutsche Forschungsgemeinschaft. Nicolas Duprey reports financial support was provided by Paul Crutzen post-doctoral fellowship. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Coral sampling was conducted under the sampling permit #2019–901/GNC granted by the Government of New Caledonia and The Parc naturel de la mer de corail.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107147.

Data availability

Data will be made available on request.

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