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RESEARCH

Active and passive pathways of nutrient transfer in coral reef ecosystems

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Abstract Coral reefs receive both passive and active nutrient subsidies, supplied via oceanographic processes and animal-mediated transfer, which can bolster reef productivity and resilience to disturbance. We examined the relative importance of these two pathways across lagoonal and seaward reefs, reefs of different depths, and those around islands either with or without breeding seabird colonies using carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and nutrient metrics (per cent N, %N and carbon-to-nitrogen ratios, C:N). We found increased passive oceanic nutrient inputs in reefs that were both deep and seaward facing, indicated by lower $\delta^{13}C$ values. Enriched $\delta^{15}N$ values and lower carbon-to-nitrogen ratios within reefs adjacent to islands with seabird colonies provided evidence of the role of seabirds as active vectors of nutrients to coral reef food webs, particularly within shallow, lagoonal reefs. Though %N values did not seem to provide a good indicator through which to disentangle active vs passive nutrient transport within this context, variation in $\delta^{13}C$ and $\delta^{15}N$ values and C:N ratios highlighted the interplay between passive oceanic processes and active seabird contributions to coral reefs. We emphasise the importance of both preserving and restoring natural nutrient pathways, particularly at a time when coral reef ecosystems are under increasing pressure from anthropogenic threats.

Keywords Cross-ecosystem nutrients · Nutrient subsidy · Seabird guano · Stable isotope analysis

Introduction

The productivity and persistence of natural systems is maintained via the cycling of essential resources. These resources can move both through ‘active’ animal-mediated mechanisms, such as the energy flows induced by animal migrations and predation events, as well as through more ‘passive’ abiotic mechanisms, such as the movement of nutrients by winds, currents, erosion, and gravity (McInturf et al. 2019). Seeking to investigate both active and passive pathways simultaneously is increasingly garnering attention (Kéfi et al. 2012), and there is emerging interest in understanding how both forms of energy and nutrient transfer operate across a range of scales. The mechanisms behind this ecosystem connectivity, driven by both the active and passive transfer of energy and nutrients, are complex (Montoya et al. 2006). However, understanding how both forms of transfer operate at cross-ecosystem scales is important at a time when anthropogenic-induced change within one ecosystem is likely to have impacts that cascade into others (Peller and Altermatt 2024).

Coral reef ecosystems host high levels of biological diversity, providing spawning, breeding, nursery, and feeding

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habitats for a multitude of species (Small et al. 1998). Furthermore, they are of global social, economic, and ecological importance, providing a plethora of goods and services and supporting the livelihoods of millions of people (Woodhead et al. 2019). This biodiversity and importance is supported via active and passive energy and nutrient pathways that cycle both within coral reef ecosystems themselves (Brandl et al. 2019), as well as between coral reefs and other ecosystems (Mumby and Hastings 2007). Indeed, whilst once perceived as isolated features within otherwise indistinct oceans, coral reefs are increasingly recognised as being highly connected with the ecosystems that surround them (Lowe and Falter 2015; Gove et al. 2016).

Passive mechanisms such as coastal upwelling and internal waves, caused by surface winds, current-driven water movements, stratified waters, and rough bottom topography, drive the movement of nutrients and plankton between deep oceans and reefs (Spring and Williams 2023). These influxes are vital, supporting both mixotrophic reef-building corals as well as planktivorous reef fish that depend on them for shelter (Hamner et al. 1988; Fox et al. 2018). The importance of these passive pathways between open oceans and coral reefs varies spatially with reef type and bathymetry, with lagoonal reefs being less exposed to oceanic nutrients and plankton than seaward and barrier reefs (Hamner et al. 2007; Brandl et al. 2025). Coral reefs are also connected to pelagic ecosystems via more active pathways of energy and nutrient transfer, driven by 'mobile link' organisms (Lundberg and Moberg 2003). For example, wide-ranging marine predators, including seabirds, sharks, and large mobile fishes, often feed in pelagic areas and excrete waste within coral reef ecosystems, thereby actively transporting energy and nutrients across ecosystem boundaries (Young et al. 2010; Benkwitt et al. 2022; Dunn et al. 2022). Even within lagoonal reefs, reef fish communities are sustained by oceanic-based production sources, planktonic dependence extending beyond communities that inhabit more oceanic atoll edges (Skinner et al. 2019, 2021). Ultimately, there is incredible complexity to the mechanisms of connectivity that exist in coral reef ecosystems. Untangling the influence of active and passive ecosystem connectivity on coral reefs can help predict how these connections might change in future, with alterations to ocean currents (Wilson et al. 2016), invasive species introductions (Peller and Altermatt 2024), and reduced predator populations (Dedman et al. 2024). This understanding will, therefore, help to inform which reefs are likely to benefit most from the removal of invasive species and the restoration of predator populations, their movements, and roles within ecosystem connectivity (Dunn et al. 2024).

Here, we investigate the influence of both passive and active pathways (i.e. oceanographic processes and seabird movements) on the provisioning of nutrients to coral reef ecosystems within the Chagos Archipelago, a remote archipelago within the central Indian Ocean that provides a unique opportunity to examine ecosystem connectivity amongst coral reef habitats without direct human influence. The Chagos Archipelago is situated in an area of strong trade-winds and a thermocline that causes ocean upwellings (McCreary et al. 1993). Furthermore, its islands host a diverse range of predatory seabird species that subsidise coral reef food webs with nutrients from their pelagic foraging areas (Graham et al. 2018; Benkwitt et al. 2022). We used natural markers as tools to help elucidate the active and passive pathways that connect ecosystems within the Chagos Archipelago, investigating stable isotope signatures that allow the quantification of an organism's resource and habitat use (Newsome et al. 2007), as well as nutrient levels and ratios. Specifically, we investigated carbon ($\eth^{13}$C) stable isotopes, nitrogen ($\eth^{15}$N) stable isotopes, nutrient levels (per cent nitrogen, %N), and nutrient ratios (carbon-to-nitrogen ratios, C:N) within taxa collected from two depths within lagoonal reefs and from more exposed seaward reefs within the Chagos Archipelago, including from reefs surrounding islands where high densities of seabirds were present as well as those where they were absent. Carbon stable isotopes reflect the primary carbon sources within a food web, and lower values can, therefore, be indicative of nearshore and benthic vs passive oceanic signatures, due to higher nutrient concentrations and greater productivity nearshore (McMahon et al. 2013). Contrastingly, nitrogen stable isotopes increase with trophic level and are, therefore, used as a proxy for the uptake of seabird-derived nutrients (Benkwitt et al. 2021a). Higher nutrient levels and lower C:N nutrient ratios (indicators of nutrient supply) might also be indicative of this active transport mechanism.

We collected samples of three benthic organisms that are representative of the base of the food web: two primary producers (macroalgae, *Halimeda* sp. and turf algae) and a sponge (*Spheciospongia* spp.) that filter feeds on zooplankton and, therefore, provides an isotopic signature reflective of this food source. We also collected tissues from two heterotrophic taxa to explore how cross-ecosystem nutrients progress through the food web: shallow subtidal gastropod snails and hermit crabs. We predicted that organisms from seaward reefs would have lower $\eth^{13}$C values compared to those from lagoonal reefs, and that this difference would be more pronounced at deeper depths on seaward reefs, due to a reliance on passive nutrient inputs from more oceanic sources (Fig. 1). We also predicted that taxa from reefs around islands where seabirds were present would have higher nutrient levels, enriched $\eth^{15}$N values, and lower nutrient ratios in comparison with those without seabirds, due to these ecosystems being enriched by the active transfer of higher trophic level seabird guano (Fig. 1). We predicted that due to seabird guano inputs being diluted by the passive input of oceanic nutrients, and potentially washed

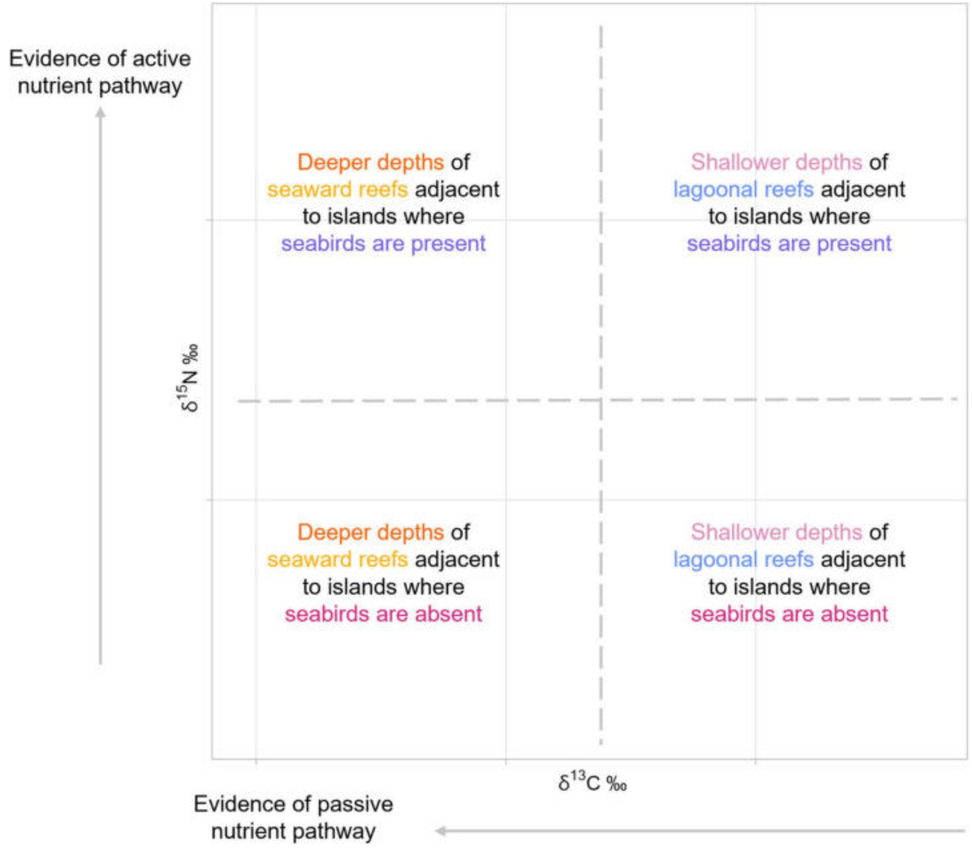

Fig. 1 Conceptual isotopic biplot of δ^{13}C and δ^{15}N demonstrating our hypotheses for the isotopic space that macroalgae, turf, sponge, hermit crabs, and gastropods sampled across reefs within the Chagos Archipelago will occupy

away more quickly due to currents and wave exposure, these differences would be lower on seaward reefs than within lagoonal reefs, and would diminish with depth in the basal food source species.

Materials and methods

Data collection

Sampling was conducted at low-lying atoll islands throughout the Chagos Archipelago within the central Indian Ocean (5°50′ S, 72°00′ E). Sampling was across 4 years, with sampling in 2019, 2021, and 2022 in the January–April pre-trade-wind season, and sampling in 2023 in October following the trade-winds. Within each year, samples were collected within a 3-week period. Whilst the phenology of the seabirds that breed in the Chagos Archipelago is varied, many species are present within the Archipelago throughout the year, with high abundances throughout October–April (Carr et al. 2020; Votier et al. 2024). Within the central equatorial Indian Ocean, wind-driven upwelling is low during inter-monsoon periods (Kumar et al. 2016), with peak upwelling across the Salomon, Peros Banhos, and Egmont atolls (Fig. 2) being between May and June in both 2019 and 2022 (Spring et al., *unpublished data*). Our sampling was, therefore, consistently outside peak upwelling periods for the Chagos Archipelago. Whilst all islands have been uninhabited since the 1970s (with the exception of the military facility on the island of Diego Garcia), introduced black rats (*Rattus rattus*) and coconut palm (*Cocos nucifera*) plantations have led to differences in seabird abundances (Fig. 2) and flows of active nutrient transfer across the islands (Graham et al. 2018; Carr et al. 2021).

All islands in this study were similar in size, location, and environment (with the exception of seabird abundances) and were encompassed by a large marine protected area thereby protecting them from extrinsic human influences (Hays et al. 2020). Our sampling took place across four of the Chagos Archipelago's atolls and encompassed coral reef sites that were approximately 100–200 m from shore, both adjacent to islands with seabirds ($n_{\text{islands}} = 7$), and presumed 'active' nutrient input, as well as those where seabirds were absent due to rats ($n_{\text{islands}} = 7$; Fig. 2). Seabird presence was determined via previous work within the region (Graham et al. 2018; Carr et al. 2021). Samples were collected from both the lagoonal reefs adjacent to these islands as well as from adjacent seaward reefs that were likely more exposed to more 'passive', oceanic nutrient inputs. Samples of three basal food sources (primary producers *Halimeda* sp. macroalgae [5 cm] and turf algae [2 g], and zooplankton-feeding sponge *Spheciospongia* spp. [2 g]) were collected at

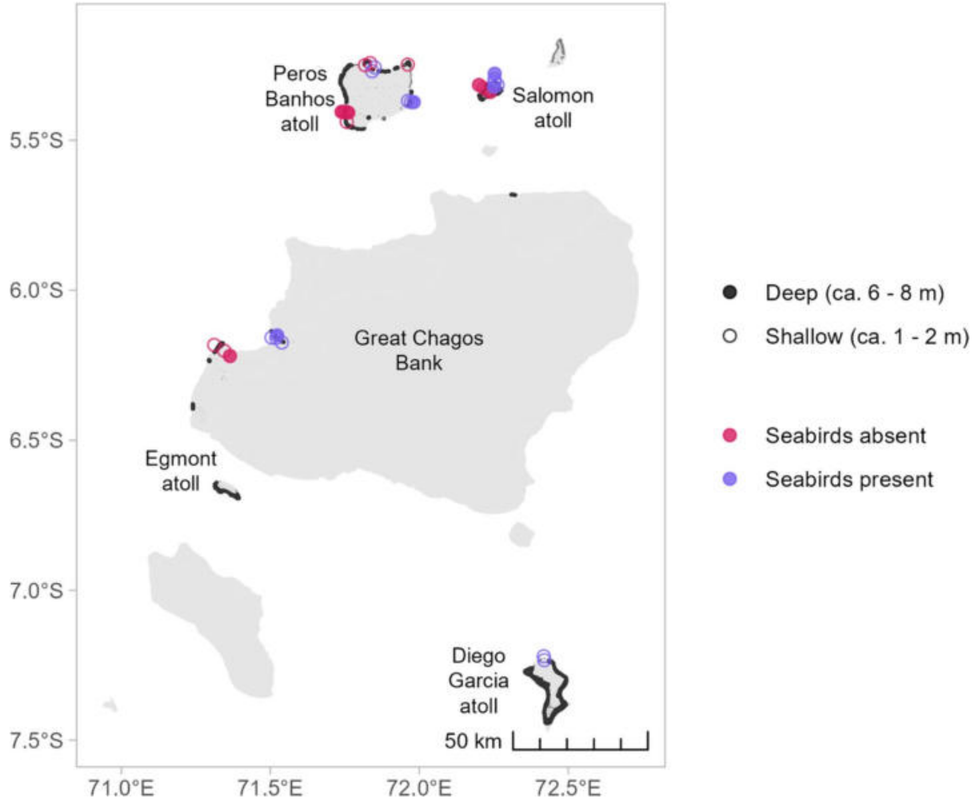

Fig. 2 Locations of sample collection throughout the Chagos Archipelago: Île Anglaise, Île Mapou, and Île de la Passe in Salomon atoll; Anglaise, Grand Île Coquillage, Moresby Island, Île Parasol, Île de la Passe, Île Poule, and Île Yeye in Peros Banhos; Eagle Island, Middle Brother, and South Brother in the Great Chagos Bank; East Island within the Diego Garcia atoll. Where symbols overlap, this is indicative of sampling taking place within lagoonal reefs as well as seaward reefs at the same island. Open circles indicate sampling at shallow depths, and closed circles indicate sampling at deeper depths. Islands are illustrated in black, and submerged banks are illustrated in grey

both 'shallow' (ca. 1–2 m) and 'deep' (ca. 6–8 m) depths, whereas samples of heterotrophs (shallow subtidal hermit crabs and gastropods [individuals]) were aggregated across the two depths due to logistical constraints whilst sampling (Table 1). Sample sizes varied due to logistical constraints, including variable time in the field and conditions restricting access to certain sites at certain times. Fieldwork was conducted, and samples were collected under permit numbers 0001SE19, 0002SE21, 0001SE22, and 0009SE23 in 2019, 2021, 2022, and 2023, respectively.

Hermit crabs and gastropods were extracted from their shells, to analyse only the body of the animal. All samples were kept separate on collection, dried at 60 °C for at least 48 h following collection, and stored in sterile airtight vials, following previously used methodologies (Graham et al. 2018; Benkwitt et al. 2021a). Macroalgae samples were washed with hydrochloric acid to dissolve any calcareous matter and were then analysed using an Elementar Vario MICRO cube Elementar Analyser and an Isoprime 100 Isotope Ratio Mass Spectrometer at Lancaster Environment Centre, Lancaster University, UK. Based on international standards IAEA 600 and USGS 41, accuracy was 0.2‰ standard deviation. Furthermore,

Table 1 Number of samples collected from each of the different reef habitats across 14 islands in 2019, 2021, 2022, and 2023 (the number of samples collected per year are shown in Table S1). Samples collected from islands where seabirds were present were predicted to exhibit evidence of greater active nutrient transfer, whereas samples collected from seaward reefs and deeper depths were predicted to exhibit evidence of greater passive nutrient transfer

Sample	Seabirds	Present				Absent			
	Habitat	Lagoonal		Seaward		Lagoonal		Seaward	
	Depth	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
Macroalgae		54	11	78	11	72	30	42	39
Turf algae		24	8	40	8	45	21	29	9
Sponge		47	10	58	10	40	30	26	30
Hermit crab		26		25		27		31	
Gastropod		35		22		35		26	

a subset of samples were run in duplicate or triplicate to ensure accuracy of readings, and the first reading was used for analyses.

Statistical analyses

Data processing, statistical analyses, and data visualisation were undertaken in R (R Core Team 2024) using the 'tidyverse' (Wickham et al. 2019), 'SIBER' (Layman et al. 2007; Jackson et al. 2011), 'brms' (Bürkner 2017), and 'MixSIAR' (Stock and Semmens 2016) R packages.

First, to investigate the isotopic niche space occupied by macroalgae, turf, sponge, hermit crabs, and gastropods sampled across reefs (Fig. 1), we conducted Shapiro–Wilk tests and drew quantile–quantile plots to ensure that all isotope data were adequately described by a multivariate normal distribution (Royston 1982). We then calculated Bayesian standard ellipses areas that provide measures of core niche space, as well as the proportion of overlap in isotopic niches (Jackson et al. 2011).

To investigate the uptake of active nutrients, passive nutrients, and subsequent nutrient levels and ratios whilst accounting for non-independence within our sampling design, we fit multilevel Bayesian models using Stan to compare ð^{13}C, ð^{15}N, %N and C:N values within samples from reefs surrounding islands with seabirds vs islands with rats, lagoonal reefs vs seaward reefs, and shallow vs deep waters (Bürkner 2017). For the basal food source samples, we ran models that included interactions between the explanatory variables for sample taxa, 'seabirds' (a categorical variable outlining whether seabirds were present or absent on the adjacent island), 'habitat' (a categorical variable describing whether the reef was lagoonal or seaward), and 'depth' (a categorical variable indicating whether samples were collected from deep or shallow depths). For the heterotroph samples, the full model included interactions between the explanatory variables for taxa, 'seabirds', and 'habitat'. All models included an additive term for the year of sampling, and a random effect of the island that they were collected from nested within the atoll that the island was part of. To reflect the distributional properties of the data, we used a Gaussian distribution with an identity link for the ð^{13}C, ð^{15}N, and consumer %N values, and a lognormal distribution for the models investigating basal food source %N values and nutrient ratios of both basal food sources and heterotrophs. These models were run using 4 Markov chain Monte Carlo chains for 5000 iterations, following a warm-up of 2000, using the weakly informative priors provided by the 'brms' package (Bürkner 2017). We confirmed model convergence and fit via visual inspection of the chains, posterior predictive checks (to compare the observed data in comparison with the simulated data distributions) and by checking that the Gelman–Rubin convergence statistic ($\hat{R}$) was close to 1 (Bürkner 2017; McElreath 2020). We examined patterns of the models' residuals to ensure good model specification and visualised the posterior distributions to verify that they had been meaningfully updated by the data, indicating that the priors had not dominated inference. Model results are presented as effect estimates and 95% credible intervals, unless stated otherwise, and the influence of year is explored within the Supporting Information (Fig. S1). Evidence of an effect was determined via the direction and magnitude of the posterior distribution, as well as the proportion that lay away from zero (McElreath 2020).

To quantify the contribution of passive vs active nutrient sources to the two heterotroph taxa across the two reef habitats, we ran four Bayesian mixing models (Moore and Semmens 2008) following the MixSIAR model framework (Stock et al. 2018). For the sources, we calculated mean and standard deviation values for i) sponge as a proxy for passive, oceanic nutrients (Van Duyl et al. 2018) and ii) turf algae as a proxy for actively transferred, seabird-enriched nutrients due to higher ð^{15}N values near seabird islands, indicative of seabird-derived nutrient uptake (Graham et al. 2018). We restricted these analyses to data collected within Salomon atoll (Fig. 2) due to sources overlapping in isospace at the other atolls (see Fig. S2 for isospace plots of the Salomon atoll samples). The trophic discrimination factors were set to 0.1 ± 2.2 ‰ and 2.6 ± 2.0 ‰ for ð^{13}C and ð^{15}N, respectively, based on a literature review on discrimination factors for aquatic invertebrates (Brauns et al. 2018). The models were run with two process and residual error terms, and whether seabirds were present or absent on the adjacent island was included as a fixed factor. For these analyses, we used 'normal' Markov chain Monte Carlo parameters, i.e. a chain length of 100,000, with a burn of 50,000 and a thin of 50 for three chains. As before, model convergence was assessed using Gelman–Rubin as well as Geweke diagnostic tests.

Results

Nutrient pathways and sources

The different taxa generally occupied different core niche spaces (Fig. 3a) as well as different amounts of core niche space, demonstrated by differences in the areas of their sample size-corrected standard ellipses: macroalgae = 4.4; turf algae = 14.4; sponge = 12.2; hermit crab = 6.8; and gastropod = 10.4. Values of ð^{15}N were higher in hermit crabs (mean = 7.2 ± 0.9 ‰ sd) and gastropods (10.0 ± 1.5 ‰) than in macroalgae (5.5 ± 0.8‰), turf algae (5.8 ± 1.1‰), and sponge (6.1 ± 1.2‰) and ð^{13}C values also varied between taxa (macroalgae = −19.7 ± 2.0‰; turf algae = −13.6

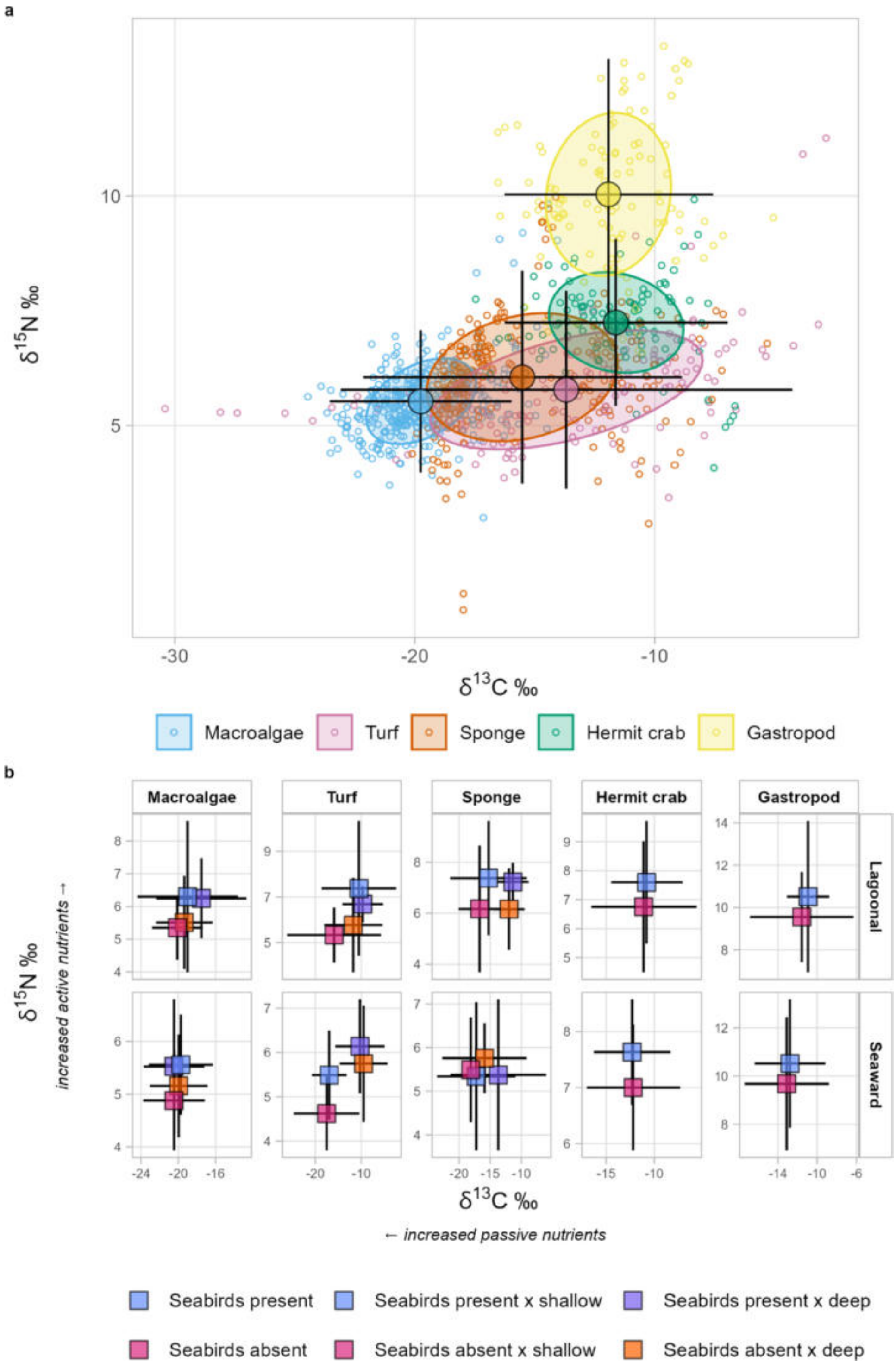

Fig. 3 Isotopic biplots of δ^{13}C and δ^{15}N for macroalgae, turf, sponge, hermit crabs, and gastropods sampled across reefs within the Chagos Archipelago. Ellipses are drawn using the normal distribution at a 50% confidence level, and large circles and squares represent mean values, and error bars represent standard deviation. Panel **a** illustrates the means and standard deviations of each taxon, with small open points representing individual samples, and **b** shows the means and standard deviations of each taxon from each reef habitat type (lagoonal or seaward) grouped by seabird presence and by depth for the basal food source samples (macroalgae *Halimeda* sp., turf algae, and sponge *Spheciospongia* spp.) and by seabird presence for the heterotroph samples (hermit crabs and gastropods) as these samples were aggregated by depth. Axes scales differ between the panels

± 4.8‰; sponge = −15.4 ± 3.4‰; hermit crab = −11.6 ± 2.36‰; and gastropod = −11.9 ± 2.2; Fig. 3a–b‰).

When pooled across the basal food source samples (macroalgae, turf algae, and sponge), values of ð^{13}C were not strongly impacted by the individual effects of reef habitat (estimate of the effect of seaward reefs = −0.22, CIs = −0.62, 1.07) or depth (estimate of the effect of deeper reefs = −1.07, CIs = −2.64, 0.56), though deeper seaward reefs generally had lower values, indicating increased reliance on passive, oceanic nutrients (estimate of effect of the interaction between seaward reefs and deeper depths = −1.83, CIs = −3.65, −0.01; Fig. 4a). Despite there not being an overall effect of just reef habitat on ð^{13}C values when pooled across sample types, a difference in the passive nutrient pathway

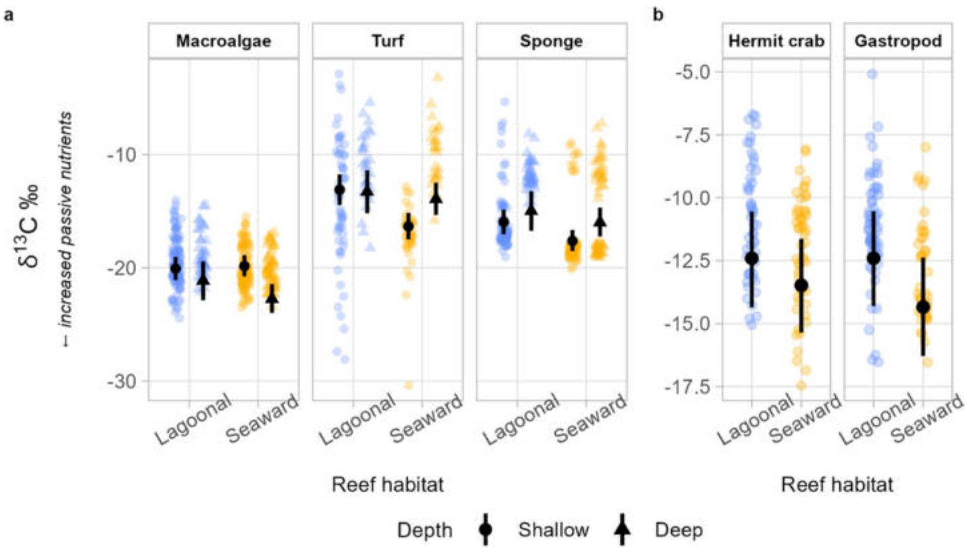

Fig. 4 Predicted conditional effects and 95% uncertainty intervals of **a)** basal food source δ^{13}C values under the effect of the interaction between sample type (macroalgae *Halimeda* sp., turf algae, and sponge *Spheciospongia* spp.), seabirds (present or absent), habitat (lagoonal or seaward reefs), and depth ('shallow' ca. 1–2 m and 'deep' ca. 6–8 m), and the fixed effect of year and **b)** heterotroph δ^{13}C values under the effect of the interaction between sample type (hermit crabs and gastropods), seabirds, and habitat, and the fixed effect of year. Conditional effects are displayed, with predictions marginalised over the effect of seabird presence and year. Translucent dots represent raw data

between lagoonal and seaward reefs (implied via lower ð^{13}C values at seaward reefs) was more evident within turf and sponge (estimate of effect of turf and seaward reefs = −3.46, CIs = −5.07, −1.87; estimate of effect of the interaction between sponge and seaward reefs = −1.9, CIs = −3.14, −0.67). Turf and sponge both had higher ð^{13}C values than macroalgae overall (estimate of effect of turf = 6.96, CIs = 5.75, 8.19; sponge = 4.12, CIs = 3.19, 5.05; Fig. 4a). The absence of birds did not influence ð^{13}C values (effect estimate = −0.7, CIs = −1.8, 0.45).

Gastropods and hermit crabs had similar ð^{13}C values to each other (effect estimate = 0, CIs = −1.04, 1.0). Values were generally lower (possibly indicative of a passive nutrient pathway) within samples from seaward reefs (effect estimate = −1.07, CIs = 0.04, −2.2; Fig. 4b), although credible intervals overlapped with zero, indicating uncertainty (Fig. S3a). As was observed within the basal food sources, the absence of seabirds did not influence ð^{13}C values within the heterotroph samples (effect estimate = 0.14, CIs = −2.34, 2.50).

Within the basal food source samples, values of ð^{15}N were higher in samples from around islands where seabirds were present, indicating an active nutrient pathway via the input of seabird-vectored nutrients (estimate of effect of seabirds being absent = −1.38, CIs = −2.27, −0.53; Fig. 3b; Fig. 5a). Basal food source ð^{15}N values were also higher within lagoonal reefs (estimate of the effect of seaward reefs = −0.69, CIs = −0.96, −0.43; Fig. 5a), but were not influenced by depth (effect estimate = 0, CIs = −0.49, 0.50). Values of ð^{15}N were highest within turf algae (effect estimate = 0.81, CIs = 0.43, 1.18) and in sponge (effect estimate = 0.73, CIs = 0.43, 1.02), in comparison with macroalgae.

To a lesser extent than in the basal food source samples, ð^{15}N values in the heterotrophs tended to be higher in samples from around islands with seabirds (estimate of effect of seabirds being absent = −0.53, CIs = −1.74, 0.7; Fig. 5b), although the 95% credible interval included zero, indicating uncertainty around this result (Fig. S3b). Contrary to basal food sources, values of ð^{15}N were not influenced by whether samples were from seaward or lagoonal reefs (estimate of effect of habitat = −0.01, CIs = −0.64, 0.66; Fig. 5b).

For the most part, our Bayesian stable isotope mixing models showed that gastropods and hermit crabs were primarily sustained by a nutrient pathway that we had hypothesised was a proxy for active nutrient transfer (Fig. 6). Both hermit crabs and gastropods sampled from seaward reefs surrounding islands where seabirds were present had a slight increased reliance on passively transferred nutrients than on seaward reefs when seabirds were absent (Fig. 6a & c). Within lagoonal reefs, there was very little difference in the contribution of active vs passive nutrients to hermit crabs between islands with seabirds vs those without seabirds (Fig. 6b). However, within gastropods from lagoonal reefs, there was a shift from the proxy for a passive, oceanic nutrient pathway (mean contribution estimate where seabirds were absent of the passive pathway = 0.59 and the active pathway = 0.41) to the proxy for a more active nutrient pathway when adjacent to islands where seabirds were

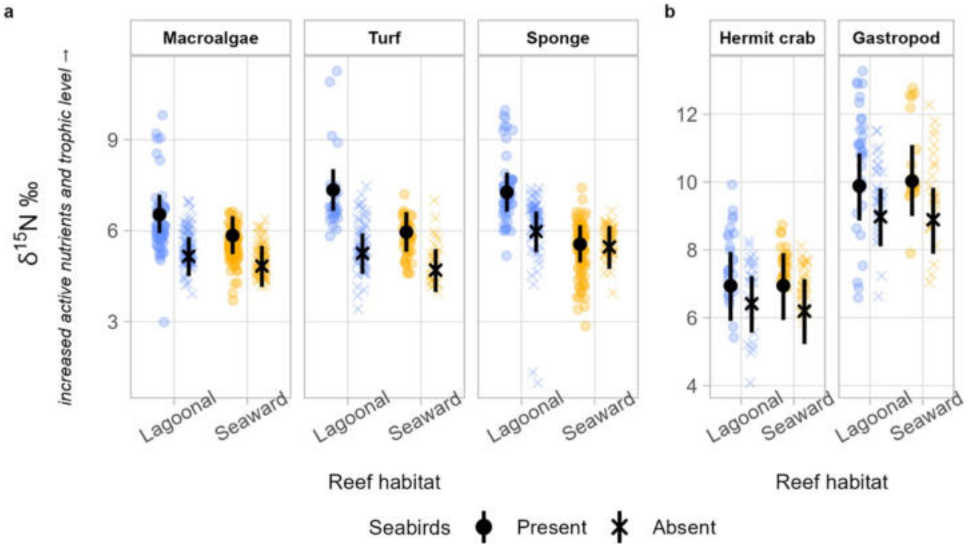

Fig. 5 Predicted conditional effects and 95% uncertainty intervals of **a** basal food source δ^{15}N values under the effect of the interaction between sample type (macroalgae *Halimeda* sp., turf algae, and sponge *Spheciospongia* spp.), seabirds (present or absent) habitat (lagoonal or seaward reefs), and depth ('shallow' ca. 1–2 m and 'deep' ca. 6–8 m), and the fixed effect of year and **b** heterotroph δ^{15}N values under the effect of the interaction between sample type (hermit crabs and gastropods), seabirds, and habitat, and the fixed effect of year. Conditional effects are displayed, with predictions marginalised over the effect of depth and year. Translucent dots represent raw data

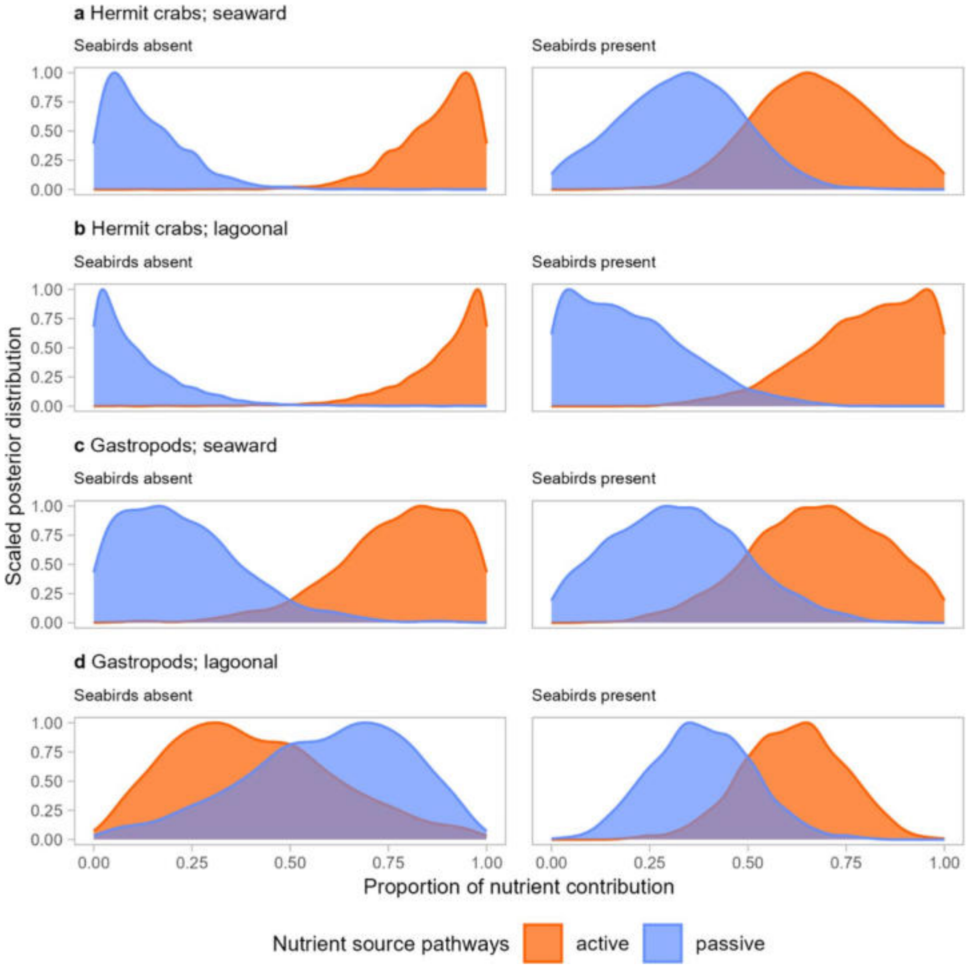

Fig. 6 Proportion of proxies for active and passive nutrient pathway contributions to heterotrophic taxa, as determined using Bayesian stable isotope mixing models. Scaled posterior density plots of the contribution of nutrient source pathways to **a** hermit crabs from seaward reefs adjacent to islands where seabirds were either absent or present, **b** hermit crabs from lagoonal reefs adjacent to islands where seabirds were either absent or present, **c** gastropods from seaward reefs adjacent to islands where seabirds were either absent or present, and **d** gastropods from lagoonal reefs adjacent to islands where seabirds were either absent or present

present (mean contribution estimate where seabirds were present of the passive pathway = 0.39 and the active pathway = 0.61; Fig. 6d).

Nutrient enrichment

Whilst there was no evidence of an effect of seabird presence on basal food source %N values (estimate of the effect of seabirds being absent = −0.25, CIs = −0.57, 0.07), nutrient levels were generally higher within lagoonal reefs (estimate of effect of seaward reefs = −0.39, CIs = −0.60, −0.19) and at deeper depths (effect estimate = 0.71, CIs = 0.33, 1.1; Fig. 7a). Values of %N were highest within samples of sponge (effect estimate = 0.89, CIs = 0.66, 1.12) and lowest within samples of turf algae (effect estimate = −0.95, CIs = −1.24, −0.66).

There was minimal impact of the presence of seabirds or habitat type (lagoonal vs seaward reef) on %N values within the heterotroph taxa (estimated effect of seabirds being absent = −0.48, CIs = −1.91, 0.96; estimated effect of seaward reefs = 0.12, CIs = −0.92, 1.16). Nitrogen percentages were higher within gastropods (effect estimate = 2.79, CIs = 1.81, 3.76) than in hermit crabs (Fig. 7b).

Lower carbon-to-nitrogen ratios can be indicative of higher nitrogen availability, and the ratio of C:N in basal food source samples was generally lower on reefs surrounding islands where there were seabird populations in comparison with those without seabirds (estimate of the effect of seabirds being absent = 0.2, CIs = 0.04, 0.37). For macroalgae, C:N ratios were lower within samples from lagoonal reefs (estimate of the effect of seaward reefs = 0.3, CIs = 0.18, 0.42) and at deeper depths (effect estimate = −0.27, CIs = −0.5, −0.04; Fig. 7c), though they were higher within

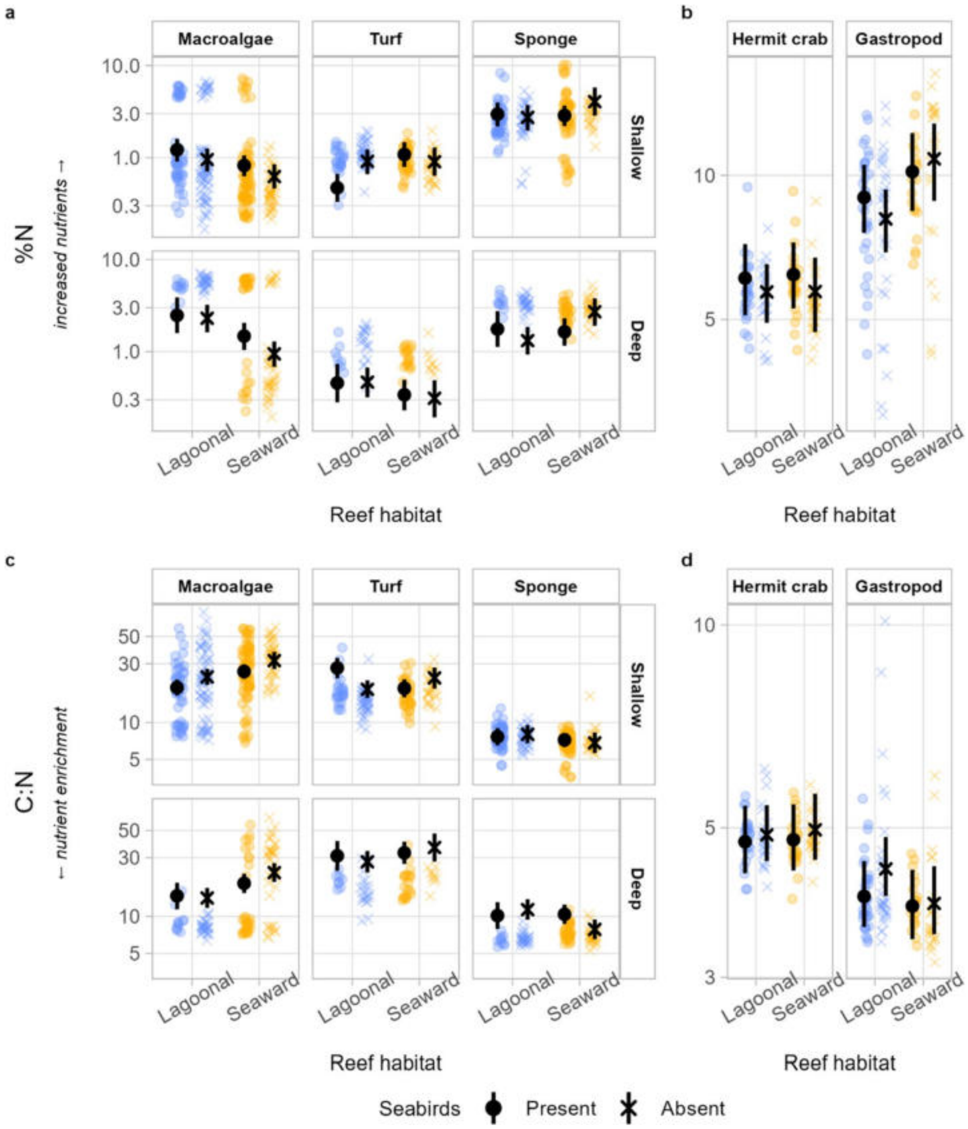

Fig. 7 Predicted conditional effects and 95% uncertainty intervals of **a** basal food source %N values (on log scale) under the effect of the interaction between sample type (macroalgae *Halimeda* sp., turf algae, and sponge *Spheciospongia* spp.), seabirds (present or absent), habitat (lagoonal or seaward reefs), and depth (‘shallow’ ca. 1–2 m and ‘deep’ ca. 6–8 m), and the fixed effect of year, **b** heterotroph %N values under the effect of the interaction between sample type (hermit crabs and gastropods), seabirds, and habitat, and the fixed effect of year, **c** basal food source C:N ratios (on log scale) under the effect of the interaction between sample type, seabirds, habitat, and depth, and the fixed effect of year, and **d** heterotroph C:N ratios under the effect of the interaction between sample type, seabirds, and habitat, and the fixed effect of year. Conditional effects are displayed, with predictions marginalised over the effect of year. Translucent dots represent raw data

turf from lagoonal reefs (estimate of the effect of the interaction between turf and seaward reefs = −0.68, CIs = −0.91, −0.46). Ratios of C:N were similar within sponge from both reef habitats (estimate of the effect of the interaction between sponge and seaward reefs = −0.36, CIs = −0.54, −0.18; Fig. 7c), although sponges collected from shallower depths had lower C:N ratios (estimate of the effect of the interaction between sponge and deeper depths = 0.55, CIs = 0.24, 0.87).

Finally, C:N ratios in heterotroph samples were similar between islands with and without seabirds (effect estimate = 0.02, CIs = −0.12, 0.16), as well as between seaward and lagoonal reefs (effect estimate = −0.01, CIs = −0.07, 0.08). Ratios of C:N were lower within gastropods than within hermit crabs (effect estimate = −0.19, CIs = −0.26, −0.12).

Discussion

Coral reefs are subsidised from a range of nutrient sources. Our study explores the relative contributions of different nutrient pathways to coral reef taxa by using the ð^{13}C, ð^{15}N, %N, and C:N values of samples collected from different coral reef habitats as proxies for passive and active nutrient transfer. Whilst patterns varied across taxa, we show that oceanic nutrients, moved via passive abiotic mechanisms such as currents and upwelling, may underpin elements of coral reef food webs, particularly at deeper depths on seaward reefs, whilst 'mobile link' organisms (i.e. seabirds that actively transport nutrients) can influence shallow and lagoonal coral reef food webs when present.

Lower ð^{13}C values were found in both basal food source samples and heterotrophic samples from seaward reefs, in comparison with those from lagoonal reefs (Fig. 4), indicating variation in the baseline carbon sources underpinning these habitats (Le Bourg et al. 2018), although the signal was weaker in heterotrophic taxa (Fig. S3a) and not evident in macroalgae. Plants and pelagic phytoplankton that inhabit high turbulence systems generally have low ð^{13}C values (France 1995), therefore influencing the ð^{13}C values of turf algae, sponge, and potentially other consumers that feed on phytoplankton and turf algae (Fig. 4a, b). Despite a lack of habitat effect, values of ð^{13}C were lowest within the macroalgae samples, indicative of the genus (*Halimeda*) being a fast-growing primary producer that must rapidly assimilate and photosynthesis carbon (Vogel et al. 2015). Moving forward, carbon isotope analysis of essential amino acids (a method robust to differing growth rates and other extrinsic impacts) and other integrative approaches (such as isotopically informed demographic modelling) are likely to provide novel insights into the different passive pathways that subsidise coral reef food webs (Larsen et al. 2015; Skinner et al. 2022; Brandl et al. 2025). For example, these techniques allow the traces of biogeochemical fluxes through food webs, as well as distinctions between different planktonic pathways, such as those that are either nearshore or offshore in origin (Skinner et al. 2021; Brandl et al. 2025). Compound-specific stable isotope analysis may also allow for further insights into seasonal variability in nutrient pathways (Skinner et al. 2022). Indeed, the Indian Ocean's complex current systems are influenced by climate, sea level, and temperature (Hood et al. 2017), and much of its climatology is dominated by differing monsoon seasons (Lévy et al. 2007). These cycles have cascading influences on biological productivity and nutrient pathways (Hood et al. 2017) and, whilst we do not yet know how long it takes for variation in environmental conditions to reveal changes in the isotopic values for many coral reef taxa (Skinner et al. 2022), they are likely the reason for interannual differences in ð^{13}C across both the basal food source and heterotroph samples (Fig. S1). In the face of unprecedented environmental change, understanding how passive nutrient pathways support coral reef ecosystems, and how this might vary between years, seasons, and with changing ocean current regimes, is vital (Hays 2017).

Regarding the active transport of nutrients to coral reefs, the uptake of seabird-derived nutrients was evident via higher ð^{15}N values within samples from around islands where seabirds were present, congruent with previous studies (Graham et al. 2018; Benkwitt et al. 2021a). This signal (higher ð^{15}N values as well as lower carbon-to-nitrogen ratios) was observed across all basal food source samples, indicating that the actively transferred seabird guano led to increased availability and, therefore, absorption of limited nutrients (i.e. nitrogen) by primary producers such as phytoplankton and algae (Figs. 5a and 7c). Though previous studies have identified evidence of active nutrient transfer within lagoonal reef taxa (Graham et al. 2018; Benkwitt et al. 2021a), we now also find higher ð^{15}N values in samples from seaward reefs adjacent to islands with seabirds in comparison with those without seabirds (Fig. 5). We did not observe an influence of depth on this signal, suggesting that the influence of seabird nutrient enrichment extended to deeper depths. Though the difference in the depth that we collected samples from was not large (ca. 1–2 m and ca. 6–8 m), the horizontal distance that this related to range from approximately 100 to 200 m. In previous studies, evidence of a seabird nutrient pathway has been observed within macroalgae, turf algae, and reef fish at least 300 m from shore (Benkwitt et al. 2021a). Future work should seek to interrogate the spatial footprint of seabird nutrient transfer, its pathways from land to sea, and its influence over the extents and depths of the reefs that surround atoll islands (Choisnard et al. 2024).

Though less strong than the patterns observed within the basal food source samples, heterotrophic taxa showed a tendency towards higher ð^{15}N values, consistent with trophic fractionation (Fig. 5b). Though there was uncertainty around the strength of this effect (Fig. S3b), gastropods, in particular, had high ð^{15}N values (Fig. 5b), particularly in 2023 in comparison with 2022 (Figure S1d), low C:N ratios (Fig. 7d), and underwent a shift from passive, oceanic nutrient pathways to more active nutrient pathways when inhabiting lagoonal reefs adjacent to islands where seabirds were present (Fig. 6d). This is likely due to gastropods grazing directly on enriched algae, similar to herbivorous detritivorous reef fishes which also exhibited higher ð^{15}N than omnivorous reef fishes when close to islands with seabirds (Andrades et al. 2024). The heightened relative reliance of gastropods on the proxy for the active pathway in lagoonal reefs where seabirds were present, therefore, likely reflects the heightened ability of seabird-derived nutrients to accumulate within lagoons in contrast with rapidly-flushed seaward reefs. Furthermore, these inter-habitat differences may also reflect shifts in gastropod diet between lagoonal and seaward reefs, indicative of variation in nutrient availability, community composition, and competitive interactions. Influxes of seabird nutrients to lagoonal reefs may therefore alleviate constraints that may have otherwise limited gastropods to forage on sources sustained by passive nutrient pathways.

The trophic pathways of omnivorous hermit crabs are likely longer and more complex than those of herbivorous gastropods and they, therefore, did not demonstrate the same switch to a reliance on an active nutrient pathway when in the presence of seabirds (Fig. 6a, b). Instead, hermit crabs always relied on the active nutrient pathway, highlighting the complexity of this system and the likelihood that though we considered ð15N a proxy for active nutrient transfer, the nutrient signal of the turf algae was also influenced by differing benthic nutrient sources, such as the substrate that it grows on (García-Seoane et al. 2023), and other interacting active mechanisms like fish excretion (Van Wert et al. 2023). How important the active pathway of seabird-derived nutrient enrichment is for heterotrophic taxa, both in terms of its overall contribution as well as its influence on their life histories, abundance, behaviour, and functioning, therefore, remains to be determined. For example, though increased seabird nutrients causes heightened growth rates in corals (Benkwitt et al. 2023; Lange and Benkwitt 2024) and altered demographic rates in parrotfish (Benkwitt et al. 2021b), knowledge gaps remain regarding its influence on other aspects of coral reef food webs. Understanding the influence of allochthonous nutrient inputs on the ecology of gastropods and hermit crabs is important due to the link that they provide between primary producers and secondary consumer invertivorous fishes, a group that composes a high proportion of fish biomass on coral reefs (Robinson et al. 2023). This is particularly timely during a period where, despite their importance (Steibl et al. 2024), tropical seabird abundances are in flux, with many species experiencing declines due to a multitude of threats, such as invasive species (Spatz et al. 2023). Despite these declines, certain populations are increasing due to conservation efforts, with the restoration of native vegetation and eradications of invasive species being particularly encouraged across atoll ecosystems (Dunn et al. 2024).

Though we hypothesised that samples from around islands with seabirds might have higher nutrient levels, seabird presence did not influence %N values. Instead, nitrogen levels were higher within lagoonal basal food source samples, and those collected from deeper depths (Fig. 7a). Perhaps, instead of being indicative of a seabird fertilisation signal, increased %N within this context was reflective of more passive nutrient enrichment mechanisms such as wave-driven circulation and sediment recycling (Adam et al. 2021), although these factors can interact (Thibault et al. 2022; Appoo et al. 2024b). It could be due to these interactions and our lack of ability to model this ecological variability, that our fitted values sometimes deviate from the raw data (Fig. 7a). Of the basal food sources, values of %N were highest within sponge (Fig. 7a), likely due to its high efficiency at taking up dissolved organic material together with planktonic food sources (de Goeij et al. 2013). Furthermore, macroalgae samples collected in 2022 had higher %N values than those collected during other years (and consequently lower C:N ratios; Fig. 7a, c; Figure S1), possibly due to heavier than normal rainfall inputting nutrients to the system (5 days of > 30 mm precipitation; www.meteoblue.com, Basel, Switzerland) or temporal variation in the reproductive ecology of *Halimeda* sp. (Clifton 1997; Clifton and Clifton 2002). Though these sources of ecological variability likely had consequences for variation in isotope values, we were only able to account for the effect of year as an additive term within our modelling (although see Supporting Information Fig. S1), which may have led to discrepancies between our model predictions and the raw data (Fig. 7a & c). Gastropods and hermit crabs also differed in their %N values (Fig. 7b), due to differences in their diet, nitrogen retention, and other aspects of their ecologies (Davis et al. 2015). Ultimately, it is likely that different taxa apportion different quantities of nutrients to a range of different avenues (e.g. into rapid growth). Though %N values did not seem to provide a good indicator through which to disentangle active vs passive nutrient transport within this context, it has been useful within other more vegetation-dominated ecosystems such as tropical mangrove and seagrass habitats, likely due to plants having more predictable and direct nutrient requirements (Appoo et al. 2024a).

Overall, we have highlighted that allochthonous nutrients are supplied to coral reef ecosystems via a combination of both active and passive pathways. Values of ð^{13}C indicated that passive pelagic nutrient transfer has an important role in sustaining elements of deeper, seaward coral reef food webs, whereas active pathways of nutrient transfer, namely that from nutrient-rich seabird guano, are more likely to influence coral reef organisms within lagoonal reefs. This being said, lagoonal reefs provide nursery habitat for a diversity of fishes which, later in their life cycles, migrate to seaward reefs, therefore potentially extending the benefits of active nutrient transfer across multiple reef habitats (Adams and Ebersole 2002). Further investigation into the ecological implications of variation in nutrient supply to various taxa will likely provide insights into how coral reefs might respond to environmental changes. Values of ð^{15}N, ð^{13}C, and carbon-to-nitrogen ratios, but perhaps not %N, provide useful tools through which to answer these questions. Human activity can lead to excess nutrients entering coral reef ecosystems (D'Angelo and Wiedenmann 2014) and disrupt natural nutrient pathways with wide-reaching consequences (Gunn et al. 2023). We, therefore, encourage continued research into the mechanisms behind these pathways as well as their impacts on ecosystem function. This is especially pertinent at a time when habitat restoration and eradications of invasive species are being encouraged as a way of restoring seabird populations across tropical island ecosystems, with potential benefits for nutrient connectivity and coral reef ecosystems (Dunn et al. 2024).

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Author's contribution RED, CEB, and NAJG conceived and designed the study. All authors collected the data. RED and L-LJ did the analyses. RED prepared the figures. RED wrote the first draft of the manuscript. All authors reviewed and contributed to the final version of the manuscript.

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Declarations

Competing interests The authors declare that they have no relevant competing interests to declare.

References

Adam TC, Burkepile DE, Holbrook SJ, Carpenter RC, Claudet J, Loiseau C, Thiault L, Brooks AJ, Washburn L, Schmitt RJ (2021) Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. Ecol Appl 31:e2227

Adams AJ, Ebersole JP (2002) Use of back-reef and lagoon habitats by coral reef fishes. Mar Ecol Prog Ser 228:213–226

Andrades R, Cardozo-Ferreira GC, Benevides LJ, Pimentel CR, Mancini PL, Ferreira CEL, Giarrizzo T, Joyeux J-C, Macieira RM (2024) Seabird guano reshapes intertidal reef food web in an isolated oceanic islet. Coral Reefs 43:347–355

Appoo J, Bunbury N, Jaquemet S, Graham NAJ (2024a) Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats. iScience 27:109404

Appoo J, Bunbury N, Letori J, Hector A, Gendron A, Graham NAJ, Rocamora G, Le Corre M, Jaquemet S (2024b) Seabird presence and seasonality influence nutrient dynamics of atoll habitats. Biotropica 56:e13354

Benkwitt CE, Carr P, Wilson SK, Graham NAJ (2022) Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. Proceedings of the Royal Society B: Biological Sciences 289:20220195

Benkwitt CE, D'Angelo C, Dunn RE, Gunn RL, Healing S, Mardones ML, Wiedenmann J, Wilson SK, Graham NAJ (2023) Seabirds boost coral reef resilience. Sci Adv 9:eadj0390

Benkwitt CE, Gunn RL, Le Corre M, Carr P, Graham NAJ (2021a) Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. Curr Biol 31:2704–2711

Benkwitt CE, Taylor BM, Meekan MG, Graham NAJ (2021b) Natural nutrient subsidies alter demographic rates in a functionally important coral-reef fish. Sci Rep 11:1–13

Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, Duffy JE (2019) Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Front Ecol Environ 17:445–454

Brandl SJ, Yan HF, Casey JM, Schiettekatte NMD, Renzi JJ, Mercière A, Morat F, Côté IM, Parravicini V (2025) A Seascape Dichotomy in the Role of Small Consumers for Coral Reef Energy Fluxes. Ecology 106:e70065

Brauns M, Boëchat IG, de Carvalho APC, Graeber D, Gücker B, Mehner T, von Schiller D (2018) Consumer-resource stoichiometry as a predictor of trophic discrimination (Δ^{13}C, Δ^{15}N) in aquatic invertebrates. Freshw Biol 63:1240–1249

Bürkner P-C (2017) brms: An R Package for Bayesian Multilevel Models Using Stan. J Stat Softw 80:1–28

Carr P, Trevail A, Bárrios S, Clubbe C, Freeman R, Koldewey HJ, Votier SC, Wilkinson T, Nicoll MAC (2021) Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. Restor Ecol 29:e13386

Carr P, Votier S, Koldewey H, Godley B, Wood H, Nicoll MAC (2020) Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conserv Int 31:14–34

Choisnard N, Duprey NN, Wald T, Thibault M, Houlbrèque F, Foreman AD, Cuet P, Guillaume MMM, Vonhof H, Sigman DM, Haug GH, Maguer J-F, L'Helguen S, Martínez-García A, Lorrain A (2024) Tracing the fate of seabird-derived nitrogen in a coral reef using nitrate and coral skeleton nitrogen isotopes. Limnol Oceanogr 69:309–324

Clifton KE (1997) Mass spawning by green algae on coral reefs. Science 275:1116–1118

Clifton KE, Clifton LM (2002) The phenology of sexual reproduction by green algae (Byopsidales) on Caribbean coral reefs. J Phycol 35:24–34

D'Angelo C, Wiedenmann J (2014) Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Curr Opin Environ Sustain 7:82–93

Davis JP, Pitt KA, Connolly RM, Fry B (2015) Community structure and dietary pathways for invertebrates on intertidal coral reef flats. Food Webs 3:7–16

Dedman S, Moxley JH, Papastamatiou YP, Braccini M, Caselle JE, Chapman DD, Cinner JE, Dillon EM, Dulvy NK, Dunn RE, Espinoza M, Harborne AR, Harvey ES, Heupel MR, Huveneers C, Graham NAJ, Ketchum JT, Klinard NV, Kock AA, Lowe CG, MacNeil MA, Madin EMP, McCauley DJ, Meekan MG, Meier AC, Simpfendorfer CA, Tinker MT, Winton M, Wirsing AJ, Heithaus MR (2024) Ecological roles and importance of sharks in the Anthropocene Ocean. Science 385:adl2362

Dunn RE, Benkwitt CE, Maury O, Barrier N, Carr P, Graham NAJ (2024) Island restoration to rebuild seabird populations and amplify coral reef functioning. Conserv Biol 39:e14313

Dunn RE, Bradley D, Heithaus MR, Caselle JE, Papastamatiou YP (2022) Conservation implications of forage base requirements of a marine predator population at carrying capacity. iScience 25:103646

Fox MD, Williams GJ, Johnson MD, Radice VZ, Zgliczynski BJ, Kelly ELA, Rohwer FL, Sandin SA, Smith JE (2018) Gradients in Primary Production Predict Trophic Strategies of Mixotrophic Corals across Spatial Scales. Curr Biol 28:3355-3363.e4

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae:foodweb implications. Mar Ecol Prog Ser 124:307–312

García-Seoane R, Viana IG, Bode A (2023) Using MixSIAR to quantify mixed contributions of primary producers from amino acid δ15N of marine consumers. Mar Environ Res 183:105792

de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342:108–110

Gove JM, McManus MA, Neuheimer AB, Polovina JJ, Drazen JC, Smith CR, Merrifield MA, Friedlander AM, Ehses JS, Young CW, Dillon AK, Williams GJ (2016) Near-island biological hotspots in barren ocean basins. Nat Commun 7:10581

Graham NAJ, Wilson SK, Carr P, Hoey AS, Jennings S, MacNeil MA (2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559:250–253

Gunn RL, Benkwitt CE, Graham NAJ, Hartley IR, Algar AC, Keith SA (2023) Terrestrial invasive species alter marine vertebrate behaviour. Nat Ecol Evol 7:82–91

Hamner WM, Colin PL, Hamner PP (2007) Export–import dynamics of zooplankton on a coral reef in Palau. Mar Ecol Prog Ser 334:83–92

Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, Planktivorous Fish, and Water Currents on a Windward Reef Face: Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Hays GC (2017) Ocean currents and marine life. Curr Biol 27:R470–R473

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Sannassy Pilly S, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MA, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard C, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier S, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H, Curnick DJ (2020) A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. Mar Biol 167:159

Hood RR, Beckley LE, Wiggert JD (2017) Biogeochemical and ecological impacts of boundary currents in the Indian Ocean. Prog Oceanogr 156:290–325

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Kéfi S, Berlow EL, Wieters EA, Navarrete SA, Petchey OL, Wood SA, Boit A, Joppa LN, Lafferty KD, Williams RJ, Martinez ND, Menge BA, Blanchette CA, Iles AC, Brose U (2012) More than a meal… integrating non-feeding interactions into food webs. Ecol Lett 15:291–300

Kumar GS, Prakash S, Ravichandran M, Narayana AC (2016) Trends and relationship between chlorophyll-a and sea surface temperature in the central equatorial Indian Ocean. Remote Sens Lett 7:1093–1101

Lange ID, Benkwitt CE (2024) Seabird nutrients increase coral calcification rates and boost reef carbonate production. Sci Rep 14:24937

Larsen T, Bach LT, Salvatteci R, Wang YV, Andersen N, Ventura M, McCarthy MD (2015) Assessing the potential of amino acid ^{13}C patterns as a carbon source tracer in marine sediments: effects of algal growth conditions and sedimentary diagenesis. Biogeosciences 12:4979–4992

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Le Bourg B, Letourneur Y, Bănaru D, Blanchot J, Chevalier C, Mou-Tham G, Lebreton B, Pagano M (2018) The same but different: Stable isotopes reveal two distinguishable, yet similar, neighbouring food chains in a coral reef. J Mar Biol Assoc UK 98:1589–1597

Lévy M, Shankar D, André J-M, Shenoi SSC, Durand F, de Boyer Montégut C (2007) Basin-wide seasonal evolution of the Indian Ocean's phytoplankton blooms. J Geophys Res 112:

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

Lundberg J, Moberg F (2003) Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. Ecosystems 6:87–98

McCreary JP Jr, Kundu PK, Molinari RL (1993) A numerical investigation of dynamics, thermodynamics and mixed-layer processes in the Indian Ocean. Prog Oceanogr 31:181–244

McElreath R (2020) Statistical Rethinking: A Bayesian Course with Examples in R and Stan. Chapman & Hall, London

McInturf AG, Pollack L, Yang LH, Spiegel O (2019) Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? Biol Rev Camb Philos Soc 94:1761–1773

McMahon KW, Hamady LL, Thorrold SR (2013) Ocean ecogeochemistry: a review. Oceanogr Mar Biol Annu Rev 51:327–374

Montoya JM, Pimm SL, Solé RV (2006) Ecological networks and their fragility. Nature 442:259–264

Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. Ecol Lett 11:470–480

Mumby PJ, Hastings A (2007) The impact of ecosystem connectivity on coral reef resilience. J Appl Ecol 45:854–862

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Peller T, Altermatt F (2024) Invasive species drive cross-ecosystem effects worldwide. Nat Ecol Evol

R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Robinson JPW, Darling ES, Maire E, Hamilton M, Hicks CC, Jupiter SD, Aaron MacNeil M, Mangubhai S, McClanahan T, Nand Y, Graham NAJ (2023) Trophic distribution of nutrient production in coral reef fisheries. Proc Biol Sci 290:20231601

Royston JP (1982) Algorithm AS 181: The W Test for Normality. J R Stat Soc Ser C Appl Stat 31:176–180

Skinner C, Cobain MRD, Zhu Y, Wyatt ASJ, Polunin NVC (2022) Progress and direction in the use of stable isotopes to understand complex coral reef ecosystems: A review. Oceanography and Marine Biology: An Annual Review, Volume 60. CRC Press, pp 373–432

Skinner C, Mill AC, Fox MD, Newman SP, Zhu Y, Kuhl A, Polunin NVC (2021) Offshore pelagic subsidies dominate carbon inputs to coral reef predators. Sci Adv 7:3792

Skinner C, Newman SP, Mill AC, Newton J, Polunin NVC (2019) Prevalence of pelagic dependence among coral reef predators across an atoll seascape. J Anim Ecol 88:1564–1574

Small A, Adey WH, Spoon D (1998) Are current estimates of coral reef biodiversity too low? The view through the window of a microcosm. Atoll Res Bull 458:1–20

Spatz DR, Jones HP, Bonnaud E, Kappes P, Holmes ND, Guzmán YB (2023) Invasive species threats to seabirds. In: Young L, VanderWerf E (eds) Conservation of Marine Birds. Elsevier, pp 97–130

Spring D, Fox M, Green M, Guillaume-Castel R, Jacobs Z, Roche R, Turner J, Williams G (*In revision*) Oceanographic and atmospheric drivers of localized upwelling across an ocean coral reef archipelago. Limnol Oceanogr.

Spring DL, Williams GJ (2023) Influence of upwelling on coral reef benthic communities: a systematic review and meta-analysis. Proc Biol Sci 290:20230023

Steibl S, Steiger S, Wegmann AS, Holmes ND, Young HS, Carr P, Russell JC (2024) Atolls are globally significant sites for tropical seabirds. Nat Ecol Evol 1907–1915

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Stock BC, Semmens BX (2016) MixSIAR GUI User Manual.

Thibault M, Houlbreque F, Duprey NN, Choisnard N, Gillikin DP, Meunier V, Benzoni F, Ravache A, Lorrain A (2022) Seabird-derived nutrients supply modulates the trophic strategies of mixotrophic corals. Front Mar Sci 8:

Van Duyl FC, Mueller B, Meesters EH (2018) Spatio-temporal variation in stable isotope signatures (δ13C and δ15N) of sponges on the Saba Bank. PeerJ 6:e5460

Van Wert JC, Ezzat L, Munsterman KS, Landfield K, Schiettekatte NMD, Parravicini V, Casey JM, Brandl SJ, Burkepile DE, Eliason EJ (2023) Fish feces reveal diverse nutrient sources for coral reefs. Ecology 104:e4119

Vogel N, Fabricius KE, Strahl J, Noonan SHC, Wild C, Uthicke S (2015) Calcareous green alga *Halimeda* tolerates ocean acidification conditions at tropical carbon dioxide seeps. Limnol Oceanogr 60:263–275

Votier SC, Corcoran G, Carr P, Dunn RE, Freeman R, Nicoll MAC, Wood H, Trevail AM (2024) Geolocation and immersion loggers reveal year-round residency and facilitate nutrient deposition rate estimation of adult red-footed boobies in the Chagos Archipelago, tropical Indian Ocean. J Avian Biol 2024:

Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. J Open Source Softw 4:1686

Wilson LJ, Fulton CJ, Hogg AM, Joyce KE, Radford BTM, Fraser CI (2016) Climate-driven changes to ocean circulation and their inferred impacts on marine dispersal patterns. Glob Ecol Biogeogr 25:923–939

Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NAJ (2019) Coral reef ecosystem services in the Anthropocene. Funct Ecol 33:1023–1034

Young HS, McCauley DJ, Dunbar RB, Dirzo R (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. Proc Natl Acad Sci USA 107:2072–2077