



## Fine-scale foraging ecology and habitat use of sympatric green and hawksbill turtles in the Western Indian ocean

Cheryl L. Sanchez<sup>a,b,c</sup>, Paolo Casale<sup>a,\*</sup>, Nancy Bunbury<sup>c,d</sup>, Luke A'Bear<sup>c</sup>, Veronique Banane<sup>c</sup>, Frances Benstrong<sup>c</sup>, Maria Bielsa<sup>c</sup>, Christopher W. Jones<sup>c</sup>, Anna Koester<sup>c</sup>, Susan Murasko<sup>b</sup>, Martin C. van Rooyen<sup>c</sup>, Frauke Fleischer-Dogley<sup>c</sup>, Simona A. Ceriani<sup>b</sup>

<sup>a</sup> Department of Biology, University of Pisa, Via A. Volta 6, 56126 Pisa, Italy

<sup>b</sup> Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Saint Petersburg, FL, USA

<sup>c</sup> Seychelles Islands Foundation, Mahé, P.O. Box 853, Victoria, Seychelles

<sup>d</sup> Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR10 9FE, UK

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### ABSTRACT

Using stable isotope analysis of carbon and nitrogen of turtle tissues and putative prey items, we investigated the diet of immature green turtles and hawksbill turtles foraging in the lagoon of Aldabra Atoll, a relatively undisturbed atoll in the southern Seychelles. Aldabra offers a unique environment for understanding sea turtle ecology. Green turtles mostly consumed seagrass and brown algae while hawksbill turtles mainly consumed mangroves and invertebrates. Green turtles showed a dietary shift with size (a proxy for age). There was minimal niche overlap between species and evidence of small-scale foraging site fidelity with turtle tissue reflecting site-specific prey. This highlights the ecological importance of seagrass and mangrove habitats and suggests that turtles play a role in controlling algal biomass at Aldabra. This study is the first to closely examine the foraging ecology of these sympatric turtle species in the Western Indian Ocean, a globally important region for both species.

### 1. Introduction

Green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) commonly share coastal foraging areas (Bjorndal 1996; Stringell et al., 2016; Clyde-Brockway et al., 2022; Sanchez et al., 2023) and can have an impact on the benthos. For instance, foraging green turtles influence primary producer community structure and dynamics (Bjorndal 1996; Fourqurean et al., 2010; Burkholder et al., 2013). On the other hand, foraging hawksbill turtles create space for coral settlement (Meylan 1988; Hill 1998; León and Bjorndal 2002; Bjorndal and Jackson 2003).

Dietary plasticity occurs in turtle foraging aggregations globally (Esteban et al., 2020); green turtle diet varies from mostly herbivorous (seagrass or macroalgae dominated, or in-between) to large percentages of animal matter (Fukuoka et al., 2016; Esteban et al., 2020; Piovano et al., 2020). At foraging sites, diet is usually dominated by the most common food resource (Esteban et al., 2020), although there are exceptions, such as in Shark Bay, Australia, where green turtle diet is

mostly macroalgae and gelatinous animals, despite abundant seagrass meadows (Burkholder et al., 2011). Hawksbill turtles specialize in eating sponges (Meylan 1988; Hill 1998; León and Bjorndal 2002) but also eat other invertebrates (von Brandis et al., 2014; Méndez-Salgado et al., 2020; Reynolds et al., 2023) and vegetation (Bell 2013).

In marine megafauna foraging areas, identifying dietary composition is crucial for understanding their ecological functions, trophic positions, and whether there is competition for resources (Duffy et al., 2007). The habitats used by green and hawksbill turtles overlap (Bjorndal and Bolten 2010; Gaos et al., 2012, 2017), and may overlap more as coral reefs decline (Bjorndal and Bolten 2010). Sympatric species can reduce resource competition through distinct diets (Stringell et al., 2016; Ferreira et al., 2018), or by shifting dietary resources with age (Miller and Rudolf 2011). When resources are limited, both interspecific and intraspecific competition can occur, potentially affecting growth, survival, or reproductive success, or triggering changes in resource consumption (Schoener 1974). Shifting resources might have implications for ecosystem dynamics, subsequently modifying the functional role of

\* Corresponding author.

E-mail address: [paolo.casale@unipi.it](mailto:paolo.casale@unipi.it) (P. Casale).

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certain species within their habitats (Wong and Candolin 2015).

There are various ways to assess turtle diet, including through direct observation (e.g., SCUBA, snorkel), extractive methods (gut contents of dead turtles, esophageal lavage), and indirect methods (biogeochemical, e.g., stable isotope analysis; SIA; Esteban et al., 2020). SIA is a powerful tool for assessing diet and trophic ecology (Haywood et al., 2019). It has been used to infer site fidelity and identify newly recruited animals (Vélez-Rubio et al., 2016; Piovano et al., 2020); estimate the relative importance of different dietary items (Piovano et al., 2020; Gama et al., 2021; Reynolds et al., 2023); identify changes in diet with the size of individuals (Shimada et al., 2014; Vélez-Rubio et al., 2016; Burgett et al., 2018); and quantify the isotopic niche that species occupy (Newsome et al., 2007; Weber et al., 2023).

Green turtles and hawksbill turtles are listed on the IUCN Red List, respectively, as Endangered (Seminoff et al., 2015) and Critically Endangered (Mortimer and Donnelly 2008). Where these species co-occur at foraging grounds, they show diet partitioning, as seen in the Caribbean (Bjorndal and Bolten 2010; Stringell et al., 2016) and Atlantic (Martins et al., 2020). Since diet can be influenced by various factors, such as water temperature, habitat health (e.g., level of degradation) and run-off (Santos et al., 2015; Esteban et al., 2020), determining dietary composition provides important insights into the ecological roles of these turtles. A more detailed understanding of these roles is particularly valuable from undisturbed systems. This information is needed to predict turtle population dynamics and ecosystem changes with environmental changes and population increases (Hamann et al., 2010).

In the Western Indian Ocean, Aldabra Atoll in Seychelles is a rare example of a relatively undisturbed ecosystem. The closest inhabited island (Madagascar) is ca. 400 km away and the main Seychelles islands lie >1000 km north. Aldabra's remoteness and protection (inscribed UNESCO World Heritage Site in 1982; UNESCO 2022) have kept the atoll free of fishing for nearly 40 years besides a small, highly monitored fishery by the team at the research station, and it now has among the highest fish biomasses in Seychelles, particularly of apex predators (Friedlander et al., 2015), as well as thriving green and hawksbill turtle populations (Pritchard et al., 2022; Sanchez et al., 2023).

Aldabra falls within Southwest Indian (SWI) regional management units (RMUs) for green and hawksbill turtles (Wallace et al., 2023). These RMUs include important nesting populations for both species (Mortimer and Donnelly 2008; Seminoff et al., 2015), with an estimated 103,000–144,000 green turtle and 12,000–16,000 hawksbill clutches per year (Mortimer et al., 2020). The majority of hawksbill nests occur in Seychelles and Chagos Archipelago (Mortimer et al., 2020), with Aldabra accounting for >10% of green turtle RMU nesters (Mortimer et al., 2020; Pritchard et al., 2022). Few in-water estimates exist for immature turtles in the RMU (Stokes et al., 2023; Sanchez et al., 2023) and little is known about foraging ecology (von Brandis et al., 2014). More broadly, there is a lack of information from the Indian Ocean concerning turtles and SIA; SIA studies have great potential in increasing turtle research and conservation (Pearson et al., 2017; Figgenger et al., 2019; Haywood et al., 2019).

With substantial aggregations of foraging green and hawksbill turtles within Aldabra's lagoon (Sanchez et al., 2023), we aimed to: (i) estimate contributions of different prey groups to the diet of both species; (ii) assess if turtle diet changes between younger and older turtles by using size group as a proxy for age, since size is a good predictor of age (i.e., Mayne et al., 2022); (iii) estimate the niche space of both species; and (iv) assess site fidelity to local sites of Aldabra. With Aldabra's minimal human pressure and a relatively intact, healthy marine ecosystem, our predictions are based on the assumption that resources are not limited and that turtles are not at carrying capacity (recovery from substantial population declines is ongoing; Pritchard et al., 2022). The results will provide important information for conservation management of the turtles in this RMU.

## 2. Materials and methods

### 2.1. Study site

Aldabra (9°25'S, 46°20'E) is a remote atoll (34 × 14 km) in the Western Indian Ocean managed by the Seychelles Islands Foundation (SIF), with only a small team of staff (<20 people) residing at the research station on the atoll. Aldabra consists of four main islands surrounding a large, shallow lagoon (203 km<sup>2</sup>, <3 m deep) with deeper channels to the open ocean. Aldabra has a 2–3 m tidal range (Farrow and Brander 1971). The climate is driven by two main seasons; the north-west monsoon (warmer, wetter; approx. Nov–Mar; hereafter “wet season”) and the south-east trade winds (cooler, drier; Apr–Oct; hereafter “dry season”) (Stoddart and Mole 1977).

Nine sampling sites were selected based on the heterogeneity of the study area (Fig. 1; A–I): five in the lagoon (A–E) and four outside (F–I). All sites were systematically sampled for potential prey items during the wet season; sites A and C in the lagoon were also sampled in the dry season for potential prey items at a smaller scale to examine seasonal isotopic variation. Sites were based on locations that are part of a long-term capture-mark-recapture program (Sanchez et al., 2023) and the lagoon habitat map (Hamylton et al., 2018), to ensure habitat type was represented. Turtles were captured at four sites (A, B, C and E) year-round. Site D (which is not a capture location in the long-term capture-mark-recapture program) was not a turtle capture site but was sampled for putative prey items to ensure representation of different habitats of the lagoon. Turtles have been observed at site D but not in the density seen at the capture sites used in this study (pers. obs). Potential prey items were sampled at multiple stations (2–5) at all sites (Fig. 1; A–I).

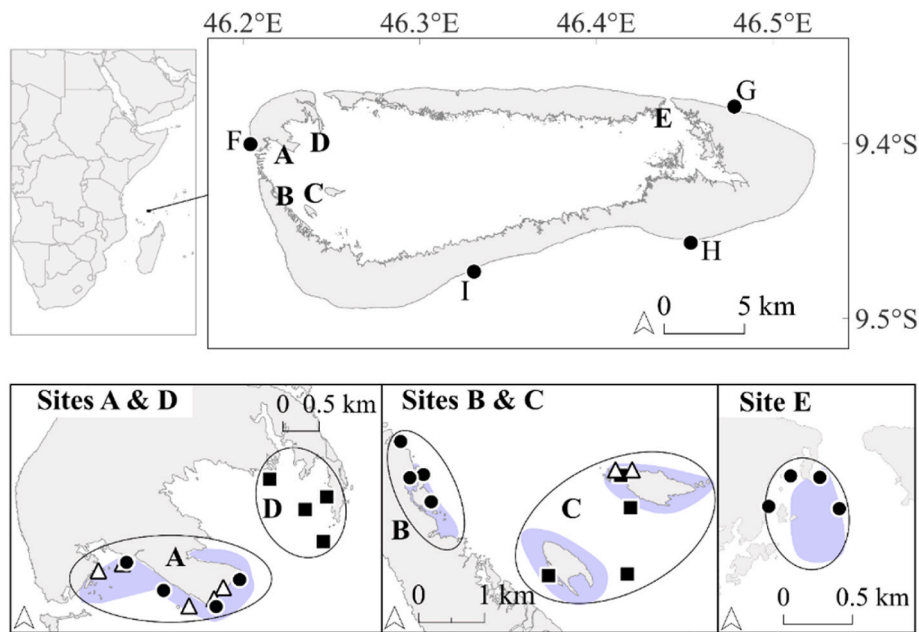
### 2.2. Turtle sample collection

Turtle skin tissues for stable isotope analysis were taken from 9 Feb 2021–7 April 2022. Turtles were captured by the ‘rodeo’ method (Ehrhart and Ogren 1999) or by walking along non-reef patches at low tide, as part of the long-term in-water monitoring program. Once captured, curved carapace length notch-to-tip (CCLn-t; cm) was measured using a flexible tape measure to the nearest 0.1 cm (Bolten 1999). Inconel tags (National & Tag Co. Style 681) were applied to both front flippers of smaller turtles, and titanium tags (Stockbrands Co., Aust. ‘Turtle’ tags) to turtles >10 kg. If turtles were recaptured, tag numbers were recorded. A tissue sample <3 mm<sup>2</sup> of the top epidermal layer (hereafter referred to as skin sample) was taken from between the shoulder and the neck with a sterile razor blade. Skin samples were stored in iodized NaCl.

### 2.3. Prey item collection

Vegetation and animal items (referred to as prey items) were targeted based on reports in the literature for the diet of both turtle species and what was available at the nine stations (Table 1). Prey items were collected by snorkeling, walking at low tide, or by SCUBA (<7 m depth for the outside reef). During the wet season (Nov–Dec 2021, Mar 2022), prey items were collected at five lagoon sites (Fig. 1; A–E), and four stations were sampled per site. At each station, 3–5 blades per cluster of the two most common seagrass species each were collected. For each algae group, one branch from three different clusters were collected, and two mangrove propagules and two leaves collected. Two each of sponges, tunicates, snails, and crabs were collected. Tissue was taken from sponge and zoanthid, while whole snails and crabs were collected. Two stations at each of the four reef sites (F–I) were sampled. Five samples per station were targeted for each taxon (except algae and mangroves). Sites were sampled less intensively (less items were collected due to logistic reasons) during the dry season (June 2021) at two lagoon sites (A, C; Fig. 1), to account for seasonal variation.

At each station, prey items were collected within a 20-m radius of an



**Fig. 1.** Top row: Aldabra’s location in the Western Indian Ocean, and the nine prey sampling sites, A–I: A–E are in the lagoon; F–I along the outer reef of the atoll. Bottom row: Several stations occurred within a site. Wet season stations (A–E) are filled with black, and sites in the same bottom panel are differentiated by circles or squares; dry season stations (triangles; sites A and C) are filled with white. Turtle capture sites (A, B, C and E) are shown in purple shading.

**Table 1**

Putative prey item categories collected for stable isotope analysis. If multiple species were collected, bold indicates the most commonly found/collected when applicable. Common name is given when species was not identified.

Phylum	Class	Category	Species
Porifera		Sponge	Sponge
Chordata	Asciacea	Tunicate	<b><i>Didemnum mole</i></b> <i>Didemnidae</i> spp.
		Zoanthid	<i>Palythoa caesia</i>
Cnidaria	Hexacorallia		
Mollusca	Gastropoda	Snail	Snails
Arthropoda	Crustacea	Crab	Crab
			Hermit crab
Tracheophyta	Monocots	Mangrove	<i>Rhizophora mucronata</i> <i>Avicennia marina</i>
		Seagrass	<i>Cymodocea</i> spp. <i>Halodule</i> spp. <i>Halophila ovalis</i> <i>Thalassia hemprichii</i> <i>Thalassodendron ciliatum</i> <i>Dictyurus purpurascens</i>
Rhodophyta	Florideophyceae	Red algae	<i>Eucheuma</i> spp. <i>Gracilaria</i> spp. <i>Hypnea</i> spp. <i>Jania</i> spp. <i>Leveillea jungermannioides</i> <i>Sarconema filiforme</i>
Chlorophyta	Ulvophyceae	Green algae	<b><i>Halimeda</i> spp.</b> <i>Boergesenia forgesii</i> <i>Rhizoclonium grande</i>
Ochrophyta	Phaeophyceae	Brown algae	<b><i>Padina</i> spp.</b> <i>Polycladia myrica</i> <i>Sargassum oligocystum</i> <i>Turbinaria conoides</i>

anchored boat and were kept on ice. In the lab, samples were rinsed and sand/epibiota removed with a razor blade (Burkholder et al., 2011; Burgett et al., 2018). Vegetation items were dried in a drying oven at 60 °C until dry and stored in aluminum foil packets. Crab and snail muscle was removed and either immersed in iodized NaCl or dried (if small amount; first thoroughly rinsed) until analysis.

#### 2.4. Stable isotope preparation and analysis

Turtle tissue and putative prey items were rinsed, dried and homogenized for stable isotope analysis (SIA) following standard procedures (Ceriani et al., 2014, 2015; Gillis et al., 2018; Ceriani et al. 2014, 2014, 2015, 2015, 2015). Each tissue underwent successive deionized water baths to remove NaCl then the targeted surface epidermis (referred to as ‘skin’) was separated from any dermal tissue underneath. Skin tissue was placed in a drying oven overnight (>12 h) at 60 °C. Each tissue was cut into several small pieces. Vegetation samples were visually inspected under the microscope for any epibiota (which was removed if found). Half of calcified samples (i.e., Halimeda) were submerged in hydrochloric acid until no reaction was seen, then thoroughly rinsed with deionized water. Samples were placed in the drying oven overnight, and a subsample of each vegetation cluster was combined and homogenized per seagrass species or category (i.e., red algae) for all others, per station, to form a single sample for that time/site (Burkholder et al., 2011). Animals were soaked individually in deionized water for 2 h, and the water was changed and soaked overnight (ca. 12 h). Water was changed again for 2 h. Salinity was checked and was never higher than the deionized water after this process. Each animal was inspected under the microscope and any biota was removed. Half of each zoanthid sample was decalcified following the same process as vegetation above. Samples were lyophilized and each animal homogenized separately.

For all samples, lipids were extracted using an accelerated solvent extractor (Model 200, Dionex) with petroleum ether. Each batch underwent 5 min of heating followed by 5 min of static purging, three times. The following amounts were weighed with a microbalance and sealed in tin capsules: 0.18–0.57 mg turtle skin, 0.2–1.13 mg crab/hermit crab, 0.15–0.80 mg snail, 0.51–0.77 mg sponge, 0.53–3.33 mg tunicate, 0.51–3.05 mg zoanthid. Analyses for % carbon, % nitrogen,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  values were performed at the Marine Environmental Chemistry Laboratory (MECLab) at the University of South Florida College of Marine Science (St. Petersburg, FL, USA), where samples were converted to N<sub>2</sub> and CO<sub>2</sub> using a Carlo-Erba NA EA1108 Elemental Analyzer (Thermoquest Italia, S. p.A., Rodano, Italy) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan, Bremen, Germany). Stable isotope ratios were

expressed in conventional notation as parts per thousand (‰) according to the following equation:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1,000$$

where X is  $^{15}\text{N}$  or  $^{13}\text{C}$ , and R represents the corresponding ratios of heavy to light isotopes ( $^{15}\text{N}:^{14}\text{N}$  and  $^{13}\text{C}:^{12}\text{C}$ ) in the sample and international standard, respectively. Raw measurements were calibrated relative to VPDB ( $\delta^{13}\text{C}$ ) and AT-Air ( $\delta^{15}\text{N}$ ) with certified reference materials USGS 41a ( $\delta^{13}\text{C} = 36.55 \pm 0.08$  ‰,  $\delta^{15}\text{N} = 47.77 \pm 0.15$  ‰, N = 9.52 ‰, C = 40.81 ‰, C:N [molar] = 5.0) and USGS 40 ( $\delta^{13}\text{C} = -26.39 \pm 0.04$  ‰,  $\delta^{15}\text{N} = -4.52 \pm 0.06$  ‰, N = 9.52 ‰, C = 40.81 ‰, C:N [molar] = 5.0). Estimates of analytical precision were obtained by replicate (n = 58) measurements of an internal laboratory reference material (NIST1577b Bovine liver,  $\delta^{13}\text{C} = -21.7 \pm 0.1$  ‰,  $\delta^{15}\text{N} = 7.8 \pm 0.2$  ‰, % N =  $10.0 \pm 0.2$  ‰, % C =  $48.0 \pm 0.9$  ‰, C:N [molar] =  $5.6 \pm 0.1$ ) and yielded a precision (reflecting  $\pm 1$  SD)  $\leq 0.1$  ‰ for  $\delta^{13}\text{C}$  and  $\leq 0.1$  ‰ for  $\delta^{15}\text{N}$ . Vegetation and animal tissue precision was  $0.2 \pm 0.1$  ‰ (‰N),  $3.0 \pm 0.7$  ‰ (‰C),  $0.4 \pm 0.1$  ‰ (C:N mass),  $0.4 \pm 0.1$  ‰ (C:N molar),  $0.2 \pm 0.1$  ‰ ( $\delta^{13}\text{C}$ ), and  $0.1 \pm 0.1$  ‰ ( $\delta^{15}\text{N}$ ).

## 2.5. Statistical analyses

Analyses were run in R (v4.3.0; R Core Team 2023) using RStudio (v1.2.5; Posit team, 2022). Data were tested for normality and equal variance (Shapiro-Wilk and Levene's tests) leading to the use of non-parametric tests. Permutational multivariate analyses of variance (PERMANOVA) were conducted using "vegan" package (Oksanen et al., 2022) and function "adonis2" with Euclidean distance and 999 permutations. Post-hoc tests were conducted using the package "RVAideMemoire" (Herve 2023) and function "pairwise.perm.manova" with a Benjamini-Hochberg correction. To assess possible seasonal differences in turtle diet, isotopic ratios of both turtle species separately (all sites combined) and seagrass (sites A and C) were investigated through PERMANOVAs in the form  $c(N,C) \sim \text{SEASON}$ . Seagrass was included to detect changes in baseline isotopic values between seasons. Since no differences were detected, season was not considered in the analyses.

### 2.5.1. Diet

To investigate isotopic differences among sites (to support fidelity to capture areas) and between sizes, for each turtle species a two-factor PERMANOVA was conducted in the form,  $c(N,C) \sim \text{SITE} * \text{SIZE}$ , where N and C were the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic values, SITE was a factor with four levels (sites A, B, C and E) and SIZE GROUP was a factor with two levels (larger group  $\geq$  median size and smaller group  $<$  median size). The interaction of the two variables was considered to account for the change of diet with age and for turtles of different age possibly frequenting different sites. To better understand/contextualize the green turtle and hawksbill turtle results, a one-way PERMANOVA was conducted for each prey item category, with SITE as the explanatory variable.

To further investigate if diet changes between younger (smaller) and older (larger) turtles, a second approach consisted of excluding site as a possible confounding factor by considering data from only one site. For convenience, the site with the highest sample size was selected for each turtle species. A two-factor PERMANOVA with size group (smaller vs larger; same as above) as an explanatory variable was conducted per species.

To identify groups of prey items isotopically similar, a PERMANOVA for each site in the form  $c(N,C) \sim \text{GROUP}$  was performed as well as a visual assessment of the site-specific prey isospace. Prey contribution to both turtle species' diet was assessed using the Bayesian mixing model MixSIAR (Stock and Semmens 2016). All JAGS (Just Another Gibbs Sampler) models were run with the "extreme" MCMC parameters (chain length = 3000000, burn = 1500000, thin = 5, chains = 3) and evaluated

by the Gelman-Rubin and Geweke in-built diagnostics. Prey contribution analyses were fourfold. First, to determine overall diet of each turtle species, the sites with the most captures for each species were analyzed for green (site A) and hawksbill turtles (site E). Second, to determine if there were differences in diet between turtle species, a mixing model was run for each species at the same site with the same prey item groupings (e.g., turtle comparison at site E). Third, to explore if isotopic differences of turtles among sites were due to a different diet or to varied isotopic baselines, we analyzed the next highest capture site for green turtles that was isotopically different to the first site (site B). Due to low sample size of hawksbill turtles at most sites, hawksbill turtle diet was assessed at one site (E) while green turtle diet was assessed at three sites (A, B and E).

Since tissues have different rates of incorporating isotopes, for green turtles we used previously established trophic discrimination factors (TDFs) from captive and wild green turtles in the Pacific ( $4.1 \pm 0.4$   $\delta^{15}\text{N}$ ,  $2.3 \pm 0.3$   $\delta^{13}\text{C}$ ; Turner Tomaszewicz et al., 2017). Since TDFs have not been estimated for hawksbill turtles, we ran two models for hawksbill turtles at site E: one with TDFs for loggerhead turtles ( $1.54 \pm 0.12$   $\delta^{15}\text{N}$ ,  $2.62 \pm 0.34$   $\delta^{13}\text{C}$ ; Reich et al., 2008) and one with TDFs from captive and wild green turtles in the Pacific, as used for the green turtles in this study (Turner Tomaszewicz et al., 2017). Both green turtle and loggerhead TDFs have been used in hawksbill turtle stable isotope diet studies, in the East Pacific: Turner Tomaszewicz et al. (2017) in the Gulf of California, Mexico (Reynolds et al., 2023), and Reich et al. (2008) in Golfo Dulce, Costa Rica (Méndez-Salgado et al., 2020). We considered the loggerhead TDFs most appropriate for our hawksbill turtle models since hawksbill turtles are generally omnivorous throughout their lives, while green turtles become more specialized in vegetation as they get larger (Bjorndal 1996).

### 2.5.2. Isotopic niche

Isotopic niche width and overlap among and between the two turtle species was investigated through Stable Isotope Bayesian Ellipses (SIBER v2.1.7; Jackson et al., 2011). Total area (TA) encompassed by all the isotopic ratios of the convex hull area in the biplots and standard ellipse area corrected (SEAc) for small sample sizes ( $<50$ ) were calculated (Layman et al., 2008; Jackson et al., 2011). Bayesian standard ellipses (SEAB) were calculated by combining equal priors, likelihoods and iterations from the MCMC simulation. SEAB is a more robust approach, used to account for the uncertainty with small sample sizes and outliers (Jackson et al., 2011). Overlap was calculated based on the posterior distributions of the fitted ellipses (Jackson et al., 2011).

## 3. Results

### 3.1. Turtles and their isotopic values

A total of 180 individuals were caught: 129 green turtles and 51 hawksbill turtles (Table S1). The overall size in CCLN-t (mean  $\pm$  SD; range) for green turtles was  $47.5 \pm 7.0$  cm (38.6–73.1) and for hawksbill turtles was  $45.5 \pm 6.9$  cm (29.6–63.8). Mean size for both species was mostly in the 40–49.9 cm size class (Table 2). For green turtles (n = 129), the  $\delta^{15}\text{N}$  range was 2.5–12.5 ‰ (mean  $7.3 \pm 2.5$  ‰ SD) and  $\delta^{13}\text{C}$  was  $-17.5$  to  $-5.6$  ‰ ( $-9.9 \pm 2.7$  ‰ SD). For hawksbill turtles (n = 51), the  $\delta^{15}\text{N}$  range was 6.3–11.9 ‰ ( $9.7 \pm 1.1$  ‰ SD) and  $\delta^{13}\text{C}$  was  $-18.7$  to  $-10.8$  ‰ ( $-13.7 \pm 1.1$  ‰ SD; Fig. 2).

We found no seasonal differences isotopically in green turtles (PERMANOVA; n = 129), hawksbill turtles (PERMANOVA; n = 51) or seagrasses in sites A and C (PERMANOVA; n = 12, n = 9, respectively), therefore further analyses combined samples from the two seasons.

### 3.2. Prey items

$\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of prey values across all sites for animal and vegetation categories were  $-24.94$ – $0.28$  ‰ ( $-13.34 \pm 5.25$  ‰, mean  $\pm$

**Table 2**

The number (n) of green and hawksbill turtles caught by site, and the mean ± standard deviation and range of the size (CCLn-t; cm) and isotopic values δ<sup>15</sup>N (‰) and δ<sup>13</sup>C (‰) for the sites turtles were grouped into. Sites A-C were in the west lagoon, and site E was in the east lagoon.

		SITE A	SITE B	SITE C	SITE E	
<b>Green turtles</b>	<b>n</b>	47	41	24	17	
	(mean ± SD; range)	48.2 ± 7.6; 38.6–65.5	48.4 ± 7.4; 38.8–73.1	46.2 ± 6.6; 39.5–62.0	44.8 ± 4.1; 39.5–58.9	
	δ <sup>15</sup> N (‰)	7.5 ± 2.3; 2.5–12.5	7.0 ± 2.4; 2.8–12.3	6.0 ± 2.3; 2.8–10.0	9.6 ± 1.4; 7.1–12.1	
	δ <sup>13</sup> C (‰)	-8.6 ± 2.5; -17.4 to -5.6	-11.0 ± 2.6; -17.5 to -6.6	-10.7 ± 2.5; -16.2 to -6.6	-9.3 ± 2.1; -13.5 to -6.8	
	<b>Hawksbill turtles</b>	<b>n</b>	2	10	11	28
	(mean ± SD; range)	43.7 ± 7.6; 38.3–49.1	50.1 ± 6.1; 38.7–61.4	46.7 ± 7.1; 37.1–63.8	43.6 ± 6.6; 29.6–56.3	
δ <sup>15</sup> N (‰)	10.5 ± 0.6; 10.1–10.9	8.6 ± 1.1; 6.3–10.4	8.7 ± 0.3; 8.3–9.3	10.4 ± 0.6; 9.4–11.9		
δ <sup>13</sup> C (‰)	-15.5 ± 2.3; -17.6 to -13.4	-13.6 ± 1.9; -18.7 to -12.3	-12.5 ± 1.1; -14.1 to -10.8	-14.1 ± 0.5; -15.1 to -12.4		

SD, hereafter; n = 147) and -29.7–2.39‰ (-16.02 ± 8.18% SD; n = 135). Isotopic values among sites varied, e.g., site A had more depleted δ<sup>15</sup>N values (i.e., negative; -7.86 to -0.87‰ SD; n = 51) than site E (-2.74–7.93‰ SD; n = 46) (Table S2–3).

Among-site differences were found for several prey items (Table 3; Fig. S1–2). Pairwise comparisons detected isotopic differences for different taxa between the east and west lagoon sites, and differences between the reef and lagoon sites (Table S4–5).

**3.3. Diet**

Isotopic ratios among prey groups varied (PERMANOVAs p < 0.02; n: A = 9, B = 10, C = 9, D = 9, E = 10, F = 2, G = 4, H = 3) (Fig. 3, Table S6), indicating different site isotopic baselines. Therefore, site-specific prey isotopic values were used in the mixing models.

For all mixing model comparisons, turtles and prey overlapped in the isospaces (Fig. S3). The following prey contributions are reported by the 95% credible intervals (CI; mean ± SD) (Fig. 4, Table S7–9). Overall green turtle diet was similar across sites and included multiple prey items, with seagrass and brown algae being the main components (Fig. 4). Seagrass comprised approximately half the diet of green turtles at site A (19.1–66.5% CI; 43 ± 12.5 SD; n = 12) and site E (2.7–65.8%

CI; 36.7 ± 17.9 SD; n = 9), and less for site B (5.9–47.2% CI; 25.4 ± 10.4 SD; n = 9). Brown algae was important to green turtle diet at all sites (site A: 2.4–60.2% CI; 29.7 ± 15.8 SD; n = 4; site B: 2.8–52.2% CI; 28.2 ± 13.1 SD; n = 4; site E: 0.7–59.4% CI; 21.1 ± 16.6 SD; n = 3).

For hawksbill turtles (site E; n = 28) using loggerhead TDFs, the highest contribution was from mangroves 6.8–43.1% CI (26 ± 9.2 SD), followed by invertebrates (crabs, snails and zoanthids; 0.9–40.0% CI; 16.2 ± 10.6 SD). The lowest contribution was from seagrass (5.9–22.2% CI; 7.7 ± 5.9 SD) (Fig. 4, Table S8). When running the model with green turtle TDFs at site E, the highest contribution was from mangroves (11.9–44.4% CI; 30.5 ± 8.1 SD) followed by seagrass (2.6–45.4; 25.9 ± 11.4 SD) and brown algae (0.6–44.9; 15.2 ± 12.1 SD). Other dietary items were <10% (see Fig. S4, for matrix plots).

**3.4. Age and site effects**

In green turtles both site and size (small vs large) affected isotopic values (PERMANOVA; n = 129; p < 0.001), but the interaction did not. Isotopic values differed between all sites, except for between B and C (Table 2). Site E (east lagoon site) δ<sup>15</sup>N value had the highest mean and smallest range, while west lagoon site A had the largest δ<sup>15</sup>N range (Table 2). Smaller turtles had more enriched δ<sup>15</sup>N mean values (8.23 ± 2.18, n = 64) than larger turtles (6.47 ± 2.40, n = 65). Mean δ<sup>13</sup>C values were slightly more enriched for the larger turtles (-9.45 ± 2.8) compared to the smaller turtles (-10.3 ± 2.5).

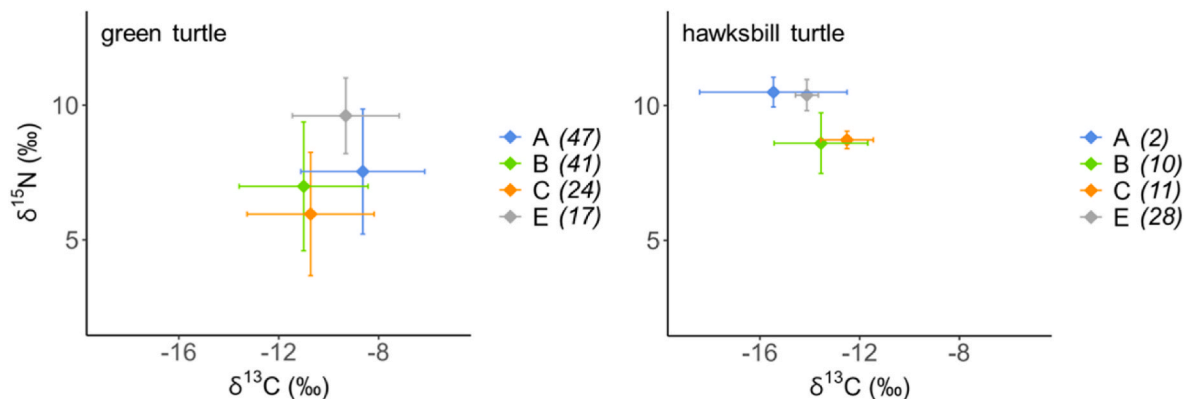
In hawksbill turtles, site (PERMANOVA; n = 51; p < 0.001) but not size (small vs large) affected isotopic values. Their interaction did not affect isotopic values. Site E had higher δ<sup>15</sup>N and δ<sup>13</sup>C values and a smaller CCLn-t mean from sites B and C (Table 2).

There were differences in isotopic values of green turtle size groups when only looking at site A (PERMANOVA; n = 47; p = 0.005). The small size group had more enriched δ<sup>15</sup>N (8.76 ± 1.42, n = 23; 6.36 ± 2.43, n = 24, respectively) and more depleted δ<sup>13</sup>C than the large size

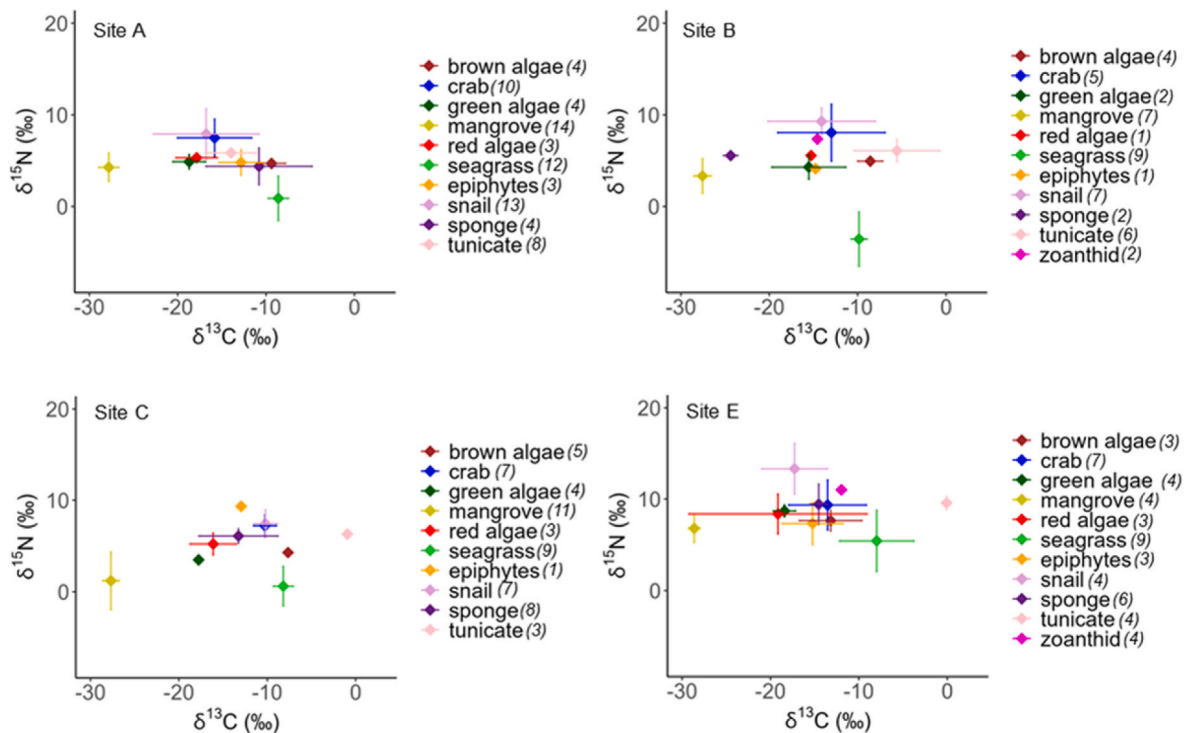
**Table 3**

Among site comparison PERMANOVA results for each prey item grouping.

	F	Df	n	Pr(>F)
Brown algae	6.75	4	19	<0.01
Green algae	6.47	4	18	<0.01
Mangrove	7.26	4	38	<0.01
Red algae	0.86	4	11	0.86
Seagrass	6.23	7	49	<0.01
Crab	2.17	5	36	0.07
Snail	2.60	6	42	<0.01
Sponge	6.20	6	36	<0.01
Tunicate	27.39	4	27	<0.01
Zoanthid	8.45	2	6	0.20



**Fig. 2.** δ<sup>15</sup>N and δ<sup>13</sup>C values for green turtles (n = 129) and hawksbill turtles (n = 51). Lagoon capture site is shown in color. Mean and SD are shown with sample size in brackets.



**Fig. 3.** Prey category  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  by lagoon site. For all, PERMANOVA p-value <0.001. Each category/grouping is represented by mean and SD and has sample size in brackets. No trophic discrimination factors were added.

group ( $-9.21 \pm 2.39$ ,  $n = 23$ ;  $-8.08 \pm 2.49$ ,  $n = 24$ , respectively).

With only one site considered for hawksbill turtles, there was no difference between isotopic values and size at site E (small vs large), based on median size 44.5 cm (PERMANOVA;  $n = 28$ ). The small and large groups had similar  $\delta^{15}\text{N}$  ( $10.4 \pm 0.6$  SD,  $n = 13$ ;  $10.4 \pm 0.6$  SD,  $n = 15$ , respectively) and  $\delta^{13}\text{C}$  ( $-14.2 \pm 0.6$  SD,  $n = 13$ ;  $-14.1 \pm 0.3$  SD,  $n = 15$ , respectively).

For green turtles at site A, seagrass had the highest contribution for both size groups, but increased from the small (6–49.9% CI;  $26.2 \pm 11.7$  SD;  $n = 23$ ) to large group (32.4–75.9% CI;  $55.7 \pm 11.4$  SD;  $n = 24$ ). The proportion of brown algae decreased from younger (small; 2.5–75.7% CI;  $38.6 \pm 20.4$  SD,  $n = 23$ ) to older turtles (large; 2–49.1% CI;  $21.4 \pm 12.8$  SD,  $n = 24$ ). Zoanthids also decreased from the small (0.4–43.1% CI;  $17 \pm 12.4$  SD;  $n = 23$ ) to large size group (0.5–20.3% CI;  $7.8 \pm 5.3$  SD,  $n = 24$ ; Fig. 5, Table S7).

### 3.5. Isotopic niche

At site A, small green turtles had a smaller isotopic niche than large turtles (TA = 39.1 and 57.3; SEAB = 10.1 and 17.5, respectively) with only a 5.6% overlap (Table S10, Fig. S5). When comparing green turtles and hawksbill turtles at site E, green turtles had a wider isotopic niche than hawksbill turtles (TA = 16.9 and 3.52; SEAB = 7.6 and 0.80, respectively (Fig. 6, Table S10). The diet of both species at site E (hawksbill TDFs from Reich et al., 2008) complements these findings with different main prey items for each species (Fig. 4, Table S8).

At site E, hawksbill turtles occupied a smaller TA and SEAB ( $n = 28$ ; 3.52 and 0.80 with 0.56–1.20 credible intervals, respectively) than green turtles ( $n = 17$ ; 16.89 and 7.55 with credible intervals of 4.5–12.9), with only a 5% overlap (Table S10). The TA and SEAB for green turtles decreased from site A (67.6, 16.9) to B (51.3, 14.8) to C (28.8, 7.6) to E (16.9, 7.6). Site E had the smallest isotopic niche width and the least overlap with the other sites. Sites A and B overlapped the most with other sites and each other (Table S10, Fig. S6). The TA and SEAB for hawksbill turtles was largest at site B (13.3, 7.5) and smaller,

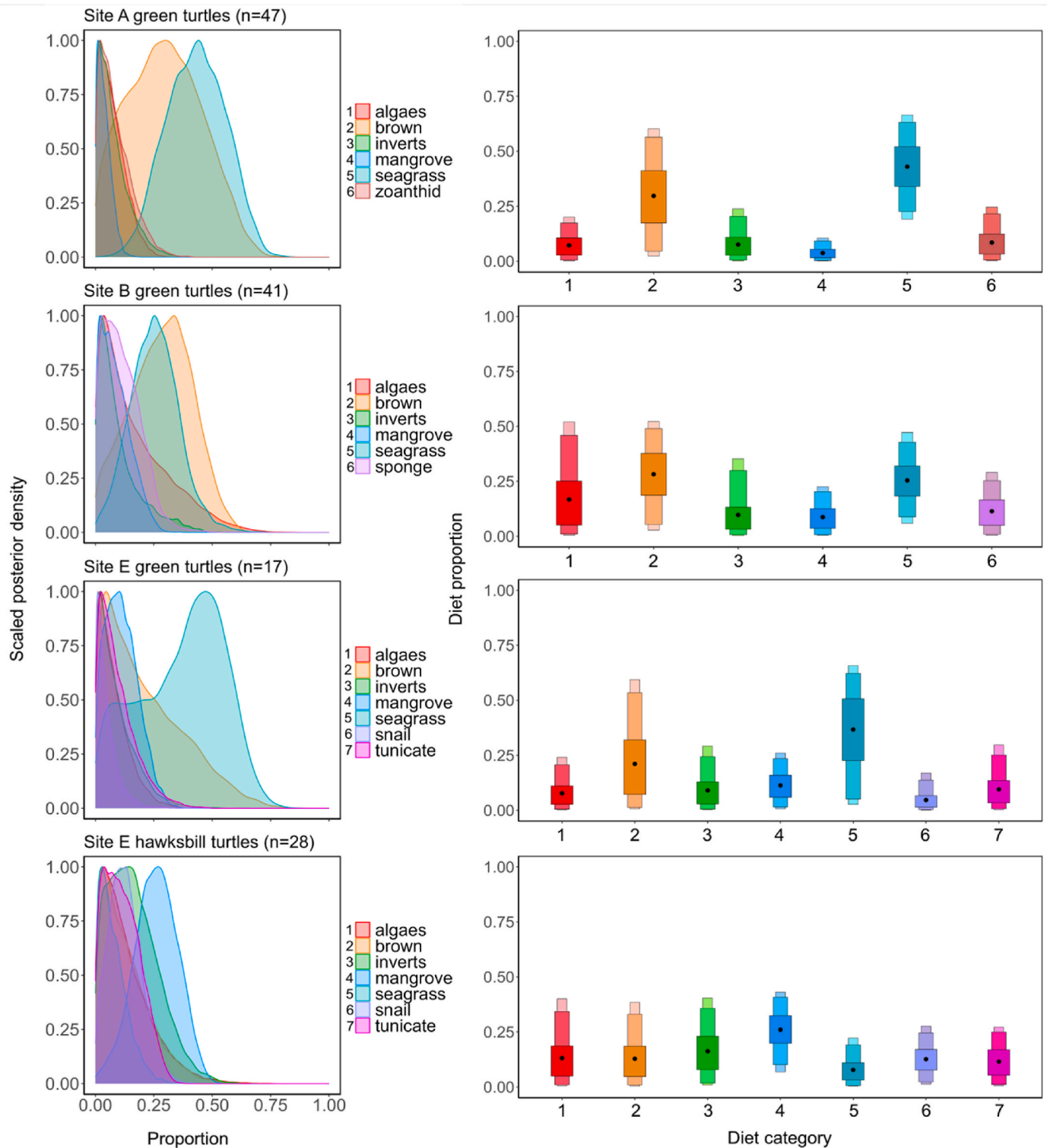
yet similar, for sites C (2.2, 1.0) and E (3.5, 0.8), and there was very little overlap among sites (range of 1.7–7.5%; Table S10, Fig. S6).

## 4. Discussion

Our study provides substantial new insight into the behavior and foraging preferences of marine turtles in a relatively undisturbed system with minimal direct anthropogenic impact. We found distinct isotopic ratios of putative prey items between sites at one of the smallest spatial scales (1 km) that isotopic differences have been detected, which is likely due to the unique isotopic spatial differences within the Aldabra lagoon and to strong turtle foraging site fidelity.

Stable isotope ratios can change in a predictable and systematic way due to biogeochemical processes (Hobson 1999; McMahon et al., 2013). Spatial isotope composition has been well-documented in the literature and is affected by, but not limited to, temperature, upwellings, and eddies (e.g., Kurle and McWhorter 2017; Magozzi et al., 2017; Pethybridge et al., 2018). Very little is known about biogeochemical processes in the lagoon or around the atoll. Bulk nitrogen stable isotope baselines at sites have been found to also be influenced by nitrogen runoff from anthropogenic activities (Valiela et al., 1997). At Aldabra, isotopic baselines are likely not influenced by anthropogenic presence. In fact, the highest nitrogen values were at the eastern site of the atoll (the research station is on the northwestern side of the atoll).

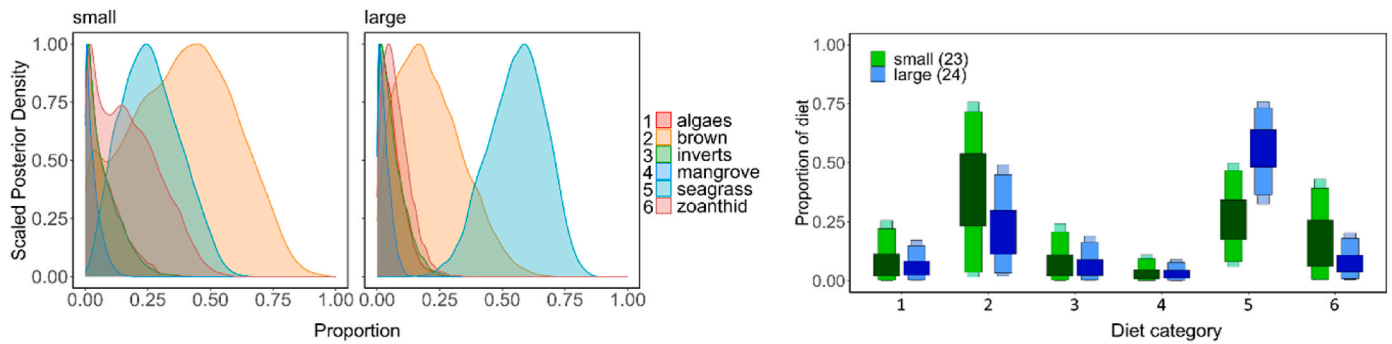
Additionally, in other studies, large amounts of vertebrates, such as nesting seabirds, have been shown to affect nutrient flow (De La Peña-Lastra 2021). For example giant tortoises play a major role in the terrestrial organic matter of Aldabra (Falcón and Hansen 2018). Constance et al. (2022) suggested that the spatial distribution of nutrients in mangrove soils in Aldabra's lagoon was due to macrofauna such as Aldabra giant tortoises. In general, mangroves lead to more depleted  $\delta^{13}\text{C}$  being incorporated into seagrasses (Bouillon et al., 2008), and mangroves dominate over half of Aldabra's lagoon coastline (Constance et al., 2022). Furthermore, large seabird breeding colonies in the mangroves around the lagoon (Diamond 1974; Súr et al., 2013) can



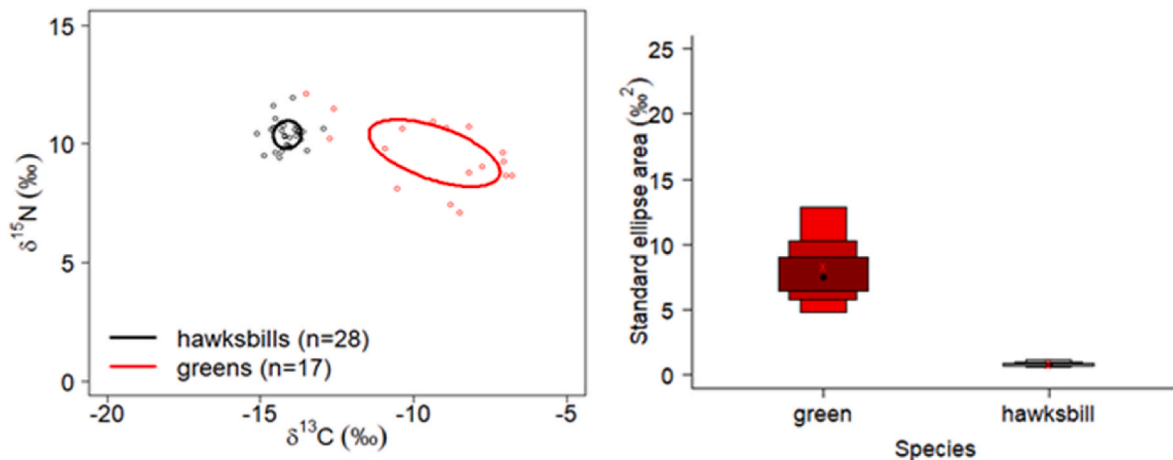
**Fig. 4.** Prey contributions to diet for green turtles at sites A, B, and E and for hawksbill turtles at site E. The left column has posterior densities and the right column credible interval boxplots. Rows are by site/turtle species. Mean  $\pm$  SD of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from mostly site-specific prey groups and turtle skin were incorporated into the model. Trophic discrimination factors were added to prey values:  $+4.1 \pm 0.4$  SD  $\delta^{15}\text{N}$  and  $+2.3 \pm 0.03$  SD  $\delta^{13}\text{C}$  (Turner Tomaszewicz et al., 2017) for green turtle mixing models;  $+1.65 \pm 0.12$  SD  $\delta^{15}\text{N}$  and  $2.62 \pm 0.34$  SD  $\delta^{13}\text{C}$  (Reich et al., 2008) for the hawksbill turtle mixing model.

contribute large amounts of bio-available nitrogen, phosphorous and trace elements into the surrounding ecosystems (De La Peña-Lastra 2021). Nutrients from seabird colonies have been shown to enrich nitrogen and nutrient availability in adjacent waters and within the food chain as well as accelerate coral reef growth (Graham et al., 2018;

Benkwitt et al., 2023). Isotopic baselines and the nutrient flows of the atoll should be investigated further, including investigating whether large vertebrates are playing a role in how/why the baseline isotopic ratios are different between the various sites.



**Fig. 5.** Estimated prey contributions to green turtle diet at site A ( $n = 47$ ) for the small ( $n = 23$ ) and large ( $n = 24$ ) size groups based on green turtle median size of site A (45.2 cm CCL) by incorporating mean  $\pm$  SD of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from the prey groups and turtle skin. Trophic discrimination factors of  $+4.1 \pm 0.4$  SD to  $\delta^{15}\text{N}$  and  $+2.3 \pm 0.03$  SD to  $\delta^{13}\text{C}$  were added to prey values (Turner Tomaszewicz et al., 2017).



**Fig. 6.** (A) Standard ellipses calculated using a maximum likelihood approach (SEAc) for green turtles ( $n = 17$ ) and hawksbill turtles ( $n = 28$ ) at site E; (B) Bayesian standard ellipse areas (SEAB) with black dots representing the mode, and shaded boxes represent 50%, 75% and 95% credible intervals of the SEAB, from dark to light. The SEAc mode is shown as red crosses. Produced in SIBER (Jackson and Parnell 2023).

#### 4.1. Diet

Green turtles in our study predominantly consumed vegetation (mainly seagrass and brown algae), but showed some foraging plasticity among sites. Green turtles globally have variable feeding habits (Esteban et al., 2020). In the Eastern Pacific, green turtles eat seagrass, algae and invertebrates (Amorocho and Reina 2007; Lemons et al., 2011; Clyde-Brockway et al., 2022; Vanderklift et al., 2023), with invertebrates sometimes comprising the highest dietary contribution (Lemons et al., 2011). However, at three other Seychelles' atolls, adult green turtles contained mostly seagrass in their gut, with a small percentage of algae, sponges and bryozoans (Stokes et al., 2019). With SIA, we have expanded the list of turtle dietary items, with non-seagrass items contributing a larger part of green turtle diet in Seychelles than previously found.

Hawksbill turtles are noted for specializing in sponges (Bjorndal 1996), with detailed studies in the Caribbean showing 70 to > 90% of their diet composed of sponges (Meylan 1988). However, in the Pacific, hawksbill turtle diet is a mix of animal and vegetation items (Bjorndal 1996; Bell 2013), especially in the Eastern Pacific (Carrion-Cortez et al., 2013; Méndez-Salgado et al., 2020; Martínez-Estévez et al., 2022; Reynolds et al., 2023), where mangroves and algae/vegetation had major contributions to hawksbill turtle diet, a result that is similar to our study. In Seychelles, a previous diet study (lavage and stomach contents of dead turtles) found that hawksbill turtles predominantly ate sponges (von Brandis et al., 2014). The authors presumed that algae and seagrass were incidentally ingested when hawksbill turtles targeted sponges

within algae/seagrass beds. In the same study, turtles at Aldabra ( $n = 20$ ) notably ingested a large amount of red algae, which was scarce in turtle diets at the other Seychelles' sites. Additionally, at D'Arros, Seychelles, a hawksbill turtle was directly observed eating brown algae (von Brandis et al., 2014).

At Aldabra, mangroves were not detected in the lavage study of hawksbill turtles (von Brandis et al., 2014) but were through SIA (present study). Other studies elsewhere have found diet estimations of hawksbill turtles to vary based on the method used. For example, in Mexico, seagrass was found in hawksbill diet (not a main contributor) through SIA (Reynolds et al., 2023) but not in scat (Martínez-Estévez et al., 2022). In Costa Rica, Méndez-Salgado et al. (2020) explored hawksbill diet on the same individuals using both SIA and lavage, and they found mangroves to be an important part of the diet using SIA but not using lavage. Methods such as lavage and scat sampling are simpler and less costly, but it can be difficult to recover/identify different prey items (Forbes 1999; Seminoff et al., 2002). For SIA studies, models depend on the data that is provided and can therefore be wrong. What these SIA studies indicate is that these food items might be consumed. This emphasizes the need for multiple, complementary methods to get a comprehensive picture of turtle diet, and the value of SIA for being included as one of the methods.

Mangroves in particular are known to be important habitats and food sources in the Eastern Pacific hawksbill turtles (Gaos et al., 2012, 2017; Martínez-Estévez et al., 2022). This aligns with our findings, as our study is the first to show that mangroves are an important part of hawksbill turtle diet in the Seychelles. Hawksbill turtles may be more herbivorous



in a macroalgae-dominated area if invertebrates are not abundant.

Our study, while comprehensive, has certain limitations. Several prey categories included multiple rather than a single species. Having a common species across sites (the initial aim) would have allowed easier interpretation of results, but sampling was guided by what was found in the field. Additionally, not all items searched for, such as ctenophores and shrimp, were found at each site despite extensive searching; therefore, the isospaces could be missing potential diet sources. More than one species of snail and crab was collected, due to lack of common species across the sites, and these were not identified to species. Due to the different foraging strategy of different species within these two taxa, the isotopic signatures could be confounded (e.g., Piovano et al., 2020). Moreover, the absence of notable seasonal variation in isotopic ratios might suggest either consistent food source availability or it may highlight the study's constraints in identifying such seasonal differences. Lastly, finding isotopic differences at sites prevented us from pooling hawksbill turtles, meaning we could only assess hawksbill turtle diet at one site.

Mixing models are also sensitive to the TDF used. Since TDFs have not been estimated for hawksbill turtles, we ran two models from the same site using TDFs from other sea turtle species: loggerhead turtles (Reich et al., 2008) and green turtles (Turner Tomaszewicz et al., 2017). The loggerhead TDFs were from small, fast growing juveniles in captivity (Reich et al., 2008), while the green turtle TDFs were from partially wild and captive green turtles (Turner Tomaszewicz et al., 2017). Both of these TDFs have been used in mixing models for hawksbill turtles: Turner Tomaszewicz et al. (2017) in Mexico (Reynolds et al., 2023) and Reich et al. (2008) in Costa Rica (Méndez-Salgado et al., 2020), but they have not been applied together and compared. When done so in this study, the two models gave different results. By comparing the MixSIAR results of the two TDFs to the SIBER results for this same study, and with previous lavage/necropsy results of hawksbill turtles in Seychelles including hawksbill turtles sampled at Aldabra (von Brandis et al., 2014), we found the Reich et al. (2008) TDFs more appropriate for our hawksbill turtle models and possibly for the ocean basin. Future studies should consider using multiple TDFs in combination with other lines of evidence (such as lavage and/or necropsy results) to estimate diet.

#### 4.2. Diet change with age

We found isotopic differences between small and large green turtles, with the  $\delta^{15}\text{N}$  becoming more depleted with age. Green turtles, especially in warmer waters, have flexible ontogenetic shifts, from a mostly carnivorous, oceanic juvenile stage to a neritic juvenile stage, shifting to a plant-dominated diet in adulthood (Howell et al., 2016; Burgett et al., 2018); however, diet can vary by region/temperature (Esteban et al., 2020). In north-western Australia, seagrass was found important for all sizes, with macroalgae possibly being important to smaller sized green turtles, and jellyfish increased in diet with size (Vanderklift et al., 2023). Decreasing  $\delta^{15}\text{N}$  with larger green turtle sizes was also seen on the Bermuda Platform while turtles were transitioning to a predominantly seagrass diet (Burgett et al., 2018). Shifting proportions of dietary items from smaller to larger turtles indicates that although seagrass is an important part of diet of all green turtles in the Aldabra lagoon, it becomes the main food source with age. The observed differences among sizes can therefore be explained by dietary shift.

Hawksbill turtles showed no change in diet with size. Of the few studies on hawksbill turtle diet using stomach contents (Stringell et al., 2016) or stable isotopes (Méndez-Salgado et al., 2020; Martínez-Estévez et al., 2022; Clyde-Brockway et al., 2022; Reynolds et al., 2023), none have found dietary changes with size when excluding recently recruited individuals. This suggests that hawksbill turtles do not change diet once they have settled in their neritic environment.

There was no indication of recently recruited turtles based on the isotopic ratios. Green turtles in the Pacific can recruit to neritic foraging

grounds from >30 cm (Northern Mariana Islands; Summers et al., 2017) up to 48 cm (Fiji; Piovano et al., 2020). Turtles within this study overlapped with putative prey items, indicating they were in the environment long enough for the site-specific isotopic signatures to integrate into their skin.

#### 4.3. Isotopic niche

We found trophic diversity between green and hawksbill turtles, and green turtles became more specialized as they got larger. Small niche overlap between the two species suggests resource partitioning, a result that is supported by the species-specific diet estimates obtained using mixing models. Several prey items contributed similarly to hawksbill turtle diet, while green turtles were more specialized, but the hawksbill turtle isotopic niche was smaller than the green turtles. The large size of the green turtle isotopic niche can be explained by the differences in diet between size, but also, as seen in other places, from individual specialization (Vander Zanden et al., 2013; Thomson et al., 2018). Reasons for the small hawksbill isotopic niche are not as clear and may require further investigation of their foraging ecology to understand how the varied diet and small isotopic niche co-occur. Another factor that could impact the diet includes the TDF used, as discussed above; as shown in our results when using different TDFs, the diet contributions change.

For both species, isotopic niche width was different among the sites. Green turtle niche width increased from the east to west lagoon where the greatest niche width (site B) had a larger dietary contribution from brown, red and green algae and a larger range in  $\delta^{13}\text{C}$ . The niche width for hawksbill turtles at site B was also larger, indicating less partitioning, as the overlap between species was larger from E to B. These differences among and between sites could be related to availability of prey items, which may increase or relieve competition (Chandelier et al., 2023).

When comparing niche widths among green turtle sizes, the smaller niche width of small turtles at site A compared to the large size class. This was unexpected, since smaller turtles are usually more generalist, and niche spaces shrink as animals get larger and more specialized (Vander Zanden et al., 2013). However, our study only included immature neritic individuals and no adults, the former of which have a narrower niche width (Vander Zanden et al., 2013). Turtles can exhibit variability in their life history behaviors. Research indicates that turtles may delay their shift from pelagic to benthic prey when in neritic habitats (Cardona et al., 2009), move between neritic and pelagic environments (Parker et al., 2011), or even remain long-term as pelagic consumers (Turner Tomaszewicz et al., 2018). Should turtles in our study display any of these behaviors, it could potentially lead to misinterpretations in our findings.

Each site at Aldabra has mangrove forests and passageways, along with sandy bottom areas. Therefore, if individuals are specializing within this generalist population, the habitat is likely heterogeneous enough for turtles to specialize on different items and still be found near one another, and maintain high site fidelity. Individual specialization has been found for green turtles in other areas (Vander Zanden et al., 2013; Thomson et al., 2018).

#### 4.4. Fidelity

We found isotopic differences for turtles among sites, not related to body size. The variations in isotopic differences among the sites are likely attributed to differences in nutrient flow around the lagoon, as discussed above, but could be from individual specialization or prey availability/selectivity (Burkholder et al., 2011; Vander Zanden et al., 2013; Stringell et al., 2016).

Since bulk SIA is not able to distinguish between trophic enrichment and baseline differences for  $\delta^{15}\text{N}$  values (Jennings and Warr 2003), we established baselines for the sites through primary producers (e.g., Lemons et al., 2011). Several of our prey categories had significant differences in isotopic values among the sites supporting that several

sites were isotopically distinct. Moreover, the diet of green turtles was similar among sites analyzed, therefore a different diet is not a likely explanation for the observed different isotopic values. These findings indicate that turtles tend to frequent the same site to forage, with their tissues reflecting preys that are isotopically different from other sites. We interpret these results as evidence of fidelity.

Immature green and hawksbill turtles have been found to have fidelity to foraging grounds through different methods such as satellite telemetry and/or capture-mark-recapture (Chevis et al., 2017; Siegwalt et al., 2020; Meylan et al., 2022) as well as inferred through stable isotope analysis (Méndez-Salgado et al., 2020; Turner Tomaszewicz et al., 2022a; Clyde-Brockway et al., 2022). Further spatio-temporal understandings of isotopic baselines throughout the atoll should be prioritized to allow a clearer understanding of the differences detected for turtles and prey items at the different sites.

To establish foraging site fidelity, other studies have evaluated the consistency in isotopic ratios of individuals over time by including methods such as skeletochronology (e.g., Ferreira et al., 2018; Turner Tomaszewicz et al., 2022b) or sampling the same individuals across years (Thomson et al., 2012) (summarized in Haywood et al., 2019). However, the use of skin, with a low turnover rate was estimated to be 3–4 months in fast-growing, small juvenile sea turtles (Reich et al., 2008) and, thus, likely longer in this study which included bigger turtles. Turtle and prey item differences among sites in this study suggest fidelity for time it takes for tissue to turnover. Additionally, differences were not seen in prey items between the two different seasons of the atoll alleviating the complication of seasonal differences.

#### 4.5. Conclusions

Our study's isotopic values for green turtles and hawksbill turtles are the first such data for Seychelles, and only the second known in the Western Indian Ocean region (Chandelier et al., 2023; Reunion Island). The Indian Ocean is the most underrepresented region for stable isotope studies on sea turtles (Haywood et al., 2019), despite the region's high turtle numbers and recovering populations (e.g. Allen et al., 2010; Mortimer et al., 2020; Pritchard et al., 2022). At an isolated, relatively undisturbed system such as Aldabra, stable isotopes can be used to understand distribution and resource use of these two foraging species. We found evidence of site fidelity for both species, supported by site differences detected with putative prey items. We also found that green turtle diet changed with age, adding to our understanding of ontogenetic shifts.

Use of SIA in Aldabra's lagoon demonstrated how, even at this small scale, the isotopic baselines at different sites varied considerably. We demonstrate how valuable knowing local baselines is for interpreting data and the scales to which they vary. We were able to show that at each site, green turtles and hawksbill turtles share similar diet items, but in different proportions – including for green turtles of different sizes. Therefore, green turtles of different sizes and hawksbill turtles occupy different isotopic niches.

The results emphasize the importance of seagrass and mangrove habitats within the region and globally. Lagoonal mangroves make up a small percent (11%) of global total mangrove area, but are being lost at double the rate of other mangrove ecosystems (Worthington et al., 2020). Algae was found to possibly contribute to the diet of both turtles species, therefore future research should investigate if these species have any role in controlling algal biomass at Aldabra. Nesting populations for green turtles and hawksbills turtles have been increasing in the region (e.g., Allen et al., 2010; Burt et al., 2015; Pritchard et al., 2022), and it is unknown if and/or how the increase in turtles could change the habitat composition. Increased populations of green turtles in other places have seen collapses in seagrass beds attributed partially to turtle overgrazing (Lal et al., 2010; Christianen et al., 2014; Fourqurean et al., 2019; Gangal et al., 2021). Aldabra, with higher regional fish biomass including sharks (Friedlander et al., 2015), could potentially have a

balanced ecosystem (Heithaus et al., 2012, 2014). Future research should investigate if species of megafauna at Aldabra are able to coexist (green turtles, hawksbill turtles and dugongs) without being resource limited or depleting their resources. Little is known, however, about shark and dugong distribution and abundance at the atoll, nor about the abundance of foraging turtles.

We recommend that future studies establish trophic discrimination factors for hawksbill turtles, which should improve confidence in mixing model results. Although there have been a few studies on turtle diet in the WIO (e.g., hawksbill turtles, von Brandis et al., 2014; green turtles, Stokes et al., 2019), this is the first stable isotope study for diet in this region on these species. Given the identified underrepresentation of stable isotope studies on sea turtles in the Western Indian Ocean, it is essential to expand such studies across the region, and to build a comprehensive dataset for understanding the ecology of these species. Comparisons could then be made to the various diet studies including the different methods (SIA, lavage, direct observation, etc.) in other parts of the Indian Ocean (e.g., Whiting et al., 2014; Thomson et al., 2018; Kale et al., 2021; Vanderklift et al., 2021, 2023; Stubbs et al., 2022). Due to its unique and undisturbed status, Aldabra provides an invaluable ecosystem to study. Periodic sampling and isotopic studies can give insights into the temporal variations in turtle diets and their overall impact on the ecosystem. Considering the coexistence of these two megafauna species, and others that were not included here (dugongs, sharks), comprehensive research is needed to evaluate their interactions, competition and mutual impacts on resource distribution and consumption. To understand the ecological balance, dedicated studies focusing on dugong and shark distribution, abundance, and behavior of megafauna, including their roles in maintaining seagrass and algae populations and the potential interactions with turtle species should be elucidated.

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#### CRediT authorship contribution statement

**Cheryl L. Sanchez:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Paolo Casale:** Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Nancy Bunbury:** Writing – review & editing, Supervision, Project administration. **Luke A'Bear:** Writing – review & editing, Investigation, Data curation. **Veronique Banane:** Writing – review & editing, Investigation. **Frances Benstrong:** Writing – review & editing, Investigation. **Maria Bielsa:** Investigation. **Christopher W. Jones:** Writing – review & editing, Investigation. **Anna Koester:** Writing – review & editing, Investigation, Formal analysis. **Susan Murasko:** Writing – review & editing, Methodology, Investigation. **Martin C. van Rooyen:** Writing – review & editing, Investigation. **Frauke Fleischer-Dogley:** Writing – review & editing, Project administration, Funding acquisition. **Simona A. Ceriani:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106529>.

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