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Diet and recruitment of green turtles in Fiji, South Pacific, inferred from in-water capture and stable isotope analysis

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ABSTRACT: Green turtles *Chelonia mydas* are listed as Endangered on the IUCN Red List, yet in the South Pacific few conservation-relevant data are available for the species, especially relating to foraging and habitat use. Here, *in situ* observations and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) were used to evaluate green turtle diet and recruitment patterns at Yadua Island and Makogai Island, Fiji. Juvenile green turtles (N = 110) were hand-captured, measured, and sampled. Stable isotope analysis was performed on skin samples and on putative prey items. 'Resident' turtles versus 'recent recruits' were classified based on their bulk skin tissue isotope values, which were compared with stable isotope values of local prey items and analyzed via cluster analysis. Green turtle diet composition was estimated using MixSIAR, a Bayesian mixing model. Recent recruits were characterized by 'low $\delta^{13}C$/high $\delta^{15}N$' values and ranged in curved carapace length (CCL) from 25.5 to 60.0 cm (mean ± SD = 48.5 ± 5.7 cm). Recruitment mostly occurred in summer. Green turtles identified as 'residents' had CCLs ranging from 43.5 to 89.0 cm (mean ± SD = 57.4 ± 9.0 cm) and were characterized by 'high $\delta^{13}C$/low $\delta^{15}N$' values; mixing model results indicate they fed primarily on invertebrates (40%), fishes (31%), and marine plants (29%). This study confirms the value of seagrass pastures as both an essential habitat and a primary food source for green turtles, and can serve as a baseline for evaluations of natural and anthropogenic changes in local green turtle aggregations.

KEY WORDS: *Chelonia mydas* · Stable isotope analysis · $\delta^{13}C$ · $\delta^{15}N$ · Mixing models · SIAR · Foraging ground · Fiji

1. INTRODUCTION

Many species undergo ontogenetic habitat shifts, during which individuals exploit specific habitats and resources at different life stages to maximize their fitness (Alerstam et al. 2003). For taxa with indeterminate growth, such as sea turtles, ontogenetic habitat shifts also enhance growth rates and enable individuals to transition among life-history stages more rapidly, and reach adulthood as quickly as possible (Snover 2008). Indeed, there are several different life history strategies employed by sea turtles, all of which involve multiple habitats spread out over large geographic distances (Bolten 2003). Knowledge about the patterns of transition among marine habitats and the diets of turtles within these areas are key to better understanding the principal locations and resources for sea turtles, and can help elucidate their susceptibility to anthropogenic threats (Burkholder et al. 2011, Clusa et al. 2016).

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Green turtles *Chelonia mydas* transition among various ocean regions through life. After departing nesting beaches as hatchlings, they begin an oceanic stage termed the 'lost years' during which they associate with floating hard matter such as flotsam, debris, and marine algae (Carr 1987, Reich et al. 2007). This stage may last for several years or more, after which they transition to a coastal existence, establishing residence in neritic foraging areas where nutrient cycling is often dominated by seagrass and/or marine algae primary production regimes (Bjorndal 1997). Upon entering these areas, juveniles usually switch from a largely omnivorous diet to one that is more typically herbivorous, with resource use depending on local food availability (Miller 1997, Musick & Limpus 1997, Di Beneditto et al. 2017). However, there is emerging evidence that epipelagic foraging behavior can be retained by green turtles at some locations (Turner Tomaszewicz et al. 2018). Although the size and age of transition to neritic habitats varies widely among populations and marine regions (Musick & Limpus 1997, Reich et al. 2007, Avens & Snover 2013), this ontogenetic habitat shift is a fundamental characteristic of most green turtle populations worldwide (e.g. Musick & Limpus 1997, Bresette et al. 2010, Vander Zanden et al. 2013).

Studying the diet of green turtles is challenging because they are difficult to observe in their natural habitat, and traditional diet study techniques, such as fecal analyses and stomach lavage, are biased towards recently consumed foods (Bjorndal 1997). In contrast, stable isotope analysis (SIA) of bulk tissues reveals longer-term records of assimilated nutrients, and can provide a less biased assessment of individual trophic status. SIA has proven useful to explore the diet and trophic ecology of a wide diversity of marine megafauna (Rubenstein & Hobson 2004, Newsome et al. 2010, Bird et al. 2018, Haywood et al. 2019).

The premise of SIA is that tissues of predator species, such as sea turtles, integrate and reflect the isotope values of their prey (Hobson 1999, Rubenstein & Hobson 2004, Fry 2006), and the isotope values of both predators and prey are influenced by the baseline isotopic profile of the habitat within which they forage (Hatase et al. 2006, Newsome et al. 2007, Turner Tomaszewicz et al. 2018). Ratios of ^{15}N to ^{14}N values (expressed as $\delta^{15}N‰$) exhibit a stepwise enrichment with each trophic step, and $\delta^{15}N$ values in consumer tissues can thus be used to estimate the relative trophic position of an organism when isotope values of primary producers are known (DeNiro & Epstein 1981, Hobson 1999, Fry 2006). Nevertheless, such interpretations can be hampered by human-derived nitrogen enrichments at the base of the food chain, such as release of agricultural runoff and sewage discharge (Connolly et al. 2013, Haywood et al. 2019), that can result in artificially high trophic level estimates for consumers.

In contrast, ratios of ^{13}C to ^{12}C values (expressed as $\delta^{13}C‰$) undergo only slight trophic enrichment, and thus are not necessarily good indicators of trophic levels, but more effectively are used to trace the importance of different carbon pools to a consumer. For example, the $\delta^{13}C$ values of marine algae are much higher than those of terrestrial plants, such as mangroves, largely because of differences between the sources of carbon used for primary production in the 2 systems (Peterson & Fry 1987, Marshall et al. 2007, Inger & Bearhop 2008). Thus, when values of $\delta^{13}C$ and $\delta^{15}N$ of consumer tissues and putative foods are analyzed together, SIA can provide insights about individual diet composition (Wallace et al. 2009, Lemons et al. 2011). However, the ability of SIA to distinguish different prey in the diet of consumers can be limited by low isotopic specificity among prey species (Jones & Seminoff 2013), as well as a lack of accurate predator–prey discrimination values (Bond & Diamond 2011).

Several analytical approaches have been used to interpret stable isotope ratios in consumer tissues (see review by Layman et al. 2012). Among them, Bayesian mixing models quantify the relative contribution of different prey items to the diet of a consumer (Burkholder et al. 2011, Lemons et al. 2011, Hancock et al. 2018). This approach allows for the incorporation of uncertainty, which is a major limitation of linear mixing models (Layman et al. 2012). Further, by evaluating all information available (i.e. 'priors'), and using both fixed and random covariates, Bayesian mixing models achieve a better representation of input parameter variability by providing error parameterizations that can account for the variation of the input. Thus, in terms of outputs, Bayesian mixing models produce more accurate dietary input probability distributions for each prey group (Layman et al. 2012, Phillips et al. 2014, Stock et al. 2018).

SIA is a powerful tool to investigate diet composition and trophic level of local resident immature green turtles (Cardona et al. 2009, Lemons et al. 2011, Haywood et al. 2019). SIA can also help determine settlement and residency patterns for individuals aggregating at neritic foraging grounds (Arthur et al. 2008, Hancock et al. 2018, Vélez-Rubio et al.

2018). This is possible because consumers integrate stable isotope profiles from their foraging environments into their own tissues (DeNiro & Epstein 1981), and thus, when an animal moves among spatially discrete food webs that are isotopically distinct, stable isotope values of tissues can provide information about the previous location (Marra 1998, Rubenstein & Hobson 2004, Hobson & Wassenaar 2008, Turner Tomaszewicz et al. 2016). Therefore, comparison of bulk isotope values of sea turtle tissues with local isoscapes can depict if a turtle 'matches' local isotopic regimes, which would suggest it has been resident in the area long enough to integrate local isotope values into its tissues. Conversely, if a turtle has disparate isotope values relative to local patterns, this would indicate that it arrived in the study habitat relatively recently (Reich et al. 2007, 2008, Arthur et al. 2008).

Seagrass meadows and algal beds in Fiji are known foraging grounds for adult green turtles originating from multiple rookeries in the South Pacific (see summary in Piovano et al. 2019). Juvenile green turtles are also present in Fijian waters, and they represent more than half of the estimated local green turtle population (Batibasaga et al. 2006). A recent genetic study conducted in Fiji showed that a majority of the 150 individuals sampled were from the American Samoa management unit, with a smaller number of individuals from the New Caledonia and French Polynesia management units (Piovano et al. 2019).

In this study, we examined the recruitment, habitat use, and diet composition of green turtles at Yadua Island and Makogai Island, Fiji. Stable carbon and nitrogen isotope analyses were conducted on green turtle bulk skin tissue, and these values were compared to those of local putative prey items. This is the first stable isotope study of green turtles at a neritic habitat in the central South Pacific region (see reviews by Pearson et al. 2017, Haywood et al. 2019). As the region is affected by natural (e.g. El Niño–Southern Oscillation) and anthropogenic (e.g. climate change, overfishing, habitat degradation) changes in environmental conditions, this study provides a baseline to which future comparisons will be possible.

2. MATERIALS AND METHODS

2.1. Study area

Yadua and Makogai Islands are known to host aggregations of juvenile green turtles (Piovano et al. 2019). The distance between the 2 islands is about 100 km. Both islands present several similarities: they are located at the 2 opposite ends of the same channel (Vatu-i-Ra Channel), their coasts are protected by coral reefs, and they are in relatively close proximity to oceanic conditions (Fig. 1). The foraging grounds consist of intertidal (semidiurnal tidal cycle, with average tide height of 1–1.2 m) and subtidal (average max depth = 4 m) patchy seagrass meadows, delimited by coral reefs on the seaward side and, mostly, by sandy beaches on the landward side. The surveys conducted during this study occurred over 10 km^2 (7 km^2 at Yadua Island and 3 km^2 at Makogai Island) of benthic habitat and extended along a total of 54 km of coastline (38 km at Yadua Island and 16 km at Makogai Island). Abundance of green turtles is not equal across the bays of the 2

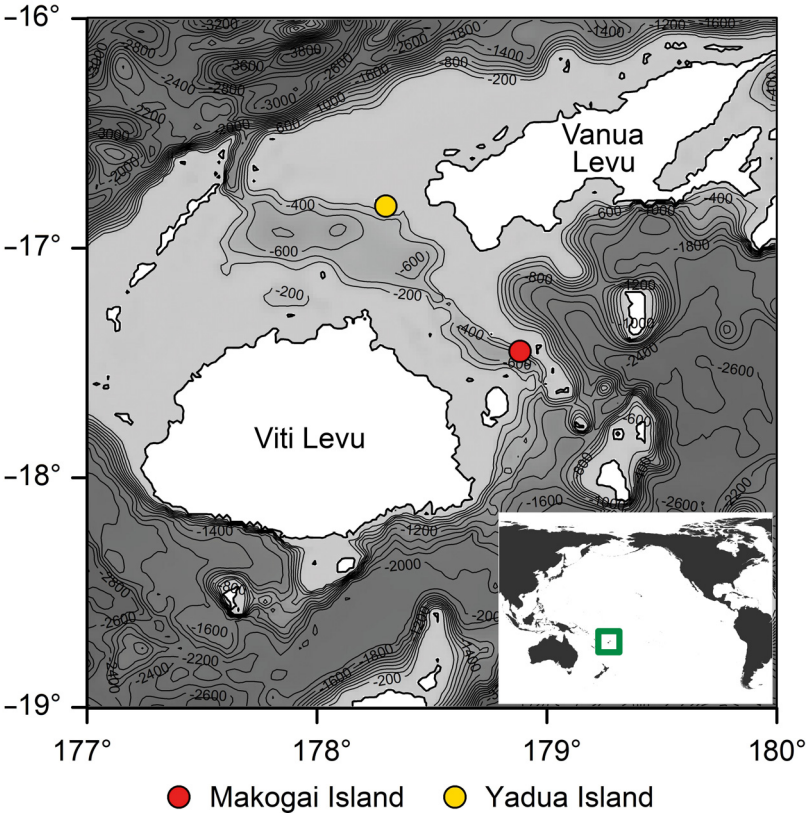

Fig. 1. Bathymetric map showing proximity of Yadua and Makogai Islands to oceanic conditions. Inset map: location of Fiji within the Pacific Ocean. Maps created with the ETOPO1 dataset (Amante & Eakins 2009) in R (R Core Team 2017) with the packages 'marmap', 'mapproj', 'maps' and 'ggplot2'

islands, and to date no turtle tagged at one island has been found at the other island (S. Piovano unpubl. data).

2.2. Turtle capture and measurement

Four-day capture–mark–recapture surveys were carried out at each island during winter 2015 (July–August: 1 survey performed at each island) and the following summer (November to March: 3 surveys at Yadua Island and 2 surveys at Makogai Island). During each visit, turtles were hand-captured at high tide via the 'rodeo' technique (Ehrhart & Ogren 1999), after which species identification, minimum curved carapace length (CCL; Bolten 1999), and weight were recorded. Captured turtles were also checked for the presence of external injuries and fibropapilloma tumors. Each turtle had a uniquely coded Inconel flipper tag (National Band and Tag, Style 681) applied to the trailing edge of 1 front flipper (Eckert & Beggs 2006) upon initial capture. This research was part of a larger study, and here the focus is only on the turtles that were sampled for SIA.

2.3. Turtle tissue and habitat sampling

After measurement, 2 epidermis (hereafter 'skin') samples were collected from the front shoulder region using a disposable biopsy punch (2 mm diameter on turtles <50 cm CCL, 6 mm diameter on turtles of larger sizes). Skin samples were stored in a saturated NaCl solution until analysis. Efforts were made to only collect the epidermal layer, with no underlying connective tissue.

Samples of prey items in the area were collected to characterize the stable isotope ratios of the putative prey taxa of green turtles. Putative diet items included seagrasses, macroalgae, and invertebrates (Table 1); the items were sampled from each island at low tide during habitat characterization activities (see Section 2.5). To account for potential opportunistic feeding on discarded fishes (Turner Tomaszewicz et al. 2018), samples of fish were obtained from local subsistence fishermen. Putative diet items were chosen based on prior knowledge about green turtle diet and availability of the items at each island. Samples were either dried (seagrasses and algae) or preserved in 70% ethanol (invertebrates and vertebrates) until analysis.

2.4. SIA

Skin and putative diet samples were rinsed, lyophilized, and homogenized prior to isotope analysis. The effect of lipid extraction on the isotope values

Table 1. Putative diet items sampled for stable isotope analysis. Common name is given in brackets when species was not identified. Three samples were collected for each item

Category	Phylum	Class	Species
Macroalgae	Chlorophyta	Ulvophyceae	*Halimeda opuntia*
			Halimeda discoidea
			Rhizoclonium sp.
	Ochrophyta	Phaeophyceae	*Chnoospora minima*
			Colpomenia sinuosa
			Hydroclathrus clathratus
			Padina boryana
			Padina pavonica
			Sargassum polycystum
	Rhodophyta	Florideophyceae	*Acanthopora spicifera*
			Gelidiopsis intricata
			Jania sp.
			Tricleocarpa fragilis
Seagrasses	Tracheophyta	Monocots	*Halodule pinifolia*
			Halodule uninervis
			Halophila ovalis
Marine invertebrates	Arthropoda	Crustacea	(Crab)
			(Hermit crab)
			(Shrimp)
	Echinodermata	Echinoidea	*Tripneustes gratilla*
	Mollusca	Bivalvia	(Cockle)
		Gastropoda	*Cerithium* sp.
			Conus ebreus
			Engina sp.
			Littorina sp.
			Monetaria annulus
			Morula sp.
			Nassarius sp.
			Natica sp.
			Nerita sp.
			Nucella sp.
			Strombus sp.
	Porifera		(Sponge)
Marine fishes	Chordata	Actinopterygii	*Epinephelus* sp.
			Gymnothorax sp.
			Scarus sp.

of skin samples has been tested elsewhere (Vander Zanden et al. 2012, Turner Tomaszewicz et al. 2017) and in light of this, lipid extraction was deemed to be unnecessary; therefore, isotopic analyses were conducted on non-lipid-extracted skin samples.

Approximately 1.0 mg of green turtle skin or prey tissue was weighed and loaded into tin capsules and analyzed by a continuous-flow isotope ratio mass spectrometer (IRMS) at the stable isotope laboratory at the University of Florida, Gainesville, USA. All samples were analyzed for their $\delta^{13}C$, $\delta^{15}N$, %C, and %N values. A Carlo Erba NA 1500 Elemental Analyzer system interfaced via a ConFlo II device (Finningan MAT) to a Thermo Electron DeltaV Advantage gas IRMS was used. Prior to exiting the elemental analyzer, combustion gas was measured using a thermal conductivity detector to determine percent compositions. USGS40 standards (9.52% N, 40.82% C) were used for calibration. Sample stable isotope ratios relative to the isotope standard are expressed in the conventional delta (δ) notation in parts per thousand (‰):

$$\delta = ([R_{sample}/R_{standard}] - 1)] \times 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively. The standards used were USGS40 (L-glutamic acid; $\delta^{13}C$ = −26.39‰, $\delta^{15}N$ = −4.52‰) and USGS41 (L-glutamic acid enriched in ^{13}C and ^{15}N; $\delta^{13}C$ = 37.63‰, $\delta^{15}N$ = 47.57‰). All carbon isotope results are expressed relative to Vienna Pee Dee Belemnite. All nitrogen isotope results are expressed relative to atmospheric air. All analytical runs included USGS40 and USGS41 inserted after every 5–8 samples to isotopically correct the results and to estimate precision of the isotopic measurements. Replicate assays of standard materials indicated measurement errors of 0.05‰ and 0.095‰ for carbon and nitrogen, respectively.

2.5. Habitat characterization

Habitat characterization to determine marine plant biodiversity, distribution, and percent coverage was performed at seagrass meadows where green turtles were observed during the study period. Seagrass meadows were characterized in 2015 following McKenzie (2003). Briefly, biodiversity of seagrasses and macroalgae was recorded by estimating their % coverage with a standard 50 × 50 cm quadrat placed every 10 m along a 100 m linear transect perpendicular to the shore, at low tide. For invertebrate species, presence and abundance (i.e. number of individuals) within each quadrat were noted. A total of 385 quadrats were deployed along 35 transects (18 in Yadua Island and 17 in Makogai Island). Based on core areas of juvenile green turtles in other regions being less than 5 km^2 (Seminoff et al. 2002, Wildermann et al. 2019), the spatial extent of movement of the study turtles was most likely within the area over which prey were sampled.

2.6. Statistical and mixing model analysis

Statistics were run in R version 3.4.1 (R Core Team 2017). Green turtle stable isotope data were partitioned into biologically appropriate subgroups (i.e. groups with similar life histories) using a cluster analysis. The cluster analysis conducts an automated search for groups of cohesive observations within a given dataset, thus clustering the data without prior knowledge of their structure (Fraley & Raftery 2002). The analysis was run with the package 'mclust' (Fraley et al. 2018), following the procedure of Fraley & Raftery (2002). The package generates a series of normal mixture models fitted using an expectation–maximization algorithm with varying covariance parameterizations and number of clusters. Mixture models were compared with the Bayesian information criterion. The best model, with the highest Bayesian information criterion, was used to classify green turtles into groups based on their bulk tissue isotope values.

The overall contribution of each putative diet item for each study site was determined using the Bayesian mixing model package 'MixSIAR' (Stock & Semmens 2016). Prior to mixing model analyses, prey items were grouped based on taxonomy and position in the food web; i.e. invertebrates and fishes were separated into herbivorous and carnivorous groups for each respective taxon. Fishes were included to evaluate potential opportunistic feeding on fish discarded at sea by local artisanal fishers. Macroalgae and seagrasses were kept in separate categories. MixSIAR generated a series of green turtle diet proportions for each prey group using green turtle and prey $\delta^{13}C$ and $\delta^{15}N$ values. Green turtle skin isotope discrimination factors from Seminoff et al. (2006) (+0.17 ± 0.03‰ for $\delta^{13}C$; +2.80 ± 0.11‰ for $\delta^{15}N$) were applied to account for turtle–prey isotopic discrimination.

Statistical differences in CCL between the 2 study sites and the 2 clusters, as well as isotope values between the 2 sites and between the 2 seasons, were explored with Wilcoxon-Mann-Whitney (WMW) tests.

Correlations between CCL and $\delta^{13}C$ values, and CCL and $\delta^{15}N$ values, were determined using a Pearson product-moment correlation test. Differences in seagrass coverage (surface area occupied), total presence (yes/no) of invertebrates, as well as total abundance (number of individuals recorded) of herbivorous and carnivorous invertebrates, at the 2 islands were tested with a Pearson's chi-squared (χ^2) test.

3. RESULTS

3.1. Turtle captures

During this study, 110 juvenile green turtles were captured and sampled (64 at Yadua Island and 46 at Makogai Island). Turtle CCL ranged from 25.5 to 89.0 cm (mean ± SD = 54.6 ± 9.0 cm), and mean CCL was not statistically different between the 2 sites (Yadua Island: 53.1 ± 8.0 cm; Makogai Island: 56.7 ± 10.1 cm; WMW test: Z = 1.60, p = 0.109). No adult green turtle was encountered. No fibropapilloma tumors or external injuries were recorded.

3.2. Stable isotope ratios and elemental concentrations

Green turtle stable isotope ratios were similar between the 2 islands (Table 2), although the range of $\delta^{15}N$ values was slightly broader at Makogai Island (range = 3.93–19.05‰, mean ± SD = 11.38 ± 3.38‰) than at Yadua Island (4.88–17.67‰, 11.15 ± 3.09‰; WMW test: Z = −0.40, p = 0.693), and the range of $\delta^{13}C$ values was slightly shifted towards more negative values at Makogai Island (−15.12 to −7.96‰, −12.15 ± 1.76‰) versus Yadua Island (−14.99 to −6.74‰, −11.59 ± 1.76‰; WMW test: Z = 1.80, p = 0.072). A significant seasonal difference in $\delta^{15}N$ and $\delta^{13}C$ values was observed among turtles sampled in the 2 seasons, with individuals captured in winter having lower $\delta^{15}N$ values ($\delta^{15}N$ winter: 9.65 ± 3.48‰, summer: 11.79 ± 2.95‰; WMW test: Z = 3.09, p < 0.002) and higher $\delta^{13}C$ values ($\delta^{13}C$ winter: −10.86 ± −1.85‰, summer: −12.25 ± −1.63‰; WMW test: Z = −3.29, p < 0.001). Turtle size (CCL) had a significant moderate negative correlation with $\delta^{15}N$ values (Pearson product-moment correlation test: r [108] = −0.56, p < 0.001) and a significant moderate positive correlation with $\delta^{13}C$ values (Pearson product-moment correlation test: r [108] = 0.57, p < 0.001).

Among putative prey items, the lowest $\delta^{13}C$ values (−14.68 ± 3.42‰) and the highest $\delta^{15}N$ values (9.75 ± 0.58‰) were recorded in carnivorous fishes (Table 2). The highest $\delta^{13}C$ values (−8.18 ± 0.95‰) were found in herbivorous fishes whilst the lowest $\delta^{15}N$ values (3.70 ± 2.31‰) were found in seagrasses.

3.3. Cluster analyses

The cluster analyses of discrimination-calibrated isotope values for green turtles identified 2 clusters (Fig. 2). One cluster (with mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of −13.18 ± 0.72‰ and 15.16 ± 1.50‰, respectively) showed green turtle isotope values that were higher in $\delta^{15}N$ compared to local putative prey after accounting for nitrogen discrimination. A second cluster ($\delta^{13}C$ and $\delta^{15}N$ = −11.35 ± 1.79‰ and 9.46 ± 1.87‰, respectively) fell within the range of isotope values found among putative prey sampled within the 2 foraging grounds.

Table 2. Mean (SD) percent nitrogen (N) and carbon (C) and mean (SD) stable isotope values $\delta^{15}N$ and $\delta^{13}C$ for green turtles and aggregated diet items used in the mixing model analysis. Turtle isotope values are presented in 3 groups: the 2 foraging aggregations (Yadua and Makogai Islands) and all green turtles in this study (all)

Green turtles (Mixture)	n	N (%)	$\delta^{15}N$ (‰)		C (%)	$\delta^{13}C$ (‰)	
		Mean (SD)	Mean (SD)	Range	Mean (SD)	Mean (SD)	Range
Yadua Island	64	14.10 (2.32)	11.29 (3.20)	4.88 to 17.67	40.46 (6.32)	−12.07 (1.76)	−14.99 to −6.74
Makogai Island	46	14.49 (1.71)	10.98 (3.20)	3.93 to 19.05	41.79 (4.96)	−11.56 (1.70)	−15.12 to −7.96
All	110	14.25 (2.01)	11.19 (3.10)	3.93 to 19.05	41.03 (5.72)	−11.87 (1.78)	−15.12 to −6.74
Diet items							
Macroalgae	20	1.58 (0.66)	4.03 (1.05)	1.10 to 6.16	35.04 (5.59)	−11.39 (4.44)	−18.54 to −2.23
Seagrasses	9	3.63 (4.23)	3.70 (2.31)	1.40 to 9.10	39.56 (8.58)	−9.38 (4.50)	−19.34 to −3.41
Herbivorous invertebrates	29	8.11 (4.30)	5.16 (1.70)	−0.72 to 8.00	32.52 (11.68)	−9.42 (2.66)	−15.56 to −5.48
Herbivorous fishes	3	14.74 (0.15)	5.11 (0.11)	4.96 to 5.21	48.18 (0.31)	−8.18 (0.95)	−8.83 to −7.80
Carnivorous invertebrates	6	10.71 (4.08)	8.02 (1.60)	5.02 to 9.50	39.79 (10.50)	−14.20 (2.08)	−17.93 to −10.30
Carnivorous fishes	8	14.95 (0.14)	9.75 (0.58)	8.86 to 10.50	48.01 (0.73)	−14.68 (3.42)	−18.83 to −10.43

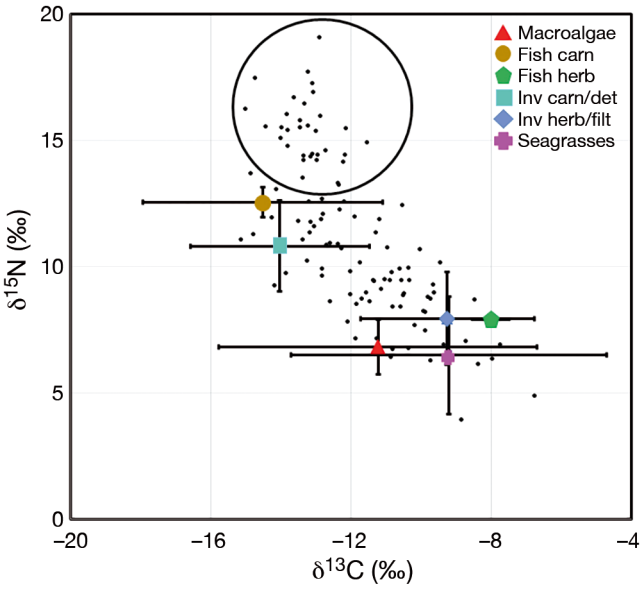

Fig. 2. Cluster analysis grouping with MixSIAR-generated isoplot of all green turtle $\delta^{13}C$ and $\delta^{15}N$ (black dots) with mean $\delta^{13}C$ and $\delta^{15}N$ values for the aggregated prey items, identified by color. The circle encompasses a group of green turtles whose tissues are likely not yet equilibrated to the local isotope regime. Fish carn: carnivorous fishes; Fish herb: herbivorous fishes; Inv carn/det: carnivorous (included detritivorous) invertebrates; Inv herb/filt: herbivorous (included filter feeding) invertebrates

The mean size of the green turtles making up the first group (48.5 ± 5.7 cm CCL) was smaller than that of second group (57.4 ± 9.0 cm CCL; WMW test: $Z = -5.20$, $p < 0.005$). On average, the first group was composed of individuals ranging in size from 25.5–60.0 cm CCL (Yadua Island = 47.0 ± 5.6 cm; Makogai Island = 50.8 ± 5.3 cm; Fig. 3), and included 31.8% of individuals sampled at Yadua Island and 28.3% of individuals sampled at Makogai Island. After accounting for diet–tissue discrimination, the mean $\delta^{15}N$ of turtles in the 'high $\delta^{15}N$ group' (15.16 ± 1.50‰) was still higher than the mean $\delta^{15}N$ of the highest trophic level fish in the study area (carnivorous fishes: 9.75 ± 0.58‰). This group made up 30% of the green turtles sampled in winter and 50% of those sampled in summer. Because turtles assigned to this cluster are likely to have tissues that had not yet equilibrated to the local isotope regime, these individuals were excluded from the mixSIAR analyses.

The other group identified by cluster analysis was composed of green turtles whose discrimination-calibrated stable isotope values fit well within the range of $\delta^{13}C$ and $\delta^{15}N$ values of prey items, encompassing local organisms from seagrasses to carnivorous fishes (Table 2). This group was composed of individuals ranging in size from 43.5–89.0 cm CCL (Yadua Island = 56.0 ± 7.3 cm; Makogai Island = 59.3 ± 10.6 cm; Fig. 3), and included 68.2% of individuals sampled at Yadua Island and 71.7% of individuals sampled at Makogai Island. This group made up 70% of the green turtles sampled in winter and 50% of those sampled in summer.

3.4. Mixing model

MixSIAR results indicate variable foraging strategies of green turtles present at both islands. When examined individually on a per-turtle basis, some green turtles had bulk skin isotope values indicative of lower trophic level (i.e. mostly herbivorous diet) and others had isotope values suggesting a higher trophic level (i.e. a more omnivorous diet) (Fig. 4). However, at the population level, MixSIAR results were similar between the 2 islands, indicating that diets were mostly comprised of invertebrates (herbivorous and carnivorous invertebrates totaled 40% of the diet sources at both islands), with the rest almost equally composed of fishes (herbivorous and carnivorous fishes totaled 32% at Yadua Island and 31% at Makogai Island) and plants (macroalgae and seagrasses totaled 29% at both islands; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m640p201_supp.pdf). A matrix plot of diet item group sources is presented in Fig. S1.

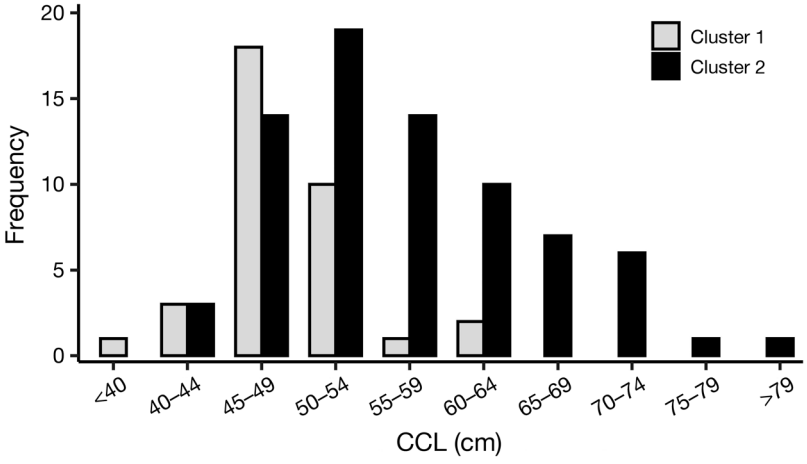

Fig. 3. Green turtle minimum curved carapace length (CCL) in 5 cm categories, grouped by results of the cluster analysis. Black bars represent 'recent recruits;' grey bars represent 'residents'

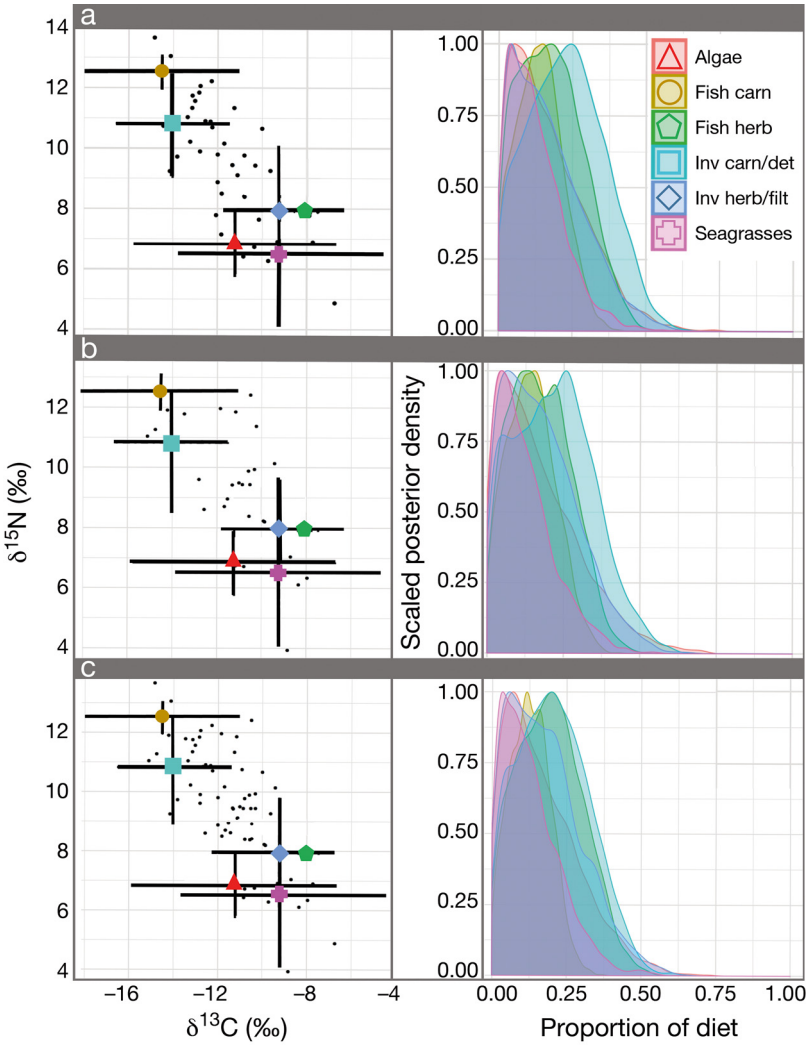

Fig. 4. Post-cluster analysis of MixSIAR results for (a) Yadua Island foraging aggregation, (b) Makogai Island foraging aggregation, and (c) all turtles. Figures are presented for each group as isoplots on the left and diet proportion distributions on the right

3.5. Habitat characterization

Benthic habitats at the 2 islands hosted seagrasses (up to 46% of the sampled benthic surface area at Yadua Island and up to 28% at Makogai Island, Table S2), with relatively little macroalgae (on average, less than 7% at both islands). At Yadua Island, 3 species made up 96% of the seagrass coverage, particularly *Halodule pinifolia* (mean ± SD = 72.7 ± 32.6%), followed by *H. uninervis* (17.0 ± 24.0%) and *Halophila ovalis* (5.8 ± 12.1%). Overall, the seagrass coverage was highly variable; for example, *H. ovalis* had a mean coverage of 5.8% but coverage was greater than 50% in 3 transects where it was the dominant seagrass species.

At Makogai Island, 2 species made up 98% of the seagrass coverage, with *H. uninervis* being the dominant seagrass (94.6 ± 9.4%) and *H. ovalis* showing a much lower coverage (3.3 ± 4.7%, with only 2 transects in which the species made up more than 10%). Benthic coverage of *H. pinifolia*, *H. uninervis*, and *H. ovalis* was different between the 2 islands ($\chi^2_{1,5730} = 5730$, $p < 0.001$, $\chi^2_{1,6596} = 694$, $p < 0.001$, and $\chi^2_{1,713} = 694$, $p < 0.001$, for each seagrass, respectively). *Syringodium isoetifolium* had lower coverage at both islands (Yadua Island: 0.5 ± 1.8%, Makogai Island: 2.1 ± 7.9%; $\chi^2_{1,203} = 0.8$, $p = 0.362$).

Herbivorous and carnivorous invertebrates had a similar presence ($\chi^2_{1,35} = 0.7$, $p = 0.404$) between the 2 sites, with herbivorous invertebrates (e.g. *Tripneustes gratilla*, *Nerita* sp., and *Strombus* sp.) recorded in 50% of the 198 quadrats deployed at Yadua Island and in 47% of the 187 quadrats deployed at Makogai Island, while carnivorous invertebrates (e.g. *Conus ebreus*, *Natica* sp., and *Morula* sp.) were present in 22% of the quadrats at Yadua Island and in 24% of the quadrats at Makogai Island. The abundance of carnivorous invertebrates recorded in the quadrats was similar between the 2 islands ($\chi^2_{1,28} = 1.3$, $p = 0.257$), while the total number of herbivorous invertebrates recorded at Yadua Island was lower than at Makogai Island ($\chi^2_{1,275} = 72$, $p < 0.001$).

4. DISCUSSION

This is the first characterization of recruitment and diet composition of juvenile green turtles present at 2 foraging grounds in a South Pacific Island Country. Two groups of green turtles were present at both foraging grounds: a 'low $\delta^{13}C$/high $\delta^{15}N$' group (likely 'recent recruits'), and a 'high $\delta^{13}C$/low $\delta^{15}N$' group (likely 'residents'), which underscores that these areas provide necessary resources for neritic juveniles of varied recruitment histories. This discovery also highlights that these Fijian habitats host neritic juveniles of a broad size range, which likely equates to turtles of different ages.

4.1. Recruitment

The lower $\delta^{15}N$ values of putative 'resident' turtles are consistent with $\delta^{15}N$ values of local prey items, whereas the relatively higher $\delta^{15}N$ values of putative 'recent recruits' are thought to reflect values from areas outside of Yadua and Makogai Islands, owing to the fact that no prey resources were found within the study areas that had sufficiently high $\delta^{15}N$ values after accounting for turtle–prey discrimination. Therefore, green turtles with high $\delta^{15}N$ are interpreted to be individuals that recently departed an isotopically disparate region and recruited to the local habitat, but had not been present long enough to reach isotopic steady state with the local isotope regime. The isotope residence time in skin of small juvenile loggerhead turtles *Caretta caretta*, the only sea turtle for which isotopic residence times have been established, is ca. 67 d for nitrogen and ca. 83 d for carbon (Reich et al. 2008). Thus, green turtles in the putative 'recent recruit' group likely recruited within the previous ~80 d, with individuals least resembling the local isotope regime thought to be the most recent of recruits.

In this context, the most likely origin of these 'high $\delta^{15}N$' turtles is oceanic habitat. Oceanic waters with depths greater than 1000 m are within 50 km of both study sites (Fig. 1), and in the eastern Pacific, green turtles that occupy offshore, oceanic waters had significantly higher skin $\delta^{15}N$ values than individuals residing in nearby neritic habitats (Turner Tomaszewicz et al. 2018). Moreover, the observed disparity in $\delta^{15}N$ values between 'recent recruits' and 'residents' is consistent with ontogenetic shifts from oceanic to neritic regions elsewhere (Hatase et al. 2006, Arthur et al. 2008, Hancock et al. 2018, Turner Tomaszewicz et al. 2018). During occupation of oceanic habitats, green turtles feed primarily on coelenterates, crustaceans, and gastropods (Bolten 2003, Parker et al. 2011), all of which are expected to have relatively higher $\delta^{15}N$ values compared to primary producers, which feature prominently in the diet of juvenile green turtles upon recruitment to neritic foraging areas (Di Beneditto et al. 2017, Hancock et al. 2018, Turner Tomaszewicz et al. 2018).

Lower $\delta^{13}C$ in the 'recent recruit' group is also consistent with a more oceanic existence (Reich et al. 2007) due to the assimilation of ^{13}C-depleted nutrients that are characteristic of pelagic systems (Rubenstein & Hobson 2004). Similarly, Arthur et al. (2008) reported a recruitment pattern for green turtles in Australia whereby new recruits were characterized by lower $\delta^{13}C$ values than known resident turtles, and similar to those of juvenile green turtles captured in offshore waters. In Fiji as well as Australia, it is likely that turtles characterized as new recruits still maintained $\delta^{13}C$ values that reflected their pelagic existence.

The possibility that turtles in the 'low $\delta^{13}C$/high $\delta^{15}N$' group were recent recruits is also supported by their size (mean CCL = 48.5 cm) being about 9 cm smaller than putative 'resident' turtles (mean CCL = 57.4 cm). Green turtles recruit from oceanic waters to neritic habitats at similar sizes across tropical and temperate waters of the North Pacific Ocean and of the western South Pacific (about 35–50 cm CCL and 40–44 cm CCL, respectively; Table S3). Thus, the apparent recruitment size for Fijian green turtles appears consistent with previously reported average sizes of recruits at other Pacific inshore foraging grounds and confirms this trend in the central South Pacific.

As an alternate scenario, high $\delta^{15}N$ values of green turtles in the present study may have resulted from consumption of prey items that were not sampled during this study, for example, gelatinous organisms such as cnidarians or ctenophores, both of which have been reported in the diet of juvenile green turtles elsewhere (González Carman et al. 2014). Additional sampling of putative prey species within Yadua and Makogai Islands and expansion of sampling techniques to include plankton tows may help to exclude this possibility.

It is also conceivable that the 'low $\delta^{13}C$/high $\delta^{15}N$' group included turtles that transitioned back and forth between neritic and oceanic environments in and around Fiji instead of undertaking a 1-way oceanic-to-neritic ontogenetic habitat shift. Although the prevalent life-history paradigm for green turtles suggests that once recruited to neritic habitats as small turtles, individuals remain in these areas (Lutz & Musick 1997), larger, post-neritic-recruitment size turtles have been observed in oceanic habitats (Turner Tomaszewicz et al. 2018). It is thus possible that some Fijian green turtles may transition back to the oceanic environment after recruitment as has been shown for juvenile loggerheads in the Atlantic Ocean (Witzell 2002) and Mediterranean Sea (Casale et al. 2008). A combination of SIA and other techniques, such as satellite tracking (Seminoff et al. 2012) of green turtles captured in Fijian foraging grounds, serial sampling of scute tissue (Reich et al. 2007), and use of amino acids (Seminoff et al. 2012), may shed light on the prevalence of this alternate life-history strategy.

More 'recent recruit' turtles were present in summer, suggesting that recruitment at the tropical

Fijian sites occurred seasonally. Seasonal recruitment, possibly influenced by water temperatures and prey availability, is common in juvenile green and loggerhead turtles living in temperate and sub-tropical regions (Avens et al. 2003, Avens & Lohmann 2004, Silva et al. 2017), but is not always noticeable within 1 yr projects at tropical sites, as a lack of seasonality can be observed for juvenile green turtles in some years (Torezani et al. 2010, Silva et al. 2017). As an effect of seasonality, CCL of the green turtles present in summer can be used as a proxy for 'recent recruits' whereby, at the Fijian sites, 52 cm would be the pivotal size below which green turtles would be 'likely recent recruits' (based on the summer subset only, correct assignation is 78% for the 'recent recruit' group and 95% for the 'resident' group). This makes 52 cm CCL a good proxy size threshold for monitoring population dynamics.

4.2. Foraging ecology: diet composition and habitat use

In this study, mixing model-derived diet distributions highlight that Fijian green turtles at both islands consume a substantial amount of invertebrates, followed by fishes and marine plants. The consistent presence of invertebrates in green turtle diet at both sites (40%) was somewhat unexpected, considering that a lower abundance of herbivorous invertebrates was reported in Yadua Island. Perhaps the consistency of invertebrate consumption resulted from the low coverage of seagrass (15%) and marine algae (<7%), and presumed lesser availability of these vegetative resources in the study area. Alternatively, heavy consumption of invertebrates by Fijian green turtles may be an opportunistic strategy to gain important nutrients otherwise not provided via consumption of seagrass and/or marine algae, such as been suggested for green turtles in the southeastern Pacific Ocean (Hays Brown & Brown 1982, Amorocho & Reina 2007). Regardless of the reason, neritic habitats of Fiji can be added to the growing list of areas where green turtle diet is dominated by invertebrates (see Jones & Seminoff 2013).

Trophic opportunism may also be reflected in the apparent significant consumption of herbivorous and carnivorous fishes. Although fishes have rarely been recorded as a diet item for green turtles, the possibility of opportunistic foraging on small fish discards from the local artisanal fishery cannot be excluded, nor can foraging on fishes poisoned by the traditional fishing technique 'duva ni Niukini' (e.g. Golden et al. 2014). Consumption of fisheries discards has been reported for loggerhead turtles in the eastern Pacific, where Peckham et al. (2011) noted that sea robins (*Prionotus* spp.), sand perches (*Diplectrum* spp.), and lizardfish (*Synodus* spp.) were recovered from up to 30% of the stomachs examined from dead-stranded turtles; all 3 genera were commonly caught and discarded as bycatch from gillnets in the area (S. H. Peckham unpubl. data). A stable isotope study on green turtles stranding in the same area interpreted high $\delta^{15}N$ values as reflecting consumption of fishery discards (Turner Tomaszewicz et al. 2018). Direct observational studies (Thomson et al. 2018) or traditional stomach and gut content analyses (Bjorndal 1980) may help elucidate this possibility.

Seagrasses and macroalgae together contributed about one-third of the diet of the 'resident' turtles, which is surprisingly low considering that both foods have been reported as primary diet items for green turtles (Bjorndal 1997). Seagrass consumption (13% average diet proportion) mirrored its benthic coverage (15% coverage), a finding which suggests that local green turtle diet is influenced by food availability, such as has been shown for seagrass consumption at other foraging sites around the world (Mortimer 1981, Bjorndal 1982). However, in Fiji, marine algae were consumed (17% average diet proportion) in greater proportions than would be expected by their low (<7%) mean benthic coverage, thus suggesting a degree of dietary preference for this diet item. Preference for marine algae has also been reported in the eastern Pacific, where López-Mendilaharsu et al. (2008) found that green turtles selectively consumed the green algae *Codium* spp. and red algae *Gracilaria* spp. in a neritic foraging area. Taken together, the apparent preference for marine algae and the consistent use and availability of seagrasses at the same site indicate that green turtles may employ multiple foraging strategies within the same foraging ground. A greater understanding of the availability and nutritional value of different foods as well as the energy requirements and intestinal microflora communities of green turtles will help decipher the mechanisms that cause green turtles to shift between generalist and preferential foraging strategies.

4.3. Caveats and limitations of mixing model analyses

Grouping prey items with similar isotopic values and foraging strategies prevents erroneous interpre-

tation of mixing model results, yet this is offset by less diet contribution specificity. However, carnivorous fishes and carnivorous invertebrates, as well as herbivorous fishes and herbivorous invertebrates were not aggregated in this study due to taxonomical differences. The similarities in isotope values for these prey groups (i.e. carnivorous invertebrates vs. carnivorous fishes) suggest that the contributions of fish species to Fijian green turtle diet is a result of isotopic similarities influencing analyses rather than direct feeding on fish species. In addition, a strong negative isotopic correlation between carnivorous fishes and carnivorous invertebrates at both islands was noted (Fig. S1). The joint uncertainty in each source proportion might have influenced the model output, creating an artificially inflated proportion, as covariation can affect the mixing model results and interpretation (Phillips et al. 2014). A mixing model analysis incorporating prior stomach content information, based on gut content observations, would relax the influence of prey group non-specificity, and provide more ecologically realistic model outputs depicting green turtle diet composition.

5. CONCLUSIONS

This is the first stable isotope study of sea turtles in the Fijian region. Via cluster analysis, 2 isotopically disparate clusters driven by differences in $\delta^{15}N$ values were found. The difference in $\delta^{15}N$ values is thought to result from animals switching from a largely carnivorous diet in the open ocean, to a more omnivorous diet upon recruiting to neritic foraging areas. The presumed isotopic differences between these 2 life history stages also offers opportunities to determine size at recruitment to foraging grounds. Green turtles recruit to Fijian coastal foraging areas starting at ca. 25 cm CCL, and we consider 52 cm CCL as a good size threshold for distinguishing long-term residents vs. recently recruited green turtles. Two separate analytical approaches were used: cluster analysis and Bayesian mixing models. Together these tools provided a novel glimpse into the foraging ecology and recruitment of green turtles in Fiji. This study is a first step in our understanding of green turtle foraging ecology in the region, and we recommend that future investigations endeavor to collect larger green turtle sample sizes over longer time frames, and to isotopically analyze greater numbers and diversity of putative prey species to further depict the resources most important to local green turtles. In addition, use of complementary techniques, such as satellite telemetry and SIA of amino acids, is highly recommended to evaluate the influence of trophic and geographic differences on the diet of the green turtles.

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