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RESEARCH ARTICLE

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Diet of hawksbill turtles (*Eretmochelys imbricata*) in the Gulf of California, Mexico

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Abstract

1. Hawksbill turtles ($n = 56$) in a foraging ground around Isla San Jose, Gulf of California, Mexico, were caught, measured, and their skin and scutes sampled. Tissue samples from putative prey species were collected from observed hawksbill feeding areas in the foraging ground.
2. Measurements of each turtle's straight carapace length were used to estimate the average life stage of the population. Tissue samples were processed for stable carbon and nitrogen isotope analysis to estimate foraging habits of turtles in this location.
3. The majority (96.4%) of measured individuals' straight carapace length fell in the size range considered to be juveniles.
4. A Bayesian mixing model analysis of the $\delta^{13}C$ and $\delta^{15}N$ values of hawksbill skin and potential prey indicated that hawksbills consume primarily invertebrates and algae, with lesser contributions from seagrass and mangrove material.
5. There was a positive linear relationship between turtle size and the $\delta^{13}C$ values from scute samples, and an increase in the $\delta^{13}C$ values of five individuals recaptured in subsequent years suggested a potential location shift from a pelagic habitat in the turtles' post-hatching, earliest juvenile years to the nearshore foraging area around Isla San Jose in their later juvenile years.

KEYWORDS
foraging ecology, marine vertebrate diet, Pacific Ocean, sea turtle, stable isotope analysis, $\delta^{13}C$, $\delta^{15}N$

1 | INTRODUCTION

Hawksbill sea turtles (*Eretmochelys imbricata*) are listed as Critically Endangered on the IUCN red list of threatened species, with the primary threats to their survival being the international shell trade, the destruction of nesting and foraging areas, and the illegal harvest of individuals and eggs for consumption (Mortimer & Donnelly, 2008). Hawksbills have an approximate 35–45-year generation time and are estimated to reach sexual maturity at between 15 and 25 years of age, with some ranging from as low as 15 years to as high as 40 years (Chacón, 2009; Snover et al., 2012; Avens et al., 2021; Turner Tomaszewicz et al., 2022), leaving them vulnerable to multiple natural and anthropogenic risks for many years before reproduction.

Hawksbills can be found in the Atlantic, Indian, and Pacific oceans (U.S. Department of Commerce, National Oceanic and Atmospheric Administration, & US Department of the Interior, U.S. Fish and Wildlife Service, 2013). Like most sea turtle species, they undergo a migratory phase in their life history (Limpus, 1996; Bolten, 2003). Eastern Pacific hawksbill movement patterns and foraging choices during their early life and development are not yet fully understood or documented, though recent studies have sought to establish a baseline for the population (e.g. Liles et al., 2015; Gaos et al., 2017a; Gaos et al., 2017b; Martínez-Estévez et al., 2022b; Turner Tomaszewicz et al., 2022). Understanding their resource needs and habitat use throughout their early years is critical for developing strategies to recover hawksbill populations.

Soon after hatching, hawksbills spend an unknown period of time potentially occupying a number of habitats, from pelagic areas to shallow reefs, with little evidence for the oceanic phase observed in all other sea turtle species (Van Houtan et al., 2016a). Little is known about this stage, to the point where it is referred to as the 'lost years' (Chacón, 2009). Hawksbills in the eastern Pacific are thought to spend their earliest, post-hatchling stage (∼0–5 years or <35–37 cm curved carapace length (CCL) in pelagic, offshore habitats before transitioning to nearshore habitats at ∼5 years of age (Carrión-Cortez et al., 2013; Wedemeyer-Strombel et al., 2021; Turner Tomaszewicz et al., 2022). Juvenile eastern Pacific hawksbills are strongly associated with mangrove and estuarine habitats for foraging (Gaos et al., 2012; Carrión-Cortez et al., 2013; Martínez-Estévez et al., 2021; Wedemeyer-Strombel et al., 2021; Turner Tomaszewicz et al., 2022), and hawksbills in the Gulf of California appear to occupy relatively small home ranges of 0.05–17 km^2 throughout their juvenile years (Martínez-Estévez et al., 2021) and into adulthood, with populations from Central America having their nesting habitats located close to their foraging grounds (Gaos et al., 2017b). Mangrove ecosystems are important nearshore nursery habitats for coastal and pelagic fish species, providing biologically productive areas for many developing juveniles (Aburto-Oropeza et al., 2008; Miththapala, 2008), including fish species that are commercially important for small-scale fishing communities. The overlap of turtles and fisheries in these highly productive habitats raises potential challenges for hawksbill conservation (Aburto-Oropeza et al., 2008).

In the Atlantic Ocean, hawksbills are primarily spongivores (Bjorndal, 1996). However, multiple studies based upon stomach and faecal analysis indicate hawksbills in the Pacific Ocean are omnivorous, consuming large quantities of vegetation and algae in addition to invertebrates such as sponges and tunicates (Hornell, 1927; Carr, 1952; Frazier & Stoddart, 1984; Meylan, 1984; Bjorndal, 1996; Martínez-Estévez et al., 2022b).

Stable isotope analysis (SIA) can be used to examine dietary composition and habitat use in animals (Fry, 2006), and it is especially useful for cryptic, highly migratory, or otherwise difficult to assess species (Hobson & Wassenaar, 2019), including sea turtles (Seminoff et al., 2012; Turner Tomaszewicz et al., 2015; Hetherington et al., 2018). Tissue samples from the consumer and putative prey are processed to measure the ratios of heavy to light stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes (reported in parts per thousand (‰)). These ratios are used to estimate the proportional composition of prey types in a consumer's diet as well as information about the habitat within which the prey were consumed (Fry, 2006; Ben-David & Flaherty, 2012). SIA is especially useful for elucidating diet and movement patterns of marine vertebrates that utilize multiple habitats over their lifetimes (Hobson, Piatt & Pitocchelli, 1994; Turner Tomaszewicz et al., 2017a). In particular, differences in δ^{13}C values measured in marine animals can indicate changes in habitat use related to regional differences in productivity, distance from shore, and other factors (Ramos & González-Solís, 2012). For example, the δ^{13}C values in marine environments are generally higher in nearshore or benthic regions and lower in offshore, pelagic environments (McConnaughey & McRoy, 1979; Hobson, Alisauskas & Clark, 1993; France, 1995). Stable nitrogen isotope values can also be used to assess animal habitat use (e.g. Turner Tomaszewicz et al., 2017a) but are most commonly used to estimate animal trophic position and the contributions of potential diet items to a consumer (Hobson, Piatt & Pitocchelli, 1994; Newsome, Clementz & Koch, 2010).

The time required for assimilation of stable isotopes from diet sources into consumer tissues varies with tissue type (Kurle, 2009). Therefore, animal diets can be reconstructed for multiple timescales using stable isotope values measured across various tissues (Kurle, 2009) as well as within tissues that are continuously growing (e.g. sea turtle scutes) (Reich, Bjorndal & Martínez del Rio, 2008). This can be especially useful for reconstructing dietary information for cryptic species that are only available for sampling during certain life-history stages, such as sea turtles that come ashore to lay eggs, occupy nearshore ecosystems during their juvenile years, or wash ashore after death. SIA has been used as a means of tracking marine predators (Ramos & González-Solís, 2012) and as a method to examine dietary make-up for a number of sea turtle species, including green (Lemons et al., 2011), loggerhead (Seminoff et al., 2012; Vander Zanden et al., 2014; Turner Tomaszewicz et al., 2017a), and hawksbills (Méndez-Salgado et al., 2020; Martínez-Estévez et al., 2022b).

Sampling stable isotope values from different areas across a turtle scute allows for estimating temporal changes in their diet because turtles deposit scute material in growth layers, with the oldest portion in the posterior of the scute and the most recent in the anterior (Hobson, 1999; Alibardi & Dipietrangelo, 2005; Palaniappan, 2007; López-Castro, Bjorndal & Bolten, 2014; Van Houtan et al., 2016b). Hawksbill turtles deposit the keratin in these growth layers at rates of 5 to 14 layers per year (Vander Zanden et al., 2010; Van Houtan et al., 2016b), and the tissue is inert once the scute growth layers are formed, retaining the stable isotope values that reflect the diet ingested by the turtle during the time the layers were deposited (Hobson, 1999; Van Houtan et al., 2016b). Thus, scutes have the potential to contain extensive chronologies, locking multiple years of diet data in their growth layers.

This study examined the foraging habits of juvenile hawksbill sea turtles in a foraging ground off Isla San Jose in the southern Gulf of California (hereafter referred to as the San Jose foraging ground; Figure 1). Specifically, hawksbill morphometric data and the δ^{13}C and δ^{15}N values from hawksbill shell (scute) and skin samples were used in combination with the δ^{13}C and δ^{15}N values of their potential diet items to (1) estimate the average life stage of hawksbill turtles utilizing the San Jose foraging ground, (2) estimate their foraging ecology, and (3) estimate temporal shifts in diet and/or habitat use that could reflect an ontogenetic shift from a pelagic to a nearshore habitat with age or movement in and out of the San Jose foraging ground throughout their juvenile years.

FIGURE 1 San Jose foraging ground located off Isla San Jose in the Gulf of California, Mexico, including three closely located microhabitats—rocky reef, sandy reef, and mangrove estuary.

Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

2 | METHODS

2.1 | Study site

The San Jose foraging ground is located at the southern end of Isla San Jose in the southern Gulf of California, 5.7 km offshore of the Baja California Sur Peninsula. It is characterized by a mangrove estuary covering an area of 1.09 km^2, a sandy bottom embayment west to the estuary with small patches of rocky boulder substrate, and a rocky reef habitat south of the mangrove estuary (Figure 1). The whole area is approximately 12.8 km^2. The mangrove estuary is a no-take marine protected area established by the Comisión Nacional de Acuacultura y Pesca, local fishers, and a local non-governmental organization in 2012 (Niparaja (Sociedad de Historia Natural Niparaja A.C.), 2015). The other two habitats that comprise the foraging ground are not protected.

FIGURE 2 Locations for the posterior and anterior scute samples collected from hawksbill turtles for stable isotope analyses. Photograph used with permission from LiveAuctioneers.

2.2 | Sample collection

Between 2014 and 2019, hawksbill sea turtles were captured (n = 56) using three methods: (1) a live-entanglement net (118 m long, 5 m deep, and 25 cm stretch monofilament mesh size) that was checked at regular intervals (about every 60 min); (2) strike netting, where the entanglement net was deployed from a small skiff to surround and capture an individual; and (3) hand capture by free diving. Owing to the variety of capture methods, catch per unit effort (CPUE) was calculated as the total number of captured hawksbills per habitat divided by the total time of each monitoring event, expressed as captures per hour. Each captured turtle was measured for straight carapace length (SCL), CCL, straight carapace width, curved carapace width, body depth, plastron length, total tail length, and body weight (Bolten, 1999). Turtles were tagged with and identified by a small, numbered metal tag attached to each of the rear flippers. There were 51 turtles captured between 2014 and 2019, with five turtles captured a second time in 2019 with initial captures in 2016 (n = 3) and 2017 (n = 2). Samples were collected from the skin of the posterior flipper using surgical scissors (n = 55) and the anterior and posterior portions of the central anterior scute by scraping the scute with a surgical knife (n = 48 and 51 respectively) (Figure 2). Skin samples were placed in vials containing 95% ethanol and refrigerated within 10 days of the sampling date. Scute samples were stored in vials at room temperature until processed for SIA.

Samples of putative dietary items were collected in June 2017 and 2019. In 2017, one to six samples each of 23 separate species ($n = 75$) were collected, whereas in 2019, 5–10 samples each of 23 separate species ($n = 129$) were collected (Supporting Information Table S1). Samples were washed in clean seawater and dried at ~150 °F (~66 °C) in a foil-lined cooler until dry. Dried samples were stored in airtight zippered bags with desiccant until prepared for SIA.

2.3 | SIA processing

All samples were prepared for SIA at the University of California San Diego by washing each in deionized water, lyophilizing for ≥24 h, homogenizing by hand, and packing subsamples of 0.001 g (±0.0005 g) in 5 mm × 9 mm tin capsules. All samples were analysed for their δ^{13}C and δ^{15}N values using a Carlo Erba CE1108 elemental analyser interfaced via a CONFLO III device to a Thermo-Electron Delta Plus XP mass spectrometer at the Stable Isotope Laboratory, University of California, Santa Cruz. Average precision for these data was determined using the standard deviations around the means for a subset of internal laboratory standards run at set intervals throughout analysis, and these were 0.04‰ for δ^{13}C and 0.14‰ for δ^{15}N.

2.4 | Stable isotope model

The proportional contribution of putative prey items to the diets of the turtles was estimated using the Bayesian stable isotope mixing model MixSIAR (R v4.2.2). The posterior distributions from the model provide an estimate, with associated uncertainty, for the contributions of each source category to the diets of the hawksbill turtles (Phillips, 2012). The consumer stable isotope values used in the model were those measured from the hawksbill skin samples ($n = 55$) (Supporting Information Table S2). Based on observations of the turtles in the study and diet data obtained from hawksbill scats collected from the same population of turtles (Martínez-Estévez et al., 2021; 2022b), the stable isotope values from putative hawksbill prey were used to create four source categories: invertebrates (tunicates and sponges), algae (*Caulerpa* spp., *Dictyota* spp., *Halimeda* spp., and *Padina* spp.), seagrass (*Halophila* spp.), and mangrove (*Rhizophora mangle*) leaves and stems. The mean (±*SD*) δ^{13}C and δ^{15}N values for each of the four source categories were used in the model (Table 2 and Supporting Information Table S1). The trophic discrimination factors used in the model were measured from captive eastern Pacific green sea turtles (skin Δ^{13}C = 2.3 ± 0.3‰ and Δ^{15}N = 4.1 ± 0.4‰) (Turner Tomaszewicz et al., 2017b).

2.5 | SIA: Spatial and temporal changes in diet

To determine whether juvenile hawksbills in the San Jose foraging ground exhibited temporal shifts in diet and/or habitat use over time, the δ^{13}C and δ^{15}N values from the posterior scute samples ($n = 51$) were compared with the size of each turtle (SCL) using simple linear regression models. Scutes grow from front (anterior) to back (posterior), so the isotope values from the posterior portion of the scute were used for this analysis because they reflect the oldest recorded dietary data, increasing the likelihood of capturing recorded stable isotope values that reflect data incorporated while the turtles may have been inhabiting pelagic habitats in their earliest juvenile years (Wedemeyer-Strombel et al., 2021; Turner Tomaszewicz et al., 2022). A change in stable isotope values measured in posterior scutes that corresponds with increasing size could indicate a potential transition from the turtles' earliest years in unknown, likely pelagic habitats to their later juvenile years in the nearshore San Jose foraging ground. Finally, to further detect the potential for a shift in isotope values that may reflect a shift in diet and/or habitat over time, an additional scute sample was collected from animals that were captured more than once ($n = 5$ pairs). For this analysis, the stable isotope values from the posterior scute collected at the first capture (2016, $n = 3$; 2017, $n = 2$) were compared with the anterior scute collected at the second capture ($n = 5$; recaptured in 2019). The δ^{13}C and δ^{15}N values from scutes between the first and second captures were compared using a Wilcoxon signed-rank test. All means are reported with ±*SD*, unless noted otherwise, and significance was tested at the $\alpha = 0.05$ level.

3 | RESULTS

3.1 | Population morphometrics

Hawksbill turtles ($n = 51$) were captured and processed between 2014 and 2019, with five individuals recaptured a second time within that interval ($n = 56$ total). The captures occurred in the sandy reef ($n = 17$, mean CPUE = 0.3, *SE* = 0.1), mangrove estuary ($n = 35$, mean CPUE = 1.3, *SE* = 0.2), and rocky reef ($n = 4$, mean CPUE = 0.2, *SE* = 0.1) habitats comprising the San Jose foraging ground. Turtle body size ranged from 33.8 to 82.6 cm SCL (mean: 48.2 ± 9.6 cm) (Supporting Information Table S2). Most of the turtles (54 of 56, 96%) fit within the size range estimates for juveniles (Table 1), whereas two individuals (76.6 cm and 82.6 cm SCL) were classified as putative adults based on the mean nesting female hawksbill size reported for the region (CITES, 2002; Van Houtan et al., 2016b; Martínez-Estévez et al., 2022a).

Group	*n*	SCL (cm)	Weight (kg)	δ^{13}C skin (‰)	δ^{15}N skin (‰)
All turtles	56	48.2 ± 9.6	14.9 ± 7.6	−15.1 ± 0.9	12.7 ± 1.8
Juveniles	54	47.1 ± 7.6	13.2 ± 6.3	−15.1 ± 0.8	12.7 ± 1.8
Putative adults	2	79.6 ± 4.2	60.3 ± 11.0	−13.9 ± 0.01	13.8 ± 0.1

TABLE 1 Mean (±*SD*) straight carapace length (SCL), weight, and stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from skin samples of hawksbill turtle groups sampled in the San Jose foraging ground, Gulf of California, Mexico, 2014–2019.

3.2 | Stable isotope analyses

The $\delta^{13}C$ and $\delta^{15}N$ values (range: $\delta^{13}C$ -17.3‰ to −13.5‰; $\delta^{15}N$ 8.2–15.6‰) from the skin of all sampled turtles along with the mean (±*SD*) $\delta^{13}C$ and $\delta^{15}N$ values of the four source categories (algae, invertebrates, seagrass, and mangrove) were included in the MixSIAR models to estimate overall diet for hawksbills in the San Jose foraging ground. The probable contribution of the four source categories to hawksbill diets was dominated by invertebrates (mean 32.3%) and algae (mean 29.8%), followed by seagrass (mean 20.1%) and mangrove (17.9%) (Table 3 and Figure 3).

3.3 | SIA: Spatial and temporal changes in diet

The $\delta^{13}C$ values of the posterior hawksbill scute samples increased significantly with increasing hawksbill SCL ($F_{1,49} = 11.48$, $P = 0.001$, $R^2 = 0.19$) (Figure 4a). There was no significant relationship between the associated $\delta^{15}N$ values and the hawksbill SCL measurements ($F_{1,49} = 0.24$, $P = 0.63$, $R^2 = 0.005$) (Figure 4b).

3.4 | SIA: Recaptured turtles

There was no significant change in the $\delta^{15}N$ values from the posterior scutes sampled from five hawksbills during their first capture (14.3 ± 0.3‰) versus those sampled from the anterior scute of those same five hawksbills at their recapture (13.3 ± 1.3‰; $n = 5$ pairs of turtles, $Z = -1.214$, $P = 0.225$). However, the $\delta^{13}C$ values were significantly higher for the anterior scute from the recapture (−15.7 ± 0.7‰) than those from the initial capture's posterior scute (−16.9 ± 0.7; $n = 5$ pairs of turtles, $Z = 2.023$, $P = 0.043$), indicating a potential shift from a pelagic to a nearshore habitat, as pelagic marine habitats generally have lower $\delta^{13}C$ values than those from nearshore and benthic marine habitats (McConnaughey & McRoy, 1979; Hobson, Alisauskas & Clark, 1993; France, 1995).

TABLE 2 Mean (±*SD*) stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for the four prey categories used to estimate turtle diets in the San Jose foraging ground, Gulf of California, Mexico, with MixSIAR.

Source	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Invertebrates	41	−18.2 ± 2.7	10.8 ± 1.4
Algae	41	−15.9 ± 2.3	8.4 ± 0.9
Seagrass	9	−9.5 ± 0.7	6.9 ± 0.8
Mangrove	10	−27.2 ± 0.9	6.4 ± 0.6

Note: See Supporting Information Table S1 for full details of all diet items collected. The isotope values for all skin samples collected from the hawksbill turtles and used in the MixSIAR model can also be found in Supporting Information Table S2.

4 | DISCUSSION

4.1 | Population morphometrics

Based on abundance estimates in foraging sites of north-west Mexico, including the Gulf of California (Martínez-Estévez et al., 2022a), the San Jose foraging ground appears to be one of the most important developmental hotspots for hawksbills in the Mexican Pacific. The smallest turtle captured in the study was 33.8 cm, supporting the idea that turtles in this population transition into this area as later juveniles after spending some amount of time in offshore, pelagic regions during their earliest, post-hatching, juvenile stage. This transition has been hypothesized to occur at ∼35 cm SCL (Palaniappan, 2007; Gaos et al., 2012; Turner Tomaszewicz et al., 2022). In addition, most individuals (54 of 56, 96.4%) were smaller than the SCL size believed to indicate transition to the adult stage (nesting adult females range from 69.4 to 109.0 cm SCL) (Palaniappan, 2007) and the population was comprised of body sizes ranging across the full spectrum of SCLs considered indicative of the later juvenile developmental stage (Seitz et al., 2012; Van Houtan et al., 2016b; Turner Tomaszewicz et al., 2022). In addition, the five recaptured individuals grew an average of 4.8 cm (SCL) over 2–3 years (individual measurement changes over 2 years: 42.0–45.0 cm, 45.5–48.8 cm; over 3 years: 43.5–48 cm, 45.3–51.5 cm, 36.8–44.2 cm), and their recapture supports the hypothesis that this is a long-term foraging habitat for juvenile hawksbills in the Gulf of California.

4.2 | SIA and MixSIAR model analysis

This is the first stable isotope study of hawksbill sea turtles in the Gulf of California, Mexico. The MixSIAR results using the stable isotope

TABLE 3 Proportional dietary contributions for hawksbill turtles sampled in the San Jose foraging ground, Gulf of California, Mexico, 2014–2019.

			Credible interval		
Food source	Population mean (%)	1 *SD* (%)	2.5%	50%	97.5%
Algae	29.8	18.9	0.7	28.0	62.9
Invertebrates	32.3	9.9	12.1	32.9	47.3
Mangrove	17.9	4.5	9.0	17.9	25.2
Seagrass	20.1	8.8	2.6	20.8	33.1

Note: Parameters were estimated using the Bayesian stable isotope mixing model MixSIAR with stable isotope values from hawksbill skin samples and their potential prey sources.

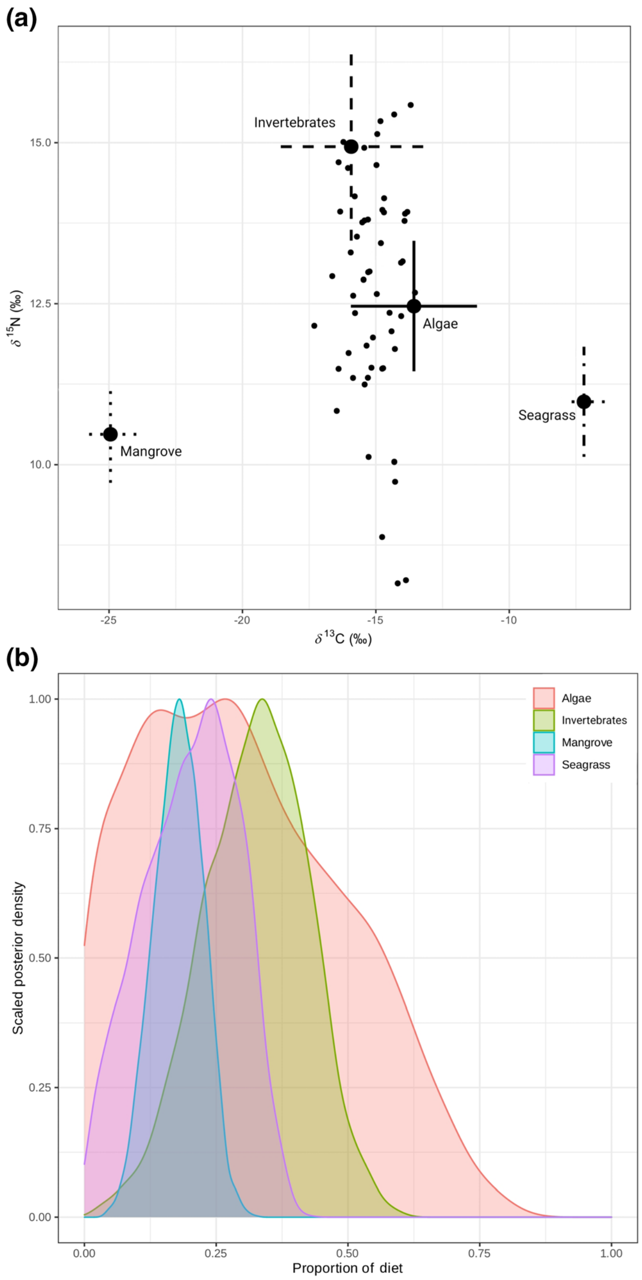

FIGURE 3 (a) The isospace plot of the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from the skin collected from hawksbill turtles within the San Jose foraging ground and the mean (±*SD*) stable isotope values from the four putative prey categories (invertebrates, algae, seagrass, and mangrove) collected from the study site. Each coloured point represents a single turtle's pair of stable isotope values, grouped by habitat (mangrove estuary, rocky reef, and sandy reef) in which the turtles were captured. (b) Estimated prey contributions to the diet of hawksbill turtles sampled within the San Jose foraging ground. The estimates were obtained using MixSIAR, a Bayesian stable isotope mixing model incorporating the mean (±*SD*) δ^{13}C and δ^{15}N values from four aggregated prey sources and the skin samples collected from the turtles.

values from the hawksbill skin and their presumed prey indicate they were eating primarily algae and invertebrates, with smaller contributions from seagrass and mangrove material (Table 3 and Figure 3). Martinez-Estevez et al. (2021) found similar results from the analysis of 13 scat samples collected from this same population of hawksbills that were dominated by invertebrates, algae, and mangroves. They did not find evidence of seagrass ingestion within the scat material, but scats provide only a snapshot of an animal's most recent diet, and thus seagrass could have been missing from the samples they collected. Juvenile hawksbill turtles are generally believed to be omnivorous (Bjorndal, 1996; Nichols, 2003), thus the finding that the hawksbills in the San Jose foraging ground consume a mix of vegetation and invertebrates fits with estimated diets of other populations of eastern Pacific hawksbills (Carrión-Cortez et al., 2013; Méndez-Salgado et al., 2020). Recent research in Punta Coyote, Costa Rica, suggests their population of eastern Pacific hawksbills transition to spongivory in adulthood (Carrión-Cortez et al., 2013), and hawksbills in Puerto Rico have been documented with 90–100% demosponges in their stomach contents (Bjorndal, 1996). Historical records for the eastern Pacific suggest that hawksbills remain omnivorous throughout their life (Bjorndal, 1996). This study did not have samples from or access to adequate numbers of adults to examine potential ontogenetic diet shifts with the transition to adulthood, but it is encouraged for future study to further understanding of this cryptic species.

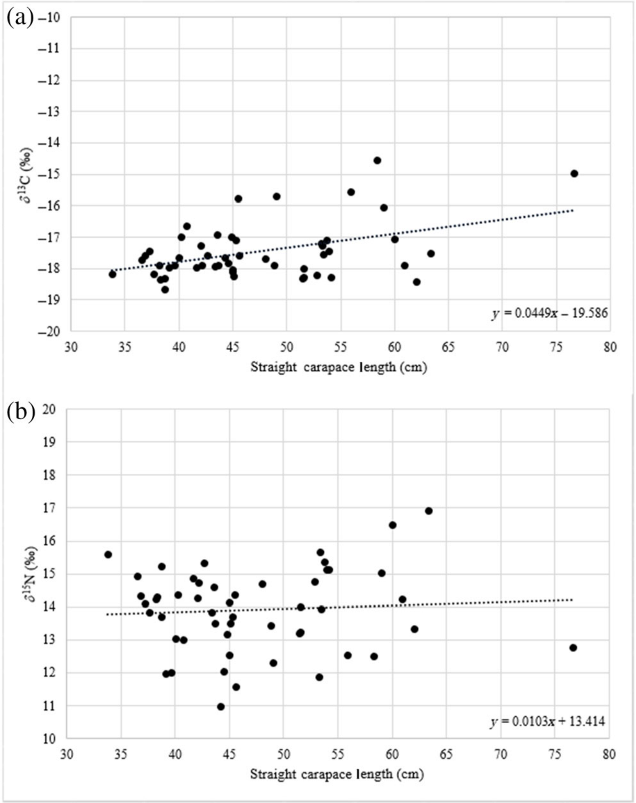

FIGURE 4 The stable (a) carbon (δ^{13}C; $P = 0.001$, $R^2 = 0.19$) and (b) nitrogen (δ^{15}N; $P = 0.63$, $R^2 = 0.005$) isotope values from posterior scutes sampled from hawksbill turtles in the San Jose foraging ground and their corresponding straight carapace length measurement.

One study in Hawaii found the time between posterior and anterior growth layer deposition varied from 3 to 8 years for juvenile hawksbills (Van Houtan et al., 2016b), meaning stable isotope values from an anterior portion of scute represent historical conditions several years after the material in the posterior portion. Scute layers are very thin and difficult to sample precisely, thus the stable isotope values from the scute samples may have reflected slightly different timescales across animals. Though this prevents detailed timelines from the older posterior scute samples, their age suggests that they reflect the general foraging ecology of the hawksbills prior to their transition as juveniles into the nearshore San Jose foraging ground.

Marine offshore pelagic habitats generally have lower δ^{13}C values than nearshore habitats do (Ramos & González-Solís, 2012); thus, the positive linear relationship observed between the increasing δ^{13}C values from hawksbill scutes and their increasing size (Figure 4a) may reflect a habitat transition from a post-hatching/early juvenile pelagic, oceanic phase to the nearshore San Jose foraging ground during their later juvenile phase. The increase in the δ^{13}C values observed in scutes collected at the later of two time intervals also reflects a potential habitat transition from the pelagic to the nearshore San Jose foraging ground. Such a juvenile ontogenetic shift has been suggested for other hawksbill populations in the eastern Pacific (Wedemeyer-Strombel et al., 2021; Turner Tomaszewicz et al., 2022) and in the Atlantic (Avens et al., 2021). Two previous studies (Wedemeyer-Strombel et al., 2021; Turner Tomaszewicz et al., 2022) found lower δ^{13}C values in scutes and bone growth layers from hawksbills with increasing size class in different areas of the eastern Pacific Ocean. This increase in hawksbill δ^{13}C values with size was attributed to an increasing reliance on mangrove estuarine habitats as they transition from their pelagic, post-hatching juvenile stage, as the mangrove area in which they were foraging had lower δ^{13}C values than the coastal rocky reef and oceanic habitats.

The observed change in the δ^{13}C values with increasing size could also indicate a dietary shift, but this is not likely as there was no observed change in the δ^{15}N values from turtles between the early and later scute samples, nor any observed relationship between their δ^{15}N values and SCL. Thus, regardless of foraging location, these turtles are likely foraging at the same trophic level across these time periods. SIA of tissues collected from very small individuals (<40 cm CCL) would allow for a better understanding of the potential for ontogenetic habitat shifts. With continued sampling and further recaptures, especially those targeting the youngest/smallest turtles, these timelines could be extended and replicated for more turtles, allowing for further insights into the movements of the species during the little-understood ‘lost years’ of their development.

4.3 | Implications for conservation

These data demonstrate the juvenile size ranges and omnivorous nature of these turtles. Along with the recent spatial ecology information revealing the extreme site-fidelity, small home ranges, and strong preference for mangrove estuaries exhibited by juvenile hawksbill turtles in the Gulf of California (Martínez-Estévez et al., 2021), this strongly indicates that the San Jose foraging ground is an important, long-term developmental ground for a relatively large number of juvenile hawksbills. The SCL measurements from the turtles within this population indicate that 96.4% of the hawksbills in the San Jose foraging ground could be classified as juveniles rather than putative adults. This suggests the area's protected status has allowed for safer conditions for hawksbills to mature, underscoring the importance of habitat protection in the recovery of hawksbill turtles in the eastern Pacific. The estimated number of mature females in the eastern Pacific is still less than 700 (Gaos et al., 2017b), further demonstrating the need for similar management and conservation efforts at other important foraging grounds in the Gulf of California and the eastern Pacific.

AUTHOR CONTRIBUTIONS

Kara Satomi Reynolds: Data curation; formal analysis; investigation; writing—original draft. **Carolyn M. Kurle:** Conceptualization; methodology; project administration; resources; supervision; writing—review and editing. **Donald A. Croll:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing—review and editing. **Diana L. Steller:** Conceptualization; investigation. **Dorota Szuta:** Conceptualization; investigation. **Scott D. Miller:** Conceptualization; investigation. **Lourdes Martínez-Estévez:** Conceptualization; investigation; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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