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Large-scale patterns of green turtle trophic ecology in the eastern Pacific Ocean

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Abstract. Trophic position and niche width are fundamental components of a species' ecology, reflecting resource use, and influencing key demographic parameters such as somatic growth, maturation, and survival. Concepts about a species' trophic niche space have important implications for local management and habitat protection, and can shed light about resilience to changing climate for species occurring over broad spatial scales. For elusive marine animals such as sea turtles, trophic niche is challenging to study, and researchers often rely on other metrics, such as isotopic niche, as a proxy. Here, stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$ values) was conducted on bulk skin tissue of 718 green turtles (*Chelonia mydas*) distributed among 16 foraging areas in the eastern Pacific from the USA to Chile, a range spanning ~10,000 km. Compound-specific nitrogen isotope analysis of amino acids (CSIA-AA) was applied to 21 turtles among seven sites. Isotopic niche space was determined via Bayesian ellipse area (BEA) and convex hull area (CHA) analyses of bulk isotope values, which were also used along with amino acid $\delta^{15}N$ values to determine trophic position (TP). Substantial variability in bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values was found within and among sites, and amino acid $\delta^{15}N$ values confirmed this was largely due to spatial differences in baseline nitrogen isotopic compositions, but also to a lesser extent from TP differences among the green turtle

foraging populations. Isotope niche space varied among sites, influenced by the diversity of prey types and relative input of terrestrial- vs. marine-derived nutrients; BEAs were the most suitable measurement of isotopic niche space due to the larger influence of outlying values with the CHA approach. Amino acid isotope-derived TP estimates that accounted for local habitat conditions (e.g., mixed seagrass/macroalgae diet) performed the best among several approaches; TP ranged from 2.3 to 3.6, which indicates an omnivorous diet for most populations. In addition to providing additional spatial resolution for $\delta^{13}C$ and $\delta^{15}N$ isoscapes in the eastern Pacific, especially in coastal habitats, this study further establishes CSIA-AA as an effective tool to study the trophic ecology of sea turtles across a variety of food webs and habitats.

Key words: amino acids; Bayesian ellipse; carbon; *Chelonia mydas*; convex hull; ectotherm; isoscape; isotopic niche; nitrogen; stable isotope analysis; trophic position.

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Introduction

Trophic niche is an important concept in ecology for understanding species interactions and the structuring of communities (Chase and Leibold 2003). Among the most important metrics defining an animal's niche are its trophic position (TP) and trophic niche width, both of which influence somatic growth, ontogeny, and reproduction (Post 2002, Newsome et al. 2007, Jaeger et al. 2010) and have important implications for species resilience to environmental change (Estes et al. 2003, Layman et al. 2007*a*, Peterson et al. 2011). Whereas TP indicates the extent to which plant- vs. animal-based foods are consumed, and can be established on individual and population levels, trophic niche width is considered at population scales and is influenced by degree and diversity of individual specialization (Van Valen 1965, Bolnick et al. 2003). Trophic niche width may also be influenced by extrinsic factors such as prey availability and habitat complexity (Bearhop et al. 2004, Newsome et al. 2007), and discrete subpopulations of the same species may have unique trophic niches that are shaped by resource use and local habitat conditions. Trophic niches of consumer species have been widely examined (Chase and Leibold 2003, Peterson et al. 2011); however, the extent to which trophic niche varies among disparate populations on broad regional scales is less understood.

Consumer trophic status has often been examined via stomach content analyses, fecal analyses, or by direct observation; however, these approaches have some well-understood limitations (Votier et al. 2003). Instead, stable isotope analysis (SIA) has become a useful tool to evaluate the trophic status of consumers, because the isotope values in their tissues integrate and reflect the isotope values of their prey and habitat (Peterson and Fry 1987, Rubenstein and Hobson 2004, Newsome et al. 2007). The advantage of this approach is that small quantities of body tissue can be collected and analyzed to gain insight about a consumer's trophic status without the need for direct observation or retrieval of diet components via invasive procedures. When examined on more than one axis (i.e., isotopes of two or more elements), SIA is a valuable way to study isotopic niche space, which although

different from ecological niche space, can yield important insights about consumer resource use, habitat complexity, and nutrient flow (Bearhop et al. 2004, Newsome et al. 2007, Layman et al. 2007*b*, Flaherty and Ben-David. 2010, Newsome et al. 2012).

The two most common stable isotope values used in ecological study are for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Because differing photosynthetic pathways and inorganic carbon acquisition strategies among other factors result in variable $\delta^{13}C$ values among plant types, these values can be used to trace the importance of different carbon sources to a consumer (DeNiro and Epstein 1978). For example, in coastal estuarine habitats, mangroves, which are marine angiosperms, can have substantially lower $\delta^{13}C$ values relative to submerged seagrass and marine macroalgae located only a few meters away (Lepoint et al. 2004, Marshall et al. 2007, Bouillon et al. 2008). Further, seagrasses often have higher $\delta^{13}C$ values than adjacent macroalgae due to their ability to use bicarbonate (HCO_3^-) in addition to dissolved CO_2 (which is used by algae) as an inorganic carbon source (Touchette and Burkholder 2000). Because at equilibrium HCO_3^- is enriched in ^{13}C relative to $CO_{2(aq)}$ ($\delta^{13}C$ values of 0‰ vs. –9‰, at ~20°C, respectively), its utilization by seagrass leads to relatively high $\delta^{13}C$ values (Raven et al. 2002, LePoint et al. 2004). Thus, primary producers in coastal marine ecosystems may fall into three categories, with $\delta^{13}C$ values being lowest in mangroves, intermediate in marine algae, and highest in seagrasses.

Consumer tissues have higher $\delta^{15}N$ values relative to their prey due to preferential retention of ^{15}N during metabolism and tissue maintenance, among other less understood factors (DeNiro and Epstein 1981). As a result, there is predictable, stepwise ^{15}N enrichment with each trophic step, and thus, $\delta^{15}N$ values can be used to estimate an organism's trophic position (Post 2002, Newsome et al. 2007, Nielsen et al. 2015). Bulk tissue $\delta^{15}N$ values have been used to evaluate the trophic niche of a variety of marine animals (e.g., Jaeger et al. 2010, Navarro et al. 2013); however, a major limitation of this approach is its inability to discern trophic vs. baseline influences on consumer bulk tissue $\delta^{15}N$ values (Chikaraishi et al. 2007, Décima et al. 2013), which can limit the value of SIA for comparing trophic status between populations that live in different areas.

The application of compound-specific nitrogen isotopic analyses of amino acids (CSIA-AA) can complement bulk tissue isotopic results and can distinguish trophic level relationships in a food web from changes in isotope composition at the base of the food web (McClelland and Montoya 2002, Chikaraishi et al. 2007, Popp et al. 2007). This is possible because the $\delta^{15}N$ value of some AAs, such as phenylalanine, do not change appreciably during consumer nutrient assimilation and thus retain the isotopic composition of "source" nitrogen at the base of the food web, whereas other AAs, such as glutamic acid, are enriched in ^{15}N relative to source amino acids with each trophic transfer (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Baseline and trophic information can therefore be obtained from consumer tissues without the need for analyses of prey items or basal food web samples (Popp et al. 2007, Chikaraishi et al. 2009, Ohkouchi et al. 2017). Previous studies using CSIA-AA have quantified trophic levels of a variety of marine taxa (Dale et al. 2011, Bradley et al. 2015, Hetherington et al. 2019), but rarely has TP been determined for multiple subpopulations of the same species across ocean basins (but see Vander Zanden et al. 2013*b*, Arthur et al. 2014).

In marine systems, spatial patterns of isotopic abundances (i.e., isoscapes) are influenced by a variety of biotic and abiotic factors. For example, marine microplankton $\delta^{13}C$ values tend to decrease (become more negative) from low to high latitudes due to broad-scale shifts in rates of growth caused in part by changes in water temperature, cell size, and CO_2 concentration effects on carbon fixation by phytoplankton, as well as other environmental factors that are not yet clear (Goericke and Fry 1994, Laws et al. 1995, Popp et al. 1998, Wilkes and Pearson 2019). Nitrogen isotope values vary depending on the predominant form of nitrogen cycling and primary production of a given oceanic region, such that basal primary producers in regions of partial water column denitrification have elevated $\delta^{15}N$ values due to ^{15}N-fractionation during the reduction of NO_3^- to N_2O or N_2 in oxygen-deficient zones (Montoya 2007, Somes et al. 2010, Deutsch et al. 2011). Given these influences, isotope values in baseline producers can vary spatially, especially

over extreme distances. Isoscapes have been developed for some marine regions (e.g., Olson et al. 2010), but the spatial resolution of isotope maps is often of 1000s of kilometers, and cannot account for the local and regional spatiotemporal variability in ocean circulation and isotope patterns (Ramos and González-Solís 2012). Moreover, marine isoscapes are less understood in coastal, neritic habitats due to the influence of terrestrial and benthic energy pathways (McMahon et al. 2013).

The Eastern Pacific Ocean (EP) is a vast, highly dynamic region with substantial spatiotemporal variability in physical and biological characteristics (Strub 1998, Chavez et al. 1999, Fiedler 2002, Pennington et al. 2006). These oceanographic conditions coupled with the presence of numerous well-described biological hotspots provide an ideal opportunity to examine physical and biological oceanographic influences on broad-scale stable isotope patterns in marine species. Prior studies in the EP have found considerable disparity in bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values of wide-ranging marine taxa including squid (Ruiz-Cooley and Gerrodette 2012), pinnipeds (Aurioles-Gamboa et al. 2009), sea turtles (Kelez 2011, Peavey et al. 2017), and zooplankton and fishes (Olson et al. 2010, Hetherington et al. 2017). However, the extent to which these patterns are driven by intrinsic differences in species life history vs. baseline influences is often unknown. Also, most animals studied so far are pelagic taxa, and almost no information is available about broad spatial isotope patterns for coastal-dwelling species. Thus, it would be insightful to couple SIA analyses of bulk tissue and amino acids to decipher these patterns for a coastal consumer, especially one that taps into both seagrass- and marine algae-based nutrient pathways.

Green turtles (*Chelonia mydas*) are present throughout tropical to temperate coastal marine habitats worldwide and are important for shaping habitat structure and influencing nutrient flow (Thayer et al. 1982, Bjorndal and Jackson 2003). Historical paradigms suggest green turtles are obligate herbivores that consume seagrasses and/or marine algae (Parsons 1962, Carr 1967). There is growing evidence that the species also consumes invertebrate foods in many areas (Bjorndal 1997, Jones and Seminoff 2013), drawing intrigue as to how and why green turtles are herbivores at some sites but omnivores at others. The mechanisms driving this disparity may be related to a facultative response by green turtles to differing prey availabilities across sites (e.g., Santos et al. 2015, Gillis et al. 2018). Diet perhaps is also influenced by a turtle's physiological capacity to digest foods in the context of local temperature regimes. For example, the digestive efficiency for seagrasses in green turtles declines with lower water temperature (Bjorndal 1980); thus, seagrass may be expected to feature less prominently in the diets of green turtles in temperate vs. tropical foraging areas. However, green turtles may engage in a food "quantity vs. quality" trade-off such that despite the lower nutritional value of seagrass due to its high fiber content and low protein availability (Bjorndal 1980), dependence on this resource may continue even in suboptimal conditions due to its overall abundance and sustained presence in coastal habitats. Thus, green turtle diet is likely shaped by extrinsic factors such as prey abundance and nutritional value, as well as a turtle's intrinsic physiological capacity to assimilate foods under different thermal regimes (e.g., Di Beneditto et al. 2017, Campos and Cardona 2020).

The eastern Pacific (EP) is an area with complex topography and substantial variability in oceanographic characteristics and nearshore habitat types (Chavez et al. 1999, Fiedler 2002, Pennington et al. 2006). Green turtles in the EP are opportunistic omnivores that live in both continental and insular habitats and consume a variety of seagrass, marine macroalgae, and invertebrate species, thus deriving nutrients from multiple origins (Amorocho and Reina 2007, Carrión-Cortez et al. 2010, Lemons et al. 2011); however, so far there has been no large-scale regional evaluation of EP green turtle trophic ecology. Green turtles are well-studied, which provides a framework for interpreting results derived from isotopic research. In the EP, they have experienced remarkable population recovery, which has likely enhanced their role as nutrient transporters and ecosystem engineers in coastal habitats (Bjorndal and Jackson 2003, Lal et al. 2010). A firm grasp of their trophic ecology can help decipher energy flow and community structure in these areas. Moreover, because the trophic status of sea turtles assembled in foraging areas influences their demography and

reproductive output (Broderick et al. 2001, Bruno et al. 2020), this information can provide context for nesting abundance and population trends.

Here, the isotope niche width and trophic position of green sea turtles are studied throughout the EP using both bulk tissue SIA and CSIA-AA. Our goals were to (1) measure these ecological traits for green turtles living in multiple sub-regions within the EP and under variable habitat conditions, (2) explore the physical and biological factors that influence green turtle trophic ecology at these sites, and (3) evaluate the efficacy of different approaches for determining green turtle trophic position. Data on source amino acids and local primary producers help depict the influence of differing baseline isotope values on the bulk tissue profiles of green turtle foraging populations in the region. In addition, there is a great deal of interest in the development of marine isoscapes (Hobson et al. 2010, Ceriani et al. 2014, Vander Zanden et al. 2015, Kurle and McWhorter 2017), and these data will help define spatial patterns for $\delta^{13}C$ and $\delta^{15}N$ values at green turtle foraging areas in the EP, a region for which isoscapes require further spatial resolution, especially in coastal habitats.

Methods

Study sites

Green turtles were studied at 16 foraging sites across a latitudinal range from 33.736 °N to 23.098 °S in the EP (Fig. 1): Long Beach, USA (LB); San Diego Bay, USA (SDB); north Gulf of Ulloa, Mexico (NGU); Magdalena Bay, Mexico (BMA); Los Angeles Bay, Mexico (BLA); Infiernillo Channel, Mexico (CIN); Navachiste Bay, Mexico (NAV); Dulce Gulf, Costa Rica (DUL); Cocos Island, Costa Rica (COC); Gorgona Island, Colombia (GOR); Punta Espinosa, Galapagos Islands, Ecuador (IGP); Bahia Elizabeth, Galapagos Islands, Ecuador (IGE); Caleta Derek, Galapagos Islands, Ecuador (IGD); oceanic waters, Peru (PPE); Pisco Paracas Bay, Peru (PAR); and Mejillones Bay, Chile (MEJ); a description of each study site is provided in Supplemental Text. Biological samples were collected from 1999 to 2016 at these sites (mean sampling duration = 3.1 ± 2.7 yr), and a total of 718 green turtles (19–87 turtles per site) was included in the study. Stable isotope data from turtles at 10 sites were part of graduate theses for students or colleagues of JAS (BMA [Santos Baca 2008]; BMA, NGU [Rodríguez-Barón 2010]; PPE [Kelez 2011]; IGP, IGE, IGD [Zárate 2013]; DUL, COC [Heidermeyer 2014]; GOR [Sampson 2015], NAV [Vejar Rubio 2017]) and data from two sites (SDB [Lemons et al. 2011]; GOR [Sampson et al. 2018]) were reported previously in the literature; all primary authors for these data sources are co-authors here. The present study conducts both site-specific and regional analyses not presented elsewhere.

Turtle capture and measurement

Three primary capture techniques were used, including manual capture (technique used at DUL, COC, IGE, IGD, IGP, GOR), entanglement netting (LB, SDB, NGU, BMA, BLA, CIN, IGE, IGD, PAR, MEJ), and retention of incidental bycatch from commercial fisheries (PPE). The general health of each turtle was assessed and missing flippers, large scars, and other external anomalies were noted. Straight carapace length (SCL; 0.1 cm) and/or curved carapace length (CCL; 0.1 cm) was measured using a caliper and flexible tape, respectively (Bolten 1999). When CCL was unavailable, we used the following conversion: $CCL = (1.0363 \times SCL) + 2.2464$ (Seminoff et al. 2003). Field efforts at each site also included tagging with Inconel tags (Style 681, National Band and Tag, Newport, Kentucky) in either the front or rear flippers to avoid double sampling.

Bulk skin and primary producer tissue collection

Epidermis (hereafter referred to as skin) was collected (ca. 0.10–0.25 g wet mass) from the dorsal neck or shoulder region of each turtle using a sterilized 6-mm biopsy punch or razor blade; the sampling location on the body was consistent at each study site. Based on SIA studies of captive sea turtles, the isotopic turnover time of skin is expected to be 3–4 months in fast growing juvenile sea turtles (Reich et al. 2008) and presumably longer for larger turtles, such as those studied here. Samples were preserved in 2-mL cryovials filled with saturated salt solution, dry salt, or 70% ethanol solution and kept cool until transfer to the laboratory where they were stored at –20°C until analysis. Barrow et al. (2008) confirmed that storage in 70% ethanol or in salt

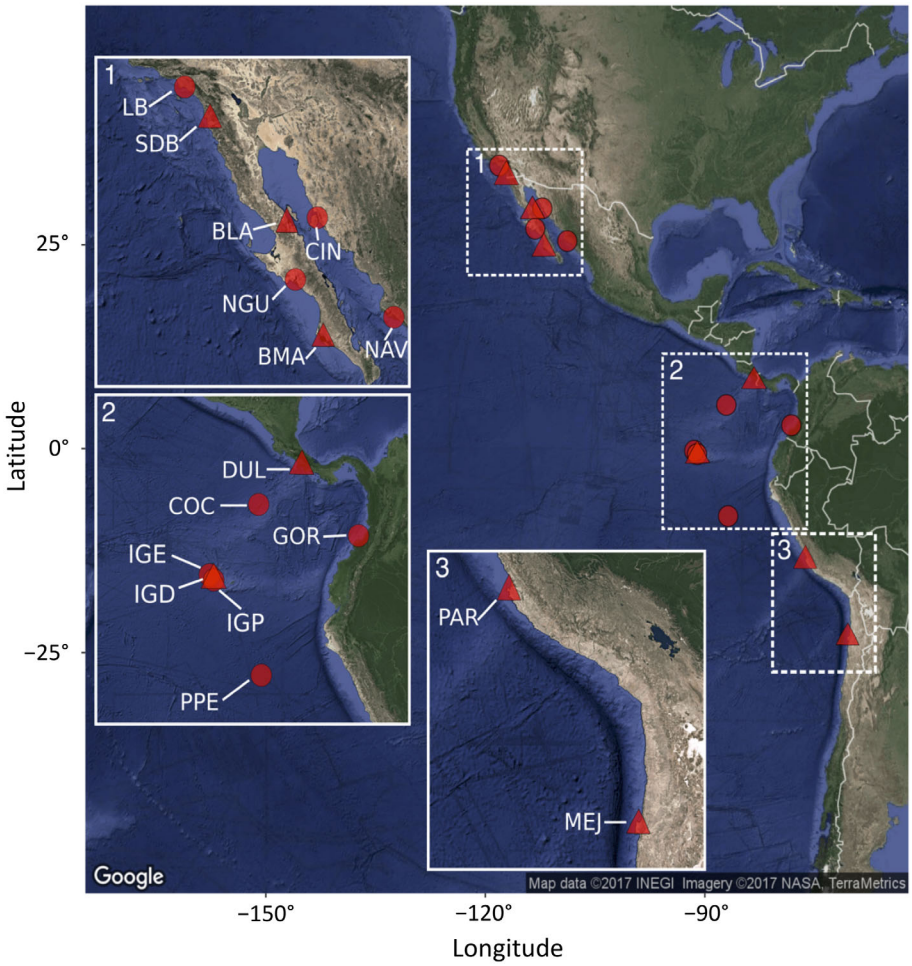

Fig. 1. Map of 16 green turtle foraging area study sites in the eastern Pacific Ocean. Triangles denote areas for which bulk tissue SIA and CSIA-AA were conducted; circles indicate sites for bulk tissue SIA only. See Table 1 for summary of site codes.

solution does not significantly affect stable isotope values of green turtle skin. Because of green turtles' strong site fidelity and long-term residency to foraging areas (Seminoff et al. 2002*a*, Koch et al. 2007, MacDonald et al. 2013), it was assumed that most individuals sampled at the neritic sites had been resident long enough for their tissues to achieve isotopic steady state with the local environment. However, it is possible that some turtles had only recently recruited, or were in the process of recruiting, to their respective neritic foraging sites. Likewise, green turtles captured in oceanic waters of Peru (PPE) were probably more mobile than their neritic counterparts, and thus may have tissue isotope values that are less reflective of their specific capture sites. Nevertheless, we include this oceanic study group to provide comparisons with green turtles sampled in neritic foraging areas.

Marine angiosperm (i.e., seagrass) and macroalgae species were collected from three sites (CIN, BLA, IGP) and combined with literature values to provide information about spatial variability in baseline $\delta^{13}C$ and $\delta^{15}N$ values among primary producers. Three taxa were selected due to their presence at multiple foraging areas and availability of $\delta^{13}C$ and $\delta^{15}N$ values in the literature (for which to provide a comparison). These included eelgrass (*Zostera marina*), the green alga *Ulva lactuca*, and the red alga *Gracilaria* sp. Each is a known prey species of green turtles in their respective areas (Seminoff

et al. 2002*b*, Felger et al. 2005, López-Mendilaharsu et al. 2005, Carrión-Cortez et al. 2010, Lemons et al. 2011, Vejar Rubio 2017, Sampson et al. 2018). Plants were hand-collected, air-dried in a plant press, and subsampled for SIA. Stable isotope values reported for red mangrove (*Rhizopora mangle*) were also explored to provide another reference point, as this marine angiosperm is found at numerous foraging areas included in this study.

Sample preparation for bulk tissue stable isotope analysis

Epidermal skin was separated from underlying dermis tissue when necessary using a razor blade. Skin samples were then rinsed with deionized water, finely diced, and freeze-dried at –50°C for 12 h in a lyophilizer (BenchTop K, VirTis, SP Industries, Gardiner, New York, USA). Lipids were removed from skin samples using a Soxhlet apparatus with a 1:1 solvent mixture of petroleum ether and ethyl ether for at least two 10-h cycles, or an accelerated solvent extractor (Model ASE300, Dionex, Bannockburn, Illinois, USA) with petroleum ether for three consecutive 5-min cycles of heating to 100°C at 1500 PSI pressurization. Following lipid extraction, the samples were freeze-dried at –50°C for 3 h to remove any residual solvent. Sub-samples of prepared homogenized tissue were weighed (0.6–1.0 mg) with a microbalance and packed in tin capsules for mass spectrometric analysis. Primary producers were also freeze-dried prior to subsampling; however, lipid extraction was not performed prior to weighing (1.0–3.0 mg) and placement in tin capsules due to the extreme low lipid content of vegetative prey types (Harwood 2012).

Bulk tissue stable isotope analysis

Bulk tissue stable isotope analyses were conducted at the University of Florida, Gainesville, Florida USA. Elemental concentrations and stable isotope ratios were measured using an on-line C-N analyzer (Carlo Erba NA1500) coupled with an isotope ratio mass spectrometer (Thermo Electron Delta V Advantage), and followed well-established procedures (see Seminoff et al. 2012). All carbon isotopic results are expressed in standard delta notation relative to VPDB. All nitrogen isotopic results are expressed in standard delta notation relative to AIR. Sample stable isotope values relative to the isotope standard are expressed in the following conventional delta (δ) notation in parts per thousand (‰):

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

where R_{sample} and R_{standard} are the corresponding values of heavy to light isotopes (e.g., $^{15}N/^{14}N$) in the sample and standard, respectively. All analytical runs included samples of a reference material with known $\delta^{13}C$ and $\delta^{15}N$ values (USGS40 and USGS41 from the USGS) inserted every 6–7 samples to calibrate the system and compensate for drift over time. Hundreds of replicate assays of reference materials indicated maximum measurement errors of 0.06‰ and 0.12‰ for carbon and nitrogen, respectively. The elemental concentrations of carbon (acceptable $\delta^{13}C$ range = 25–60‰) and nitrogen ratio (acceptable $\delta^{15}N$ range = 6–20‰) were used as quality assurance to assess stable isotope values before quantitative analyses; samples were excluded from analyses if they did not meet these criteria. The mean % C and mean % N for the retained samples was 41.1 ± 6.0% and 13.0 ± 2.2%, respectively (n = 718). The mean C:N ratio (mol/mol) for turtles at each study site was from 2.8 to 4.0 (Table 1).

Compound-specific stable isotope analysis of amino acids (CSIA-AA)

Compound-specific stable isotope analysis of amino acids was conducted on 21 skin samples from green turtles among seven foraging areas (three turtles per site; SDB, MBA, BLA, IGD, DUL, PAR, MEJ). All turtles included in CSIA-AA were also included in bulk tissue SIA. The CSIA-AA sample size was limited due to the higher cost and labor associated with this type of analysis; however, careful sample selection can yield important information to enhance understanding of bulk isotope data sampled from a larger sample pool. Green turtle samples chosen for CSIA-AA were collected from each respective site over one or two consecutive seasons. Individuals with the highest and lowest bulk tissue $\delta^{15}N$ values, as well as one turtle with a bulk tissue $\delta^{15}N$ value close to the mean, were sampled from each site so as to foster insights about trophic vs. baseline influence on bulk skin

Table 1. Summary of green turtle skin tissue sampling, curved carapace length (CCL), $\delta^{13}C$ and $\delta^{15}N$ values, C:N ratios, convex hull area, and Bayesian ellipse area for green turtles studied at 16 foraging areas in the eastern Pacific Ocean.

Study site (site code) by country	No. turtles	Collection year(s)	CCL (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N (mol/mol)	Convex hull area	Bayesian ellipse area
United States								
Long Beach (LB)	25	2010–2014	66.9 ± 12.5 (46.9, 101.0)	–16.3 ± 2.3 (–22.7, –12.4)	16.7 ± 1.2 (14.1, 18.8)	3.0 ± 0.1	26.9	7.9
San Diego Bay (SDB)	87	2002–2012	92.1 ± 19.2[a] (48.5, 116.5)	–16.0 ± 1.3 (–18.9, –13.0)	17.5 ± 1.9 (13.1, 20.2)	3.4 ± 0.6	24.2	4.3
Mexico								
North Gulf of Ulloa (NGU)	19	2006	60.0 ± 12.5[b] (42.7, 86.2)	–14.9 ± 3.1 (–19.3, –9.1)	11.6 ± 2.6 (7.6, 15.0)	3.4 ± 0.2	43.5	21.8
Magdalena Bay (BMA)	25	2005–2007	59.5 ± 9.2[c] (44.5, 81.4)	–17.1 ± 3.9 (–21.4, –8.8)	10.2 ± 2.9 (7.0, 17.1)	4.0 ± 0.5	72.0	31.9
Los Angeles Bay (BLA)	53	2002–2004	76.2 ± 9.2[d] (54.2, 99.6)	–15.6 ± 1.0 (–18.9, –14.0)	15.7 ± 1.1 (13.4, 18.0)	3.2 ± 0.4	13.3	3.5
Infiernillo Channel (CIN)	28	2007	67.4 ± 9.2[e] (55.1, 84.6)	–14.8 ± 1.0 (–17.1, –12.6)	16.1 ± 1.1 (14.0, 19.0)	3.2 ± 0.2	12.5	3.2
Navachiste Bay (NAV)	33	2011–2016	67.8 ± 8.8 (46.0, 79.3)	–16.1 ± 0.8 (–17.7, –14.0)	16.4 ± 1.2 (14.1, 19.4)	3.0 ± 0.2	10.9	2.9
Costa Rica								
Golfo Dulce (DUL)	74	2010–2011	78.8 ± 7.4[f] (53.5, 91.8)	–15.0 ± 1.0 (–18.3, –12.9)	12.5 ± 1.7 (8.2, 15.3)	3.0 ± 0.1	23.7	5.0
Cocos Island (COC)	67	2009–2011	73.6 ± 6.6 (51.0, 87.0)	–17.9 ± 2.3 (–25.5, –15.3)	13.1 ± 1.6 (7.6, 18.4)	3.2 ± 0.5	62.6	8.8
Colombia								
Gorgona Island (GOR)	76	2012	62.3 ± 7.3 (44.6, 78.1)	–16.7 ± 0.8 (–19.8, –14.7)	13.7 ± 0.8 (10.7, 15.8)	–	13.9	2.5
Ecuador								
Elizabeth Bay (IGE)	37	2004–2005	–	–15.8 ± 1.5 (–18.7, –12.6)	11.6 ± 1.0 (9.7, 13.6)	3.2 ± 0.2	17.5	4.8
Caleta Derek (IGD)	37	2004–2005	–	–15.8 ± 2.8 (–24.8, –10.7)	11.5 ± 1.5 (8.5, 14.5)	3.2 ± 0.1	45.9	12.7
Punta Espinosa (IGP)	41	2004	71.0 ± 10.2 (53.5, 99.5)	–12.3 ± 1.1 (–15.7, –10.7)	12.1 ± 0.8 (9.6, 13.9)	3.2 ± 0.1	14.2	2.4
Peru								
Paracas Bay (PAR)	21	2004–2005	53.5 ± 9.5 (44.6, 76.5)	–15.5 ± 0.9 (–16.9, –14.2)	13.1 ± 1.5 (11.0, 15.9)	3.3 ± 0.2	8.7	3.4
Oceanic Waters (PPE)	74	2003–2009	53.0 ± 8.8 (27.0, 71.2)	–16.1 ± 1.1 (–18.0, –14.5)	11.5 ± 1.4 (7.7, 16.3)	3.1 ± 0.2	14.3	1.9
Chile								
Mejillones (MEJ)	21	1999	60.1 ± 11.3[g] (46.0, 78.0)	–14.9 ± 0.4 (–15.8, –14.1)	16.1 ± 2.5 (11.3, 21.2)	2.8 ± 0.1	9.9	3.5

Notes: Values for CCL, $\delta^{13}C$, $\delta^{15}N$, and C:N are expressed as mean ± SD, with minimum and maximum in parentheses. Mean values followed by letter superscript indicate values derived from only a portion of all of turtles at that site: [a]77 turtles; [b]17 turtles; [c]20 turtles; [d]52 turtles; [e]16 turtles; [f]69 turtles; [g]seven turtles.

isotope values. Larger sample sizes for each site would have been preferred, but were not possible due to financial constraints. Nevertheless, sample sizes of three individuals have been used in prior CSIA-AA studies to effectively describe sea turtle TP (Seminoff et al. 2012, Hetherington et al. 2019).

Samples were prepared for CSIA-AA by acid hydrolysis followed by derivatization to produce trifluoroacetic (TFA) amino acid esters (Macko et al. 1997) using standard methods (Hannides et al. 2009, 2013). Nitrogen isotope values of TFA derivatives of amino acids were determined using a Delta V Plus isotope ratio mass spectrometer following the techniques outlined in Hannides et al. (2013). Measured isotopic compositions are based on 3–5 replicate analyses of each sample with norleucine and aminoadipic

acid of known $\delta^{15}N$ values as internal reference material. All amino acid isotopic values are reported in δ-notation relative to atmospheric N_2; standard deviations for each sample averaged 0.4‰ (range: <0.1‰ to 1.0‰). All CSIA-AA analyses were conducted at University of Hawaii, Honolulu, Hawaii, USA.

Amino acids measured using this technique include alanine (Ala), glycine (Gly), threonine (Thr), serine (Ser), valine (Val), leucine (Leu), isoleucine (Iso), proline (Pro), methionine (Met), phenylalanine (Phe), tyrosine (Tyr), and lysine (Lys). Additionally, the terminal amide groups in glutamine (Gln) and aspartamine (Asn) are cleaved during the chemical isolation of amino acids, the result being the conversion of these amino acids to glutamic acid (Glu) and aspartic acid (Asp), respectively. Thus, the isotope ratio of a combined Gln + Glu is measured (termed Glx), and the isotope ratio of a combined Asn + Asp is measured (termed Asx).

Comparison of bulk skin $\delta^{13}C$ and $\delta^{15}N$ values among study sites

To explore patterns in stable isotope variation among sites, the 16 foraging areas were grouped into five different biogeographic regions, each with unique physical and biological oceanographic traits: Southern California-Baja Pacific Coast (LB, SDB, NGU, BMA), Gulf of California (BLA, CIN, NAV), Central and South America Continental Coast (DUL, PAR, MEJ), Oceanic (PPE), and Eastern Tropical Pacific Islands (COC, GOR, IGE, IGD, IGP). A series of mixed models that use different variance structures were fit and compared for each of the five regions (all with fixed effect of site, random effect of region), rather than running separate models for each region.

All analyses were conducted in R (R Core Team 2013) and associated packages, such as "ggplot2" (Wickham 2009) for graphics. Hierarchical models were constructed to evaluate effects of location on $\delta^{13}C$ and $\delta^{15}N$ values ("nlme" package, Pinheiro et al. 2017) and to describe what the response variables were measuring (e.g., effects on baseline $\delta^{13}C$ and $\delta^{15}N$, TP). In particular, models using generalized least squares (GLS) were fit following methods detailed in Zuur et al. (2009). GLS is a linear regression technique that allows for correlation between model residuals and predictors via specification of variance structures. While this is frequently performed to meet linear regression assumptions (such as homogeneity of residual variance) with variance structures considered nuisance parameters, such relationships can originate from underlying biological patterns of interest that can also be explored with this approach (Zuur et al. 2009). Thus, to assess variance heterogeneity across study sites and/or regions (e.g., due to differential isotopic niche widths), GLS models were constructed in which variance was allowed to differ across study sites, regions, both, or none. In all models, a random effect of region was included to account for differences in baseline isotope values due to oceanographic and other regional factors. Turtle size was not included as a predictor in models because not all sites had size data. Relationships among $\delta^{13}C$ or $\delta^{15}N$ values with collection and run dates were also explored to assess technical biases, although no biases were found.

Model selection was performed using AIC_c estimates (Akaike Information Criterion corrected for small sample size bias), using a criterion of Akaike weight >0.90 to identify the best-supported models (Burnham and Anderson 2002, Johnson and Omland 2004). Model selection tables were generated using the "MuMIn" package (Barton 2015), and normalized residuals were visually inspected and compared among all supported models to meet model assumptions. Specific R code for model construction and selection is available on github: EPGT-SIA: models. Finally, variance parameter estimates were extracted from the strongest supported models for $\delta^{15}N$ values as a semi-quantitative indicator of trophic niche width. These are multiplication factors (MF) depicting the ratio with the estimated residual standard error, where one predictor level is set by GLS default as a reference where MF = 1 (DUL was selected as the reference site in our analysis). Predictor levels (i.e., study sites) with MF < 1 have lower residual variance relative to the reference, whereas those with MF > 1 have higher residual variance.

Calculating isotope niche space

The Stable Isotope Bayesian Ellipses in R (SIBER) routine in SIAR was used to analyze isotopic niche space for each foraging group using their bulk skin $\delta^{13}C$ and $\delta^{15}N$ values (Jackson

et al. 2011). Euclidian convex hull area (CHA), which is the total area encompassed by all points on a $\delta^{13}C$–$\delta^{15}N$ *x*-*y* scatter plot (Layman et al. 2007*b*), was calculated for each site. However, this approach is particularly sensitive to small sample sizes (<50) and CHA can be incorrectly large for populations that have outliers (Jackson et al. 2011). Thus, 95% ellipse areas for each foraging population were also calculated using the Bayesian ellipse approach from Jackson et al. (2011). The Bayesian standard ellipse area (BEA) is an approximation of isotopic niche space width, which is a proxy for trophic niche space (Jackson et al. 2011). BEAs are unbiased with respect to sample size, and they allow for robust comparison to be made among foraging areas, regardless of sample sizes. This approach allowed for the examination of variation in $\delta^{13}C$ and $\delta^{15}N$ values and estimation of isotopic niche space occupied by each population (Semmens et al. 2009), as well as comparisons of niche space among populations and regions. This approach is similar to bootstrapping in that it iteratively assigns measures of uncertainty, in this case based on Markov-Chain Monte Carlo simulation, to construct parameters of the ellipses.

Calculation of green turtle trophic position

Estimating TPs of consumers allows for the trophic placement of each individual within a food web model, and various approaches have been conducted in the past (e.g., Post 2002, Chikaraishi et al. 2009, Hebert et al. 2016). For green turtles, TPs were estimated using three approaches: one that uses green turtle and primary producer bulk tissue $\delta^{15}N$ values (TP_{bulk}), one that relies on $\delta^{15}N$ values of green turtle amino acids and assumes a diet of solely seagrass- or macroalgae/phytoplankton-derived nutrients (TP_{AA}), and one that uses amino acid $\delta^{15}N$ values and allows for a mixed diet of seagrass- and marine algae/photoplankton-derived nutrients ($TP_{AA\text{-}mixed}$). The methods for propagation of error associated with these trophic position calculations are described in Appendix S1.

If eating nothing other than marine algae and/or seagrass, green turtles would be considered primary consumers with a TP of 2 (Vander Zanden and Rasmussen 1999, Post 2002). In the EP, however, green turtles in many areas are omnivores that consume diets comprised of up to 80% invertebrates (Amorocho and Reina 2007). This animal matter consumption would make green turtles also forage as partial secondary consumers (TP = 3), and if consuming carnivorous invertebrates (e.g., Piovano et al. 2020), they would be partial tertiary consumers (TP = 4). This trophic level hierarchy does not sufficiently capture the complex interactions and trophic omnivory that are prevalent in EP green turtles, but for the purposes of this study TPs in the range of 2 to ~3.5 are considered biologically feasible based on prior knowledge of their diet.

The TP_{bulk} approach paired $\delta^{15}N$ values of green turtles with those of primary producers from the same study site. TP_{bulk} was calculated following Post (2002) using the equation:

$$TP_{bulk} = (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/TDF_{consumer} + 1 \quad (2)$$

where $\delta^{15}N_{consumer}$ is that of green turtles at each of the eight sites where primary producer isotope data were available (BLA, BMA, CIN, DUL, GOR, IGP, NAV, and SDB), $\delta^{15}N_{baseline}$ represents primary producer values (seagrass and/or marine macroalgae) from the same respective site, and $TDF_{consumer}$ (trophic discrimination factor) is set at +4.1 ± 0.4‰ (Turner Tomaszewicz et al. 2017), which was derived for wild green turtles in the eastern Pacific. When more than one marine-based (i.e., macroalgae) primary producer was collected from a single site, $\delta^{15}N_{baseline}$ was taken as the mean for all producers.

The TP_{AA} approach was applied to green turtles from the seven sites with available CSIA-AA data (SDB, BMA, BLA, DUL, IGD, PAR, MEJ). There are two key parameters when using AAs to calculate trophic position—the trophic discrimination factor (TDF), and the Beta value (β). The TDF is specific to the combination of AAs used in the analysis and is the difference in $\delta^{15}N$ values for trophic vs. source AAs in marine consumers at each trophic step. The β value is the difference in $\delta^{15}N$ values between the same trophic and source AAs used for TDF but in primary producers associated with seagrass- or algae-based food webs (Chikaraishi et al. 2009). TP_{AA} calculations followed an approach that has been applied for a variety of taxa (e.g., Chikaraishi et al. 2009) using the equation:

$$TP_{AA} = \left(\frac{(\delta^{15}N_{Trp} - \delta^{15}N_{Src}) - \beta_{Trp-Src}}{TDF_{Trp-Src}} \right) + 1 \quad (3)$$

where the trophic (Trp)/source (Src) AAs were glutamic acid-glutamine ($\delta^{15}N_{Glx}$)/phenylalanine ($\delta^{15}N_{Phe}$) in skin of local green turtles, the β value was based on the primary producers (i.e., seagrass and/or marine macroalgae) present at that area, and TDF was calculated specifically for east Pacific green turtles via captive study. Calculations of TP_{AA} used a β_{algae} value of 3.4 ± 0.9 (Chikaraishi et al. 2009) or a $\beta_{seagrass}$ value of –8.4 ± 0.06 (a proxy derived from terrestrial C_3 angiosperms; Chikaraishi et al. 2010), and a TDF of 3.97 ± 0.64 (Lemons et al. 2020). Marine algae were present at all sites for which AA data were available, and thus, TP_{AA} was calculated for all these sites using β_{algae}. For the four areas also hosting seagrass and/or mangroves (SDB, BMA, DUL, IGD), TP_{AA} was also determined using $\beta_{seagrass.\ TPAA}$ values for green turtles at each foraging area are presented as the mean among all three turtles at that site.

The $TP_{AA\text{-}mixed}$ technique was applied for the four sites with marine algae and seagrass and/or mangrove primary production and accounted for a mixed diet of these nutrient sources following Jarman et al. (2017, Eq. S5, see also Ohkouchi et al. [2017], Eq. 11) based on the equation:

$$TP_{AA-mixed} = \left(\frac{\delta^{15}N_{Glx} - \delta^{15}N_{Phe} + (1 - f_{algae})(\beta_{seagrass}) + (f_{algae})(\beta_{algae})}{TDF} \right) + 1 \quad (4)$$

where $\delta^{15}N_{Glx}$, $\delta^{15}N_{Phe}$, β_{algae}, $\beta_{seagrass}$, and TDF are the same values as described above for Eq. 3, and f_{algae} is the marine algae-derived proportion of diet for each site based on empirical data for green turtle local diet. For sites lacking diet data, f_{algae} was based on the nearest neighboring site, assuming similar habitats and green turtle diets. Values for f_{algae} were 0.75 ± 0.26 for BMA (López-Mendilaharsu et al. 2005), 0.20 ± 0.08 for DUL (based on diet at GOR; Amorocho and Reina 2007), 0.86 ± 0.04 for IGD (Carrión-Cortez et al. 2010), and 0.75 ± 0.26 for SDB (based on diet at BMA).

Green turtle TP has also been calculated using the trophic/source AA combination of Serine ($\delta^{15}N_{Ser}$)/Lysine ($\delta^{15}N_{Lys}$) (Lemons et al. 2020); however, this is not possible here because the β_{algae} based on available $\delta^{15}N_{Ser}$ and $\delta^{15}N_{Lys}$ data is too imprecise (–0.9 ± 4.0, n = 13) to yield defensible TP estimates (see McClelland and Montoya 2002, McCarthy et al. 2013). Combinations of multiple trophic and source AAs have also been used to determine TP (Décima et al. 2013, Bradley et al. 2015, Nielsen et al. 2015), but we were unable to apply this technique because it requires data on AAs that were not detected on chromatograms for all turtles in our analyses (e.g., Ala, Iso, Val, Met). Although TP_{AA} and $TP_{AA\text{-}mixed}$ are determined using only the trophic/source AA combination of Glx/Phe, it is promising that Vander Zanden et al. (2013*b*) found this approach to be a better indicator of green turtle TP than the multiple trophic and source AA approach.

Results

A total of 718 green turtles was included in this study, with an average of 45 ± 24 turtles (range = 19–87) per site (Table 1). Skin samples were collected from 1999 to 2016, but only one site (MEJ) had samples collected prior to 2002. The mean sampling duration among sites was 3.1 ± 2.7 yr. Most sites (n = 12) had samples collected over a one- to three-year interval; four sites were sampled during five or more years. Size data were available for all but two sites (IGE, IGP), although not always for all turtles at each site. Mean CCL among all neritic study sites ranged from 53.5 ± 9.5 cm (PAR) to 92.1 ± 19.2 cm (SDB); absolute size range was 42.7–116.5 cm CCL, which includes juvenile and adult life stages. Mean CCL at the sole oceanic study area (PPE) was 53.0 ± 8.8 cm; the CCL range was 27.0–71.2 cm, which includes juveniles only. The mean-of-means CCL for all sites was 63.9 ± 10.1 cm.

Bulk $\delta^{13}C$ and $\delta^{15}N$ values

Stable isotope values in bulk skin varied among foraging sites, with mean $\delta^{13}C$ values from –17.9 ± 2.3‰ (COC) to –12.3 ± 1.1‰ (IGP); absolute $\delta^{13}C$ values ranged from –25.5‰ to –8.8‰ (Table 1, Fig. 2). Mean $\delta^{15}N$ values for each site were from 10.2 ± 2.9‰ (BMA) to 17.5 ± 1.9‰ (SDB), with an absolute $\delta^{15}N$ range among all turtles of 7.0 ‰ to 21.2‰ (Table 1, Fig. 3). When examined by site and by region, the best models fit to the data were Models C.2 and N.2 (Table 2).

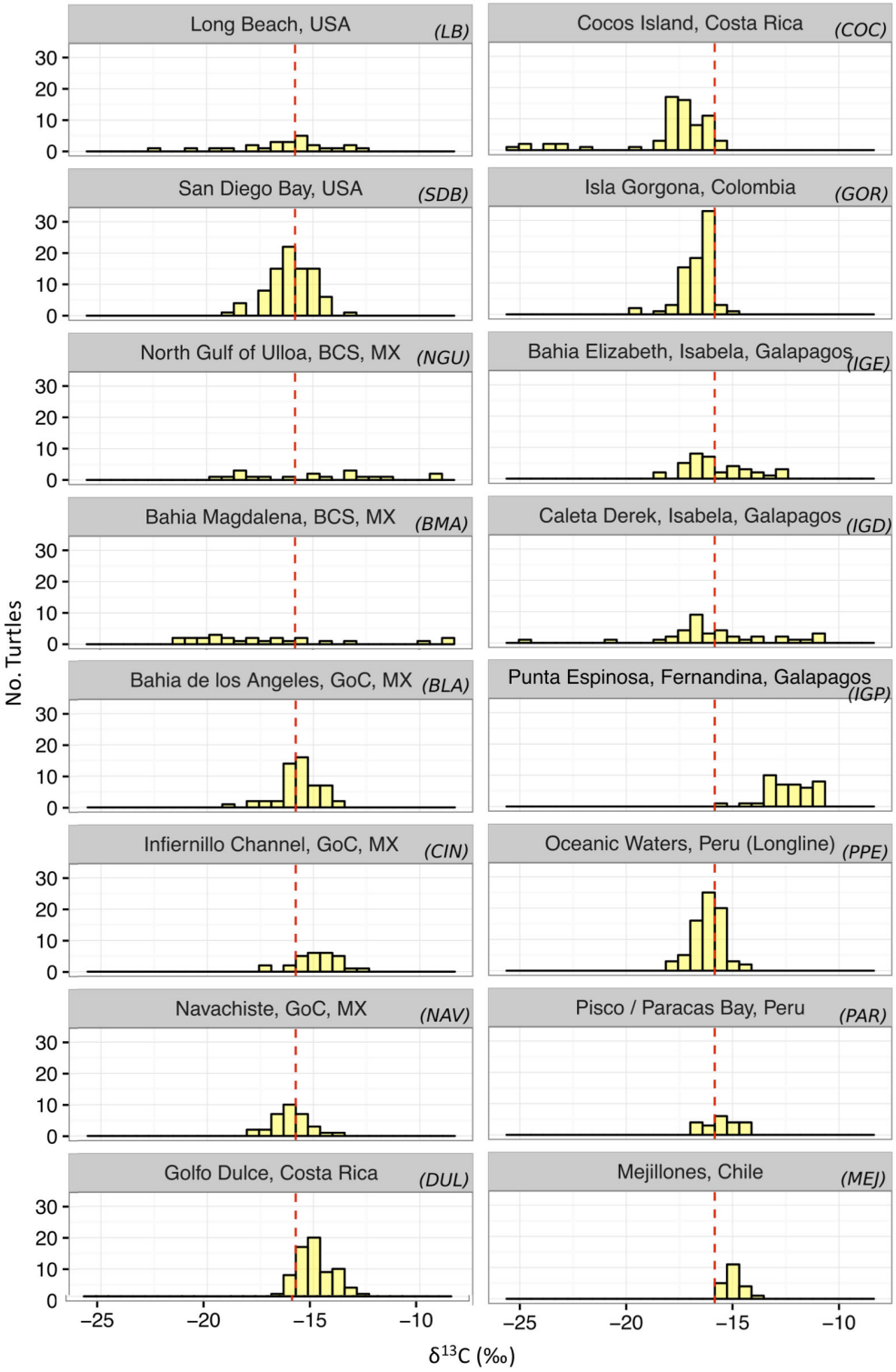

Fig. 2. Summary of bulk skin stable-carbon ($\delta^{13}C$) values for green turtles from 16 foraging areas in the eastern Pacific Ocean.

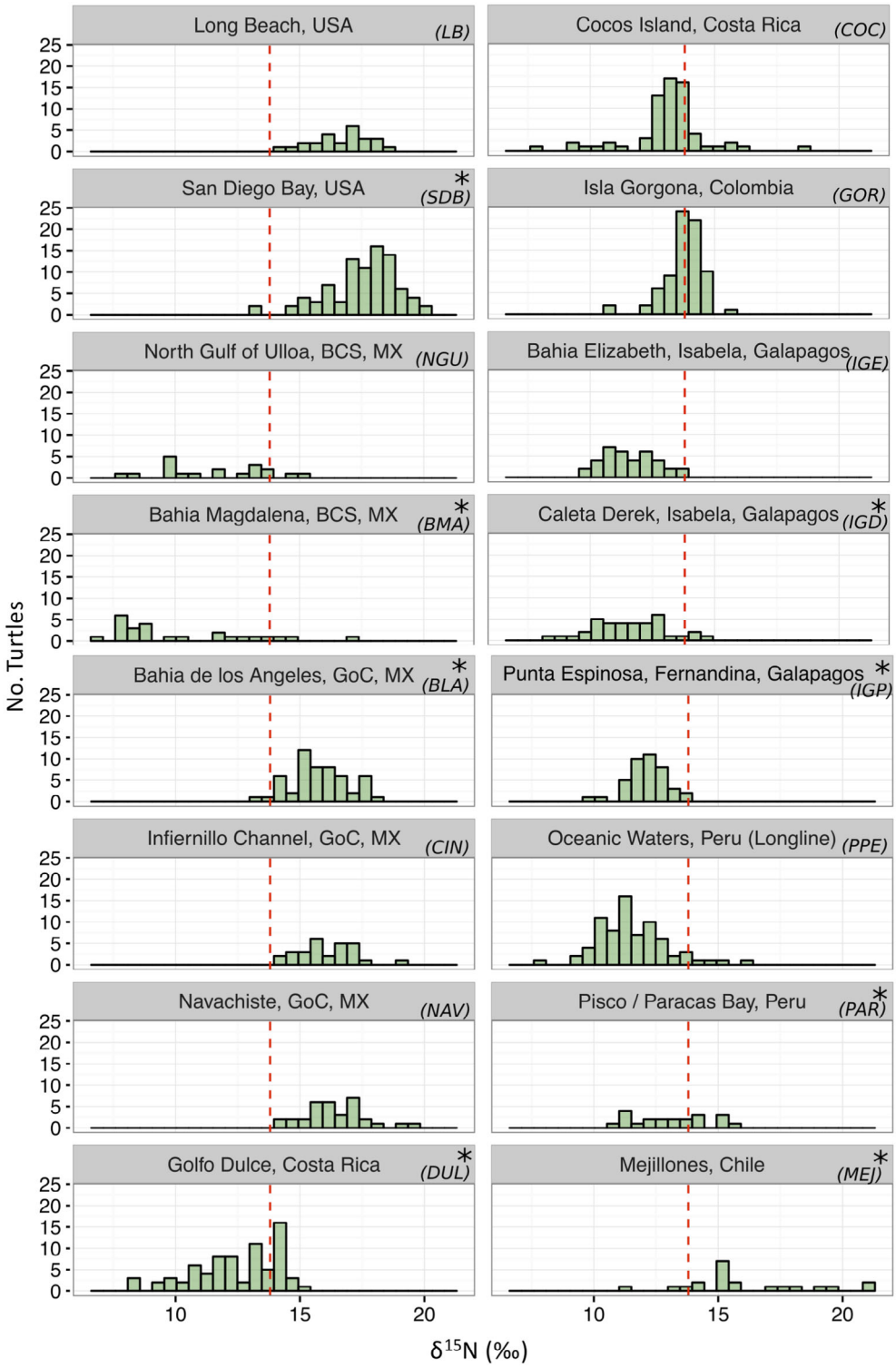

Fig. 3. Summary of bulk skin stable-nitrogen ($\delta^{15}N$) values for green turtles from 16 foraging areas in the eastern Pacific Ocean. * indicates the site also had corresponding compound-specific isotope analyses of amino acids.

Both models included only study site as a predictor and in the variance structure (Akaike weights = 0.988; Table 2), strongly supporting that study site, but not region, significantly affected the mean and variance of $\delta^{13}C$ and $\delta^{15}N$ values for green turtles. Variance multiplication factors for $\delta^{15}N$ ranged from 0.457 to 1.610 (Appendix S1: Fig. S1), and two sites (BMA, NGU) had substantially higher MF values; these two sites also had the greatest variance for $\delta^{13}C$ (Appendix S1: Fig. S2).

A $\delta^{13}C$-$\delta^{15}N$ summary bi-plot of all foraging sites is presented in Fig. 4. There were six sites (BLA, CIN, LB, NAV, MEJ, SDB) that stood out as having exceptionally high mean $\delta^{15}N$ values, all above 15.5‰ (Fig. 4). The two foraging areas in southern California, USA (SDB and LB), had the two highest mean $\delta^{15}N$ values (17.5 ± 1.9‰ and 16.7 ± 1.2‰, respectively) among all sites. High $\delta^{15}N$ values (>15.5‰) were also found for turtles in BLA (15.7 ± 1.1‰), CIN (16.1 ± 1.1‰), and NAV (16.4 ± 1.2‰)—all in the Gulf of California, and MEJ (16.1 ± 2.5‰), the southernmost foraging area in this study. The mean $\delta^{13}C$ values in green turtle skin among these six sites was from –16.3 ± 2.3‰ to –14.8 ± 1.0‰ (Table 1).

The remaining foraging areas had mean $\delta^{15}N$ values of 10.2 ± 2.9‰ (BMA) to 13.7 ± 0.8‰ (GOR), and mean $\delta^{13}C$ values from –17.9 ± 2.3‰ (COC) to –12.3 ± 1.1‰ (IGP) (Table 1, Fig. 4). With the exception of BMA and NGU, all foraging areas within this group were located in the southeastern Pacific Ocean. There were four sites that stood out as unique: COC, with lowest mean $\delta^{13}C$ values of all sites (–17.9 ± 2.3‰), IGP with the highest mean $\delta^{13}C$ values of all sites (–12.3 ± 1.1‰), GOR with the highest $\delta^{15}N$ values (13.7 ± 0.8‰), and BMA, with the lowest mean $\delta^{15}N$ values (10.2 ± 2.9‰) and second lowest mean $\delta^{13}C$ values (–17.1 ± 3.9‰) (Fig. 4).

Primary producer data from three sites (BLA, CIN, IGD) complemented information from the literature, resulting in baseline data for eight sites (Table 3). Two sites had only a single sample for each of *U. lactuca* and *Gracilaria* sp.; however, these sites remained in the analysis and the averages between the two algae were used. $\delta^{13}C$ values of *Z. marina* (seagrass) ranged from –13.6 ± 1.8‰ to –11.1 ± 1.0‰, whereas $\delta^{15}N$ was from 6.9 ± 2.5‰ to 10.4 ± 1.1‰. For macroalgae, $\delta^{13}C$ values ranged from –30.7 ± 1.2‰ to –11.6 (single sample) and $\delta^{15}N$ from 3.3 ± 1.2‰ to 12.5 ± 1.2‰, respectively.

Stable isotope niche space

Isotopic niche space was based on convex hull (CHA) and Bayesian ellipse (BEA) areas. CHA was larger than BEA for all sites (range = 12.5 to 72.0 and 1.9 to 31.9, respectively) (Table 1); likely owing to the greater influence of outlying values with this approach. This is particularly true at BMA, COC, IGD, and NGU where CHA (72.0, 62.6, 45.9, 43.5, respectively) was more than double the corresponding BEA (31.9, 8.8, 12.7, 21.8,

Table 2. Hierarchical model outputs evaluating the effects of location and region on $\delta^{13}C$ and $\delta^{15}N$ values of green turtle bulk skin tissue.

Model	Intercept	Predictor	Variance structure	df	Log likelihood	AICc	δAICc	Weight
$\delta^{13}C$								
C.2	**–16.3**	**Study Site**	**Study Site**	**33**	**–1145.8**	**2360.9**	**0.00**	**0.988**
C.4	–16.3	Study Site	Region + Study Site	37	–1145.8	2369.7	8.85	0.012
C.3	–16.3	Study Site	Region	22	–1252.8	2551.1	190.21	0.000
C.1	–16.3	Study Site	None	18	–1354.9	2746.8	385.96	0.000
C.null	–15.8	None	None	3	–1504.7	3015.5	654.65	0.000
$\delta^{15}N$								
N.2	**16.7**	**Study Site**	**Study Site**	**33**	**–1219.4**	**2508.2**	**0.00**	**0.988**
N.4	16.7	Study Site	Region + Study Site	37	–1219.4	2517.0	8.85	0.012
N.3	16.7	Study Site	Region	22	–1261.9	2569.2	61.05	0.000
N.1	16.7	Study Site	None	18	–1290.3	2617.6	109.38	0.000
N.null	13.8	None	None	3	–1578.6	3163.3	655.09	0.000

Notes: The best fitting model for each isotope is in bold. Models were fit using the base formula of (Response [$\delta^{13}C$ or $\delta^{15}N$] ~Study Site, random effect = ~1|Region, specified variance structure). See *Methods* for further details.

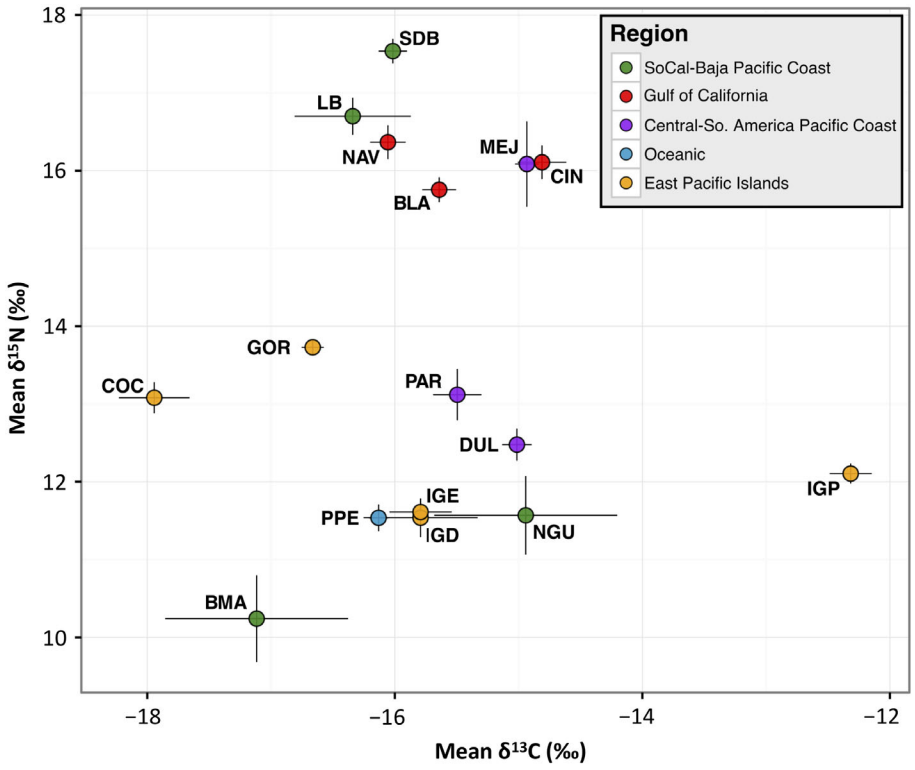

Fig. 4. Scatterplot of mean $\delta^{13}C$ (±SD) vs. mean $\delta^{15}N$ (±SD) for green turtles from 16 foraging areas in the eastern Pacific Ocean, with color denoting the general region within which each site is located. See Table 1 for summary of site codes.

respectively; Table 1, Appendix S1: Fig. S3). The Gulf of California Region had the greatest similarity in ellipse areas for any one region, and both BEA and CHA of all three populations largely overlapped (Fig. 5), even though the three sites are separated by up to 675-km straight-line distance (Fig. 1). The SoCal-Baja Pacific Coast Region had the largest variability in niche space among sites, with SDB and NGU having the largest BEAs of all sites, both of which fell outside of the ellipses of LB and SDB, which overlapped themselves and were of sizes more consistent with the remaining sites farther south (Fig. 5).

$\delta^{15}N$ values of amino acids

$\delta^{15}N$ values were determined for fourteen amino acids, but only 10 were successfully measured for all turtles (Appendix S1: Table S1). Among the 14 AAs, four behaved like source AAs (Lys, Met, Phe, Tyr), and nine were trophic AAs (Ala, Asx, Glx, Gly, Iso, Leu, Pro, Ser, Val). In addition, one AA (Thr) varied widely among sites and did not behave like either a source or trophic AA (Fig. 6, Appendix S1: Table S1). Among source AAs, mean $\delta^{15}N$ values for Lys, Met, and Phe were highest at SDB, whereas that for Tyr was highest at MEJ. For trophic AAs, mean $\delta^{15}N$ values for Ala, Asx, Glx, Iso, Leu, Pro, and Val were highest at MEJ, and mean $\delta^{15}N$ values for Gly, and Ser were highest at SDB (Fig. 6). Trophic AAs were ^{15}N-enriched relative to source AAs at all sites, but there was variability in the relative difference between source and trophic AA $\delta^{15}N$ values, as shown for $\delta^{15}N_{Phe}$ vs. $\delta^{15}N_{Glx}$ values in Fig. 7.

Trophic position

TP calculations using trophic/source AAs of Glx/Phe allowed for a diet based on a single primary producer-derived diet (using $\beta_{seagrass}$ or $\beta_{algae,}$ TP_{AA}; Eq. 3) and a diet based on mixed primary producer nutrient sources (using $\beta_{seagrass}$

Table 3. Summary of stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values for primary producers used for TP_{bulk} calculations (Table 4).

Primary producer	Study area	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Reference
Marine Angiosperms					
Seagrass	SDB	46	–11.1 ± 1.0	10.4 ± 1.1	Lemons et al. (2011)
Zostera marina	BMA	8	–12.3 ± 2.3	6.9 ± 2.5	Rodríguez-Barón (2010)
	CIN	3	–13.6 ± 1.8	9.3 ± 0.5	This study
Mangrove					
Rhizopora mangle	BAJ/EPR	27	–28.6 ± 1.6	–0.2 ± 1.9	K. Wedemeyer-Strombel, *unpublished data*
Mixed species	PP	?	–29.2 ± 1.2	3.7 ± 1.0	Viana et al. (2015)
Marine Algae	SDB	22	–15.7 ± 2.6	12.5 ± 1.2	Lemons et al. (2011)
Green algae	BMA	3	–16.3 ± 2.6	9.5 ± 0.9	Rodríguez-Barón (2010)
Ulva lactuca	NAV	1	–17.5	9.7	Vejar Rubio (2017)
	IGD	1	–11.6	6.0	Zárate (2013)
Red algae	SDB	32	–20.1 ± 4.5	11.7 ± 1.0	Lemons et al. (2011)
Gracilaria sp.	BMA	10	–17.8 ± 1.7	9.9 ± 0.5	Rodríguez-Barón (2010)
	BLA	5	–16.0 ± 0.7	12.4 ± 1.4	This study
	NAV	1	–15.4	9.8	Vejar Rubio (2017)
	IGD	1	–17.5	6.3	This study
Macroalgae	DUL	8	–30.7 ± 1.2	3.3 ± 1.2	Viana et al. (2015)
Assorted	GOR	9	–15.2 ± 1.2	5.5 ± 0.8	Sampson et al. (2018)

Notes: Study areas include Los Angeles Bay, Mexico (BLA); Magdalena Bay, Mexico (BMA); Infiernillo Channel, Mexico (CIN); Golfo Dulce, Costa Rica (DUL); Isla Gorgona, Colombia (GOR); Caleta Derek, Galapagos, Ecuador (IGD); Navachiste Bay, Mexico (NAV); Pisco/Paracas Bay, Peru (PAR); and San Diego Bay, USA (SDB). Mangrove values from El Salvador (Bahia Jiquilisco, BAJ) and Nicaragua (Estero Padre Ramos, EPR) as well as from Pacific Panama (PP, including *R. mangle*, *Pelliciera rhizophorae*, and *Avicennia germinans*) are presented for comparison. ?, no sample size provided.

and β_{algae}, $TP_{AA\text{-}mixed}$; Eq. 4). Measurements of TP_{AA} using $\beta_{seagrass}$ ranged from 4.5 ± 0.2 to 6.0 ± 0.2, and all TP values were higher than realistic limits based on empirical knowledge about green turtle diet. TP_{AA} based on β_{algae} was from 1.5 ± 0.2 to 3.6 ± 0.6 (Table 4); biologically realistic TP values were achieved for BLA (2.5 ± 0.4) and PAR (3.4 ± 0.4), while TP for MEJ was only marginally outside the feasible range (3.6 ± 0.6). In addition, when using β_{algae} three sites (BMA, DUL, SDB) had TP_{AA} below 2 (Table 4), which is impossibly low for primary consumers such as green turtles. The $TP_{AA\text{-}mixed}$ approach incorporating an f_{algae} value based on prior knowledge about green turtle diet consistently yielded the most realistic trophic position estimates for green turtles (SDB = 2.7 ± 0.2, BMA = 2.3 ± 0.2, DUL = 2.4 ± 0.1, IGD = 3.1 ± 0.1; Table 4).

TP_{bulk} estimates (Eq. 2) ranged from 1.7 ± 0.7 to 2.7 ± 0.4 when calculated using a seagrass baseline $\delta^{15}N$ value, and from 1.0 ± 0.7 to 3.0 ± 0.1 with a macroalgae baseline (Table 4). For sites with both seagrass and/or mangrove and macroalgae (BMA, CIN, SDB), TP_{bulk} calculations based on seagrass-derived primary productivity yielded the best results (Table 4), although neither TP_{bulk} calculation approach (i.e., neither seagrass nor algae) performed as well as the $TP_{AA\text{-}mixed}$ technique.

Discussion

Evaluations via SIA of the trophic status of sea turtle populations have been conducted on many occasions (e.g., Hatase et al. 2006, Cardona et al. 2009, Burkholder et al. 2011), but only sparingly have such analyses been conducted simultaneously on multiple populations or over a broad geographic scale (see Ceriani et al. 2012, Ceriani et al. 2014, Vander Zanden et al. 2015, Peavey et al. 2017). The present study included green turtles from a variety of habitat types, including seagrass meadows, rocky reefs, coral reefs, and open ocean waters, separated by up to ~10,000 km. Coupling bulk tissue and amino acid SIA provided unique insights otherwise not possible using only one approach, especially for revealing baseline influences on bulk skin $\delta^{13}C$ and $\delta^{15}N$ values. These efforts also yielded insights into the best way to characterize isotopic niche size and trophic position of green turtles, regardless of the locality, habitat type, or ocean basin.

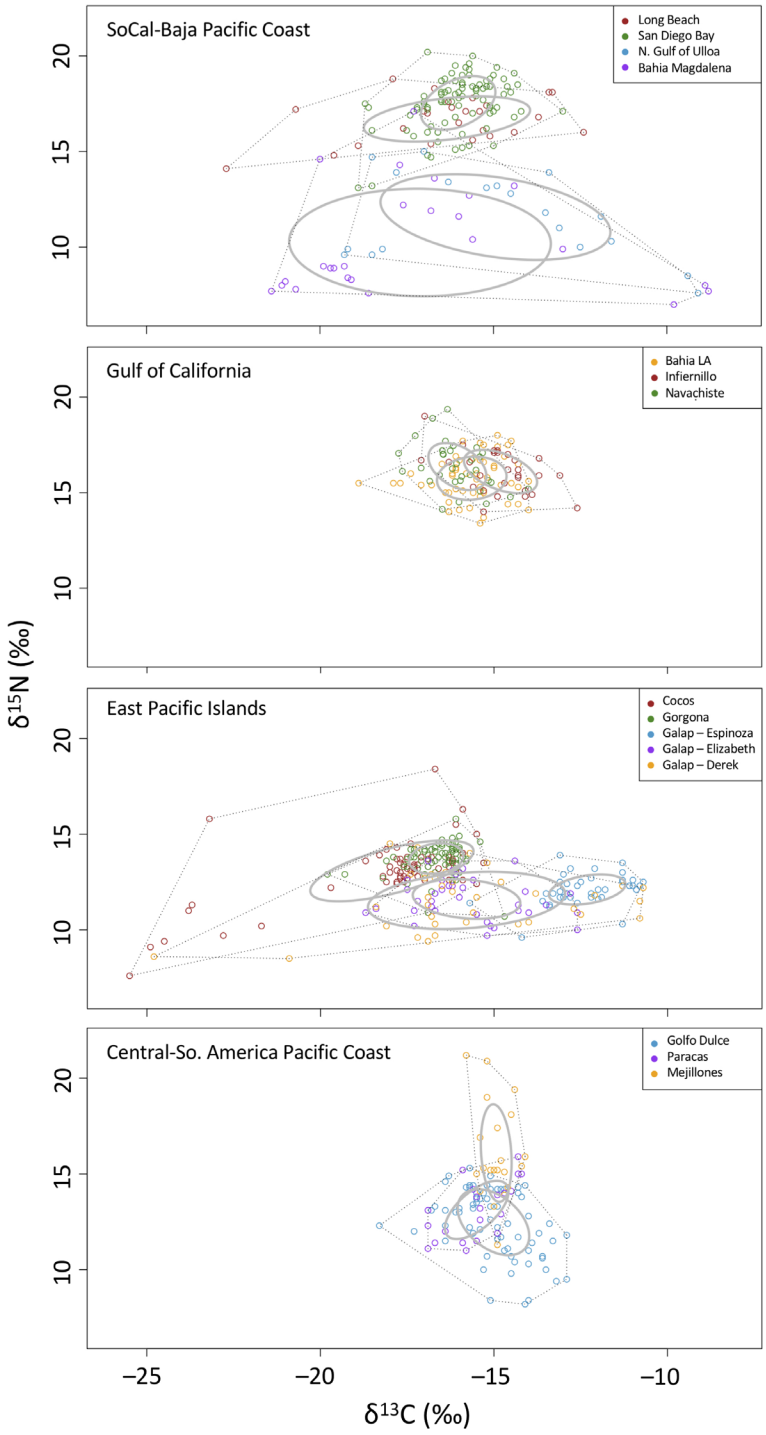

Fig. 5. Bayesian ellipses and convex hull areas for green turtles in the eastern Pacific Ocean, organized by sub-region. Analyses were based on bulk skin $\delta^{13}C$ and $\delta^{15}N$ and were conducted in SIBER (Jackson et al. 2011).

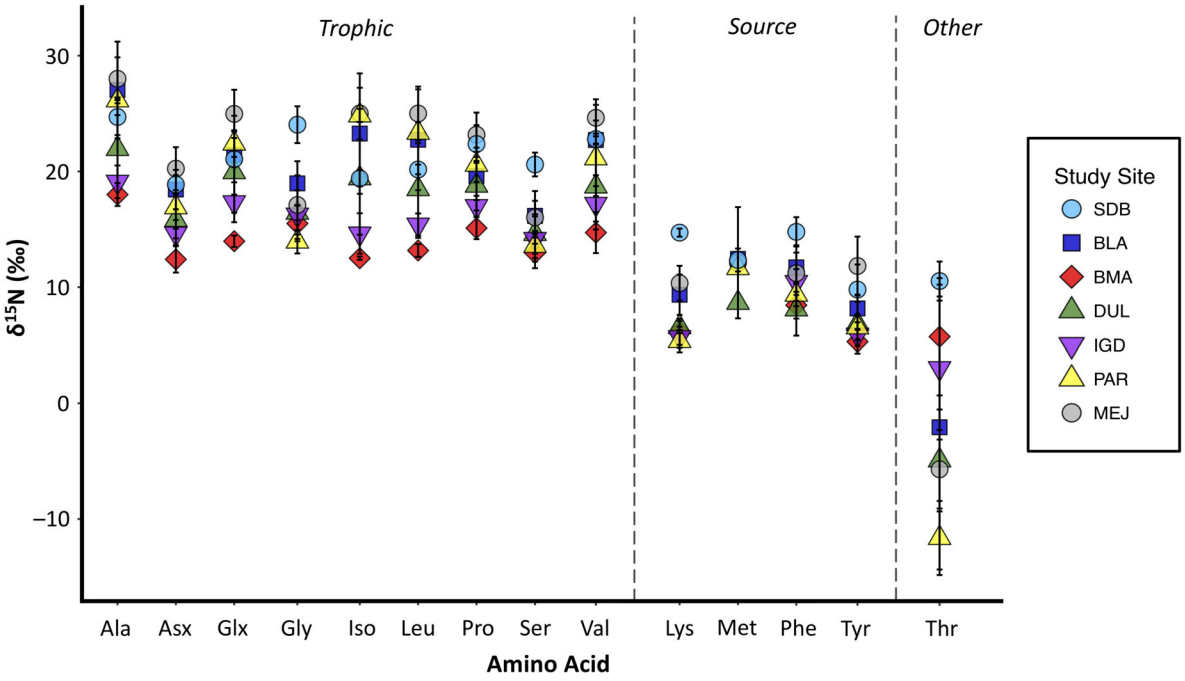

Fig. 6. Summary of $\delta^{15}N$ (‰) for 14 amino acids (AAs) in green turtle (*Chelonia mydas*) skin of three individuals from each of the seven foraging areas in the eastern Pacific Ocean. Although serine (Ser) and threonine (Thr) have been reported as source AAs elsewhere (Décima et al. 2013), Ser behaves more like a trophic AA in green turtles whereas Thr does not behave like either a source or a trophic AA.

Although there were no relationships between $\delta^{13}C$ or $\delta^{15}N$ values and sample collection or mass spectrometer analysis dates, a logical concern about this study relates to the long sample collection interval (1999–2016) and the potential for baseline isotope values or green turtle foraging strategy to shift over protracted time scales. Nevertheless, in the California Current Large Marine Ecosystem (CCLME) temporal variability in baseline phytoplankton isotope values did not significantly change over decadal time scales (Ohman et al. 2012), nor did fish bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values change over similar multi-decadal time scales in the North Pacific (Blight et al. 2015). Isotope values do however change on a semi-annual basis in at least some pelagic consumers (Ruiz-Cooley and Gerrodette 2012). For green turtles, consistency in $\delta^{15}N$ values, and to a lesser extent, $\delta^{13}C$ values was observed in bulk skin of individuals from San Diego Bay studied over six years (Lemons et al. 2011). These accounts suggest that the 17-year field overall study duration and the 3.1-yr mean sampling timeframe per site are of low concern for interpreting the data presented here.

The green turtles in this study included both juvenile and adult turtles, based on mean nesting sizes at the primary rookeries in the EP (mean size at maturity = 82–96 cm CCL; Juárez et al. 2003, Zárate 2013, Delgado-Trejo 2012). Most turtles in this study (overall mean of means 63.9 ± 10.1 cm CCL) were larger than the size of neritic recruitment for EP green turtles (~45 cm SCL; Seminoff et al. 2003, Koch et al. 2007) and thus were past the size at which the most significant ontogenetic diet shift—the transition from oceanic juvenile to neritic juvenile stage—would have already occurred; this lessens the likelihood that the observed dietary discrepancies among individuals and/or foraging populations were related to size or life-stage differences. Consistent with this, several studies have found no relationship between body size on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values of resident green turtles (Cardona et al. 2009, Burkholder et al. 2011, Lemons et al. 2011).

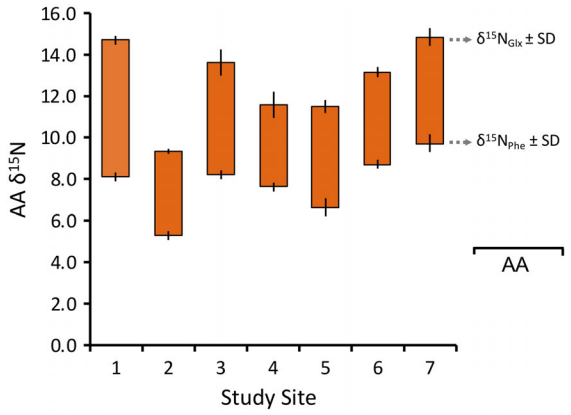

Fig. 7. Disparity in trophic and source AA $\delta^{15}N$ values for green turtle skin at seven study sites in the eastern Pacific. The trophic/source AA combination is Glutamic Acid-Glutamine/Phenylalanine (Glx-Phe). Upper extent of vertical bar for each site is mean $\delta^{15}N$ of Glx and lower extent is mean $\delta^{15}N$ of Phe. Error bars indicate SD for each respective AA.

In addition to the neritic study sites, one area (PPE) at which green turtles were sampled was a vast oceanic region off the coast of Peru. This "site" would be expected to host small oceanic juvenile green turtles, and indeed, the smallest (oceanic) juvenile in this study (27.0 cm CCL) was from PPE. Yet, larger juveniles (up to 71.2 cm CCL) were also encountered in this high seas area—which is unheard of for green turtles in most global regions, but relatively common in the eastern Pacific (e.g., Turner Tomaszewicz et al. 2018). Further, the mean CCL of turtles from PPE (53.0 ± 8.8 cm), while although the smallest of all sites, was comparable to that for turtles at the Paracas Bay (PAR) neritic foraging area (53.5 ± 9.5 cm CCL). Thus, individuals from pelagic waters of Peru represent a unique but appropriate outgroup of foraging turtles, and their analysis provides greater context for the entire EP region.

Spatial variability in bulk skin $\delta^{15}N$ values

As models indicate, study site, but not region, significantly affected both the mean and variance of $\delta^{13}C$ and $\delta^{15}N$ values for green turtles (Table 2). Nowhere is this more apparent than in the SoCal-Baja Pacific Coast Region, where the foraging areas with the two highest (SDB and LB), the lowest (BMA), and third lowest (NGU) bulk skin mean $\delta^{15}N$ values were found. The disparities in bulk $\delta^{15}N$ values were perhaps driven in part by trophic differences among the turtles; however, the difference in mean values among these areas (≥5.1‰) would indicate turtles are feeding on almost two full trophic levels apart between southern California vs. the lagoons in Baja. This is an unlikely scenario and suggests that diet alone does not account for the observed differences. The ~6.3‰ difference in source AA $\delta^{15}N$ values between the San Diego Bay ($\delta^{15}N_{Phe} = 14.9 \pm 0.6$) and Magdalena Bay ($\delta^{15}N_{Phe} = 8.6 \pm 0.5$‰) indicates that the disparity in bulk $\delta^{15}N$ values in green turtles is caused by isotopic differences at the base of the food web. Whereas BMA and NGU are largely undisturbed due to a low human population size and minimal coastal development along the Pacific coast of Baja, Mexico, both Long Beach and San Diego Bay are adjacent to major metropolitan areas in southern California, USA. With this context, perhaps anthropogenically derived nitrogen delivered via watersheds (McClelland et al. 1997) caused the higher observed $\delta^{15}N$ values. Turtles here carry heavy loads of pesticides and organic pollutants introduced via storm water runoff (Komoroske et al. 2011, Barraza et al. 2020), and delivery of allochthonous, anthropogenic nitrogen via occasional sewage spills has been confirmed by media reports (e.g., Smith 2019). Even low levels of nitrogen loading have been shown to increase $\delta^{15}N$ values of coastal consumers (Heaton 1986). Greater information about the presence thermotolerant coliforms and other human-derived pathogens in these urbanized watersheds (e.g., Poma et al. 2016) is needed to substantiate this possibility.

Green turtles at the three Gulf of California sites also have among the highest $\delta^{15}N$ values in the EP; however, the relatively pristine status of the study sites eliminates nitrogen loading as a factor. Instead, the Gulf is characterized by high $\delta^{15}N$ values in surface water phytoplankton (Rau et al. 2003, White et al. 2007, 2013) caused by denitrification in the eastern Tropical Pacific (Voss et al. 2001, Somes et al. 2010, Deutsch et al. 2011) and advection of this water mass northward into the Gulf (Liu and Kaplan 1989, Castro et al. 2001, Evans et al. 2020) where $\delta^{15}N$ values are further increased by denitrification in local

Table 4. Trophic position (TP) of green turtles in the eastern Pacific based on $\delta^{15}N$ values from bulk tissue SIA and CSIA-AA.

			CSIA-AA (Glx-Phe)				
			Single primary producer-sourced diet (Eq. 3)		Mixed primary producer-sourced diet (Eq. 4)		
Study site	Bulk SIA (Eq. 2) $TP_{seagrass}$	Bulk SIA (Eq. 2) $TP_{macroalgae}$	$TP_{seagrass}$	$TP_{macroalgae}$	TP_{mixed}	f_{algae}	f_{algae} reference
San Diego Bay[S,A]	**2.71 ± 0.56**	**2.30 ± 0.55**†	4.66 ± 0.29	1.69 ± 0.23	**2.66 ± 0.19**	0.75 ± 0.26	López-Mendilaharsu et al. (2005)
Magdalena Bay[M,S,A]	1.70 ± 0.94	1.02 ± 0.73†	4.47 ± 0.24	1.50 ± 0.20	**2.34 ± 0.18**	0.75 ± 0.26	López-Mendilaharsu et al. (2005)
Infiernillo Channel[S,A]	**2.66 ± 0.34**						
Los Angeles Bay[A]		1.82 ± 0.44‡		**2.54 ± 0.37**			
Bahia Navachiste[M,S,A]		**2.60 ± 0.71**†					
Golfo Dulce[M,S,A]		**3.24 ± 0.56**§	6.06 ± 0.24	**3.09 ± 045**	**2.43 ± 0.10**	0.20 ± 0.08	Amorocho and Reina (2007)
Isla Gorgona[M,A]		**2.98 ± 0.34**§					
Caleta Derek[M,A]		**2.31 ± 0.72**†	4.81 ± 0.25	1.84 ± 0.26	**3.14 ± 0.13**	0.86 ± 0.04	Carrión-Cortez et al. (2010)
Paracas Bay[A]				**3.39 ± 0.53**			
Mejillones[A]				**3.57 ± 0.56**			

Notes: TP based on bulk tissue SIA was determined with $\delta^{15}N$ values of green turtle skin (Table 1) and putative prey (Table 3) following Eq. 2; TDF was set at +4.1 ± 0.4 ‰ based on a study of green turtles (Turner Tomaszewicz et al. 2017). TP based on CSIA-AA $\delta^{15}N$ values used the trophic (Trp) - source (Src) AA combination of Glutamic Acid/Glutamine-Phenylalanine (Glx-Phe). TPs assuming single primary producer-sourced diets (i.e., seagrass [$TP_{seagrass}$] or macroalgae [TP_{algae}]) were determined with Eq. 3, and TPs assuming mixed primary producer-sourced diets (i.e., seagrass and macroalgae [TP_{mixed}]) were calculated with Eq. 4. TP_{mixed} was calculated only for sites known to host both seagrass and macroalgae (SDB, BMA, DUL, IGD). For error propagation of each method see Eqs. S1, S2, and S3. The marine proportion of diet (f_{algae}) was assumed to be 0 for $TP_{seagrass}$ and 1 for TP_{algae}; f_{algae} values used in TP_{mixed} calculations were based on empirical diet data at each site; for the site that that lacked diet data (San Diego Bay), f_{algae} from the nearest neighboring site (Magdalena Bay) was used, assuming similar habitats and green turtle diets. The TDF used for Glx-Phe for skin was 3.97 ± 0.64 based on a study of green turtles (Lemons et al. 2020). $\beta_{seagrass}$ for these calculations was –8.4 ± 0.06 (C_3 plants, Chikaraishi et al. 2010) and $\beta_{macroalgae}$ was 3.4 ± 0.9 (Chikaraishi et al. 2009). Biologically realistic TP estimates (see *Methods*) are in bold. Primary production type within foraging area: [M] = mangrove, [S] = seagrass, [A] = macroalgae.

† TP_{algae} calculated using baseline based on average of *Ulva lactuca* and *Gracilaria* sp.

‡ TP_{algae} calculated using baseline value based on *Gracilaria* sp.

§ TP_{algae} calculated using baseline value based on *Ulva lactuca*.

suboxic subsurface waters (Altabet et al. 1999). The processes that lead to elevated $\delta^{15}N$ values in phytoplankton likely also influence benthic macroalgae, which ultimately leads to higher $\delta^{15}N$ values in primary consumers, such as green turtles. Similarly, SIA studies spanning the EP for epi-mesopelagic squid (Ruiz Cooley and Gerrodette 2012) and olive ridley turtles (*Lepidochelys olivacea,* Peavey et al. 2017), found the highest $\delta^{15}N$ values among individuals in the Gulf of California. The influence of denitrification on the $\delta^{15}N$ values in sea turtle tissues has been described previously across ocean basins (Wallace et al. 2006, Pajuelo et al. 2010), but this is the first example suggesting a regional influence in temperate waters of the eastern Pacific.

Green turtles at the lower latitude sites in the eastern equatorial Pacific tended to have the lowest $\delta^{15}N$ values in this study, which is interesting considering the presence of the denitrification hotspot in the Eastern Pacific Warm Pool (Somes et al. 2010), and the proximity of the study sites to this area. Green turtles at the Galapagos Island sites had the lowest $\delta^{15}N$ values of all foraging areas in the region, with the exception of pelagic waters off Peru. Perhaps the low $\delta^{15}N$ results from the archipelago's exposure to the west flowing South Equatorial Current, which may buffer against influx of denitrified waters from the north. Further, the Galapagos Archipelago has been recognized as an area of high-nitrate, low-chlorophyll, and isotope fractionation associated with phytoplankton assimilation of nitrate in this region (e.g., Tyrrell et al. 2005) likely would lower the $\delta^{15}N$ values of local macroalgae resources and their predators.

Knowledge of green turtle foraging ecology at study sites in the region indicates that Galapagos green turtle's relatively low $\delta^{15}N$ values may also result from their diet. Whereas in the Galapagos, green turtles consume a macroalgae-dominated diet (Carrión-Cortez et al. 2010), turtles in Paracas Bay are known to consume some algae, but mostly scyphozoan jellies (e.g., *Chrysaora plocamia*), anenomes (*Paranthus* sp.), and fish (Quiñones et al. 2010), and turtles at Gorgona Island have a diet consisting of 80% animal matter dominated by tunicates (Salpidae and Doliolidae; Amorocho and Reina 2007). Thus, it is not surprising that the latter two sites have higher bulk skin mean $\delta^{15}N$ values.

Mejillones Bay had the highest bulk skin mean $\delta^{15}N$ value among all green turtle populations south of the equator. The mechanisms driving this pattern are less clear, but may be driven by coastal industrialization and runoff (Donoso and Dutton 2000), although probably more related to advection of partially denitrified (via conical denitrification and anammox in suboxic water; Dalsgaard et al. 2012) water onshore along the continental shelf of Chile and transferal of ^{15}N-enriched waters into the Bay (25° S) via coastal upwelling (Galán et al. 2014). A similar pattern has been found in the Peru upwelling system as far north as 15° S (Dugdale et al. 1977), which suggests that the Paracas Bay study site may also be affected by this phenomenon. The aforementioned studies by Ruiz Cooley and Gerrodette (2012) for squid and Peavey et al. (2017) for ridley turtles also found high bulk tissue $\delta^{15}N$ values in the southernmost latitudes, as did Marcoux et al. (2007) who showed a positive relationship between latitude (0° to 26° S) and $\delta^{15}N$ values for sperm whales (*Physeter macrocephalus*) and Kelez (2011) who found the highest $\delta^{15}N$ values for green turtles at the southern extremities of Peruvian offshore waters (5° to 17° S).

In the context of latitudinal $\delta^{15}N$ gradients, the high values in Mejillones coupled with those from the Gulf of California and southern California provide evidence of greater $\delta^{15}N$ values for green turtles in higher latitude foraging sites of both the Northern and Southern Hemispheres relative to equatorial regions. However, considering the array of local extrinsic influences on $\delta^{15}N$ values of foraging green turtles (e.g., urban watersheds, nitrogen loading, denitrification), latitude *per se* is likely not a contributing factor for the observed trend.

Spatial variability in bulk skin $\delta^{13}C$ values

Stable isotopic studies of sea turtles in the EP have generally found $\delta^{13}C$ values to be a less informative indicator of habitat use and diet, perhaps because these research efforts often focused on turtles in offshore waters that were not exposed to the differential influence of terrestrial and marine nutrient pathways (Turner Tomaszewicz et al. 2016, Peavey et al. 2017). Considering the diversity of habitat types, including oceanic archipelagos to coastal mangrove estuarine systems, variability in green turtle mean $\delta^{13}C$ values in this study was likely influenced by differing proximity to offshore, planktonic food webs, as well variability in exposure to terrestrial-derived carbon sources, both of which lead to ^{13}C-depletion in surface waters (France 1995) that manifest as low bulk $\delta^{13}C$ values in consumer tissues (Hobson et al. 2010). For example, Cocos Island, the site with lowest mean $\delta^{13}C$ value in the study (–17.9 ± 2.3‰), represents the summit of a seamount on the Cocos Ridge, and has been considered a stopover site with a consistent influx of non-resident turtles that may remain for short periods (Heidemeyer 2014). Pelagic existence has been reported for some green turtles in the eastern Pacific (Kelez 2011, Turner Tomaszewicz et al. 2018), and such turtles would likely have lower bulk skin $\delta^{13}C$ values, reflecting the more ^{13}C-depleted carbon pool typical of offshore waters. Indeed, there were numerous turtles present at COC that had extremely low bulk skin $\delta^{13}C$ values (i.e., outliers; Fig. S2) that perhaps were recent arrivals from the oceanic zone.

Magdalena Bay had the second lowest mean $\delta^{13}C$ ratio (–17.1 ± 3.9‰), perhaps due to the large abundance of red mangrove (*Rhizopora mangle*)—which has substantially lower $\delta^{13}C$ values than any other primary producers in the region (Table 3)—and its influence on the local food web. Magdalena Bay is a massive estuarine complex of nearly 250 km^2 in size, and its mangrove canopies are among the largest in Pacific Baja, which may lead to overall decrease in $\delta^{13}C$ values via introduction of mangrove-derived nutrients through detrital pathways (Singh et al. 2005). Moreover, green turtles in this lagoon are

known to travel into the deepest interior channels within this system, where mangrove density and leaf litter is highest (Brooks et al. 2009). It is interesting, however, that lagoons farther north in Baja did not have such low $\delta^{13}C$ values (Table 1, Figs. 2, 4). The reasons for the $\delta^{13}C$ disparity are unclear, but may relate to the greater influence of mangrove in BMA, and greater influence of seagrass and macroalgae in the NGU lagoons. Senko et al. (2010) showed green turtles here spent 69% of their time over areas of seagrass, indicating a more intimate link between turtles and seagrass in NGU vs. BMA. Emerging techniques such as CSIA of carbon can help decipher the importance of terrestrial vs. marine-derived carbon and shed light on the differing influences of mangrove vs. seagrass (e.g., Lorrain et al. 2009, Larsen et al. 2013, Whiteman et al. 2019).

The highest mean $\delta^{13}C$ value was found for green turtles at Punta Espinoza in the Galapagos Islands (–12.3 ± 1.1‰) (Table 1, Figs. 2, 4). Interestingly, this site had substantially higher $\delta^{13}C$ values than the other Galapagos foraging areas at Elizabeth Bay (–15.8 ± 1.5‰) and Caleta Derek (–15.8 ± 2.8‰), despite their close proximity. This site is known for having the greatest density of marine iguanas (*Amblyrhynchus cristatus*) in the islands, which amounts to the greatest lizard biomass of any place in the world (Bartholomew 1966). As marine iguanas are marine algivores and consume massive quantities of *Ulva* sp. at this site (J. Seminoff, *personal observation*), perhaps they short-circuit the detritus cycle by rapidly mobilizing algae (i.e., marine-)-derived nutrients via excretion (e.g., Thayer et al. 1982), which locally enhances the marine-based primary productivity, and leads to higher $\delta^{13}C$ values here vs. other sites in the Galapagos. Additional research is necessary to substantiate this possibility, but if true it would represent one of the few cases of top-down stable isotope regime modification driven by a consumer species.

Isotopic niche space

Niche space for green turtles is influenced by intrinsic differences in individual green turtle diet and habitat use, as well as extrinsic factors such as habitat diversity and local nutrient cycling regimes. These elements are depicted along two isotopic axes, with $\delta^{15}N$ range providing information on the trophic length of the population and $\delta^{13}C$ range giving an estimate of the diversity of basal resources. Interpretations of these ranges assume that the study animals are resident to the area and thus at isotopic steady state with local conditions. While green turtle residency has been established for numerous neritic foraging areas in the region (e.g., Seminoff et al. 2002*a*, Koch et al. 2007, Heidemeyer et al. 2014, Chacón-Chaverrí et al. 2015), a relatively high frequency of non-local turtles is known to occur in at least two sites, both of which are insular in nature: Cocos Island and Gorgona Island. Both areas are stopover sites for green turtles originating from distant areas (Amorocho et al. 2012, Heidemeyer 2014), and while the origin and residency patterns of these turtles has been investigated by Heidemeyer (2014), if these turtles are not present long enough to reach a steady state with local conditions, their isotope niche space would inaccurately portray the "local" isotopic niche space. Indeed, despite its small size, remoteness, and presumed lower prey diversity, Cocos Island has the second largest green turtle CHA among all study sites (Table 1), likely because of these outlying values for the putative transient turtles.

Because of the impact of outliers on the total isotopic niche area based on CHA, in most cases the BEA approach provides a more reasonable estimate of niche area that can be compared across sites, regions, and ocean basins. However, even the BEA approach will yield large areas if there is great dispersion among the $\delta^{13}C$ and $\delta^{15}N$ values for turtles within a population such as was found for green turtles in BMA and NGU (BEA = 31.9 and 21.8, respectively). After excluding these two sites, BEA isotopic areas in this study (1.9–12.7) were slightly larger, on average than those of green turtles in the western North Atlantic (Bahamas, Nicaragua, and Florida, USA: 1.8 to 6.1; Vander Zanden et al. 2013*b*) and western South Atlantic (Brazil: 2.4 to 5.3; Di Beneditto et al. 2017). This is not surprising considering that green turtles in the EP are well-known to forage on a great diversity of food types including seagrass, marine algae, and invertebrates, while turtles in the western North Atlantic are largely seagrass consumers, and those in the western South Atlantic eat mostly marine algae (reviewed in Bjorndal 1997, Jones

and Seminoff 2013). Indeed, higher levels of omnivory as seen in the EP would result in larger niche breadth along the $\delta^{15}N$ axis, and assimilation of both seagrass- and algae-derived carbon at EP foraging sites would result in greater niche width along the $\delta^{13}C$ axis.

With respect to the two sites with the largest BEA areas—Magdalena Bay and N. Gulf of Ulloa (Table 1), their BEA sizes may be influenced by a greater diversity of food resources in the area coupled with a greater prevalence of individually specialized diets. These factors could cause more variable $\delta^{13}C$ and $\delta^{15}N$ values in green turtle skin tissues and thus expand the overall ellipse areas for these populations. For example, as was found by López-Mendilaharsu et al. (2003) in BMA, some turtles closer to the mouths of the estuaries likely access the edges of the two study sites to forage on invertebrate species such as pelagic red crabs (*Pleuroncodes planipes*), which have relatively high $\delta^{15}N$ and low $\delta^{13}C$ values (J. Seminoff, *unpublished data*). At the other extreme, turtles in the innermost portions of these study sites forage in mangrove creek food webs where red mangrove is the primary source of carbon and herbivorous foods may be characterized by relatively low $\delta^{15}N$ and high $\delta^{13}C$ values (e.g., Mendoza-Carranza et al. 2010). Individual specialists in a generalist population have been reported for green turtles elsewhere (Vander Zanden et al. 2013*a*, Thomson et al. 2018), and considering the substantial variability in habitats in and around both BMA and NGU, there is an opportunity for green turtles to specialize on spatially constrained prey resources that have unique stable isotope values, which may result in larger observed isotope niche spaces.

Finally, green turtles at PPE—the only oceanic study area included in this analysis—yielded somewhat surprising results. Based on prior knowledge about non-migratory sea turtle movements in the oceanic realm, during which individuals can wander for great distances (Pitman 1990, Plotkin 2003), it was expected that green turtles from the Peruvian offshore would have originated from numerous faraway places and thus would have relatively greater $\delta^{13}C$ and $\delta^{15}N$ variability and resultant larger ellipse spaces. Yet while distant origins cannot be ruled out, it is interesting that these turtles have the smallest Bayesian ellipse area (1.9) among all sites studied and a convex hull area (14.3) that is intermediate among all sites (Table 1, Fig. S1). Perhaps this is a result of relatively low overall habitat (and prey) diversity in the southeastern Pacific Ocean high seas, as has been found for open ocean habitats elsewhere (e.g., Angel 1993). Similarly, and from a stable isotope perspective, McClellan et al. (2010) found that loggerhead turtles (*Caretta caretta*) inhabiting oceanic waters of the western North Atlantic had narrower overall $\delta^{13}C$ and $\delta^{15}N$ ranges than their counterparts living in adjacent neritic habitats.

Green turtle trophic position (TP)

As heterotrophs green turtles have a TP of at least 2, and likely not much greater than 3.5, unless individuals are consistent tertiary consumers. This framework is useful for interpreting the results found here and elsewhere, and can yield insights about the most appropriate TP measurement approach when considered in light of empirical knowledge about green turtle diet. For example, the TP_{bulk} approach (Eq. 2) yielded biologically realistic TP estimates for two of three sites when using a seagrass $\delta^{15}N_{baseline}$ and five of seven sites with a macroalgae $\delta^{15}N_{baseline}$ (Table 4). Considering that green turtle $\delta^{15}N$ values were compared with primary producer $\delta^{15}N$ values for the *same site*, consistent performance of this approach is understandable. However, a drawback of the TP_{bulk} approach is that its effective application relies on $\delta^{15}N$ values for local primary producers, which are often unavailable.

For the three sites at which TP_{bulk} did not perform effectively, the applied TDF may have been inaccurate for local conditions. There are at least three green turtle bulk skin $\delta^{15}N$ TDF values in the literature ($+2.8 \pm 0.1$, Seminoff et al. 2006; $+4.0 \pm 0.4$ for adults, 3.8 ± 0.4 for juveniles, Vander Zanden et al. 2012; $+4.1 \pm 0.4$, Turner Tomaszewicz et al. 2017). However, all but that reported by Turner Tomaszewicz et al. (2017; TDF = +4.1) were for captive animals fed a pelleted, high-protein diet. Considering that TDF of vertebrate bulk tissues is influenced by diet type and quality (e.g., Pearson et al. 2003, McCutchan Jr. et al. 2003) and that a pelleted diet may not adequately reflect diet in the wild, the value by Turner Tomaszewicz et al. (2017) which was derived for wild green turtles using novel, but

well-justified approaches is considered the most appropriate TDF to employ here. However, for the sites (BMA, BLA) with impossibly low TP (<2.0), dietary differences between the population examined by Turner Tomaszewicz et al. (2017) and those studied here may have rendered this TDF inaccurate. Because of the importance of an accurate TDF for calculating TP_{bulk}, additional studies with experimental diets that closely resemble natural diets are recommended.

The most well-performing TP estimation method for green turtles in the eastern Pacific was the $TP_{AA\text{-}mixed}$ approach (Eq. 4), which used amino acid $\delta^{15}N$ values and allowed for a mixed diet of seagrass- and marine algae/photoplankton-derived nutrients (Table 4). Green turtles from the four sites that hosted both marine macroalgae and seagrass had TPs of 2.3 (BMA), 2.4 (DUL), 2.7 (SDB), and 3.1 (IGD). These values are all highly conceivable given that green turtles are known to be omnivores at these sites (López-Mendilaharsu et al. 2005, Rodríguez-Barón 2010, Carrión-Cortez et al. 2010, Lemons et al. 2011, Bessesen and Saborío 2012). It is also notable that all three TP methods (TP_{bulk}, TP_{AA}, and $TP_{AA\text{-}mixed}$) were applied to green turtles at BMA, but only the $TP_{AA\text{-}mixed}$ approach produced a biologically realistic TP (Table 4); BMA also had the largest BEA, which coincides with the likelihood that turtles here had a highly diverse diet. Nevertheless, a potential limiting factor for this approach is that it requires an a priori understanding of the macroalgae/phytoplankton-derived nutrient dietary proportion (f_{marine}) of study animals, which is not always available. Here, for example, the lack of gut content data for green turtles in San Diego Bay required the use of data from the most adjacent foraging area (BMA). Any inaccuracies in the proxy value for f_{marine} applied in SDB would lead to erroneous TP estimates for the site. This underscores the value of combining multiple research tools including more traditional methods (e.g., SIA, gut content analysis) as well as emerging techniques (e.g., $\delta^{13}C$ patterns in amino acids, Larsen et al. 2013, Whiteman et al. 2019) to study TP in consumer species.

For study areas that do not host seagrass and/or mangrove, TP calculations based solely on macroalga/phytoplankton-derived nutrient dietary inputs (TP_{AA} with β_{marine}; Eq. 3) offer an alternative approach. Because of the limited seagrass distribution and the infrequent presence of mangrove systems in the eastern Pacific, this proved to be a viable method for green turtles. Calculations of TP_{AA} for green turtles at the three sites that do not host seagrass or mangroves generally performed well when applying a β_{algae}, with TP ranging from 2.5 to 3.6 (Table 4). Field diet data suggest that the TP estimates for two of these sites (BLA, PAR) are quite good. While green turtles at Los Angeles Bay (BLA) are known to consume a diet consisting of marine algae and invertebrates (Seminoff et al. 2002*b*), a TP_{AA} of 2.5 is in line with expectations based on such an omnivorous diet. Likewise, green turtles at Paracas Bay (PAR) are known to consume large quantities of mollusks and fish eggs and very little algae (de Paz et al. 2008, Quiñones et al. 2010), which is consistent with their relatively high calculated TP_{AA} of 3.4.

The TP_{AA} method using $\delta^{15}N_{Glx}$, $\delta^{15}N_{Phe}$, and β_{marine} (Eq. 3) has also performed well for olive ridley turtles (Peavey et al. 2017) and leatherback turtles (*Dermochelys coriacea*; Hetherington et al. 2019) both of which reported TP of 3.1, which is consistent with ecological knowledge about the trophic status of these pelagic consumers, which consume a diet of exclusively marine phytoplankton-derived nutrients. This method also yielded reasonable TP estimates for green turtles in oceanic waters of the central Pacific and Peru, where Arthur et al. (2014) reported TPs of 2.5 ± 0.1 and 2.3 ± 0.2, respectively. Again, this is not surprising considering green turtles in these areas probably only had access to nutrients derived from the pelagic phytoplankton-based food web. However, for green turtles in nearshore habitats of Hawaii, this TP_{AA} approach was less reliable—yielding a TP of 1.51 ± 0.23 (Arthur et al. 2014), perhaps owing to the influence of seagrass that a β_{algae} could not account for.

For the four EP study sites that hosted seagrass, TP_{AA} calculations using $\beta_{seagrass}$ consistently overestimated TP (4.5 to 6.1, Table 4), probably because green turtles commonly consume marine-derived prey and not solely seagrass in these areas. In contrast, in the western North Atlantic where turtle grass (*Thalassia testudinum*) is the dominant diet item for green turtles, TP_{AA} calculations using Eq. 3 with $\delta^{15}N_{Glx}$,

$\delta^{15}N_{Phe}$, and $\beta_{seagrass}$ yielded more realistic values, with TP estimates of ~1.7 to ~2.1 (Vander Zanden et al. 2013*b*). However, half (3/6) of the TP estimates were below 2.0 which indicates that TP_{AA} estimates using $\beta_{seagrass}$ may yield erroneous values even for green turtles that are largely if not exclusively seagrass consumers. Departures in TP estimates from biologically realistic values may relate to the specific $\beta_{seagrass}$ value used, as it is derived independently for each trophic-source AA combination, or perhaps due to differing behavior among amino acids in green turtle physiology. Greater understanding regarding the potential caveats for determining β and about amino acid metabolism in green turtles is needed to clarify these potential factors. Moreover, as with TP_{bulk} calculations (Eq. 2), the TP_{AA} and $TP_{AA\text{-}mixed}$ approaches (Eqs. 3, 4) relied on a $TDF_{Glx\text{-}Phe}$ derived for captive green turtles raised on a diet that included high-protein pellets (Lemons et al. 2020). Future efforts should be made to characterize $TDF_{Glx\text{-}Phe}$ for green turtles raised on a natural diet.

Conclusions

Green turtles in the EP live in continental, insular, and oceanic habitats and consume a variety of seagrass, marine macroalgae, and invertebrate species. Their array of diet strategies are reflected by variability in TP and BEA across the 16 sites studied here. In general, EP green turtles have higher TPs and larger BEAs than their counterparts elsewhere, due to the consumption of larger amounts of invertebrates and greater prey diversity. Although green turtles of the EP were expected to consume more invertebrates in temperate vs. tropical regions, there was no universal spatial or latitudinal trend for $\delta^{15}N$ or TP. However, when excluding BMA and NGU, the greatest $\delta^{15}N$ values tended to be at the northern and southern ends of the study area, which also has been reported in the EP for olive ridley turtles, sperm whales, and squid (Marcoux et al. 2007, Ruiz Cooley and Gerrodette 2012, Peavey et al. 2017). We saw no spatial pattern in BEA, although the three smallest ellipse areas were for turtles at two insular sites (GOR, IGP) and the sole oceanic "site" of PPE. Lower BEA at these areas was not surprising considering the anticipated lower prey diversity in insular and oceanic habitats vs. continental neritic habitats. However, insular sites did not always have small BEAs (e.g., COC), likely due to the influence of transient turtles that had disparate $\delta^{13}C$ and $\delta^{15}N$ values relative to local conditions. Finally, the neritic-oceanic $\delta^{13}C$ spatial gradient typical of many marine regions was only weakly seen for green turtles in the EP. This is perhaps due to the region's relatively small continental shelf and resulting infiltration of oceanic-derived nutrients into coastal habitats, and/or because "low-$\delta^{13}C$" mangrove plants in nearshore areas mimicked offshore $\delta^{13}C$ values. It would be interesting to measure bulk tissue and amino acid stable isotope values of green turtles at other EP foraging areas, especially in Central America, to clarify these possibilities and refine knowledge about green turtle trophic ecology throughout the region. Greater information about the physical and biological characteristics at each foraging site is also required, and may help to understand the mechanisms that cause EP green turtles to be so unique.

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Data Availability

All raw bulk skin isotope data are available at https://doi.org/10.5061/dryad.jdfn2z39f; all raw amino acid data can be found in Appendix S1: Table S1; computer code and model inputs are available at https://github.com/lkomoro/EPGT_stable_isotope_LMK_JAS/blob/master/JAS_SIA_models.only.Rmd

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3479/full