



Opportunism on the High Seas: Foraging Ecology of Olive Ridley Turtles in the Eastern Pacific Ocean

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Stable isotopic compositions in animal tissues have been widely used to gain insight into trophic dynamics, especially of mobile aquatic predators whose behavior and dietary preferences are difficult to directly measure. Olive ridley sea turtles (*Lepidochelys olivacea*) range across >3 million km² of the tropical and subtropical eastern Pacific Ocean and their trophic ecology in open ocean areas has not yet been adequately described. Individuals feed within biogeographic regions where varying nutrient cycling regimes result in phytoplankton with distinct $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that are assimilated by the turtles. We sampled 346 turtles at-sea between 2003 and 2009 and used bulk tissue ($n = 346$) and amino acid compound specific isotope analysis (AA-CSIA, $n = 31$) to empirically support the conventional understanding that olive ridleys are omnivores. Bulk $\delta^{15}\text{N}$ values did not significantly vary with carapace length, a proxy for age, or with putative sex of adults. We therefore hypothesize that trophic position (TP) does not vary across age or sex. In line with other isotopic studies of this biogeographic scale in the same region, we observed a trend of bulk tissue ^{15}N enrichment with increasing latitude. Using AA-CSIA to account for $\delta^{15}\text{N}$ baseline shifts among food webs (space), we estimated the TP of adult foragers using two methods. We found that across their eastern Pacific range, olive ridley $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niche area varied, but median TP of adults remained constant (~ 3.1). Using a two-amino acid TP estimation method, we detected a small but notable elevation of TP for olive ridleys on the Costa Rica Dome. This study underscores the value of large-scale in-water olive ridley sea turtle research across oceanic foraging habitats to confirm or challenge anecdotal understanding of trophic roles, susceptibility to environmental change, and critical habitats. Further, it improves our understanding of why this species is now abundant in the eastern Pacific Ocean. A prey generalist with plenty of suitable foraging habitat can recover from the brink of extinction despite the presence of major threats. However, such foraging characteristics may require dynamic open ocean management approaches to meet conservation objectives if threats persist and/or increase.

Keywords: amino acid compound specific isotope analysis, niche area, trophic position, oceanic food webs, olive ridley, *Lepidochelys olivacea*

INTRODUCTION

The complexity of ecosystem function depends on food web biodiversity, predator-prey relationships, and the degree of consumer generalism (Duffy et al., 2007). Understanding the trophic role(s) of wide-ranging consumers can shed light on spatial variation in trophic structure and/or resource availability across oceanic food webs. For example, consumers may exhibit faster trophic responses to sudden changes in food supply or phenology in simple food webs vs. complex food webs (Suryan et al., 2009). A response such as an increase in trophic position may have demographic benefits, like increased survival.

Defined by their nutrient regimes, the three main types of pelagic systems are upwelling, oligotrophic oceanic, and eutrophicated coastal systems (Sommer et al., 2002). Regardless of the mechanistic drivers of the trophic structure within these systems [e.g., resource-driven (bottom-up) and/or predation (top-down)], it is well established that the biological characteristics of dominant species regulate biogeochemical cycling in spatially subsidized (i.e., patchy) open ocean food webs (Menge and Sutherland, 1976; Longhurst and Harrison, 1989; Polis et al., 1997). Today, humans are an important element of marine food webs by influencing both bottom-up and top-down controls via nutrient enrichment and resource extraction, respectively.

Mobile marine consumers like sea turtles can have variable foraging strategies. Omnivores feed on an array of prey within a food web and often span multiple trophic levels (Thompson et al., 2007). Omnivores are considered generalists when they access prey resources across food webs (Pillai et al., 2011). In contrast, specialists feed on a lower diversity of prey items within and across food webs, generally within only a single trophic level. Both types of consumers play important roles in top-down regulation of food webs. Phenology, physiology, and/or community structure can influence changes in trophic role across space (e.g., habitat) and time (e.g., with growth). Understanding the trophic position of a consumer, along with its ecological niche within a given food web, can provide insight into foraging preferences and/or response to ecosystem heterogeneity.

Stable carbon and nitrogen isotopic compositions have been used extensively to gain insights into foraging strategy, particularly for consumers whose behavior and dietary preferences are difficult to observe directly (Fry, 1988; Olson et al., 2010). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values vary across ecosystems and are tracers of metabolic and biogeochemical processes (Montoya, 2007). For example, the variability of primary producer $\delta^{13}\text{C}$ values is driven by physical forces of the carbon cycle, temperature and $[\text{CO}_2]_{\text{aq}}$, as well as biology (Laws et al., 1995; Cassar et al., 2006; McMahan et al., 2013). Coastal and benthic systems are typically nutrient rich compared to offshore and pelagic systems, and thus have phytoplankton more ^{13}C -enriched (France, 1995). As such, $\delta^{13}\text{C}$ values of consumer tissues reflect those at the baseline of the food web. Nitrogen integrated into consumer tissues is enriched in ^{15}N relative to prey, such that top predators have the highest $\delta^{15}\text{N}$ values (DeNiro and Epstein, 1981; Fry, 1988; Cabana and Rasmussen, 1996). Because the dominant nitrogen cycling regime in a region influences

$\delta^{15}\text{N}$ values at the base of the food chain (Hobson, 1999; Vander Zanden and Rasmussen, 2001), spatially discrete food webs with differing nutrient cycling offer distinct biogeochemical frameworks to study animal movement and trophic ecology (Hobson et al., 2012). In practice, measuring $\delta^{15}\text{N}$ values of tissues from multiple individuals within a population can provide insights about local nitrogen sources, trophic level, and niche space (Thomas and Crowther, 2015).

When investigating wide-ranging consumers, it is important to consider natural variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the base of the food web, in addition to trophic fractionation. “Bulk” (whole) tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values reflect a composite view of all assimilated organic compounds (e.g., protein amino acids). Many marine studies of cryptic consumers have examined bulk tissue to infer diet composition and/or trophic interactions (Ruiz-Cooley and Gerrodette, 2012; Allen et al., 2013; Thompson et al., 2015), including isotopic niche space—a multi-dimension measure of all interactions between a consumer and its habitat and prey (Elton, 1927; Hutchinson, 1957; Bearhop et al., 2004; Newsome et al., 2007; Yeakel et al., 2016). However, the interpretation of bulk analysis results is constrained by an inability to discern trophic vs. baseline influences on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumer tissues (Hussey et al., 2014; Bowes and Thorp, 2015). A second approach, amino acid compound-specific nitrogen isotopic analyses (AA-CSIA), can help overcome this limitation.

The $\delta^{15}\text{N}$ values of amino acids fall into two groups: “source” amino acids (e.g., phenylalanine, lysine) that minimally fractionate with trophic processing, and “trophic” amino acids (e.g., glutamic acid, alanine) that undergo ^{15}N -enrichment with trophic transfers (McClelland and Montoya, 2002; Chikaraishi et al., 2007; Popp et al., 2007). Source amino acids reflect the isotopic composition at the base of the food web, whereas trophic amino acids reflect the trophic level of the consumer. Examining $\delta^{15}\text{N}$ values of both types of amino acids can thus yield insights that cannot be gained with bulk-tissue analysis alone (Chikaraishi et al., 2009, 2010).

The integration of bulk-tissue stable isotope analysis with AA-CSIA has provided insights about several marine taxa, including sea turtles (Seminoff et al., 2012; Vander Zanden et al., 2013; Arthur et al., 2014). This combined approach is useful for studying the trophic ecology of cryptic species as well as those for which empirical dietary information is limited. The olive ridley sea turtle (*Lepidochelys olivacea*) is an example of both. It is an oceanic species, and individuals live offshore in waters largely inaccessible for research for the majority of their lives. Although long-term diet studies would be challenging, it is possible to collect tissue samples from individuals at sea.

Olive ridleys are the smallest and most abundant sea turtle species in eastern Pacific Ocean and are thought to mature at a younger age (~13 years) than other turtles (Zug et al., 2006; Eguchi et al., 2007; Seminoff and Wallace, 2012). They range >3 million km² across this dynamic ocean basin and are thus present in multiple biogeographic regions (Pennington et al., 2006; Olson et al., 2010; Plotkin, 2010). As nomadic opportunistic omnivores, they don't undergo ontogenetic habitat shifts and may feed in both benthic and pelagic habitats (Bjorndal, 1997; NMFS and USFWS, 1998; Robins et al., 2002; Bolten, 2003; Whiting et al.,

2007; Behera et al., 2015). Olive ridleys often forage via passive drifting rather than active swimming, meaning they eat within the same food web for many days (Block et al., 2002; Polovina et al., 2003; McMahon et al., 2007; Whiting et al., 2007; Plotkin, 2010). Their oceanic diet consists of mostly planktonic items or items living on or near flotsam including algae, crustaceans, and salps (Kopitsky et al., 2005; Jones and Seminoff, 2013; Wedemeyer-Strombel et al., 2015; Pitman, Kopitsky and Peavey, pers. comms.). Thus, the trophic position of the olive ridley may be different than for other large vertebrates such as marine mammals, sharks, and seabirds. Despite these insights, olive ridley open ocean trophic ecology has not yet been sufficiently investigated. However, their foraging behavior and temporal scale makes them perhaps the best large consumer to study spatial differences in trophic roles across oceanic food webs.

Here we apply bulk-tissue stable isotope analysis and AA-CSIA to olive ridley sea turtles foraging in the eastern Pacific Ocean. We quantitatively describe isotopic niche variation for olive ridleys across a large portion of their range, and estimate the trophic positions of adult olive ridleys. To our knowledge, this is the first account of the isotope ecology of olive ridley turtles in the Pacific Ocean. We discuss our findings as they relate to persistent but dynamic oceanic foraging habitats, conservation implications of potentially unique open-ocean foraging areas, and the olive ridley's resilience to climate, habitat quality and prey changes.

METHODS

Study Region and Sub-Regions

The study region spans the tropical and subtropical eastern Pacific Ocean, extending from $\sim 30^\circ$ N (Gulf of California) to $\sim 16^\circ$ S (Peru Current), and $\sim 76^\circ$ W (west coast of the Americas) to $\sim 115^\circ$ W (**Figure 1**). This region is oceanographically dynamic but has persistent and predictable areas of upwelling, warm pools, cold tongues, and boundary currents that support spatially explicit nutrient cycling regimes, such as nitrogen fixation and denitrification (Fiedler and Talley, 2006). Per these regimes, $\delta^{15}\text{N}$ values are distributed across the region's oceanographic features and distinct $\delta^{15}\text{N}$ baselines are assumed to represent distinct food webs.

We examined geographic variation of stable isotope compositions in olive ridleys relative to regions of varying biogeochemical processes at two different scales. First, we grouped samples by Longhurst biogeochemical provinces (VLIZ, 2009), and second, by oceanographic features described in Fiedler and Talley (2006). Longhurst provinces (L) were defined by the following numeric labels: 7 ("Coastal—Central American Coastal Province"), 8 ("Coastal—Chile-Peru Current Coastal Province"), and 35 ("Trades—North Pacific Equatorial Countercurrent Province") (VLIZ, 2009; **Figure 1A**). Alternatively, samples were grouped into five distinct sub-regions based on the following oceanographic features: the Gulf of California (GC), the North Equatorial Current (NEC), the Eastern Pacific Warm Pool (EPWP), the Costa Rica Dome (CRD, an oceanic thermal feature), and the Peru Current (PC) (**Figure 1B**). Spatial analyses across sub-regions were limited to individuals sampled within feature boundaries. Our analyses relied on the premise that stable

isotope values of olive ridley skin reflect the local food web in which the turtle was sampled, considering the isotopic turnover of sea turtle skin tissue (ca. 40–50 d, Reich et al., 2008) and the passive movements of olive ridleys foraging at-sea.

Sample Collection and Preparation

From August to December 2006, in total, 320 olive ridley sea turtles were opportunistically hand-captured from a small boat deployed from the National Oceanographic Atmospheric Administration R/V *David Starr Jordan* during the *Stenella* Abundance Research (STAR) cruise (Jackson et al., 2008). Morphometric information was collected for all turtles, and putative sex was recorded for mature/adult individuals. Based on external morphology, individuals with straight carapace length \geq ca. 56 cm are considered adult (NMFS and USFWS, 1998). Putative sex of adult-sized turtles was based on tail length; individuals with long tails (>20 cm length) were classified as males whereas those with shorter tails were considered females. For individuals sampled within the GC ($n = 29$), NEC ($n = 36$), EPWP ($n = 192$), and CRD ($n = 63$) sub-regions [alternatively: L7 ($n = 172$), L8 ($n = 21$), and L35 ($n = 151$)], a razor blade was used to collect epidermis ("skin") samples ~ 2 mm from the dorsal neck surface, and samples were immediately frozen at -80°C and then stored at -20°C at the Southwest Fisheries Science Center (La Jolla, CA, USA) until laboratory analysis. All turtles were released unharmed within ~ 20 km of where they were captured.

Prior to stable isotope analyses, samples were thawed and rinsed with distilled water, freeze dried for one 8-h cycle, and lipid-extracted using an Accelerated Solvent Extractor (ASE 200) according to previously published methods (Lemons et al., 2011; Allen et al., 2013). Lipid extraction is not known to significantly alter $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values in sea turtle skin (Medeiros et al., 2015; Bergamo et al., 2016). All samples were analyzed for bulk-tissue stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), whereas 4–14 samples in each sub-region were processed for AA-CSIA (**Figure 1**).

In total, 22 adult olive ridleys in the Peru Current were sampled from turtles incidentally captured by Peruvian longline fishing vessels. Using a 2-mm biopsy punch, skin samples were taken from the dorsal neck surface of adult olive ridleys in 2003 ($n = 3$), 2004 ($n = 5$), 2008 ($n = 10$), and 2009 ($n = 4$), preserved with salt, and archived at -20°C at the Southwest Fisheries Science Center (La Jolla, CA, USA) until laboratory analysis. These samples were lipid extracted using the same methods as above, and analyzed for bulk-tissue stable isotope values as described in Kelez (2011) and Arthur et al. (2014). AA-CSIA was completed for five samples from 2008 and 2009 using the same methods described below and in Arthur et al. (2014). Note that these samples were originally for a separate study, and as such they are unique in their collection year and method.

Bulk Tissue Analysis

i) Mass Spectrometry

For GC, NEC, EPWP, and CRD 2006 samples ($n = 320$), 0.7–1 mg of skin was homogenized with a razor blade and loaded into tin capsules. Samples were analyzed by a Costech

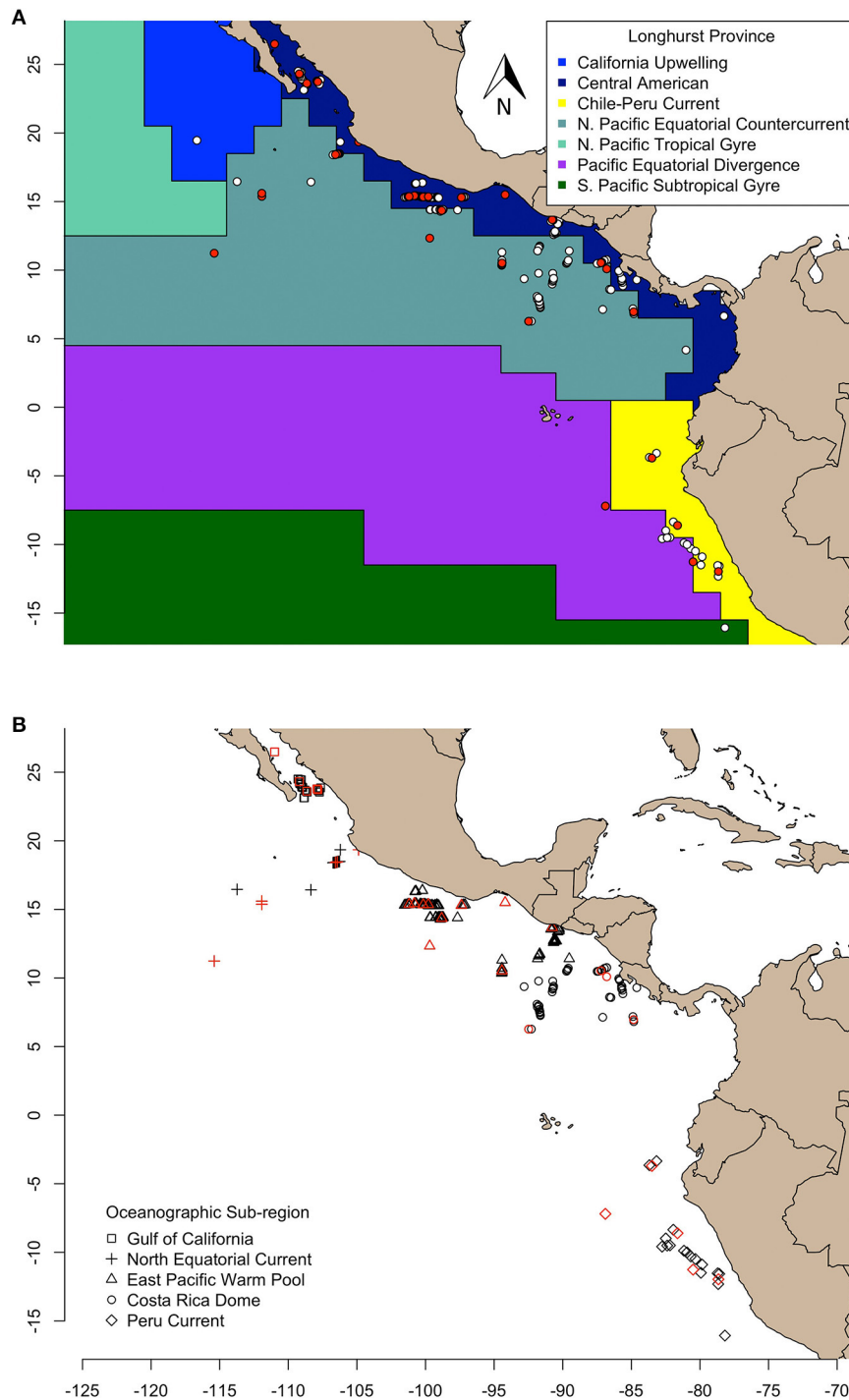


FIGURE 1 | Olive ridley turtles sampled in this study are represented as symbols and aggregated according to **(A)** Longhurst province (VLIZ, 2009), and **(B)** oceanographic sub-region (Fiedler and Talley, 2006). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of skin of all turtles were determined, and compound specific amino acid $\delta^{15}\text{N}$ values were measured for only those colored in red.

Instruments elemental combustion system (ECS4010) coupled to a continuous-flow Thermo Finnigan MAT Delta Plus XL isotope ratio mass spectrometer in the Stable Isotope Laboratory at the University of Florida, Gainesville. PC samples were

analyzed in an analogous way in the same facilities, as described in Kelez (2011). Bulk isotope values are reported in standard delta notation (δ) in parts per thousand (‰): $\delta^{\text{H}}\text{X} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times (1,000)$, where the superscript “H”

is the mass of the heavy isotope, X is the element of interest, and R is the ratio of the heavy X isotope to the light X isotope (Fry, 2006). $R_{standard}$ was atmospheric N_2 and Vienna Pee Dee Belemnite (VPDB) for $\delta^{15}N$ and $\delta^{13}C$, respectively. Continuous calibration was completed using USGS40 (L-glutamic acid: $\delta^{15}N = -4.52\text{‰}$ and $\delta^{13}C = -26.39\text{‰}$) with an average precision of 0.07‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$. To ensure accuracy, 1–3 blind sample duplicates were run per 30 samples with an average standard deviation of 0.14‰ for $\delta^{15}N$ and 0.27‰ for $\delta^{13}C$.

ii) Exploring $\delta^{15}N$ Shift with Size, Gender

Both curved carapace length (CCL) and straight carapace length (SCL) was measured for all STAR turtles. However, only CCL was measured for Peru turtles. In order to estimate SCL for Peru turtles based on the CCL measurements, we used the following model ($R^2 = 0.99$) derived from the linear relationship between SCL and CCL for STAR turtles ($n = 354$, see Supplementary Table 1):

$$y = 0.9417x + 0.1466 \quad (1)$$

Subsequently, a linear regression model ($\alpha = 0.05$) was used to explore if bulk $\delta^{15}N$ values in skin varied with SCL (cm; $n = 337$), after controlling for latitude by specifying sub-region as a factor:

$$\delta^{15}N \sim SCL + SubRegion + error \quad (2)$$

To explore if adult bulk $\delta^{15}N$ values in skin varied with gender (sex: female/male; $n = 185$) after controlling for latitude by specifying sub-region, a two-way ANOVA (Type III, $\alpha = 0.05$) was used:

$$\delta^{15}N \sim sex + SubRegion + sex*SubRegion + error \quad (3)$$

iii) Isotopic Niche Area

Standard niche width ellipse and convex hull areas were estimated using maximum likelihood, and Markov chain Monte Carlo (MCMC) credible intervals were generated to calculate uncertainty around ellipse estimates using Stable Isotope Bayesian Ellipses (SIBER) functions (Jackson et al., 2011) in the Stable Isotope Analysis in R (SIAR) package (Parnell et al., 2008, 2010). Probability of size differences between ellipses were calculated by comparing pairs of draws from the posterior MCMC distributions.

Amino Acid Compound-Specific Nitrogen Isotopic Analyses (AA-CSIA)

i) Mass Spectrometry

Of the 320 STAR samples used for bulk tissue stable isotope analysis, a subset of 26 samples from adults were dried and homogenized with a mortar and pestle and/or razor blade (2–10 mg). Samples making up the subset were chosen to cover the widest geographic area of each sub-region: GC ($n = 6$), NEC ($n = 6$), EPWP ($n = 10$), and CRD ($n = 4$); and alternatively, L7 ($n = 14$) and L35 ($n = 12$).

Samples were prepared (hydrolysis and derivatization) and analyzed for compound-specific isotopic composition of amino

acids at the Biogeochemical Stable Isotope Laboratory at the University of Hawaii at Manoa following Popp et al. (2007), Hannides et al. (2009) and Décima et al. (2013). Briefly, samples were hydrolyzed (6N HCl, 150°C), the hydrolysate purified (0.2 μ m pore size Polyethersulfone filters, cation exchange chromatography), the carboxyl terminus the amino acids esterified (4:1 C_3H_8O and CH_3COCl , 110°C) and the amino group acetylated (3:1 CH_2Cl_2 and 200 μ l $C_4F_6O_3$, 100°C). A final solvent extraction assured that the sample derivatives were pure. Samples were stored frozen at $-20^\circ C$ until analysis in triplicate using a mass spectrometer (Thermo Scientific Delta^{Plus}V or MAT 253 interfaced with a Trace GC/GCIII; see Hannides et al. (2009) and Bradley et al. (2015) for further mass spectrometry details).

The $\delta^{15}N$ values of 13 amino acids [alanine, glycine, valine, serine, leucine, isoleucine, proline, glutamic acid, phenylalanine, lysine, tyrosine, and norleucine (Nor) and amino adipic acid (AAA)], measured against internal Nor/AAA reference material of known isotopic composition, were quantified in each sample. Every block of three sample measurements was bookended by a suite of amino acids with known $\delta^{15}N$ values (alanine, threonine, isoleucine, proline, glutamic acid, and phenylalanine). Suite/samples were co-injected with Nor and AAA with known $\delta^{15}N$ values serving as internal reference material and to control for errors due to sample loss, injection variations, and variability in dilution preparations. Sample $\delta^{15}N$ values for 11 amino acids were normalized using regression (typically $R^2 > 0.9$) of either the Nor/AAA or suite standards. Accuracy was maintained to within 1‰ of the known value, and the average standard deviation of $\delta^{15}N$ across all 2006 samples and amino acids was 0.75‰.

The Peru Current samples were prepared and analyzed separately but in the same lab and with the same protocol at the University of Hawaii at Manoa. These were grouped as PC ($n = 5$), and alternatively L8 ($n = 5$), and had an average standard deviation of $\delta^{15}N$ across all samples and amino acids of 0.56 and 0.63‰, respectively (Arthur et al., 2014).

ii) Exploring Variation of Bulk $\delta^{15}N$ Values

To test our hypothesis that the variation in bulk $\delta^{15}N$ values in olive ridley sea turtle skin [standard deviation (SD) = 0.8] is driven by $\delta^{15}N$ values of source nitrogen, we built the following Deming regression (Type II, $\alpha = 0.05$) using the “mcr” package. Deming regression is an extension of simple linear regression that compares two estimation methods by accounting for measurement errors along both the x- and y-axis, instead of only along the y-axis. If two methods are parallel, a slope of one is expected.

$$\delta^{15}N_{skin} \sim \delta^{15}N_{source_{aa}} \quad (4)$$

We ran the regression two ways across the 31 samples that had both bulk and amino acid $\delta^{15}N$ values, one using phenylalanine ($SD = 0.5$) as the source amino acid (ratio of variance = 1.6), and one using the weighted mean of three source amino acids [glycine, lysine and phenylalanine] ($SD = 0.4$, ratio of variance = 2).

iii) Trophic Position Estimations

We compared two approaches to estimate trophic position (TP) according to Chikaraishi et al. (2009, 2010) and Bradley et al. (2015). We used $\delta^{15}\text{N}$ values for either phenylalanine (Phe) or the weighted mean of three source amino acids (glycine, lysine, and phenylalanine), and glutamic acid (Glu) or the weighted mean of three trophic amino acids (alanine, leucine, and glutamic acid) to estimate olive ridley TP in each sub-region. If samples had missing values for any of these amino acids, they were excluded from the weighted mean trophic position approach and the method comparison. All samples had values for Glu and Phe. We propagated error to calculate SD (see Dale et al., 2011; Choy et al., 2012; Bradley et al., 2015 for details). The two approaches were compared with a two-sided, paired Wilcoxon Signed-Rank test.

The following TP equation shows Glu and Phe as placeholders but were replaced with weighted means for the second approach (see Equation 2 in Nielsen et al., 2015). Trophic discrimination is reasonably predictable and can be accounted for with an enrichment factor (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Bradley et al., 2014). Estimates of ^{15}N enrichment among amino acids in primary producers ($\beta_{\text{Glu-Phe}} = 3.6\text{‰}$) and for each trophic level ($\Delta_{\text{Glu-Phe}} = 5.7\text{‰}$) were recommended by Bradley et al. (2015) and were equivalent across the two approaches. For trophic enrichment, others suggest $\Delta_{\text{Glu-Phe}} = 7.6\text{‰}$ (Chikaraishi et al., 2009), 6.6‰ (Nielsen et al., 2015), or other values (see Lorrain et al., 2009; Dale et al., 2011). We chose values vetted in the literature ($\beta = 3.6$, $\Delta = 5.7$), and because they resulted in more reasonable omnivorous TP estimates considering the range of known $\delta^{15}\text{N}$ values for eastern Pacific olive ridley prey (Supplementary Tables 1 and 2).

$$TP = \frac{\delta^{15}N_{\text{Glu}} - \delta^{15}N_{\text{Phe}} - \beta}{\Delta_{\text{Glu-Phe}}} + 1 \quad (5)$$

Due to the small AA-CSIA sample sizes, we did not assume that TP estimates are normally distributed, and thus used the Kruskal-Wallis non-parametric statistical test to compare TP distribution across sub-regions. Exploratory analysis of $\delta^{15}\text{N}$ probability densities, median TP, and confidence intervals of each sub-region prompted a pooled pairwise comparison (Mann-Whitney *U*-test) of trophic position estimates between the Costa Rica Dome and all others. We treated sub-region as a blocking factor in the Mann-Whitney rank sum test, and $\alpha =$

0.05 for both tests. All statistical tests were performed in R (www.r-project.org/).

RESULTS

Bulk $\delta^{13}\text{C}$ values across the study region ($n = 346$) ranged from -17.8‰ (Gulf of California) to -14.5‰ (East Pacific Warm Pool), and 8.8‰ (Peru Current) to 15.6‰ (Gulf of California) for $\delta^{15}\text{N}$ (Table 1). We observed a general trend of ^{15}N enrichment with increasing latitude (Supplementary Figure 1). Within the northern latitudes, the turtle sampled at the lowest latitude (4.17°N) had a $\delta^{15}\text{N}$ value of 11.9‰ and the turtle sampled at the highest latitude (26.48°N) had a $\delta^{15}\text{N}$ value of 15.6‰ (Figure 2). Bulk $\delta^{15}\text{N}$ values were not correlated with the $\delta^{15}\text{N}$ values of phenylalanine (Deming regression slope ≈ 2.7 , 95% confidence bounds: 1.8, 5.6) or the weighted mean $\delta^{15}\text{N}$ values of source amino acid (Deming regression slope ≈ 2.9 , 95% confidence bounds: 1.4, 12.1).

After controlling for sub-region, SCL was only a significant predictor of bulk skin $\delta^{15}\text{N}$ values when the model included PC turtles ($p = 0.02$). When PC turtles were excluded, SCL was not

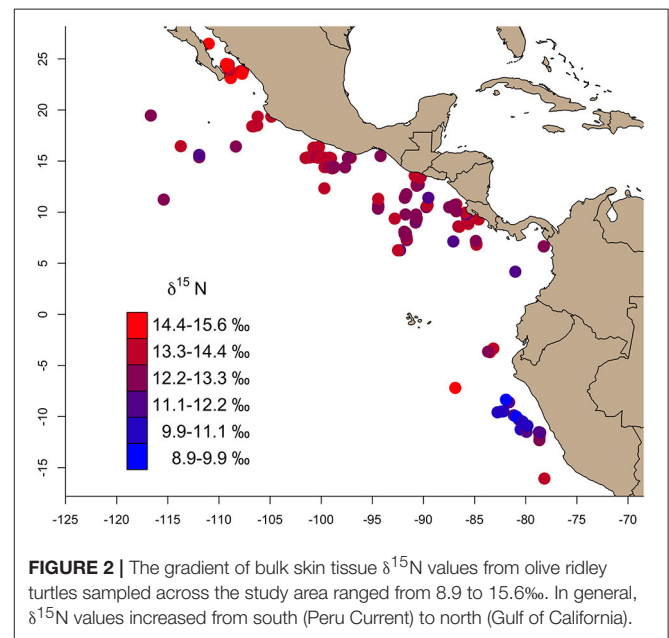


TABLE 1 | Bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) information summarized by oceanographic sub-region, listed in latitudinal order from north to south.

Sub-region	Range $\delta^{15}\text{N}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	Range $\delta^{13}\text{C}$	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$
Gulf of California	12.9, 15.6	14.4	0.71	$-17.8, -15.2$	-16.2	0.47
N. Equatorial Current	11.5, 14.5	13.6	0.57	$-16.9, -15.1$	-15.7	0.42
E. Pacific Warm Pool	11.9, 15.0	13.3	0.54	$-16.2, -14.5$	-15.4	0.34
Costa Rica Dome	11.4, 14.0	13.0	0.57	$-16.1, -14.8$	-15.4	0.29
Peru Current	8.8, 15.2	11.7	1.68	$-16.7, -14.6$	-15.9	0.96

See Supplementary Data Table 1 for the complete dataset, including sampling location, turtle size and sex.

a significant predictor of $\delta^{15}\text{N}$ values [$p = 0.06$; Supplementary Table 2; Supplementary Figure 2]. After controlling for sub-region, adult gender was not a significant predictor of bulk skin $\delta^{15}\text{N}$ values [$F_{(1)} = 0.2$, $p = 0.70$; Supplementary Table 4].

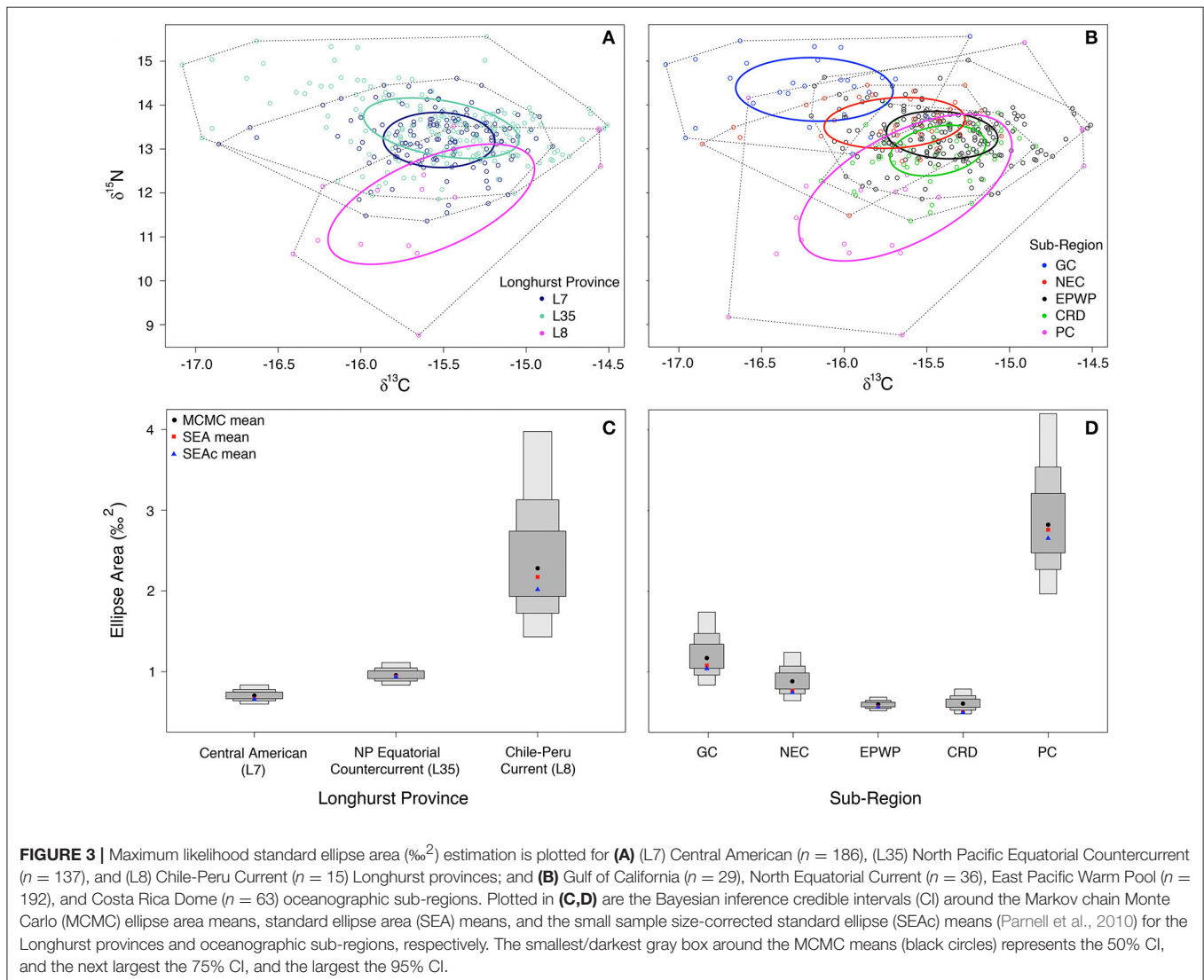
Maximum likelihood sub-region ellipse area estimates (with small sample size corrections in parentheses) are as follows: L7 = 0.7(0.7) ‰², L35 = 0.9(0.9) ‰², L8 = 2.7(2.8) ‰², CRD = 0.5(0.5) ‰², EPWP = 0.6(0.6) ‰², GC = 1.0(1.1) ‰², NEC = 0.7(0.8) ‰², PC = 2.7(2.8) ‰² (Figures 3A,B). In comparing niche area across Longhurst provinces (Figure 3C), olive ridley niche area is much larger in L8 than in either L35 or L7 (>99% probability). Further, their niche in L35 is significantly larger than in L7, even though the two are much more similar in size compared to in L8.

Comparison of niche area across oceanic food webs defined by oceanographic features (Figure 3D) shows that olive ridley niche in the Peru Current is over two and half times larger than it is in the Gulf of California (>99% probability). Further, niche is larger in the Gulf of California than in the North

Equatorial Current and the Costa Rica Dome (>89% and 99% probabilities, respectively). However, there is only moderate (~60%) confidence that niche is larger in the Costa Rica Dome than in the East Pacific Warm Pool, as their ellipse areas are quite similar.

Trophic position estimates using $\delta^{15}\text{N}_{\text{Glu}} - \delta^{15}\text{N}_{\text{Phe}}$ vs. weighted means of multiple trophic and source amino acids were not significantly different [$V = 231$, $p = 0.98$; Supplementary Table 3]. Median TP across the entire eastern Pacific seascape was 3.14 ± 0.2 SD using the $\delta^{15}\text{N}_{\text{Glu}} - \delta^{15}\text{N}_{\text{Phe}}$ approach ($n = 31$), and 3.18 ± 0.2 SD using the weighted mean approach ($n = 29$).

When comparing median TP across sub-regions, there was no significant difference across Longhurst provinces [$\chi^2(2) = 1.83$, $p = 0.40$], and no significant difference across oceanographic regions GC, NEC, EPWP, CRD, and PC [$\chi^2(4) = 5.52$, $p = 0.24$], regardless of TP estimation method. We see a significant difference in median TP between the Costa Rica Dome and all other oceanographic sub-regions pooled [$W = 20$, $p = 0.046$] when using the TPs estimated with $\delta^{15}\text{N}_{\text{Glu}} - \delta^{15}\text{N}_{\text{Phe}}$. Using this



method, we find that individuals on the Costa Rica Dome were feeding at a 0.36 median TP higher than in other oceanographic sub-regions. However, we do not see a significant difference in median TP between the Costa Rica Dome and all other sub-regions pooled [$W = 45, p = 0.70$] using the TPs estimated with weight means of $\delta^{15}\text{N}$ source and trophic amino acids. See **Figure 4** and Supplementary Table 3 for results for both approaches.

DISCUSSION

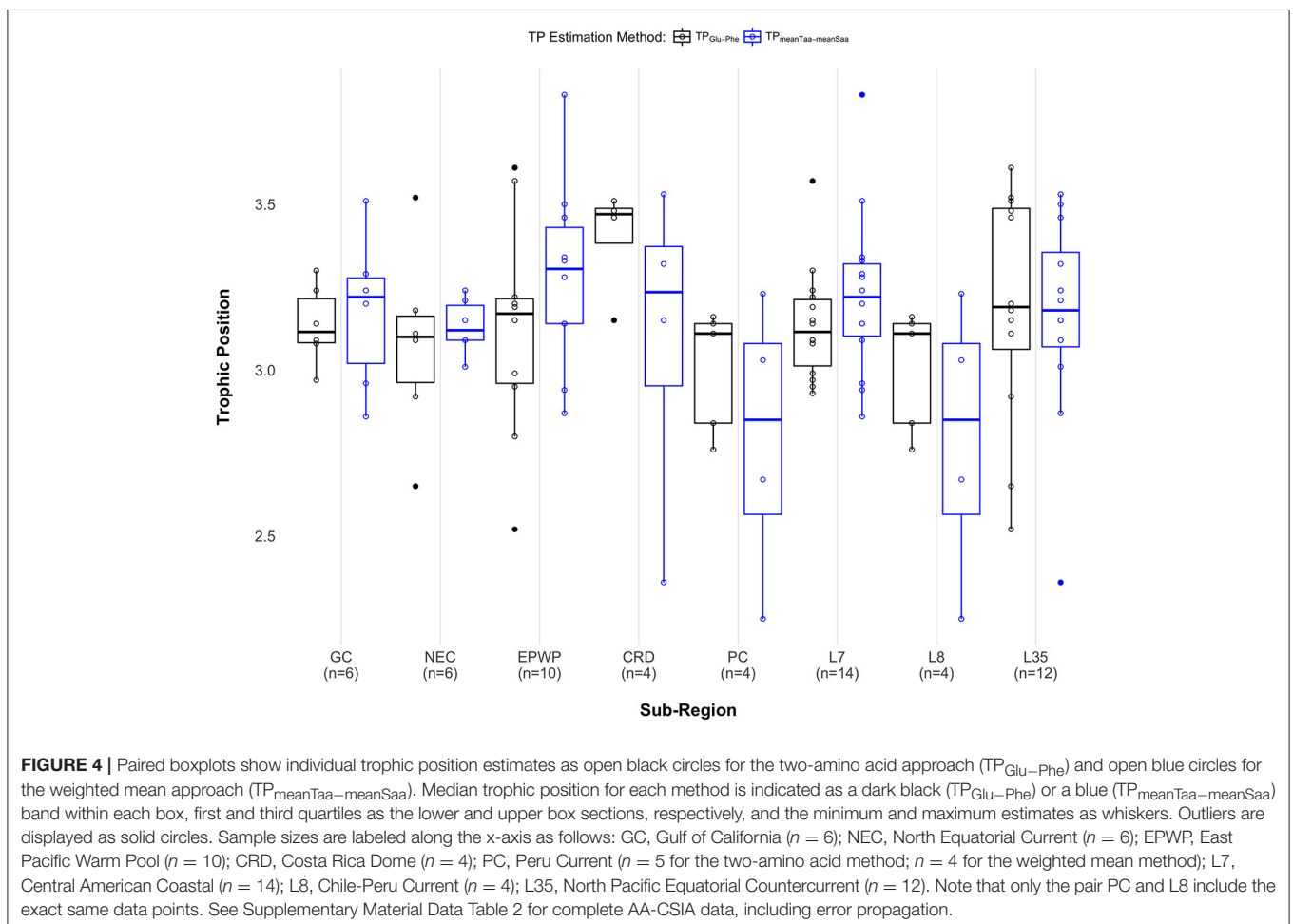
This study is the first to quantify olive ridley isotopic niche and trophic position. Whereas trophic level estimates based on bulk tissue isotopic composition exists for other wide-ranging marine consumers, few studies compare trophic position across a species' range by accounting for baseline $\delta^{15}\text{N}$ differences using AA-CSIA. We found that olive ridley trophic position is consistent across the eastern Pacific (~ 3.1), apart from perhaps on the Costa Rica Dome where it may be slightly elevated. Our AA-CSIA results also indicate that trophic position does not differ between adult males and females. Trophic consistency among olive ridleys within a given region is further supported by finding that bulk skin $\delta^{15}\text{N}$ values do not vary with size (i.e., age), and this

lack of diet shift may explain the lack of an ontogenetic habitat shift, as found in other sea turtle species (Turner Tomaszewicz et al., 2015). Together, these findings demonstrate the value of combining bulk-tissue analysis and AA-CSIA and highlights the status of the olive ridley as a unique oceanic consumer with relatively uniform foraging strategies among individuals, regardless of age, sex, or oceanic food web.

Isotopic Niche Space and Omnivory

The large ranges of $\delta^{13}\text{C}$ [$-17.08, -14.51\text{‰}$] and $\delta^{15}\text{N}$ [$11.36, 15.56\text{‰}$] values support the notion that olive ridleys are generalist omnivores, preying on a variety of primary producers (basal carbon sources) from primary and secondary trophic levels and in different areas of the ocean. Our findings suggest that despite potential individual foraging differences (e.g., prey species), the functional role of olive ridleys as omnivores, albeit largely planktivorous, remains consistent across oceanic food webs separated by thousands of kilometers. This is consistent with the few empirical dietary data for olive ridleys in this region (Bjorndal, 1997; NMFS and USFWS, 1998; Holt et al., 1999; Supplementary Tables 1, 5).

By estimating isotopic niche ellipse areas for each food web we are able to think critically about why the niche space of an



omnivore may vary across a species' range. Since baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and their within-food web variation influences niche space, we discuss each ellipse estimate in relation to the biological and physical forces acting in each food web. Although, Longhurst province boundaries are defined by physical forces that regulate the distribution of phytoplankton in the ocean, grouping foraging turtles accordingly was too coarse a scale for this investigation. While these ecological partitions are useful in guiding large-scale biogeochemical (e.g., isotope) studies concerned with nutrient cycling, they are static and quite large compared to the sub-regions that have been defined based on persistent oceanographic features with distinct biogeochemical cycling. Given this, we focus our discussion on the latter.

Ellipse area estimates suggest that the olive ridley's isotopic niche is larger in the Gulf of California and the North Equatorial Current than on the Costa Rica Dome or in East Pacific Warm Pool. Further, their Peru Current isotopic niche space is roughly three times the size of any eastern Pacific food web that we examined north of the equator, driven by large variations in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

One explanation for a broader isotopic niche ($\sim 1\text{‰}^2$) for olive ridleys in the Gulf of California compared to the other northern sub-regions might be that the majority of turtles were sampled in the Gulf entrance, where some hypothesize regional coupling of denitrification-nitrification occurs (Mee et al., 1984; White et al., 2007). There, nitrogen inputs come from a mix of ^{15}N -enriched (denitrified) subsurface water from the Eastern Tropical North Pacific (ETNP) transported via the California Undercurrent; relatively ^{15}N -depleted warm surface water from the west; and ^{15}N -enriched terrestrial inputs (sediments, guano, runoff). Whereas N_2 -fixation in the Gulf of California appears to be episodic and seasonal (White et al., 2013), all the Gulf of California olive ridleys were sampled during the month of August. During summer months, the water column is stratified and Gulf of California surface waters, including entrance zone waters, are dominated by picocynobacteria and modest N_2 fixation (White et al., 2013). We suggest turtles could have conceivably fed offshore or in deeper entrance zone waters within the month prior to sampling, retaining the "offshore" $\delta^{13}\text{C}$ signal as they moved into the Gulf (Hobson et al., 1994; Hill et al., 2006; Miller et al., 2008), or perhaps turtles fed in both pelagic and benthic habitats across the entrance zone and lower Gulf (France, 1995; Hill et al., 2014). Both scenarios could result in the observed $\delta^{13}\text{C}$ range $[-17.08, -15.24]$.

The East Pacific Warm Pool supports an impressively small isotopic niche area for olive ridleys (0.6‰^2) considering it is the largest sub-region by geography, spanning 10° of latitude and 16° of longitude. N^* values (a metric used to trace nitrate deficit relative to phosphate) in this sub-region indicate a high degree of denitrified waters that are likely a dominant control on the $\delta^{15}\text{N}$ values of bioavailable nitrogen. As such, across the entire subtropical and tropical eastern Pacific, nitrate concentrations are lowest in the East Pacific Warm Pool, as are N^* concentrations, modeled downwards of < -20 (μM ; Rafter et al., 2012). Further, characteristics that influence the bioavailable nitrogen in the euphotic zone such as temperature, pycnocline, and mixed layer depth are particularly stable and

reliable during the season in which our sampling was conducted (Fiedler and Talley, 2006). The Gulf of Tehuantepec and the Gulf of Papagayo are two especially productive gulfs (relatively higher chlorophyll and NO_3^- concentrations) within the East Pacific Warm Pool due to wind-driven upwelling. Many of the samples we examine within the East Pacific Warm Pool were in or near those two gulfs because encounter rates were so high there.

The Costa Rica Dome supports an isotopic niche area almost equal in size (0.5‰^2) to the East Pacific Warm Pool, but is considerably smaller in geographic size (we consider it 800–1,000 km in diameter). It is the most seasonally dynamic oceanographic feature in the eastern tropical Pacific (ETP) with a predictable strong and shallow thermocline (15 m at the peak of the dome, shoaling off to 50 m to the N and S) (Fiedler, 2002). Both the East Pacific Warm Pool and the Costa Rica Dome are within the Tropical Surface Water mass (Fiedler and Talley, 2006) and have high concentrations of chlorophyll and nitrate compared to other areas in the eastern Pacific (Pennington et al., 2006). While driven by different physical sources, the gulfs of Tehuantepec and Papagayo and the Costa Rica Dome share characteristics, such as upwelling, nitrate concentrations, and denitrification, that determine basal isotopic signals, which is why we believe these areas support a similar isotope niche for olive ridleys.

The Peru Current is one of the strongest upwelling regions in the world, particularly during austral winter, and thus denitrification is dominant and CO_2 efflux is high. This creates large variation in $\delta^{15}\text{N}$, upwards of 11‰, and $\delta^{13}\text{C}$, upwards of 5‰, just south of the equator and along the equatorial belt (Farrell et al., 1995; Arguelles et al., 2012). The pattern of low $\delta^{15}\text{N}$ values in olive ridley skin in this food web, specifically between 5° and 15° S, follow observations of low $\delta^{15}\text{N}$ values of particulate organic material in surface waters. This suggests that the observed variation of bulk skin $\delta^{15}\text{N}$ values was caused by baseline shifts, not trophic shifts. The large Peru Current isotopic niche area estimate ($\sim 2.7\text{‰}^2$) suggests there may be unique food web dynamics in the south equatorial region.

Trophic Position

Our understanding of olive ridleys as opportunistic foragers implies that their trophic role (i.e., trophic position) would not differ across their range. This study design provided an opportunity to test that assumption, as well as to compare the results of estimating TP using the weighted mean approach with the approach of using just two amino acids (phenylalanine and glutamic acid). Recent studies by Bradley et al. (2015) and Nielsen et al. (2015) show that using weighted means to estimate marine teleost TPs resulted in more precise estimates across taxa and trophic levels. Using the weighted mean approach, we did not find any statistical difference in TP across food webs; but using the two-amino acid approach, we detected a 0.36 TP elevation on the Costa Rica Dome.

Similar to other organisms in the eastern Pacific (e.g., copepods, lanternfishes and tuna; Popp et al., 2007; Olson et al., 2010; Hetherington et al., 2017), olive ridley bulk skin $\delta^{15}\text{N}$ values showed a tendency to be more ^{15}N -enriched in higher latitudes. Often, differences in $\delta^{15}\text{N}$ values of consumers may be driven by

trophic differences among spatially discrete foraging populations (Vander Zanden and Rasmussen, 2001). However, the TP of adult olive ridleys was remarkably constant (3.1 ± 0.2 SD) across a variety of oceanographic settings in the eastern Pacific, including the Peru Current. With this, we are confident that variation of bulk $\delta^{15}\text{N}$ values was indeed driven by the shifting $\delta^{15}\text{N}$ baseline across food webs.

TP estimates from both methods, ranging from ~ 2.4 to ~ 3.6 , make biological sense and reflect the expected omnivory. Other sea turtles studies that have estimated TP have raised concern over the reasonability of their TP estimates, driven by the beta and trophic discrimination factors used, and/or the TP estimation method (Seminoff et al., 2012; Vander Zanden et al., 2013). It is important to note that these constants can be somewhat arbitrary for species that have not been the focus of controlled feeding studies, and varying them can noticeably change TP estimates. In this study, constants from Bradley et al. (2015) were chosen carefully; they did not vary between TP estimation methods and appear to have performed well.

Source amino acids grouped nicely from trophic amino acids across samples, and the bulk skin $\delta^{15}\text{N}$ values reflected a composite of both groups. For each group of amino acids, there was a median $\delta^{15}\text{N}$ spread of about 7‰. Among the source amino acids, the largest spread was between lysine (low) and tyrosine (high), and among the trophic amino acids the largest spread was between aspartic acid (low) and alanine (high). No amino acids appeared to be intermediate. Regardless of the robustness of this study's amino acid isotope data, across taxa, to date the amino acids that seem to most reliably estimate TPs indicative of ecological expectations are phenylalanine and glutamic acid (Chikaraishi et al., 2009). Quantification of amino acid-specific incorporation rates and trophic discrimination for multiple taxa and tissues types would provide clarity as to which approach (two-amino acid vs. weight mean) is most reliable.

Costa Rica Dome—A Unique Food Web?

There was one exception to the trophic position consistency for olive ridleys: on the Costa Rica Dome, individuals fed at a 0.36 median level higher than in any other sub-region (Figure 4). As stated above, this conclusion can be drawn from estimating TPs using $\delta^{15}\text{N}_{\text{Glu}} - \delta^{15}\text{N}_{\text{Phe}}$, however it does not hold when using weighted means. While the former result seems reasonable, as many high-level consumers (cetaceans, seabirds, tuna) consistently aggregate to feed on the Costa Rica Dome's standing stocks of zooplankton and other prey (Reilly and Thayer, 1990; Sissenwine et al., 1998; Ballance et al., 2006), this discrepancy highlights the need to continue to advance the application of stable isotopes to understand sea turtle ecology.

To our knowledge, all AA-CSIA studies of wide-ranging consumers, both generalists and specialists, find the same TP consistency that we found for adult olive ridleys. For example, TPs of tuna, adult leatherbacks, lanternfishes, dragonfishes, and zooplankton do not change across ocean basins (Popp et al., 2007; Olson et al., 2010; Choy et al., 2012; Seminoff et al., 2012; Hetherington et al., 2017). This underscores the uniqueness of detecting a potential trophic shift on the Costa Rica Dome. Such a shift could be a reflection of a diet of a slightly wider variety of

prey items, or a diet of a relatively larger proportion of high order prey (see Supplementary Table 5).

The benefits of using stable isotopes are many; the analyses can be cost effective and integrated with other techniques like telemetry and genetics. However, limitations can cloud our ability to interpret results and/or can produce conflicting results, as in this case. Limitations include the lack of accurate and species-specific discrimination factors, and our understanding of what might drive variation across groups of amino acids (source, trophic). The approach used to estimate TP seems to matter, however more research on this is needed for sea turtles.

Conservation Implications

Olive ridley subpopulations in the eastern Pacific are genetically distinct from subpopulations in the western Pacific breeding population (Bowen et al., 1997; Shanker et al., 2004; Wallace et al., 2010; Jensen et al., 2013). While individuals have the ability to migrate >1,500 km, as nomads they do not have consistent home ranges (Pandav and Choudhury, 1998; Polovina et al., 2003; Whiting et al., 2007; Plotkin, 2010). Rather, they continuously forage opportunistically on a wide variety of prey. The empirical characterization of open ocean foraging ecology via stable isotope analyses has provided insight into why this turtle species has been successful compared to other, coastal species. We believe that foraging plasticity combined with relatively fast generation time allowed olive ridleys to recover quickly in the eastern Pacific, compared to other depleted turtle species, after near extinction from over-harvest in the 1960s (Abreu-Grobois and Plotkin, 2008; Plotkin et al., 2012).

The olive ridley's generalist foraging strategy is advantageous for survivorship and suggests that they may be resilient to disturbance (Heppell et al., 2005; Plotkin, 2010; Clavel et al., 2011). However, they have other biological characteristics such as low metabolism, narrow thermal niche and nesting dichotomy that may make them vulnerable to environmental change unless they are able to adapt on relevant time scales (Merchant-Larios et al., 1997; Lutz et al., 2003; Polovina et al., 2003; McMahon and Hays, 2006; Plotkin et al., 2012). Climate change may be particularly problematic for sea turtles given population sex-ratios are temperature-dependent, and they nest on beaches that may be impacted by sea level rise (Hawkes et al., 2009). As ocean temperature, chemistry, circulation, and species distributions are changing with climate (Doney et al., 2012), it is a critical time to broaden our understanding of phenology, demography, trophic roles and function of mobile consumers so that vulnerable species and their oceanic habitats can be better managed in the face of environmental variability (Micheli, 1999; Edwards and Richardson, 2004).

Since olive ridleys encounter spatially-explicit resources and threats, innovative management approaches may be necessary to achieve modern conservation objectives. A promising dynamic ecosystem-based management approach would be to predict areas where suitable foraging habitat overlaps with other areas of interest, or the presence of threats (e.g., fishing) (Howell et al., 2008; Maxwell et al., 2014, 2015; Scales et al., 2014). Given their enormous eastern Pacific range across swaths of unproductive warm waters, where they feed largely on things humans are not

yet interested in harvesting, strategic conservation measures (e.g., protecting key nesting beaches) may enable olive ridleys to be a global warming winner.

CONCLUSIONS

This study demonstrates the value of large-scale, in-water research across different foraging habitats to understand the foraging ecology of highly migratory marine species, such as the olive ridley sea turtle. As the frequency and durations of costly research cruises decrease, the value of taking advantage of research platforms of opportunity to study oceanic species like olive ridleys increases. Further, we have presented yet another example of how stable isotope analyses provide a relatively non-invasive and cost-effective analytical approach to describe the trophic ecology of a cryptic, mobile species with a large oceanic distribution. We used bulk tissue and compound-specific analyses to develop the hypotheses that in the ETP, the trophic position of the omnivorous olive ridley sea turtle remains constant with ontogenesis and sex.

We conclude that olive ridley turtles exploit persistent but dynamic oceanographic features as distinct food webs. Using AA-CSIA, we did not detect a shift in the trophic position of adult olive ridleys across any of the identified sub-regions using the weighted mean approach, indicating their energetic requirements are comparably met throughout their range. The isotopic data generated in this study adds to the growing body of work describing stable isotope baseline data for marine organisms in the eastern Pacific Ocean (Arthur et al., 2008; Olson et al., 2010; Ruiz-Cooley and Gerrodette, 2012; Seminoff et al., 2012). A natural future direction would be to estimate marine isoscapes across taxa and trophic levels to provide a systematic framework for stable isotope ecological applications, as well as empirical studies of trophic dynamics (Somes et al., 2010; Ceriani et al., 2014; Vander Zanden et al., 2015; Magozzi et al., 2017; Kurlle and McWhorter, 2017). A central repository of stable isotope data for sea turtles would support the advancement of this field and reduce duplication of efforts (Pauli, 2017). Refinement of species-specific diet-tissue $\delta^{15}\text{N}$ values and other parameters will minimize assumptions, improve interpretation, and aid our understanding of oceanic food webs.

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ETHICS STATEMENT

Peruvian research and protocol were reviewed and approved by the Duke University Ethics Committee and all necessary permits were obtained from Peruvian authorities (Peruvian Government Authorization No. 177-2008-IRENA-IFFS-DCB).

AUTHOR CONTRIBUTIONS

LP, RP, and JS conceived of and designed this study. LP, BP, KA, and SK completed the laboratory analysis. LP completed the quantitative analysis. LP and JS wrote the paper with input from all authors. LP, BP, SG, and JS provided financial support.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2017.00348/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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