The Effects of Climatic Variability on the Feeding Ecology of the Scalloped Hammerhead Shark (*Sphyrna lewini*) in the Tropical Eastern Pacific

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Climatic variability changes ocean productivity and generates systematic cascading effects in marine food webs. Studying the feeding ecology of top predators, such as sharks, can provide insights into the overall health of marine ecosystems. We conducted a 4-year study to evaluate seasonal and inter-annual trophic variations and their relationship with El Niño Southern Oscillation (ENSO) on the largest aggregation of scalloped hammerhead shark (*Sphyrna lewini*) in the Tropical Eastern Pacific (TEP). We used $\delta^{13}C$ and $\delta^{15}N$ signatures to gain a better understanding of hammerheads' feeding strategies as well as variations of their isotopic niche. Our results suggest that the hammerhead sharks in the Galapagos Marine Reserve respond to climatic fluctuations, with La Niña event potentially benefiting their trophic needs as the overall marine productivity increased in the region. This work is the first of its kind in the TEP and provides insights on how climate variability influences the feeding ecology of this critically endangered species. It also highlights the need to incorporate climate-related conservation strategies into the management of this species since ENSO events become more frequent and intense in the face of climate change.

Keywords: foraging strategies, δ13C and δ15N signatures, isotopic niche, ENSO (El Nino/Southern Oscillation), Galapagos Islands, Tropical Eastern Pacific

INTRODUCTION

The world's oceans have been under the influence of natural climatic variability for millennia (Walthers et al., 2002; Hoegh-Guldberg and Bruno, 2010), driving marine populations to develop coping adaptations to persist in this environment (Walthers et al., 2002; Sydeman et al., 2015). However, natural climatic variability is now exacerbated by the impacts of human-induced climate change on the world's oceans as it causes natural anomalous events to become more frequent and intense, stretching the capacity of marine species to adapt (Barnett et al., 2005; Pachauri and Reisinger, 2008). Human-induced climate change amplifies natural climatic events, such as El Niño Southern Oscillation (ENSO) cycles and its variations between warm (El Niño) and cold (La Niña) conditions (Cai et al., 2014; Wang et al., 2017), causing large-scale global impacts in marine ecosystems (Hoegh-Guldberg and Bruno, 2010; Doney et al., 2011).

In the Tropical Eastern Pacific (TEP), El Niño event results in increased sea surface temperature (SST) and stratification of the water column that in turn limits ocean productivity (Cai et al., 2014). Some documented effects of these events include sharp population declines of marine species (Wikelski and Thom, 2000; Edgar et al., 2010; Riofrío-Lazo et al., 2017; Páez-Rosas et al., 2021) and increased incidence of diseases (Lamb et al., 2018; Santana-Piñeros et al., 2020). Furthermore, El Niño event changes the abundance of living resources and shifts their distribution toward better quality habitats (Cheung et al., 2010), and can also negatively affect the survival of higher trophic level species (Barber and Chávez, 1986; Sydeman et al., 2015). For instance, during extreme El Niño events, the biomass of key forage groups, such as small fish and cephalopods, tends to decrease (Griffiths et al., 2010), creating a bottom-up effect that alters the demography of top predators and their feeding behavior (Robinson et al., 2009).

The recurrence of the El Niño event reduces the length and frequency of La Niña events, disrupting cold-water currents and upwellings (Chen and Dool, 1999), having significant impacts on marine predators. This has been previously documented for seabirds and marine mammals of the TEP (Sydeman et al., 2012). Particularly, in the Galapagos Islands, El Niño directly affects the reproductive and foraging success of endemic species, such as penguins, flightless cormorants, and sea lions (Valle et al., 1987; Nims et al., 2008; Páez-Rosas et al., 2012). Considering that climate change is predicted to continue increasing the magnitude and frequency of climatic events such as El Niño (Wang and Fiedler, 2006; Collins et al., 2010; Cai et al., 2014), studying the impact on the structure of marine food web and the feeding ecology of their top predators is thus key to understand ecosystem function and to develop conservation strategies.

Top predatory sharks sit at the top of marine food webs, regulating the size and dynamics of communities below them (Myers et al., 2007) and maintaining marine ecosystems balanced (Dulvy et al., 2008; Heupel et al., 2014). However, the fast depletion of sharks, mainly due to overfishing (Casini et al., 2009; Pacoureau et al., 2021), has produced negative cascading effects on marine food webs that affect the functioning of the ecosystem and its biodiversity (Heithaus et al., 2008; Baum and Worm, 2009; Estes et al., 2011). The synergistic effects of anthropogenic activities and natural climatic variability can result in a lack of top-down control exerted by top predators, ultimately degrading global marine ecosystems (Stevens et al., 2000; Dulvy et al., 2008; Ferretti et al., 2010). Presently, only few well-protected or very remote locations still harbor relative pristine food webs where sharks are abundant (Ferretti et al., 2018). The Galapagos Marine Reserve (GMR) has some of the largest global shark aggregations (Salinas-de-León et al., 2016; Acuña-Marrero et al., 2018) and is located at the epicenter of ENSO cycles, being thus an ideal natural laboratory to study the impact of climatic variability on marine ecosystems (Edgar et al., 2010; Salinas-de-León et al., 2020).

Previous studies on the feeding ecology of top predators at the GMR have been conducted mainly on seabirds and marine mammals (Awkerman et al., 2007; Paez-Rosas et al., 2017; Jimenez-Uzcategui et al., 2019; Schwarz et al., 2021), with

some studies focusing on teleost fish (Baque-Menoscal et al., 2012; Páez-Rosas et al., 2020a) and sharks (Páez-Rosas et al., 2018a; Salinas-de-León et al., 2019). These studies have used a combination of gut content and/or stable isotope analysis (SIA), with most of them focusing on single-year sampling, with just two published studies that included multi-year sampling: Whitehead et al. (1989) studied the feeding success of sperm whales (*Physeter macrocephalus*) based on scat analysis before and during the 1987 El Niño year, documenting a similar diet between both years, but revealing an apparent lower feeding success associated with increase SST during the El Niño event. More recently, Páez-Rosas et al. (2020b) revealed that Galapagos sea lions (*Zalophus wollebaeki*) exhibited trophic flexibility during the 2015 El Niño event by reducing the foraging niche and increasing the consumption of prey from greater depths. In this regard, SIA offers a methodological approach that allows to infer food source in marine predators, based on the principle that the isotopic composition of a prey item is retained in the predator's tissues (Hobson et al., 1995). This technique is a powerful tool to validate shark movements, habitat preferences, and ecological niche size over specific periods (Carlisle et al., 2012; Tamburin et al., 2019; Trueman and Glew, 2019).

The northern Galápagos islands of Darwin and Wolf are home to one of the last large aggregations of the critically endangered scalloped hammerhead shark (*Sphyrna lewini*) (Salinas-de-León et al., 2016), and these large groups are mostly composed of adult females (Klimley, 1987), some seemingly pregnant during the first months of the year (Ketchum et al., 2014). Scalloped hammerhead sharks are known to migrate between the oceanic islands of the TEP (Bessudo et al., 2011; Ketchum et al., 2014; Nalesso et al., 2019), and females have been speculated to migrate to coastal waters to give birth to their young after March (Salinas-de-León et al., 2017), when the presence of newborns has been documented in nursery areas within continental coastlines (Robles et al., 2015; Zanella et al., 2019). Despite scalloped hammerhead sharks being enlisted as Critically Endangered in the IUCN red list of endangered species due to the continuous global population declines, including across marine protected areas of the TEP (White et al., 2015; Peñaherrera-Palma et al., 2018), we still have a limited understanding about their basic life history, including their trophic ecology. In this study, we determine the $\delta^{13}C$ and $\delta^{15}N$ signatures of the critically endangered scalloped hammerhead shark (*Sphyrna lewini*) to assess seasonal and inter-annual trophic variability during a 4-year period, in which ENSO cycles occurred, with the purpose of understand how these conditions affect the feeding ecology of this species.

MATERIALS AND METHODS

Ethics Statement

This investigation was conducted under Galapagos National Park Directorate (GNPD) research permits PC-28-16, PC-27-17, PC-46-18, and PC-53-19 issued to Dr. Pelayo Salinas de León of the Charles Darwin Foundation (CDF), and research permits PC-24-17, PC-69-18, and PC-86-19 issued to

Dr. Diego Páez-Rosas from the University San Francisco de Quito (USFQ). Biopsy samples were collected *in situ* from free-swimming specimens following animal ethics protocols by the GNPD and CDF.
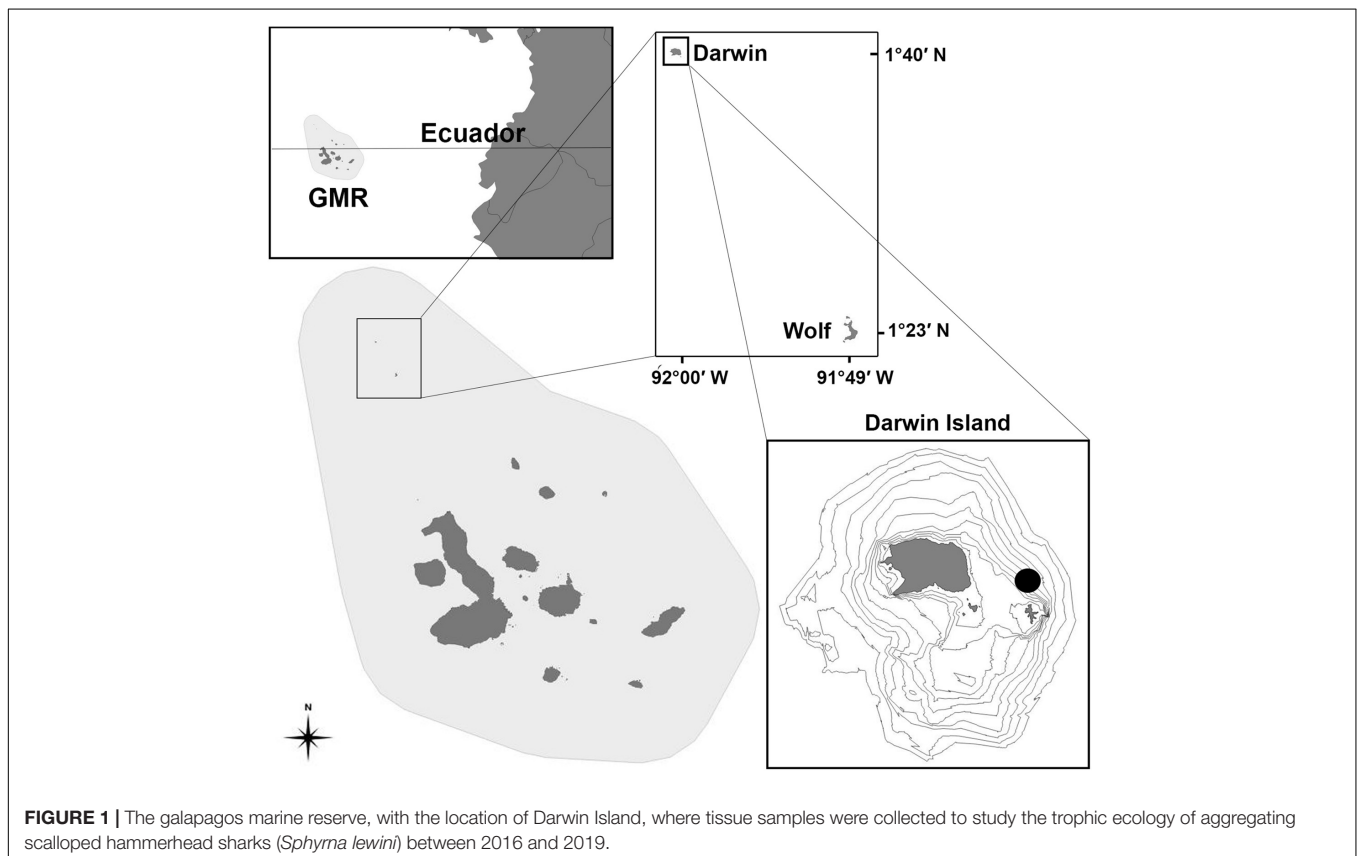
Study Site

The Galapagos Islands lie at the epicenter of the thermal anomalies that occur during ENSO cycles (Wellington et al., 2001). The oceanographic setting in this region is unique, and it is responsible for the colonization and evolution of various species whose ecological characteristics are not considered otherwise typical for a low-latitude ecosystem (Wikelski and Thom, 2000; Edgar et al., 2004). During El Niño, cold upwellings disappear resulting in a deeper thermocline and the warming of surface waters and lowering of productivity, which can last for many months up to a year (Victor et al., 2001; Wellington et al., 2001). The opposite effect occurs when La Niña brings cool Peruvian waters creating cold-water refuges and enhancing ocean productivity (Chavez et al., 2003). This recurrent climate variation serves as an opportunity for Galapagos species to adapt to these transitions, but it makes them prone to rapid population declines and risk of extinction when facing extreme ENSO cycles, such as the 1982–1983 and 1997–1998 El Niño events (Edgar et al., 2010).

Darwin and Wolf islands are located at the far northern region of the GMR (**Figure 1**), where the warm Panama Current flows in a south-western direction causing higher temperatures around these islands than in the rest of the archipelago (Banks et al., 2009). As a result, there are two defined seasons at Darwin and Wolf: the warm season that occurs from January to June and the cool season from July to December with an overall average temperature of 24°C (Acuña-Marrero et al., 2014). Moreover, these remote islands with a surface area of less than 2 km^2 each and located approximately 36 km apart (Harpp and Geist, 2002) are world-renowned hotspots for harboring large aggregations of marine megafauna, such as the critically endangered scalloped hammerhead (Ruiz et al., 2016; Salinas-de-León et al., 2016).

Sampling

Sample collection took place from 2016 to 2019 during the cool (July–December) season, and in 2019 during the warm (January–June) and cool seasons. A total of 139 tissue biopsies were collected from adult (>2.25 m TL) female scalloped hammerhead sharks. Lengths were estimated visually by experienced divers in 25 cm bins (i.e., 200–225–250–275) and based on previous stereo-video measurements (Klimley and Brown, 1983; Salinas-de-León et al., 2016). We obtained skin tissue from free-swimming scalloped hammerhead sharks by freediving among the large aggregations that occur at Darwin Island. We used a modified Hawaiian sling with a biopsy dart (Pneu-dart, Inc., United States) at the top end to collect 1 cm^3 of tissue. We targeted the base of the dorsal fin by releasing the Hawaiian sling from a perpendicular angle to the hammerhead at an approximate distance of 1 m. The skin samples were removed from the tip of

FIGURE 1 | The galapagos marine reserve, with the location of Darwin Island, where tissue samples were collected to study the trophic ecology of aggregating scalloped hammerhead sharks (*Sphyrna lewini*) between 2016 and 2019.

the biopsy dart, placed in Eppendorf tubes with 70% Ethanol, and stored at −20°C.

Stable Isotope Analysis

Tissue samples were rinsed with deionized water to eliminate residues that could alter their isotopic signature and placed in glass vials previously treated for 24 h with a chromic acid mixture prepared from sulfuric acid and potassium dichromate. Then, sampled were dried in a desiccator at 80°C for 12 h to remove all moisture. A lipid-extracted protocol was applied via three sequential 24 h soaks in a 2:1 chloroform: methanol solvent solution, then rinsed with deionized water, and dried again. This process was applied because lipids are rich in ^{12}C, which, in sufficiently large quantities, could negatively skew the ^{13}C isotopic signature (Post et al., 2007). All samples were homogenized with an agate mortar to obtain a very fine powder, of which 1 mg was weighed by means of an analytical microbalance with a precision of 0.001 mg and transferred into a tin capsule.

$\delta^{13}C$ and $\delta^{15}N$ signatures were determined by a PDZ Europa 20-20 continuous-flow isotope-ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom) at the Stable Isotope Facility of the University of California at Davis (Davis, CA, United States). The results were expressed in parts per thousand (‰) using the equation: $\delta_X = [(R_{sample}/R_{standard})−1] *1,000$, where δ_X is the heavy isotope and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and the standard, respectively. The internationally accepted standard for carbon is Vienna-Pee Dee Belemnite limestone (V-PDB) and for nitrogen is atmospheric N_2. Within-run analytical precision of $\pm 0.2‰$ for both $\delta^{13}C$ and $\delta^{15}N$ values was calculated by using two proteinaceous internal reference materials. We also measured the weight percent carbon and nitrogen concentration (C/N) of each sample, which was an indicator of lipid content (Logan et al., 2008).

Statistical Analysis

Data were tested for normality and homoscedasticity using the Shapiro–Wilk and Levene test, respectively. The statistical significance of differences in $\delta^{13}C$ and $\delta^{15}N$ values was determined using parametric or non-parametric tests, along posteriori multiple comparison tests. Significance is reported in terms of $p < 0.05$. All statistical analyses were performed in R language. The Bayesian standard ellipse areas (SEA) were used to estimate isotopic niche width and overlap among hammerhead shark samples collected in different years using the package SIBER (Stable Isotope Bayesian Ellipses in statistical software R) (Jackson et al., 2011). This Bayesian method provides a measure of the isotopic niche area at the population level, expressed as the SEA in units of area (‰^{2}) and contains 95% of the data for each group. We used Monte Carlo simulations to correct the bivariate ellipses ($\delta^{13}C$ and $\delta^{15}N$) surrounding the data points in the 95% confidence interval for the distributions of both stable isotopes (Jackson et al., 2011). These corrected standard ellipse areas (SEAc) represent the isotopic niche width and the overlap parameters. The magnitude of the isotopic overlap (‰^{2}) among years was estimated using

the estimations of the ellipses via maximum-likelihood methods (Jackson et al., 2011).

The ENSO effects on the isotopic values were examined by correlation analysis between the Southern Oscillation Index (SOI 1 + 2) and the isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for individual sharks on each year. These correlations were assessed by Pearson correlation using R program. The SOI is the average of the monthly sea surface temperature (SST) anomalies in time series data relative to historical climatological values (i.e., 1971–2000) in regions 1 + 2 (data obtained from www.ncdc.noaa.gov/teleconnections/enso/indicators/soi). Although there is not much information published about the tissue turnover rate of shark skin, it has been suggested to be between that of muscle (> 1 year) and liver (around 6 months) (MacNeil et al., 2005; Carlisle et al., 2012; Kim and Koch, 2012; Li et al., 2016). Therefore, we have used the average of 6 months of SOI 1 + 2 values in each year for this analysis.

The effects of other environmental variables were also analyzed, such as SST and chlorophyll-a concentration (mg*m^3) were examined in the region. The count data series were from 2016 to 2019 around Darwin and Wolf islands. SST and chlorophyll-a values were obtained from satellite images taken at a resolution of 4.4 km [Dataset: SST, POES AVHRR, GAC, Global, Day and Night (Monthly Composite)] and are available on the ERDDAP data server from the NOAA website[1]. Pearson's rank correlation coefficient was used to analyze the relationship between $\delta^{13}C$ and $\delta^{15}N$ signatures and the environmental variables.

RESULTS

C/N ratios in the tissue of hammerhead sharks ranged from 2.7 to 3.6: within the established range for a predator's diet (Logan et al., 2008). Mean estimated $\delta^{13}C$ and $\delta^{15}N$ values during the warm season were −13.41 ± 0.60‰ and 12.29 ± 0.56‰, respectively; and during cold season, they were −13.56 ± 0.58‰ and 12.16 ± 0.68‰, respectively (**Table 1**). There were no differences among $\delta^{13}C$ (Mann–Whitney U-test, $p = 0.261$) and $\delta^{15}N$ values (Mann–Whitney U-test, $p = 0.238$) for the year

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[1]http://coastwatch.pfeg.noaa.gov/erddap

TABLE 1 | Summary of tissue samples collected for isotopic analysis on scalloped hammerhead sharks (*Sphyrna lewini*) at Darwin Island, Galapagos Marine Reserve.

Season	n	δ ^{13}C (‰)	δ ^{15}N (‰)	C/N
August 2016	30	−13.39±0.60 (−12.38−14.53)	12.32±0.49 (11.39−13.58)	2.77±0.16 (2.62−3.23)
December 2016	30	−13.48±0.55 (−12.57−14.49)	12.20±0.41 (11.69−13.19)	2.74±0.14 (2.64−3.42)
August 2017	30	−13.49±0.48 (−12.70−14.52)	12.32±0.60 (11.23−13.72)	2.78±0.13 (2.62−3.23)
January 2018	8	−13.02±0.45 (−12.24−13.49)	12.59±0.14 (12.40−12.80)	2.85±0.06 (2.79−2.94)
February 2019	7	−13.35±0.66 (−12.80−14.49)	12.38±0.73 (11.50−13.52)	2.85±0.15 (2.67−3.08)
October 2019	34	−13.75±0.56 (−12.81−14.93)	12.01±0.87 (10.40−15.05)	3.10±0.25 (2.77−3.64)

2019 seasonal comparison (**Table 1**). We detected significant inter-annual variations in $\delta^{13}C$ and $\delta^{15}N$ values (Kruskal–Wallis test, $p = 0.028$ and 0.022, respectively), with values for 2018 differing from those of 2019 (multiple comparisons of median ranks, $p < 0.05$) (**Table 2**). The comparison of $\delta^{13}C$ and $\delta^{15}N$ values between years showed that hammerhead sharks in 2018 (mean -13.02 and $12.59‰$, respectively) maintained an inshore strategy and higher trophic level than in other years (**Table 1** and **Figure 2**).

Corrected standard ellipse area (SEAc) showed that hammerhead sharks in warm and cold seasons could be exploiting similar habitats (**Figure 3**). Mean SEA for each year and proportion of SEAc among the 4 years are shown in **Table 3**. The Bayesian ellipse of 2018 (SEAc = $0.29‰$, 95% credibility interval of $0.05–0.53‰$) and 2019 (SEAc = $1.71‰$, 95% credibility interval of $1.09–3.33‰$) had a low overlap (**Figure 4**), confirming different resource use patterns for these years. In contrast, the Bayesian ellipse of 2016 (SEAc = $0.83‰$, 95% credibility interval of $0.42–1.24‰$) and 2017 (SEAc = $0.91‰$, 95% credibility interval of $0.46–1.36‰$) are overlapped in large part with the ellipse of 2019. The overlap area (0.12) of the Bayesian ellipses from 2018 and 2019 represented the 38.1% of the ellipse surface of the former and the 4.5% of the ellipse surface of the latter. Conversely, a significant isotopic overlap was observed between 2016 and 2017 (0.61), accompanied by a high isotopic overlap between 2019 vs. 2016 and 2017 (0.46 and 0.48, respectively), showing a similar use of resources in these years. However, the Bayesian ellipse of 2019 was larger at $\delta^{13}C$ and encompassed most of the Bayesian ellipses of other years (**Figure 5**).

The relationship between the $\delta^{13}C$ and $\delta^{15}N$ values of hammerhead sharks in each year with the SOI 1 + 2 is shown in **Figure 4**. Overall, there was an increase in the mean $\delta^{13}C$ and $\delta^{15}N$ that coincided with the La Niña event of 2018. During cold year, the $\delta^{13}C$ values increased $0.52‰$, while $\delta^{15}N$ values increased $0.37‰$ in relation to the average of other years. A negative but no significant correlation was found between the ENSO and the $\delta^{13}C$ and $\delta^{15}N$ values of hammerhead sharks (Pearson's correlation, $\delta^{13}C$: $r = -0.74$, $p = 0.259$ and $\delta^{15}N$: $r = -0.78$, $p = 0.241$). There were no significant relationships between the environmental variables and $\delta^{13}C$ and $\delta^{15}N$ signatures in any years (**Table 4**). However, both isotopic signatures showed a slight positive trend with SST and chlorophyll-a values in 2018 year.

TABLE 2 | Differences in $\delta^{13}C$ (above diagonal) and $\delta^{15}N$ (below diagonal) values in females scalloped hammerhead sharks in the GMR.

	2016	2017	2018	2019
$\delta^{13}C$ (‰)				
2016	X	0.936	**0.033**	**0.041**
2017	1	X	**0.029**	**0.049**
2018	0.118	0.409	X	**0.001**
2019	1	0.286	**0.011**	X

Significant variations (Kruskal–Wallis multiple comparisons test, $p < 0.05$) are shown in bold.
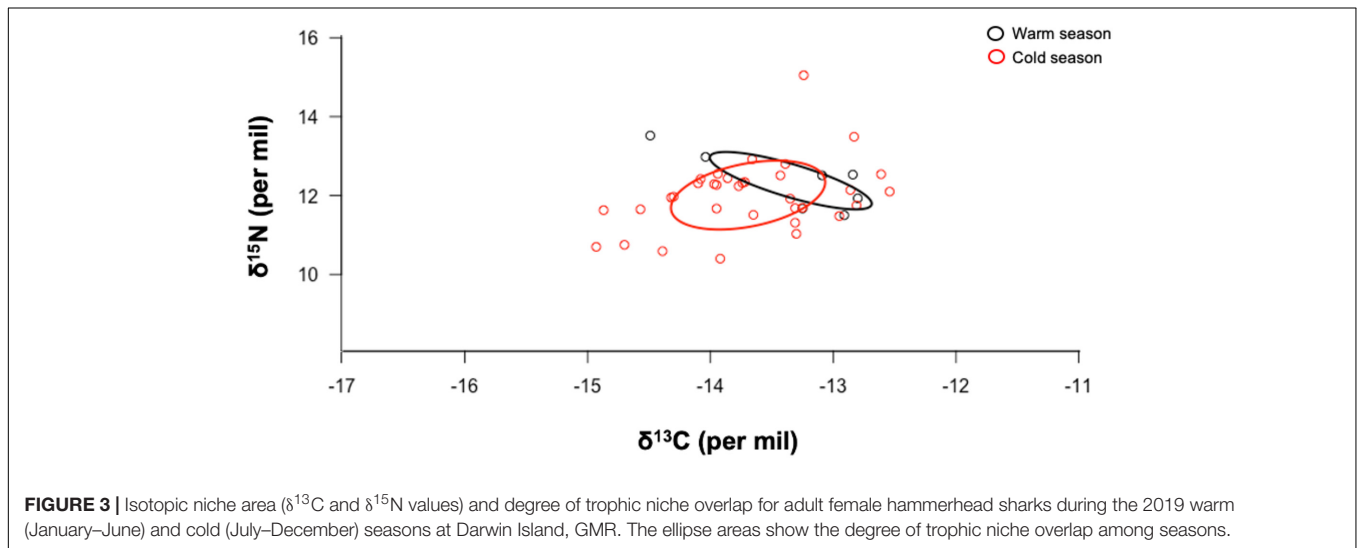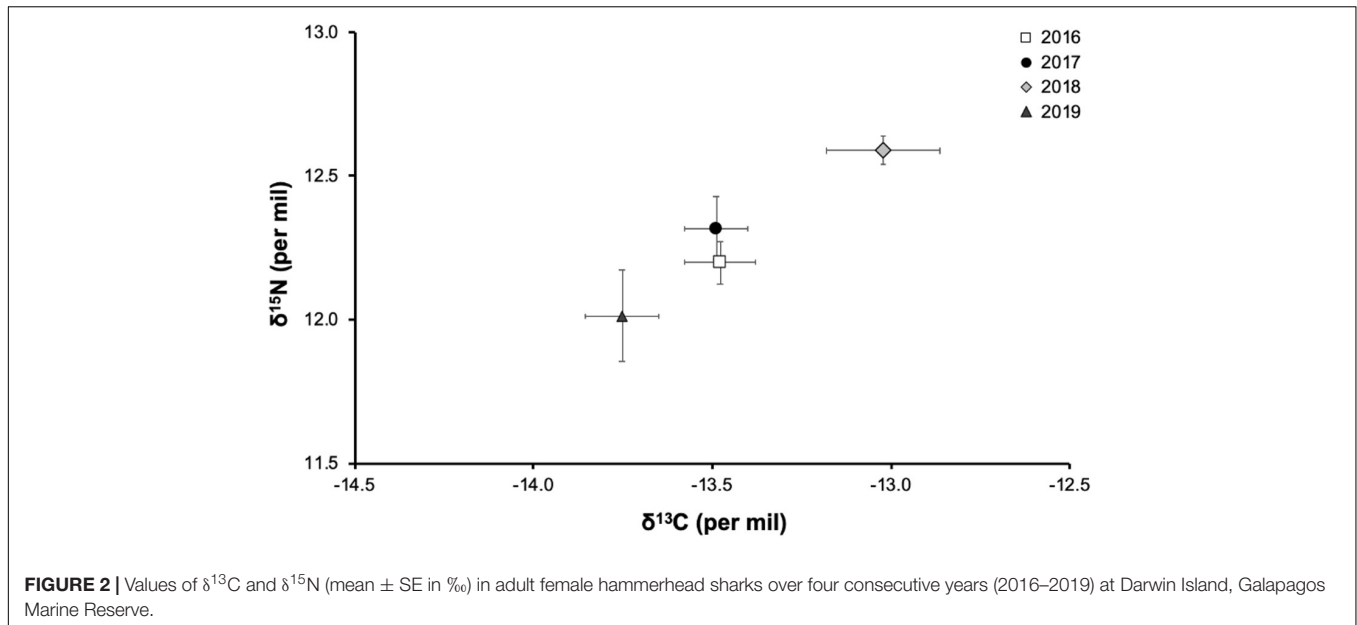
DISCUSSION

This is the first study of its kind for a top predatory shark, providing insights on how their feeding ecology varies under the influence of climatic variability in the TEP. Hammerheads showed a response on their feeding behavior to climatic fluctuations, with La Niña potentially benefiting their foraging activities as a result of the increased productivity in the region (Barber et al., 1996; Behrenfeld et al., 2006). Although our study did not include the peak (August–February) of the 2015–2016 El Niño event, our data suggest that during warmer years, hammerheads' nutritional efficiency may diminish across the region and hammerhead trophic niche may widen as they possibly adopt a more generalist feeding behavior, which might involve an increase on the use of offshore environments as feeding grounds. However, our results need to be interpreted with caution since with the present dataset, it is not possible to clearly distinguish whether these interannual changes may reflect changes in prey availability, foraging strategy, location, or a combination of the above.

El Niño Southern Oscillation Effects

NOAA reports indicate that 2018 was a strong La Niña year that brought enriched cold-water currents from southern Peru to the equatorial zone, causing SST to remain 1°C anomaly cooler than average (Páez-Rosas et al., 2018b). The warm to cold transition that occurs during ENSO cycles greatly benefits the TEP providing a negative feedback that pushes warm waters back to the western Pacific allowing the entire system to recharge its primary productivity by enhancing upwellings (Wang and Fiedler, 2006). With these productive waters, inshore prey with high $\delta^{13}C$ valued become more abundant, such as anchovies and mackerels that have been found to be dominant in pelagic sharks' stomach contents during cool-water periods (Preti et al., 2004; Rosa and Seibel, 2008). Behrenfeld et al. (2001) demonstrated that during the 1999–2000 La Niña year, surface chlorophyll concentration significantly increased in the Pacific, and this was reflected by a boost in phytoplankton biomass in the TEP.

The 1999–2000 La Niña year also featured localized upwellings producing coastal krill aggregations off Monterey Bay, California attracting large concentrations of cetaceans around the area, that benefitted of these prey distribution shifts (Benson et al., 2002). Similarly, in Peru, main pelagic resources like anchovies (*Engraulis ringens*) have being recorded during La Niña cold conditions as they become highly abundant and show a more localized distribution aggregating in coastal areas (Ñiquen and Bouchon, 2004). This has caused the pelagic fisheries off southern Peru, during La Niña years, to have higher catch per unit effort rates of blue sharks (*Prionace glauca*), which in turn has been linked to an increase in the abundance of prey in areas where blue sharks feed (Adams et al., 2016). Further research is required to elucidate how the trophic niche of these predators interacts with shark fisheries around the GMR and across the TEP (Martínez-Ortiz et al., 2015).

Our results suggest that the 2018 La Niña might have likely boosted the availability of prey items, which in turn might have resulted in changes on the foraging strategy and trophic

FIGURE 2 | Values of δ^{13}C and δ^{15}N (mean $\pm$ SE in ‰) in adult female hammerhead sharks over four consecutive years (2016–2019) at Darwin Island, Galapagos Marine Reserve.

FIGURE 3 | Isotopic niche area (δ^{13}C and δ^{15}N values) and degree of trophic niche overlap for adult female hammerhead sharks during the 2019 warm (January–June) and cold (July–December) seasons at Darwin Island, GMR. The ellipse areas show the degree of trophic niche overlap among seasons.

niche size of hammerheads, as well as enriched in the δ^{13}C and δ^{15}N. For example, diet studies in the thresher shark (*Alopias vulpinus*) off the Pacific coast of North America revealed

TABLE 3 | Basic standard ellipse area (SEA) and standard ellipse area correction (SEAc) values as an approximation of the trophic niche breadth (TNB).

Years	SEA	SEAc	TNB
2016	0.813	0.827	2.993
2017	0.850	0.912	3.544
2018	0.196	0.288	1.269
2019	1.663	1.663	6.822

The values were obtained using stable isotope Bayesian ellipses of samples from skim tissues of females scalloped hammerhead sharks in the Galapagos Marine Reserve.

that during cool water La Niña periods sharks displayed a narrower trophic spectrum and the prevalence of market squid (*Loligo opalescens*) in their diet increased significantly (Preti et al., 2004). It could also be the case that hammerheads benefit from the increase of prey items such as demersal fish and jumbo squid (*Dosidicus gigas*), species that are highly consumed by the scalloped hammerhead in other locations across the TEP (Galván-Magaña et al., 2013; Torres-Rojas et al., 2015). Other potential explanation for the changes in isotopic results observe in this study might be the fluctuations in isotopic composition of the prey due to shifts in the marine productivity and isotopic baseline, and further research is required to elucidate this.

During 2015 and early 2016, SST values increased in the region due to the presence of a strong El Niño (Penalba and Rivera, 2016; Lamb et al., 2018) resulting in lower δ^{13}C and δ^{15}N

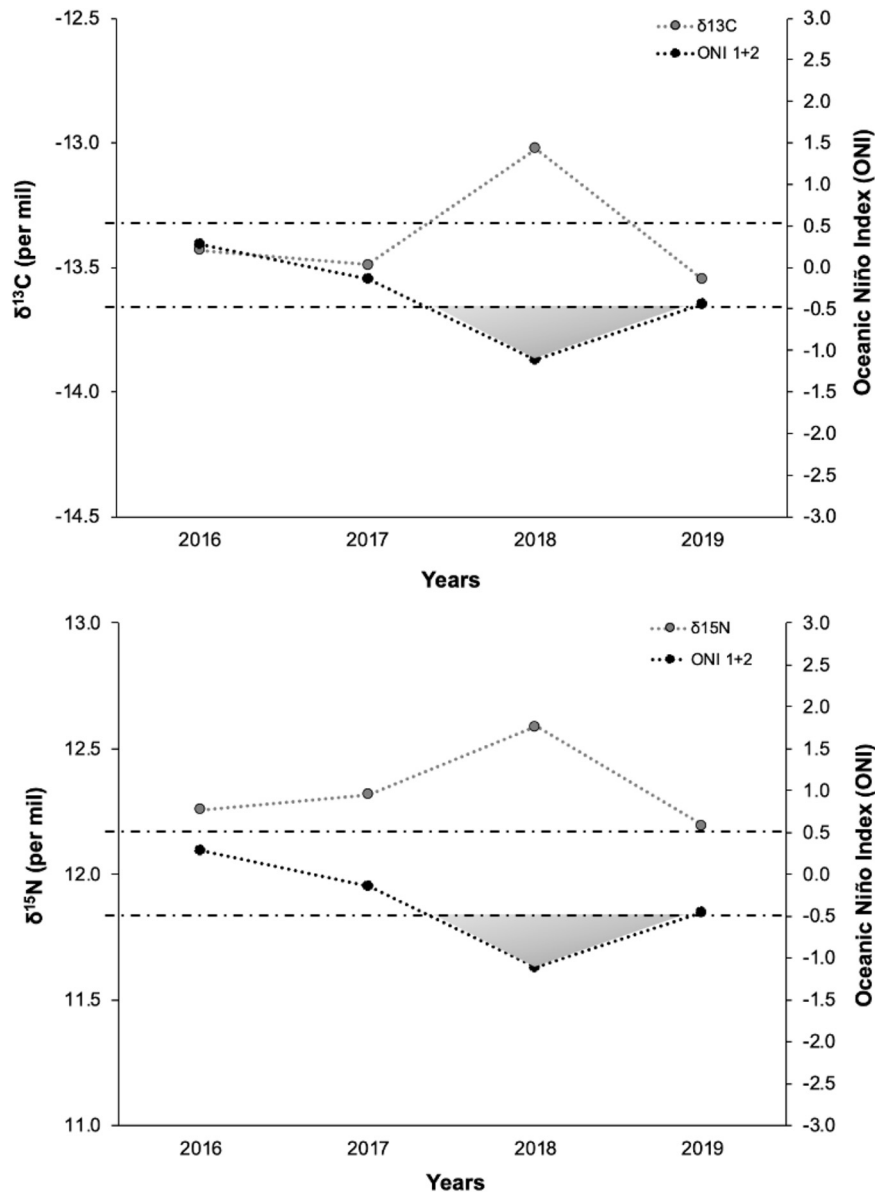**FIGURE 4 |** Mean (± SD) δ^{13}C and δ^{15}N values of adult female hammerhead sharks in relation to the Oceanic Niño Index 1 + 2. The values of the ONI 1 + 2 plotted for each year correspond to the mean of the 6 months for each season. The ONI 1 + 2 indicates the intensity of El Niño (positive values) and La Niña (negative values) events that can be considered weak (with a 0.5–0.9 SST anomaly), moderate (1.0–1.4), or strong (≥ 1.5).

signatures. These values might have decreased due to the lack of δ^{15}N rich demersal prey, which in turn might have caused foraging strategies to shift toward consuming available epipelagic prey, lower in δ^{15}N content (Torres-Rojas et al., 2015). Although El Niño years result in a decreased in ocean productivity in the eastern Pacific (Barber et al., 1996), these have also been linked to increases in pelagic diversity in this region (Ñiquen and Bouchon, 2004). Hence, the diet of some pelagic sharks becomes more varied during El Niño years of the pacific coast of North America (Preti et al., 2004, 2012). Therefore, in less favorable environments, top predators have shown to become opportunistic and diversify their diet (Preti et al., 2004), foraging

sub-optimally as nutrient depleted prey becomes more available (Preti et al., 2012; Munroe et al., 2014).

Alterations in climatic events and rising SST can also create heat waves that affect the distribution and abundance of species (Wernberg et al., 2013). The effects can be direct through physiological stress and indirect through altered predator–prey interactions (Rosa and Seibel, 2008; Wernberg et al., 2013). Both direct and indirect heat waves effects have been previously documented on sharks (Myers et al., 2007; Pistevos et al., 2015). It is predicted that by the end of the twenty-first century, the TEP will become 2–3°C warmer due to the weakening of tropical circulations (Pachauri and Reisinger, 2008), and as a result,
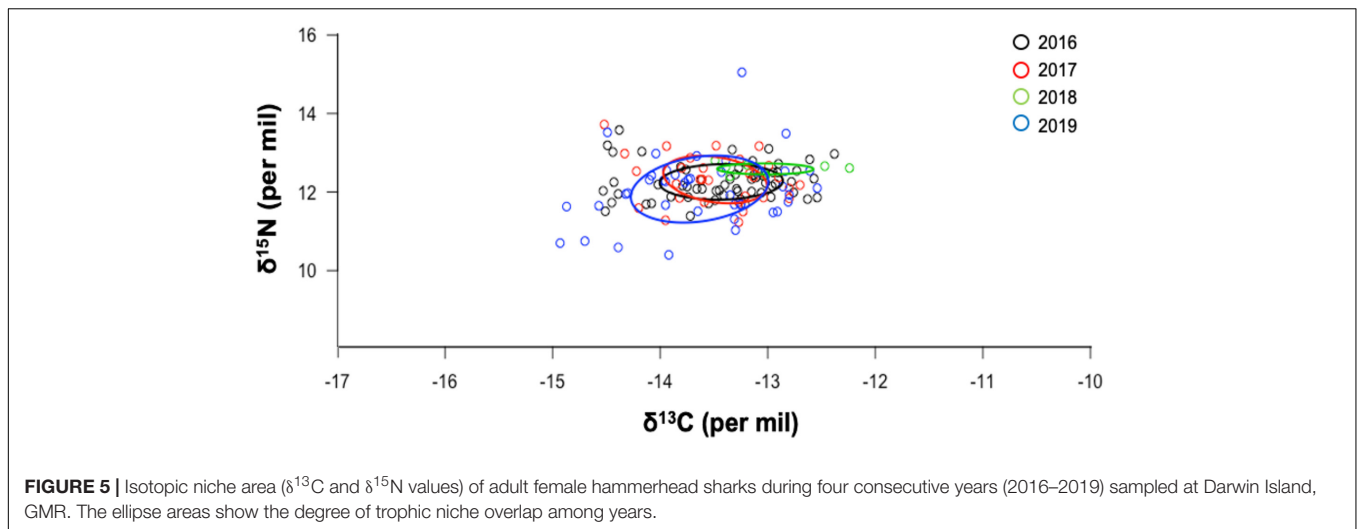
FIGURE 5 | Isotopic niche area ($\delta^{13}C$ and $\delta^{15}N$ values) of adult female hammerhead sharks during four consecutive years (2016–2019) sampled at Darwin Island, GMR. The ellipse areas show the degree of trophic niche overlap among years.

community shifts, and trophic structures alterations will follow (Wernberg et al., 2013) along with an increment on the incidence of diseases (Santana-Piñeros et al., 2020). Although further evidence is required to fully understand the impact of climatic variability, our results suggest that the high foraging adaptability and mobility of scalloped hammerhead sharks might confer this species some level of resilience to these extreme events.

Ecosystem Changes and the Role of Sharks

Generally, scalloped hammerheads feed on epipelagic and mesopelagic species (Klimley, 1987; Torres-Rojas et al., 2006), presenting high $\delta^{15}N$ values as they regularly occupy high trophic positions (Richert et al., 2015; Shiffman et al., 2019). This trait makes them vulnerable to malnutrition or starvation when preferred prey is scarce and satisfying their metabolic requirements becomes a challenge (Griffiths et al., 2010; Rojas et al., 2014; Pistevos et al., 2015). Previous studies have demonstrated that elevated temperatures increase sharks' energetic demands as well as reduce their metabolic efficiency (Pistevos et al., 2015).

Hammerheads are highly sensitive to changes in temperatures but have a strong capacity for adaptive plasticity over time (Sydeman et al., 2015). Our analyses support this statement by demonstrating how in the years 2016 and 2019 hammerhead

niche becomes wider, likely adopting a more generalist feeding approach in the face of warmer temperatures in their surrounding waters. Examples of these diet behavioral shifts have been observed in other large pelagic species; thresher shark (*Alopias vulpinus*), bull shark (*Carcharhinus leucas*), and skipjack tuna (*Katsuwonus pelamis*) as their population abundance varies and their distribution changes to inshore habitats in the face of extreme climatic events (Lehodey et al., 1997; Preti et al., 2004; Matich and Heithaus, 2012).

Hammerheads sharks are also very selective of their habitat and generally preferred warm waters (between 23 and 26°C) above the thermocline to rest and regulate their metabolism before beginning hunting activities (Hoffmayer et al., 2013; Ketchum et al., 2014). Numerous feeding studies have documented the diel vertical movements that hammerhead sharks undertake into deep waters (> 200 m) to feed on demersal fish and cephalopods (Klimley, 1993). Large adult female hammerheads are known to perform up to 70 daily deep, night foraging dives (Hoffmayer et al., 2013; Ketchum et al., 2014). Ocean warming and acidification may increase sharks' metabolism and oxygen demands leading to possibly circulatory stress (Rosa and Seibel, 2008; Pistevos et al., 2015). However, these species has demonstrated to be highly adaptive, moving from the surface of the ocean to near the bottom, even diving into anoxic waters, and likely finding prey in both environments (Jorgensen et al., 2009). Our results provide additional evidence on the foraging adaptability of this species during fluctuating climatic events.

Mobility and Management Implications

Movements and habitat use of scalloped hammerheads show a strong philopatric behavior around Darwin and Wolf islands (Ketchum et al., 2014). During the warm season (January–June), however, the water column structure around Darwin and Wolf islands becomes distinctly stratified (Palacios, 2004), with high temperatures on the surface (above 26°C), causing the thermocline to descend and so does hammerheads preferred habitat (Ketchum et al., 2014). Our isotopic analysis reveals low

TABLE 4 | Pearson's rank correlation coefficient results.

Isotopic signature	Variables	Pearson rank correlation coefficient result
$\delta^{13}C$	SST	$r = 0.30$
	Chl a	$r = 0.40$
$\delta^{15}N$	SST	$r = 0.38$
	Chl a	$r = 0.25$

Relationships between $\delta^{13}C$ and $\delta^{15}N$ signatures and environmental variables from 2016 to 2019 for sea surface temperature (SST) and Chlorophyll-a.
No relationship was significant at p = 0.05.

seasonal differences coupled with annual fluctuations depending on ENSO cycles for hammerheads in the GMR. Previous studies have shown horizontal and vertical migrations models of hammerheads around the TEP oceanic islands using acoustic and satellite telemetry to showcase two types of migratory movements: one restricted to inshore habitats and one dispersive to offshore habitats near the islands (Hearn et al., 2010; Bessudo et al., 2011; Ketchum et al., 2014). Isotopic signatures from our study showed that in years with warmer conditions hammerheads might engage in offshore foraging strategies, possible feeding outside of the GMR boundaries, thus, becoming vulnerable to fishing pressures as international fleets expand toward the GMR (Bonaccorso et al., 2021).

CONCLUSION

Our data suggest that hammerheads sharks broaden their isotopic niche when environmental fluctuations occur in their preferred environment, probably as natural behavior or physiological response to climate adaptation. Predominantly, sharks have broad thermal tolerance and a great potential for environmental adaptation, as they have demonstrated through millennia, withstanding natural climate variability (Tricas and Sisneros, 2004; Dulvy and Forrest, 2010). Our study supports this statement by showing that hammerhead sharks feeding strategies adapt to the climate variability occurring during El Niño and La Niña events within the GMR. Yet, as climate change and extreme weather events become magnified and more frequent, the future of hammerhead shark populations remains uncertain unless incorporate climate-related conservation strategies into the management of this species.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Galapagos National Park Directorate.

AUTHOR CONTRIBUTIONS

PS-D-L and DP-R conceived the study and designed the methodology. CA-U, PS-D-L, ER-L, LV-P, JS-M, and DP-R performed the field and laboratory work. CA-U, PS-D-L, and DP-R contributed to funding acquisition and wrote the original draft. DP-R conducted data analyses. ER-L, LV-P, and JS-M reviewed early manuscript versions. All authors gave final approval of the version to be published and agreed to be accountable for all aspects of the work.

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