Behavioral States Related to Environmental Conditions and Fisheries During Olive Ridley Turtle Migration From Pacific Panama

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Sea turtles migrate from breeding grounds to foraging areas through the territorial waters of several countries. Olive ridleys lack clear migratory routes, which makes it a challenge for conservation. This study aimed to evaluate if the migratory behavior of olive ridleys nesting on the Pacific Coast of Panama is correlated to environmental conditions along the migration and to identify common foraging areas. Thirty-four olive ridley turtles were tagged with satellite transmitters along the Pacific coast of Panama and tracked for up to 9 months. A Hidden Markov Model was used to identify behavioral states (foraging and migrating) and their correlation to chlorophyll a concentration, sea surface temperature (SST), eddy kinetic energy (EKE), and primary productivity. Turtle tracks overlapped with eddies and industrial fishing areas. The probability of foraging rather than migrating was positively correlated to SST, productivity and chlorophyll levels and negatively correlated to EKE. Turtles spent an average 30% of their time migrating and 70% foraging. Only 8.4% of the turtle locations occurred within an eddy, and 82.7% of the locations overlapped with previously described industrial fishing areas. Although this sea turtle species seems to migrate freely, without clear migratory corridors, turtles may have preferred foraging destinations that they travel to through different migratory routes, such as the gulfs of Tehuantepec, Fonseca, and Guayaquil. Turtles traveled up to 6,684 km through nine countries, most of them foraging in oceanic waters in Salvador, Costa Rica, and Panama, which highlights the importance of collaborative conservation strategies throughout foraging and nesting areas. The creation of a regional management unit (RMU), including Costa Rica, Panama, and Colombia, is discussed based on the observed seasonal overlap with the use of multiple fishing gears in coastal and oceanic fishing areas.

Keywords: behavioral ecology, *Lepidochelys olivacea*, Hidden Markov Model, migration, Tropical Eastern Pacific, satellite tagging

INTRODUCTION

Understanding the role played by environmental factors on animal behavior is key to developing effective conservation strategies, especially for endangered migratory species with migratory routes that are geographically unrestricted. The influence of oceanic variables such as currents or sea surface temperature (SST) on the migratory patterns and foraging behavior of marine

species may be better understood by combining the results of satellite tracking with proximate environmental data (Gaspar et al., 2006; Revelles et al., 2007; Godley et al., 2008; Schick et al., 2013). For the present study, olive ridley turtles (*Lepidochelys olivacea*) were tagged with satellite transmitters to monitor their movements within the Eastern Tropical Pacific (ETP) and evaluate any correlation between their foraging or migratory behavior and local environmental conditions, as well as the spatial and temporal overlap with industrial fishing areas.

Olive ridleys are considered the most abundant sea turtle species, inhabiting all tropical and subtropical waters (Godfrey and Godley, 2008). This species has a generalist diet (Bjorndal, 1985; McMahon et al., 2007), and mainly feeds on pelagic organisms through its extensive distribution (Polovina et al., 2006). In the Tropical Eastern Pacific this species nest from northwestern Mexico to northern Peru (Cliffton et al., 1995; Kelez et al., 2009) and has an estimated population size of 1.39 million turtles (Eguchi et al., 2007).

The nesting season for the olive ridley in the ETP occurs between July and December (Caldwell and Casebeer, 1964; Cornelius, 1982; Pitman, 1990; Eckrich and Owens, 1995; Plotkin, 2007) and may take the form of group nesting (known as Arribadas) where hundreds of individuals nest at the same location over a period of several days (Eckrich and Owens, 1995; Bernardo and Plotkin, 2007). Olive ridleys are observed to be highly vagile; moving continuously throughout novel marine areas covering hundreds of kilometers (Luschi et al., 2003; Polovina et al., 2004; Spotila, 2004; Plotkin, 2010). This migratory behavior has been termed "nomadism" and is considered to be a unique advantage to be able to adapt to a highly dynamic environment that, at times, becomes unfavorable (Seminoff et al., 2008). During migrations, routes between individuals do not generally overlap in space or time and thus may lack migratory corridors, making group analysis of tracks a particular challenge (Plotkin, 2010). This nomadic nature also presents a challenge in conservation efforts as foraging areas may vary significantly between populations and individuals. Not all olive ridley populations, however, are oceanic nomads; some groups have been observed to habitually occupy neritic waters near nesting sites, as observed in North West Australia (McMahon et al., 2007; Whiting et al., 2007), French Guiana (Plot et al., 2015), and Oman (Rees et al., 2012). This behavior may be explained by nearby food resource abundance, favorable temperatures, or other oceanic conditions (Plot et al., 2015; Chambault et al., 2016, 2017) but nevertheless demonstrates significant behavioral plasticity for the species throughout their global range.

Through their nomadic migrations these turtles can encounter different local environmental conditions, which can determine the travel direction, traveling speed, diving behavior and residence time (Chambault et al., 2016, 2017, 2019). Mesoscale eddies, which drive ocean productivity in the open ocean, transport heat, salts and nutrients (Revelles et al., 2007), are known to aggregate different sea turtle species, both in cold-core cyclonic eddies, and in warm-core anticyclonic eddies (Polovina et al., 2006; Mansfield et al., 2014; Chambault et al., 2016, 2019).

As many other marine species, olive ridleys are subject to incidental fishing, by large and small-scale fisheries (Cheng and Chen, 1997; Pandav et al., 1998; Lewison et al., 2004; Pinedo and Polacheck, 2004), in which they are caught on fishing nets (Montero et al., 2016) and in pelagic long lines fishing gears (Ramirez and Ania, 2000). Incidental catch can occur when turtles directly feed on bait, by entanglement on fishing lines or by getting incidentally caught on fishing nets (Pinedo and Polacheck, 2004). Therefore, the probability of an incidental bycatch increases when fishing areas overlap with the turtles high-use areas (Montero et al., 2016). In the Eastern Pacific region, bycatch is one of the highest on the planet and is associated to multiple fishing gear that include gillnets, long-liners and trawling (Wallace et al., 2010, 2013).

The ETP hosts several major converging current systems. Nearby mountain ranges subject to high winds can give rise to localized coastal upwelling throughout the region (D'Croz and O'Dea, 2007). Thus, regions of low temperature and high productivity (and vice versa) occur during different times of the year (Fiedler, 2002; Fiedler and Talley, 2006; Saba et al., 2008). These changes in water temperature and productivity are demonstrated during the El Niño Southern Oscillation, in which pressure gradients over the Pacific Ocean give rise to complex and intense wind–current interactions, highly influencing marine conditions within the ETP. As an oceanic realm with such contrasted oceanographic condition, resident turtles must adapt to a highly dynamic habitat, and at the same time, overlap with industrial and artisanal fisheries, which also take advantage of the high productive waters. Therefore, there is a need to determine the correlations between olive ridley movements and relevant oceanographic conditions to increase our understanding of the behavioral ecology of marine organisms that occupy dynamic habitats and to aid conservation strategies for this protected species.

MATERIALS AND METHODS

Satellite Tagging
A group of 34 solitary adult olive ridley turtles were temporarily captured from the Pacific coast of Panama for the purpose of satellite tagging from August 2009 to May 2011 on nesting beaches and the surrounding waters off the Las Perlas Archipelago in the Gulf of Panama and near Coiba Island in the Gulf of Chiriqui (**Table 1**). Turtles were tagged with SPOT5 AM-S244A satellite tags from Wildlife Computers Inc. (Redmond, WA, United States), which provided the location (latitude and longitude) of the turtle for variable time frames after release.

Upon capture, curved carapace length was measured and the area for device attachment was lightly sanded to remove encrusted organisms. Epoxy glue was applied to the shell to which the tracking device was attached and once set it was coated in anti-fouling paint. Flipper tags were applied to turtles when not already present. Tracking devices were set to transmit hourly with data collected via the Argos satellite system and imported into Seaturtle.org's Satellite Tracking and Analysis Tool (Coyne and Godley, 2005) for preliminary filtering. To ensure high quality, all locations with an accuracy classified as "Z" (unknown location) and dry were removed. Any values that

TABLE 1 | Summary of tracked olive ridley turtles tagged off the Pacific Coast of Panama, tagging location, and tracking length.

Turtle PTT	Tagging date	Transmission days	Tagging location	Distance traveled (km)	Gender
46207	11-05-23	109	Gulf of Chiriquí	1651.0	F
46238	11-05-23	78	Gulf of Chiriquí	1337.8	F
46247	11-05-02	75	Gulf of Chiriquí	1676.5	M
46248	11-05-02	123	Gulf of Chiriquí	3470.0	M
46249	11-05-26	67	Gulf of Chiriquí	1738.8	F
46252	11-05-05	57	Gulf of Chiriquí	865.7	F
46256	11-05-08	33	Gulf of Chiriquí	897.3	F
46257	11-05-23	276	Gulf of Chiriquí	6163.4	M
46258	11-05-05	183	Gulf of Chiriquí	2146.2	M
46259	11-05-05	177	Gulf of Chiriquí	2777.2	F
46260	11-05-26	123	Gulf of Chiriquí	2566.2	F
52710	09-08-25	184	Las Perlas	4609.3	F
52711	09-09-11	168	Las Perlas	3929.9	F
64494	11-05-02	57	Gulf of Chiriquí	424.1	M
64495	11-05-02	165	Gulf of Chiriquí	2475.9	M
64496	11-05-08	72	Gulf of Chiriquí	1285.9	F
68217	09-08-27	151	Las Perlas	4480.2	F
68218	07-03-07	40	Las Perlas	429.8	F
97792	09-09-28	172	Las Perlas	4627.7	F
97793	09-09-28	268	Las Perlas	6683.8	F
97794	09-09-13	248	Las Perlas	5911.4	F
97795	09-09-13	195	Las Perlas	5100.2	F
97796	10-01-31	20	Las Perlas	290.3	F
97797	10-02-15	58	Las Perlas	1112.8	F
97798	10-08-23	168	Gulf of Chiriquí	3102.7	F
97799	09-09-12	40	Las Perlas	668.1	F
97800	09-09-12	134	Las Perlas	3017.5	F
101502	10-11-14	119	Las Perlas	2786.4	F
101503	11-05-01	24	Gulf of Chiriquí	369.7	M
101504	10-10-31	106	Las Perlas	2974.2	F
101505	10-10-31	157	Las Perlas	2770.8	F
101506	11-05-01	39	Gulf of Chiriquí	957.2	M
101507	11-05-04	166	Gulf of Chiriquí	3547.7	F
101508	10-11-15	52	Las Perlas	2570.4	F

Distance traveled indicates the length of the total tracked path.

implied speeds >5 km/h were discarded in accordance with established procedures (Rees et al., 2012). The Animal Care and Use Committee of the Smithsonian Tropical Research Institute approved tagging procedures.

Track Correction

We used a Bayesian State-Space model for animal movements to correct the tracks based on Argos satellite tracking data error. This model is a first difference correlated random walk model that simultaneously deals with estimation error and observations that occurred irregularly in time (Jonsen et al., 2005). The model was run using the function "fit_ssm" in the package *bsam* (Jonsen, 2016) in R version 3.4.4 (R Core Team, 2018). It was set to have four time steps per day ($t$step = 0.25), 5000 samples during the adaptation and update phase, a thinning of 10 to minimize within-chain sample autocorrelation, and a span of 0.2 for the degree of smoothing.

Behavioral States Identification and Correlation With Environmental Variables

Each location along the corrected tracks was matched to six environmental variables: SST, chlorophyll (Chl), productivity (Prod), marine currents (Curr; U and V vectors), and the presence of eddies at the time and location of each transmission. The eddy kinetic energy (EKE) was calculated for each location using the U and V vectors extracted from the V and U- "Currents, Geostrophic, Aviso, Global (1 Day Composite)" database at a 0.25 decimal degree daily resolution[1]. Daily SST was extracted from the "Multi-scale Ultra-high Resolution (MUR) SST analysis fv04.1, Global, 0.011 Degree, Daily, Analyzed SST" data at a 0.01 decimal degree resolution[2]. Monthly composite

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[1]https://catalog.data.gov/dataset/currents-geostrophic-aviso-0-25-degrees-global-1992-2012-1-day-composite

[2]https://catalog.data.gov/dataset/multi-scale-ultra-high-resolution-mur-sst-analysis-fv04-0-global-0-011-2002-present-daily-depre

Chlorophyll-a concentration level (mg/m^3) data was extracted from the "Chlorophyll-a, Aqua MODIS, NPP, L3SMI, Global, Science Quality (Monthly Composite)" data set at a 0.0417 decimal degree spatial resolution[3]. Daily net primary productivity of Carbon (mg C/m^2) was extracted from "Primary Productivity, Aqua MODIS, NPP, Global, 1-Day, EXPERIMENTAL" data set at a 0.0147 degree spatial resolution[4]. These data sets were obtained and matched to each turtle location and date by using the function "xtracto" in the R package *xtractomatic* (Mendelssohn, 2018).

We used the Mesoscale Eddy Trajectory Atlas Product from AVISO Satellite Altimetry Data[5] to identify the presence of eddies during each transmission day and location. A circular buffer zone was created around each eddy center; the buffer diameter was equivalent to the diameter of each eddy on a given day (r^2). We overlaid the eddy spatial layer with the turtle location layer and identified turtle locations within eddies buffer zones, we filtered out spatial matches that didn't have a temporal match. These analyses were done with the Spatial analyst tool in ArcGIS (v10.6).

After all turtle locations were matched to real-time environmental conditions, we used a Hidden Markov Model (HMM) to identify different behavioral states (foraging and migrating) along corrected tracks. We used the environmental variables as model covariates to find any potential correlation between behavioral states and SST, Chl, Prod, Curr, and EKE. We fitted the model using the function "fitHMM" in the R package moveHMM (Michelot et al., 2016). We set the initial values to two states: 5 ± 5 and 50 ± 20 km for the step mean and pi to 0 for the turning angle and included the environmental variables as covariates. The presence of eddies was not included in the model owing to the small sample size. A kernel density plot was used to identify high- and intermediate-use foraging areas. The analysis was performed only using locations that the HMM model identified to be in the foraging behavioral state. Kernel density was plotted using bilinear interpolation and classified in two categories: High-use foraging areas were defined as areas where 50% of foraging transmissions occurred, intermediate-use areas were where 75% of the foraging transmissions occurred. The analysis was carried out in ArcGIS (v10.6).

Turtle Tracks Overlapping With Industrial Fishing Areas

Fishing effort was obtained from Global Fishing Watch (GFM)[6] (Kroodsma et al., 2018). The time frame of Kroodsma's data (2012–2016) did not overlap our study period (2009–2012). Therefore, we calculated a trimestral mean for our study area and used it as a reference mean for fishing effort, the first trimester corresponding to the north hemisphere's winter, the second to spring, the third to summer and the fourth to fall. We used ArcMap v10.6 (ESRI) and the Spatial Analyst tool to create kernel

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[3]https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html

[4]https://catalog.data.gov/dataset/primary-productivity-aqua-modis-npp-global-2003-present-experimental-1-day-composite

[5]https://www.aviso.altimetry.fr/en/data/products/value-added-products/global-mesoscale-eddy-trajectory-product.html

[6]https://globalfishingwatch.org

density plots and identify areas with low, intermediate, and high fishing effort along sea turtle tracks. We calculated a mean fishing effort for each trimester of the year and extracted the interpolated data to each turtle coordinate location during the corresponding trimester. Fishing effort was divided into three categories: low: from the smallest values excluding 0 to the first quartile (25% of effort); intermediate: from the first to third quartiles (50% of effort); and high: above the third quartile (75% of effort).

RESULTS

General Findings

Olive ridley turtles (n = 34) were tagged on the Pacific coast of Panama between 23 August 2009 and 22 Mach 2011 (except for one in May 2007) (**Table 1**) and were observed to travel substantial distances in numerous directions from their starting location (**Figure 1A** and **Table 1**). Females (n = 26) and males (n = 8) traveled distance was not significantly different (Mann–Whitney Z score p < 0.05) with an overall average of 2,629.9 ± 0.8 km in 121 ± 4 days representing an average speed of 21.8 km/day or 0.9 km/h. Turtles traveled through nine different countries and in international waters, with most locations occurring within the Panamanian Economic Exclusive Zone (60%) and Costa Rica (19.3%) (**Table 2**).

Four turtles (PTTs: 68218, 101503, 46256, and 64494) were not included in the bsam model because their model did not converge. The initial database, which included all turtles, had 10,566 Argos locations distributed among error classes, as follows (in descending order): B (27.4%), 0 (22.2%), A (22.1%), 1 (17.4%), 2 (8.6%), and 3 (2.4%). After track correction the database increased to 16,024 coordinate locations.

Behavioral States Identification and Correlation With Environmental Variables
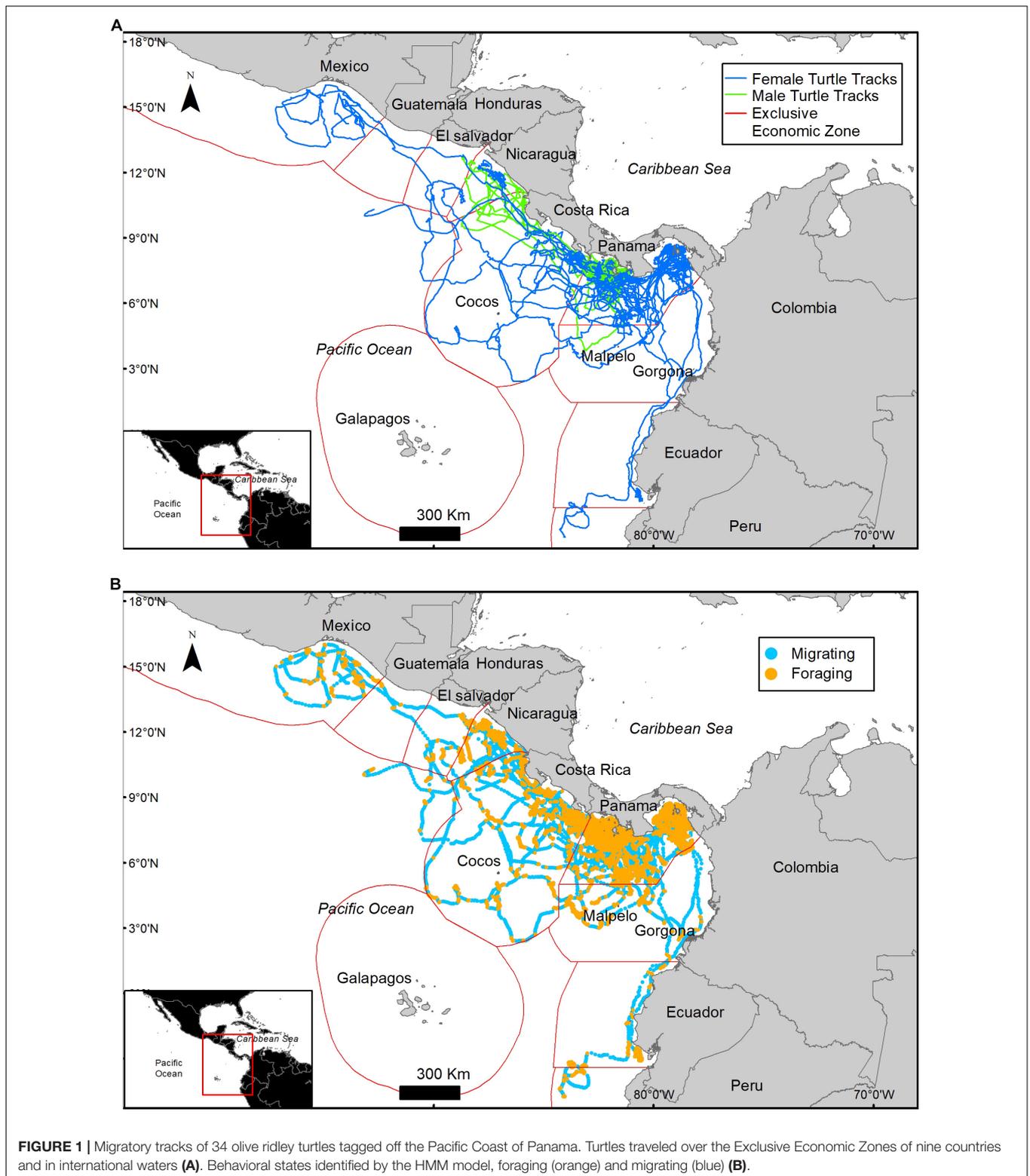
The HMM described two behavioral states: foraging (state 1) as having a step distance (distance between time intervals) of 3.9 ± 2.9 km and a turning angle of −0.02 ± 0.1^{rad} and migrating (state 2) having a step distance of 9.3 ± 5.9 km and a turning angle of 0.001 ± 13.2^{rad}. The probability of switching between behavioral states (from migrating to foraging or vice versa) was correlated with local environmental conditions under stationary long-term distribution (**Table 3**). The probability of a turtle being in state 1 (foraging) increased as SST and Chl increased, and the probability of being in state 2 (migrating) decreased as temperature and Chl decreased (**Figures 2A,B**). The effect of the EKE was the opposite, with state 1 being more probable with low EKE and state 2 more probable with high EKE (**Figure 2C**). Tracked turtles spent most of their time in water with Chl levels of 0.75 ± 0.02 mg/m^{-3}, EKE 0.02 ± 0.00 cm^2/s^2, Prod 1038.38 ± 24.41 mg C/m^2, and SST 27.82 ± 0.01°C. However, there was a significant difference in Chl levels between behavioral states; turtles foraged in waters with significantly higher Chl (0.91 ± 0.04 mg/m^{-3}) than when they were migrating (0.41 ± 0.01 mg/m^{-3}) (p < 0.005, **Figure 3**). Turtles spent an average of 30 ± 17% of their time in state 2

FIGURE 1 | Migratory tracks of 34 olive ridley turtles tagged off the Pacific Coast of Panama. Turtles traveled over the Exclusive Economic Zones of nine countries and in international waters (A). Behavioral states identified by the HMM model, foraging (orange) and migrating (blue) (B).

(migrating) and 70 ± 17% in state 1 (foraging) (**Figure 1B**). All results are presented as mean ± SE.

A total of 765 eddies occurred in the study area during the study period, 51% of these eddies were cyclonic and 49% were anti-cyclonic, with an average radius of 133.6 ± 7.3 km. Only 8.4% of the turtle locations occurred within an eddy (**Figure 4**). When migrating an average of 11 ± 12.6% of the locations were within an eddy and an average of 6.3 ± 9% were within an eddy

TABLE 2 | Turtle transmissions within Exclusive Economic Zones (percentage).

Country	Turtle transmissions (%)
Colombia	4.6
Costa Rica	19.3
Ecuador	3.3
El Salvador	1.4
Guatemala	0.4
Mexico	4.0
Nicaragua	5.3
Panama	60.1
Peru	0.7
International Waters	1.0

TABLE 3 | Model coefficient of correlation between each environmental variable (model covariate) to the probabilities of switching between behavioral states (1: foraging and 2: migration).

	From state 1 (foraging) to state 2 (migrating)	From state 2 (migrating) to state 1 (foraging)
Intercept	$-7.977187e-02$	$-1.691167e+00$
Chl	$-1.005488e+00$	$-3.088212e-03$
EKE	$4.831040e-01$	$-1.500950e+00$
Prod	$-8.420113e-06$	$8.664518e-05$
SST	$-7.557752e-02$	$-1.091996e-02$

when foraging (**Table 4**). Turtle tracks overlapped temporally and spatially with cyclonic and anti-cyclonic eddies: 4.4% of the locations within eddies were in anti-cyclonic eddies and 4% in cyclonic eddies (**Table 4** and **Figure 4**). High-use foraging areas identified by a kernel density analysis (where 50% of the locations in state 2 occurred) were primarily located in the territorial waters of Panama, Costa Rica, Nicaragua, and southern Mexico (**Figure 5**).
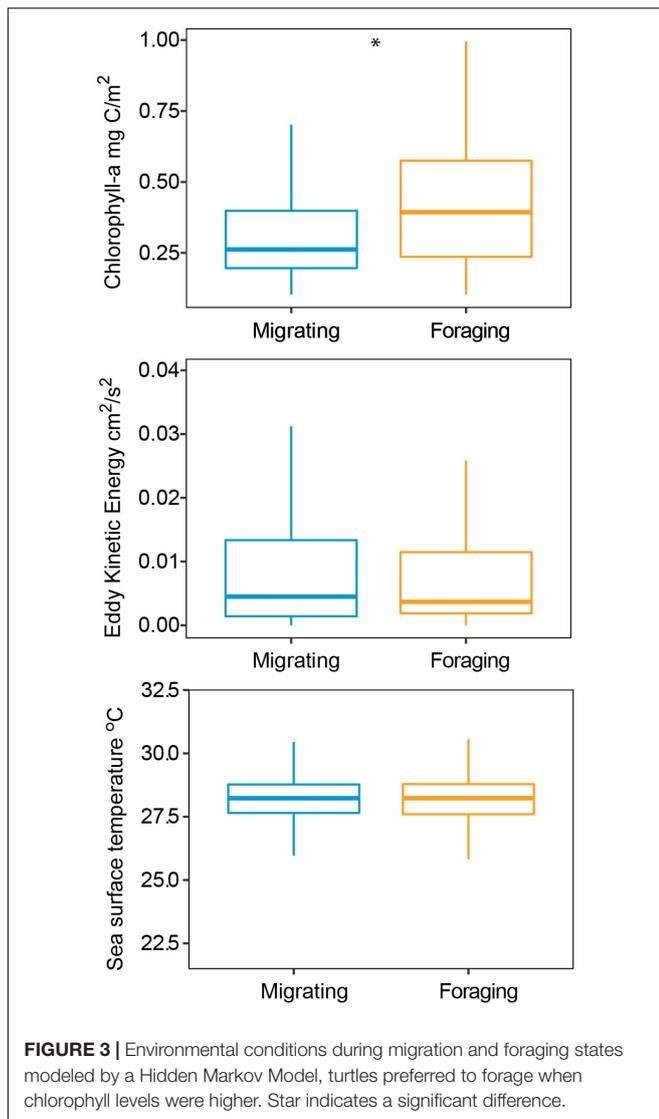
Turtle Tracks Overlap With Industrial Fishing Areas

Turtle tracks overlapped with the industrial fishing areas identified by Kroodsma et al. (2018) with 82.7% of turtle locations occurring within industrial fishing areas; 25% of them in areas with low fishing effort, 50% with intermediate, and 25% with high fishing effort. However, the extent of the overlap between turtles and industrial fisheries was dependent upon season (χ^2, $p < 0.001$), with more turtle locations in areas with high fishing effort during fall (**Figures 6**, **7A**). Purse-seine fisheries were the most common industrial fishing type in the study area during all seasons (79.4 ± 5.6%), followed by long liners (11.9 ± 1.4%), and squid jiggers (6.1 ± 4.9%), while industrial trawling represented $1.7\% \pm 0.1$ of the fishing. Squid jiggers, however, were outside the area traveled by these turtles.

On average, 24.4% of turtle locations overlapped with more than one fishing gear within industrial fishing areas, varying up to 36% in summer and a minimum of 11.7% in spring. **Figure 8** shows the spatial and seasonal distribution of the three most important fishing gears (excluding the jigger) and clearly indicates that purse-seine fishing covers the largest fishing area
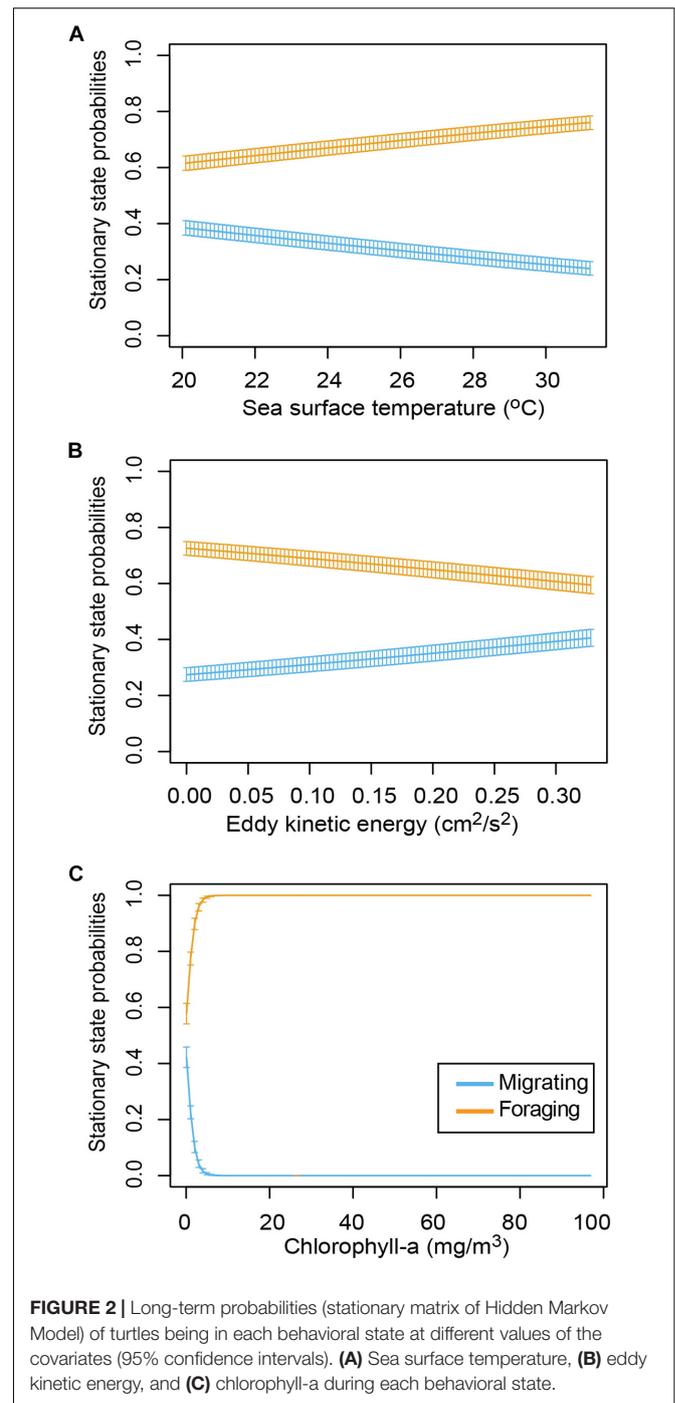
FIGURE 2 | Long-term probabilities (stationary matrix of Hidden Markov Model) of turtles being in each behavioral state at different values of the covariates (95% confidence intervals). **(A)** Sea surface temperature, **(B)** eddy kinetic energy, and **(C)** chlorophyll-a during each behavioral state.

in the region. Turtle movements coincided and overlapped with purse-seiners throughout the Eastern Pacific region by an average of 77%, varying between 65 and 89% depending on the season (**Figure 7B**). This overlap seems more intense during the summer and fall within the Costa Rican EEZ and the southwest and northwest of Panama and Colombia, respectively (**Figure 8**). Trawling seems to mainly affect Costa Rica throughout the year both the coastal zone and the EEZ, but intensely during spring with a maximum overlap of 18% (**Figure 8**). The distribution

FIGURE 3 | Environmental conditions during migration and foraging states modeled by a Hidden Markov Model, turtles preferred to forage when chlorophyll levels were higher. Star indicates a significant difference.

of longline fishing does not seem to affect the region widely, with a maximum overlap of 4.2%, except in the Gulf of Tehuantepec during winter and the northwest of the Gulf of Panama during summer and winter, in addition to international waters (**Figures 7B**, **8**). Both gulfs are affected by intense seasonal upwelling in winter, which may explain an increase in the presence of turtles and fishing vessels during this season.

Regional Foraging Patterns

Although tagged turtles migrated in multiple directions toward North and South America and toward oceanic islands, some individuals headed toward common foraging areas under different circumstances by using alternative routes at different times and crossing over the Exclusive Economic Zones of nine countries and international waters. Common foraging areas and stop-overs, included the Gulf of Guayaquil and Pampanal de Bolivar (Ecuador), Gorgona Island (Colombia), Gulf of

Fonseca (Salvador and Honduras border), and the Gulf of Tehuantepec (Mexico).

Two turtles tagged in the Las Perlas Archipelago (101504 and 97800) in October 2010 and September 2009 migrated to the foraging area at the Gulf of Guayaquil (southern Ecuador), an area known for its high Prod and high frequency of commercial fishing boats (Félix et al., 2017). Both turtles took ∼1 month (20 and 31 days, respectively) to get to Ecuador's waters, however, they used two different routes to get there, turtle 101504 used a more oceanic route than turtle 97800, having stopovers in Gorgona Island (Colombia) and in Pampanal de Bolivar (Ecuador) (**Figure 9A**) In the same way, turtles 9778 (tagged on August 2010) and 46248 (tagged on May 2011) tagged at the Gulf of Chiriqui (Panama) migrated to the Gulf of Fonseca (Salvador and Honduras border) by taking different routs, at different times, but with the same destination (**Figure 9B**).
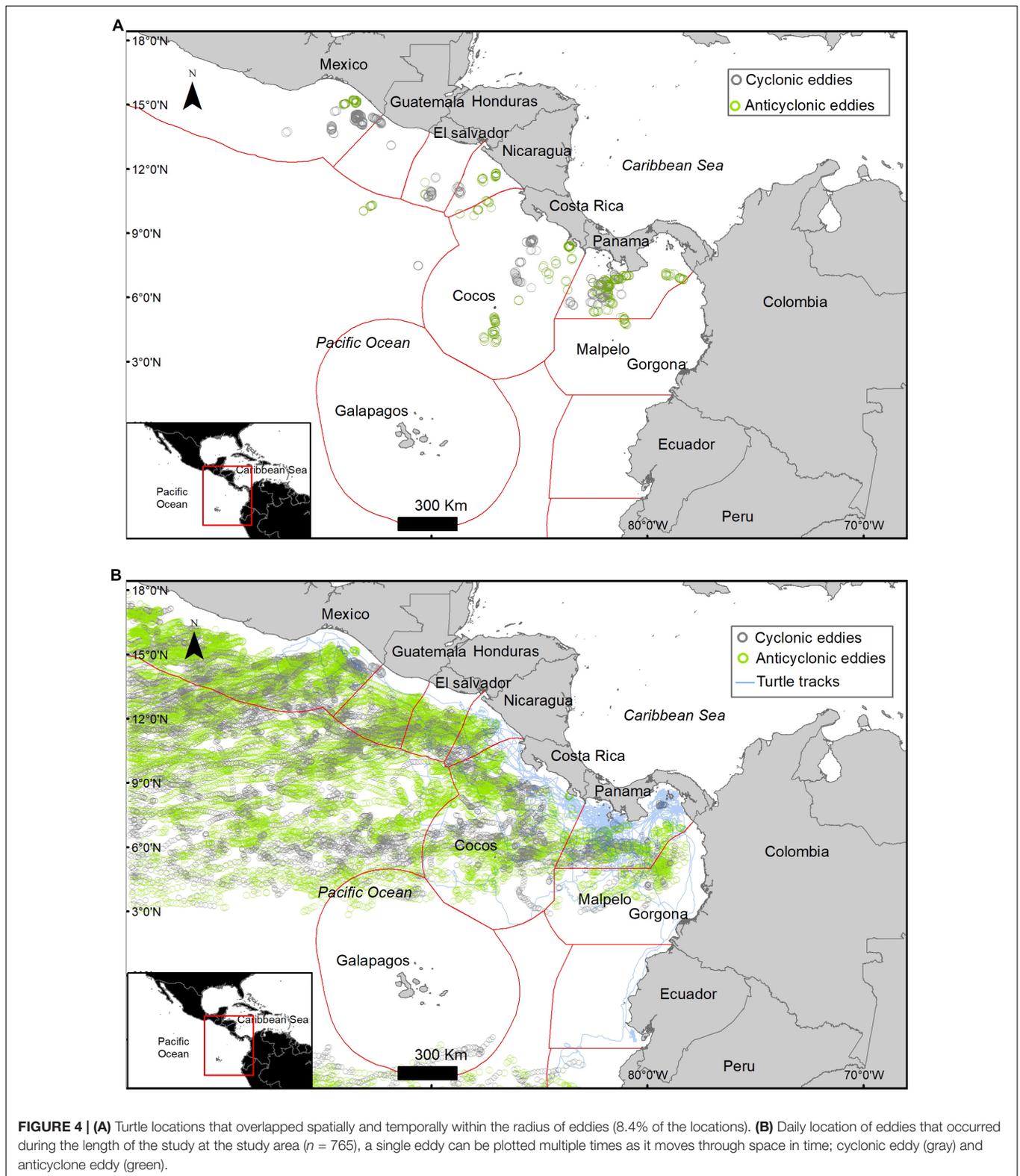
Two other turtles (97793 and 97792) migrated from the Las Perlas Archipelago to the Gulf of Tehuantepec (Mexico). Both of these turtles were tagged in September 2009 and had a similar southwestern migration until they encountered an anticyclonic eddy, started to forage, and their migratory routes diverged. Turtle 97792 headed northward with several foraging stops relatively close to the shore, and turtle 97793 continued its migration through oceanic waters. Both turtles arrived at the Gulf of Tehuantepec (Mexico) where their foraging overlapped with cyclonic and anti-cyclonic eddies (**Figure 9C**).

Two turtles had long and distinct oceanic migrations that returned to foraging grounds near their nesting area (tagging area). Both turtles were tagged simultaneously in Las Perlas Archipelago and migrated south until their routes diverged in parallel 6°N. Turtle 97795 headed northward to parallel 11°N where it foraged for 1 month in oceanic waters with high Prod and Chl concentrations and frequent eddies, and started a return until we lost the transmission. Turtle 97794 migrated south through oceanic waters and arrived to Sanquianga National Park (Colombia, south of Gorgona Island) where it foraged for 1 week, it then migrated northward back to Panama, arriving at the nesting area (tagging area) 6 months later (**Figure 9D**).

DISCUSSION

Olive ridley turtles tracked in this study migrated up to 6,684 km from the Pacific coast of Panama to different destinations without a clear migratory corridor, passing over the Economic Exclusive Zones of nine countries an over international waters and using five stop-overs and common foraging locations in the Tropical Eastern Pacific. Their plastic behavior was related to local environmental conditions, which has been described for the same species in French Guiana (Chambault et al., 2016) and for other sea turtle species that do have specific migratory corridors, such as green turtles migrating along the South American northeastern coast (Baudouin et al., 2015).

We identified two modeled behavioral states (migrating and foraging) and based on the HMM, the probability of changing from one state to another one was correlated with local

FIGURE 4 | (A) Turtle locations that overlapped spatially and temporally within the radius of eddies (8.4% of the locations). **(B)** Daily location of eddies that occurred during the length of the study at the study area (n = 765), a single eddy can be plotted multiple times as it moves through space in time; cyclonic eddy (gray) and anticyclone eddy (green).

environmental conditions. Individual movements were driven by oceanic conditions and resource availability and not by spatially explicit migratory corridors. Turtles switched from a directional migratory movement to foraging when they encountered Chl-rich and productive waters, where they spent most of their time (70%) overlapping with industrial fishing areas. Some turtles,

TABLE 4 | Percentage of turtle transmissions on each behavioral state (1: foraging and 2: migration) and the percentage of locations within an eddy during each behavioral state, overall and in anti-cyclonic and cyclonic eddies.

Turtle PTT	% of locations on each state		% of locations within an eddy				
	State 1	State 2	During State 1	During State 2	Overall	Anticyclonic	Cyclonic
46207	74.20	25.80	0.62	0.00	0.46	0.5	0.0
46238	80.25	19.75	0.00	4.84	0.96	0.0	1.0
46247	51.99	48.01	0.64	20.00	9.93	3.7	6.3
46248	54.36	45.64	10.07	12.89	11.36	7.3	4.1
46249	47.58	52.42	29.69	52.48	41.64	40.9	0.7
46252	97.38	2.62	0.00	0.00	0.00	0.0	0.0
46257	56.15	43.85	3.70	14.02	8.23	2.1	6.2
46258	88.81	11.19	0.00	0.00	0.00	0.0	0.0
46259	78.59	21.41	0.00	0.00	0.00	0.0	0.0
46260	66.19	33.81	11.38	15.66	12.83	2.0	10.8
52710	53.58	46.42	5.54	24.42	14.30	2.8	11.5
52711	72.62	27.38	12.50	11.96	12.35	0.0	12.4
64495	77.61	22.39	0.00	0.00	0.00	0.0	0.0
64496	74.39	25.61	7.91	28.38	13.15	11.1	2.1
68217	47.52	52.48	3.83	9.15	6.62	0.0	6.6
97792	54.14	45.86	31.37	18.35	25.40	21.8	3.6
97793	47.16	52.84	16.21	14.46	15.28	7.7	7.6
97794	62.40	37.60	1.94	10.99	5.34	4.4	0.9
97795	51.84	48.16	14.95	36.68	25.41	17.9	7.5
97796	100.00	0.00	0.00		0.00	0.0	0.0
97797	98.27	1.73	0.00	0.00	0.00	0.0	0.0
97798	81.40	18.60	0.00	12.00	2.23	2.2	0.0
97799	96.27	3.73	0.00	0.00	0.00	0.0	0.0
97800	72.39	27.61	0.00	0.00	0.00	0.0	0.0
101502	64.08	35.92	10.82	15.20	12.39	0.0	12.4
101504	51.54	48.46	0.00	0.00	0.00	0.0	0.0
101505	88.25	11.75	0.00	0.00	0.00	0.0	0.0
101506	62.58	37.42	23.71	8.62	18.06	0.0	18.1
101507	71.62	28.38	3.98	7.94	5.11	5.1	0.0
101508	87.92	12.08	0.00	0.00	0.00	0.0	0.0
Mean ± SD	70.37 ± 16.8	29.63 ± 16.8	6.30 ± 9.0	10.97 ± 12.6	8.04 ± 10.0	4.3 ± 8.9	3.7 ± 5.0
Range (min–max)	47.16–100	0–52.84	0–31.37	0–52.48	0–41.64	0–40.9	0–18.1
Overall %	66.89	33.11	5.46	14.43	8.43	4.4	3.99

however, coincided in some directional movements to forage in nutrient-rich destinations: the Gulf of Guayaquil (Ecuador), the Gulf of Tehuantepec (Mexico), and the Gulf of Fonseca (Salvador and Honduras border). During their migration turtles encountered a low number of eddies (only 8% of the locations), this strong mismatched could be likely due to turtle's behavior (oriented swimming outside these high-velocity structures) and low occurrence of coastal eddies.

Turtles tagged in this study (at the TEP) had more oceanic and disperse migrations compared to turtles tagged in French Guiana, which had a distinct coastal migratory route (Chambault et al., 2016). However, the average traveling distance (2,629 km) and the average traveling speed (0.9 km/h) found in this study lays within the ranged found in French Guiana (412–3651 km for traveling distance at a speed of 0.9–2.8 km/h) (Chambault et al.,

2016). Distance traveled and traveling speed was not different between male and female turtles, however, in this study only eight out or 34 tagged turtles were males, therefore, further studies with a more symmetrical sample size should support this result. Although the turtles tracked in this study traveled through coastal and oceanic waters they stayed in waters around 28°C, comparable to turtles tracked in Australia and French Guiana (McMahon et al., 2007; Chambault et al., 2016).

Turtles that migrated south to the Gulf of Guayaquil in Ecuador and north to the Gulf of Fonseca in Costa Rica did not overlap temporally during their migration (tagged in different years) but arrived at the same foraging destination via different migratory routes. The two turtles that migrated to the Gulf of Tehuantepec in Mexico did overlap temporally but also took different migratory routes to arrive at the same destination.
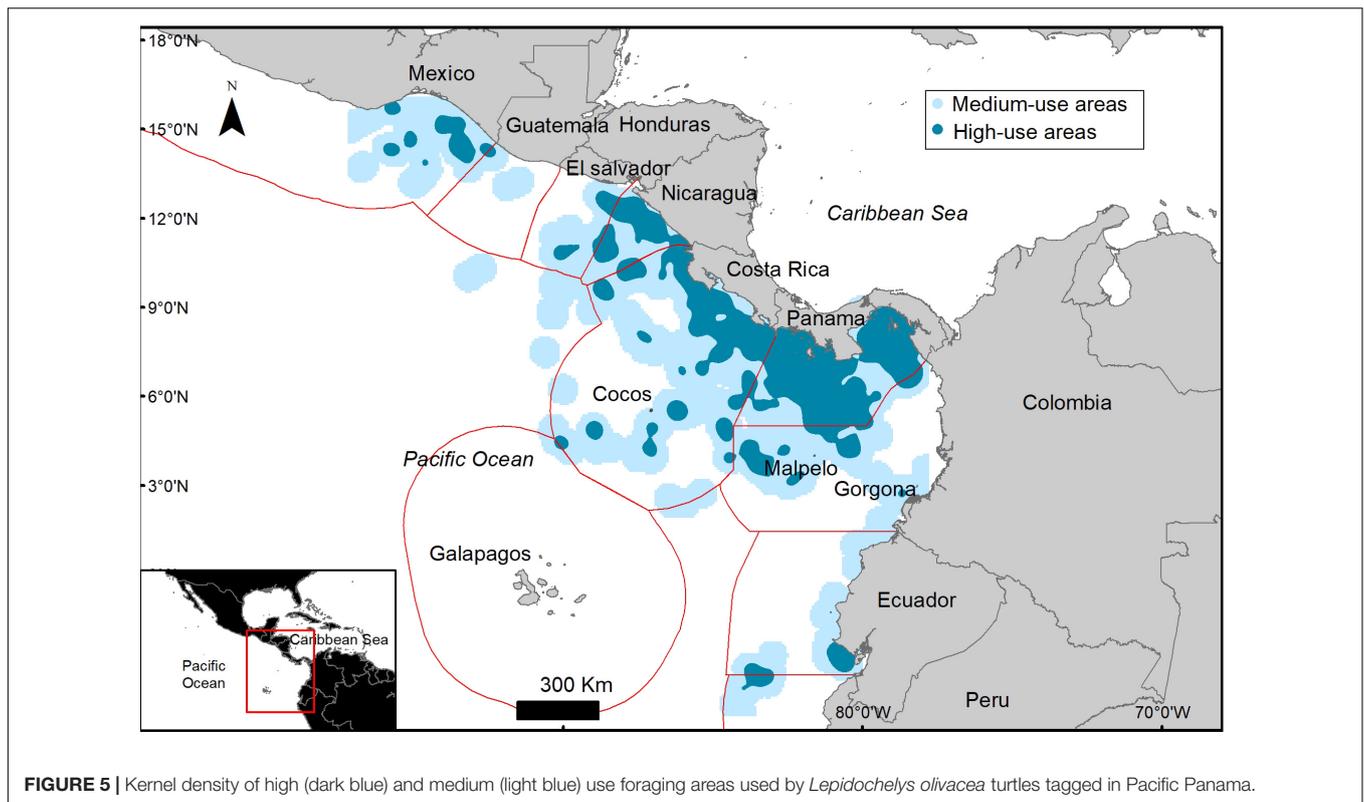
FIGURE 5 | Kernel density of high (dark blue) and medium (light blue) use foraging areas used by *Lepidochelys olivacea* turtles tagged in Pacific Panama.
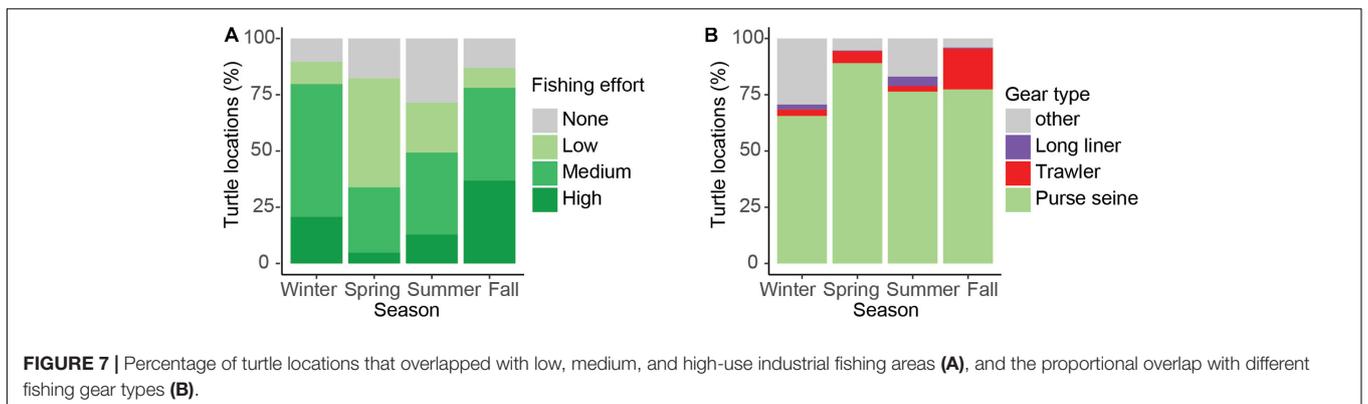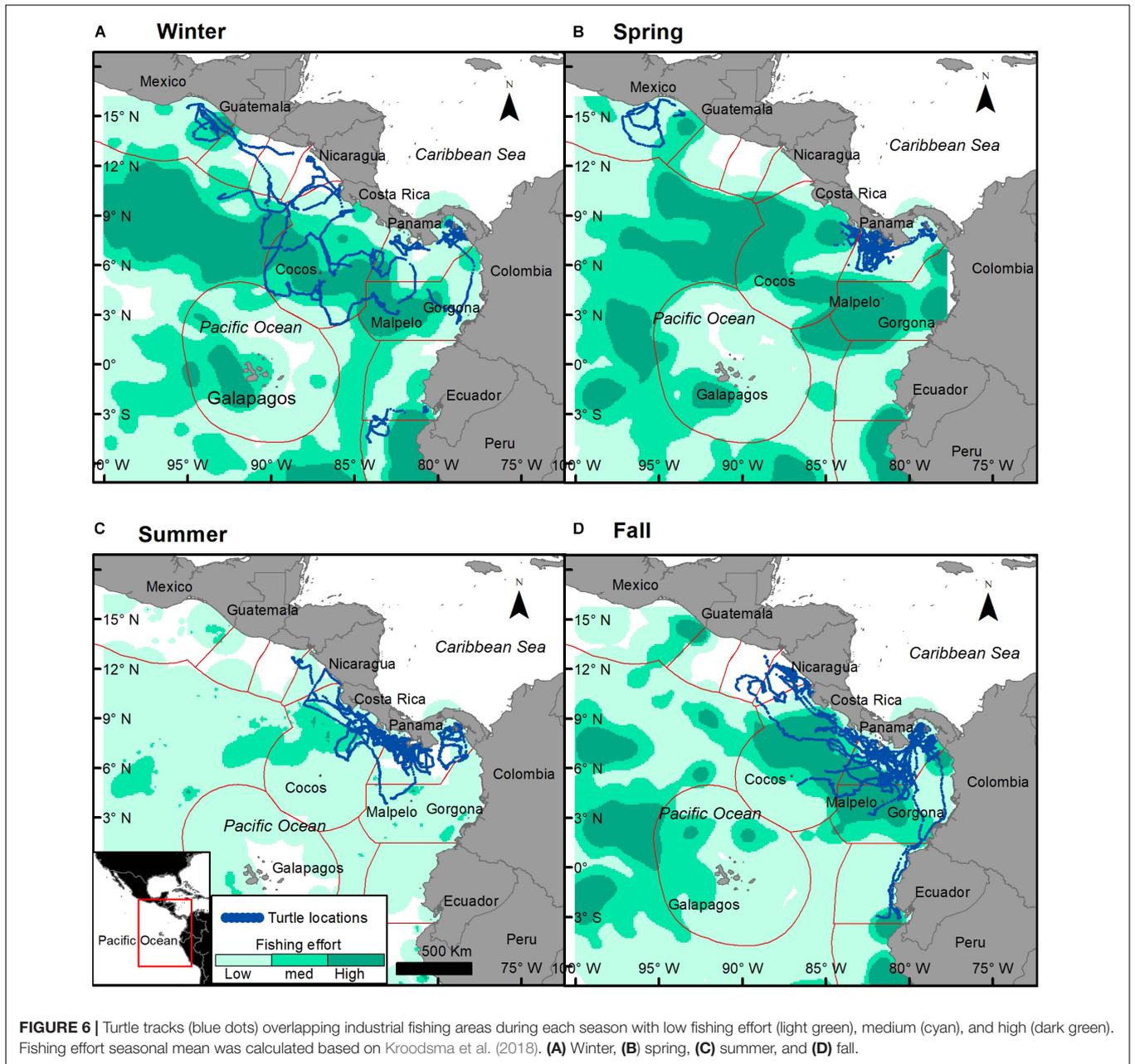
These results support the previously described nomadic behavior of this species. Our study further indicated that, although these turtles move freely in the oceans driven by resource availability, changing directional migratory behavior to foraging when resources were available (statistically confirmed herein) or changing direction in response to eddies, they do have a foraging destination to get to. They also have a remarkable ability to navigate back to the nesting area after long and improvised migration from foraging areas, as other migratory species do (Milner-Gulland et al., 2011).

Although migratory routes were scattered and different between tagged turtles, important foraging areas could be identified primarily in the territorial waters of Panama, Costa Rica, Nicaragua, and Mexico. Their overlap with high-Productive areas (e.g., Costa Rica Dome and Gulf of Guayaquil) commonly used by fishers is a matter of concern for sea turtle populations, which are threatened both in coastal waters, owing to habitat lost on nesting beaches, and offshore, owing to by-catch by fishing vessels. During the present study, data on artisanal fisheries or fishing boats not equipped with AIS devises where not included in the analysis due to lack of available reliable data. Montero et al. (2016) determined that the probability of incidental catch per unit effort by ETP purse-seine fisheries, which accounts for the majority of the fishing vessels in the study area, increases in temperatures (SST) of 26–30°C, with higher incidence occurring from June to December, in bycatch hotspots from North and south of the equator between 0–10°N; 0–10°S and from 120 to 140°W; and along the Colombian coast and surrounding regions. This indicates that turtles migrating off the

Pacific coast of Panama, such as the ones tagged in the present study, are particularly vulnerable since they overlap temporally and spatially with these high by-catch areas and seasons.

Owing to their nomadic migrations and the lack of clearly defined migratory corridors, protection of this species should focus on good fishing practices and turtle-safe fishing gear particularly through Central America, and should be added to special management programs in foraging destinations such as the gulfs of Guayaquil (Ecuador), Fonseca (Salvador and Honduras), and Tehuantepec (Mexico) and, of course, the protection of nesting habitats. Education of how to deal with incidentally caught turtles should also be implemented, since adequate handling of lightly hooked turtles incidentally caught by long liners reduces their probability of dying upon release (Swimmer et al., 2006).

This scenario shows that bycatch of turtles in the region affects all species and the scale of the problem is very difficult to analyze in order to implement adequate management and mitigation measures. In the United States for example, data from more than a decade on multiple turtle species demonstrated that implementing management or mitigation measures can have a significant change in the impact of the fisheries, with a reduction of by-catch and mortality in 60 and 94%, respectively (Finkbeiner et al., 2011). Additionally, the authors make potential management recommendations, which include increasing the presence of observers on fishing vessels, the modifications to fishing gear, the establishment of temporary closures in critical areas, and relevant to our study, consider the different countries whose Exclusive Economic Zones overlap, so that the resource
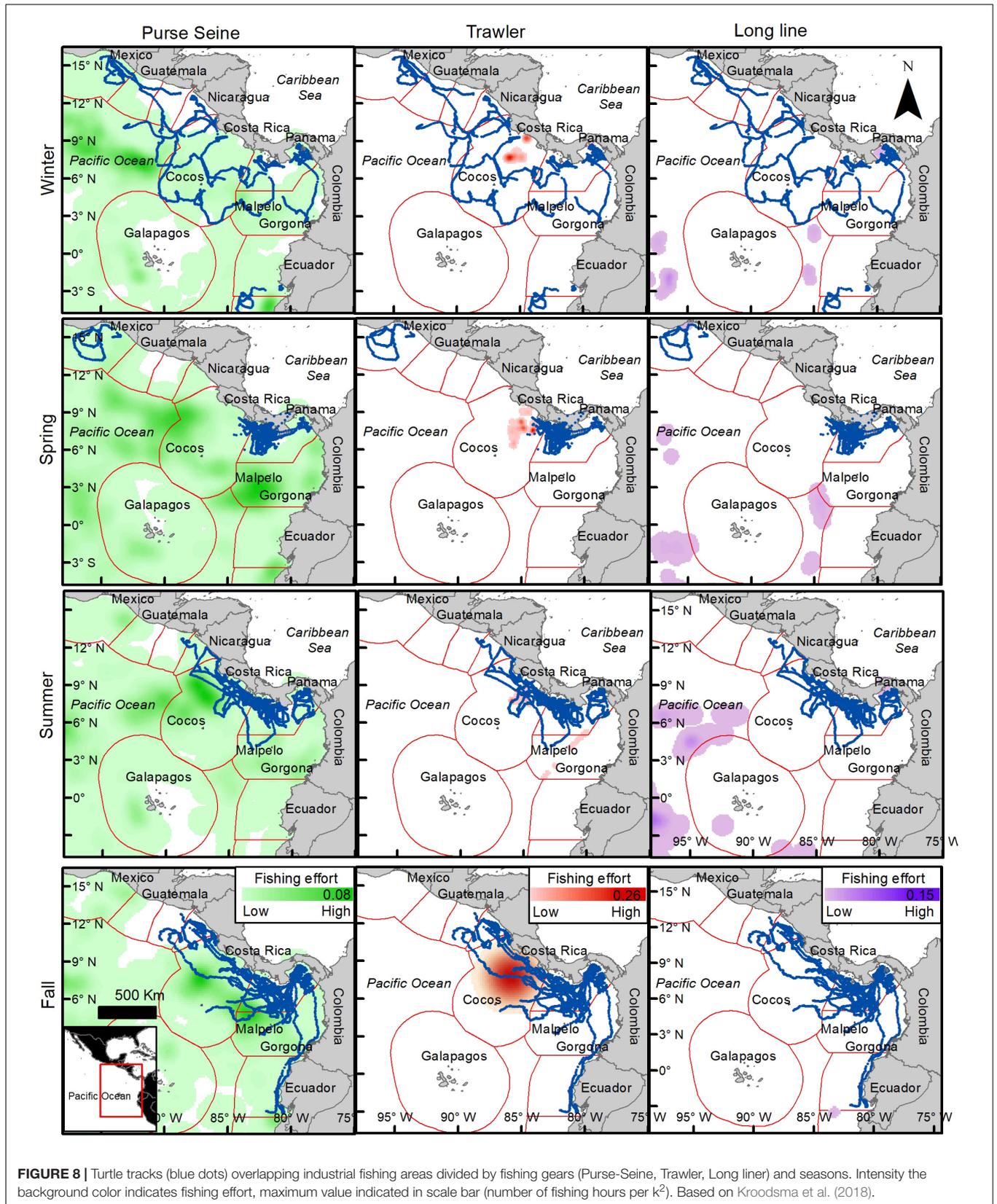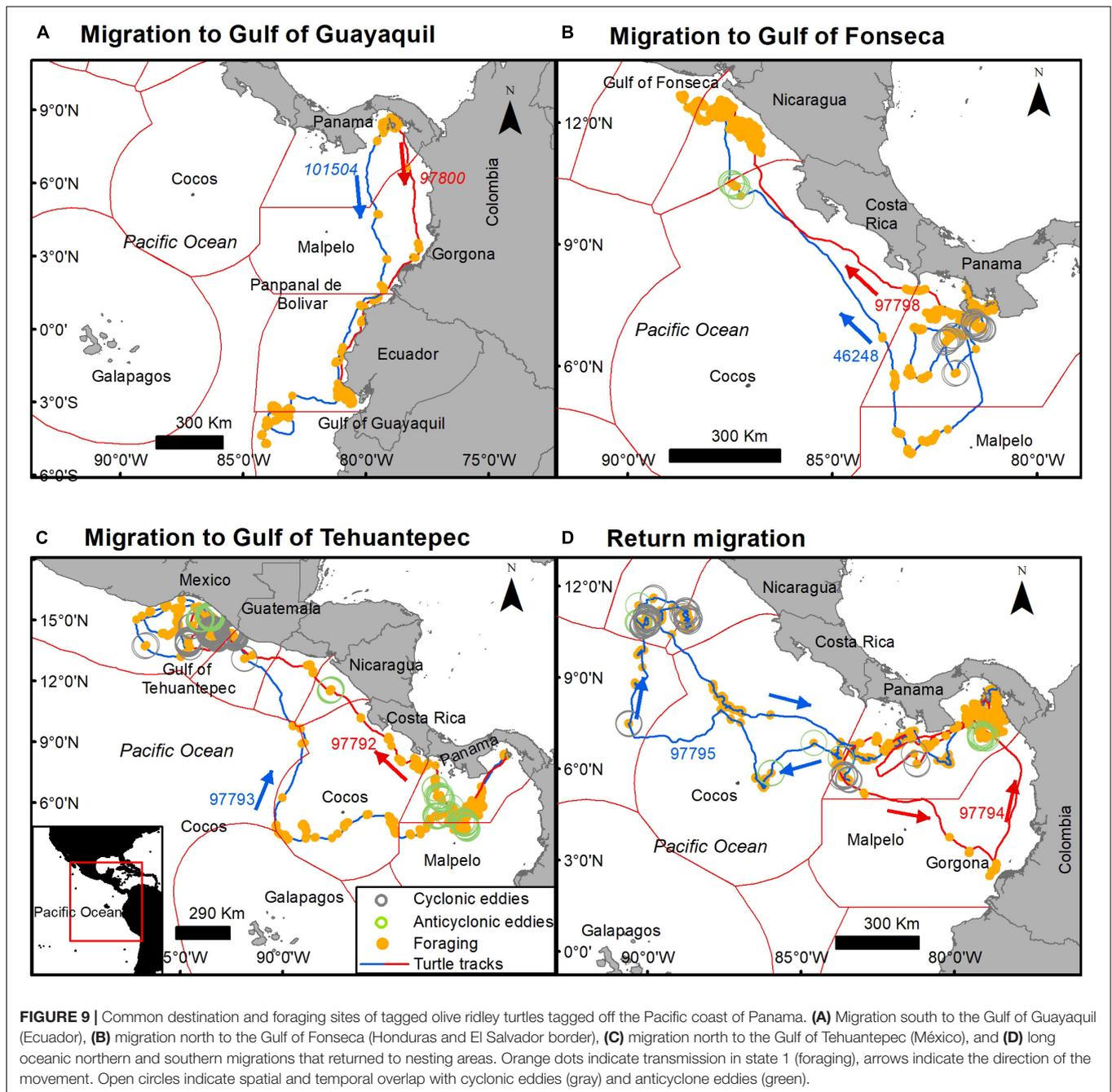
FIGURE 6 | Turtle tracks (blue dots) overlapping industrial fishing areas during each season with low fishing effort (light green), medium (cyan), and high (dark green). Fishing effort seasonal mean was calculated based on Kroodsma et al. (2018). **(A)** Winter, **(B)** spring, **(C)** summer, and **(D)** fall.

FIGURE 7 | Percentage of turtle locations that overlapped with low, medium, and high-use industrial fishing areas **(A)**, and the proportional overlap with different fishing gear types **(B)**.

FIGURE 8 | Turtle tracks (blue dots) overlapping industrial fishing areas divided by fishing gears (Purse-Seine, Trawler, Long liner) and seasons. Intensity the background color indicates fishing effort, maximum value indicated in scale bar (number of fishing hours per k^2). Based on Kroodsma et al. (2018).

FIGURE 9 | Common destination and foraging sites of tagged olive ridley turtles tagged off the Pacific coast of Panama. **(A)** Migration south to the Gulf of Guayaquil (Ecuador), **(B)** migration north to the Gulf of Fonseca (Honduras and El Salvador border), **(C)** migration north to the Gulf of Tehuantepec (México), and **(D)** long oceanic northern and southern migrations that returned to nesting areas. Orange dots indicate transmission in state 1 (foraging), arrows indicate the direction of the movement. Open circles indicate spatial and temporal overlap with cyclonic eddies (gray) and anticyclone eddies (green).

must be managed across political borders. This management plan can be designed by identifying priority areas as previously suggested (Wallace et al., 2013), and improved by using satellite monitoring of the species to obtain an enhance spatial resolution, similar to ours and other studies (Maxwell et al., 2011).

Although the nomadic nature of olive ridley turtles in the Eastern Pacific region suggests that climate change may not affect their distribution (sensu Plotkin, 2010), fishing continues to be the biggest threat. **Figures 6**, **7** showed the movements of olive ridley turtles within the countries of Central America and Costa Rica in particular, demonstrating

the overlap with fisheries within the discrete EEZs during the first and last trimesters of the year. Indeed, the need for cross-border management can be demonstrated by an example close to Panama, where bycatch of olive ridley turtles within the Costa Rica's EEZ was estimated in almost 700,000 individuals between 1999 and 2010, based on observer analysis on board the long-liners fleet (Dapp et al., 2013). Wallace et al. (2013), suggested that type of gear and species-specific information can be considered for reducing bycatch and to create or improve existing regional management units (RMUs). Regulating the use of a particular gear could

be argued necessary to reduce fishing pressure and bycatch for this species but requires well-planned political initiatives at least in some countries within the region. Our results, suggest that Colombia, Panama and Costa Rica are of particular concern due to the high level of fishing gears overlapping coastal and oceanic waters throughout the seasons and across the entire range of olive ridley turtles. Consequently, an RMU including only those three countries can be initially considered and perhaps political feasible to manage than a larger regional one (e.g., Tropical Eastern Pacific). Proposing further conservation and management measures is beyond the scope of this study, because it requires access to country-based VMS or AIS tracking databases not included in the GFW database used here. If the suggested specific RMU can be established, a priority could be to gather or update all existing information including fishing licenses for national and international vessels, size of local industrial and industrial fleets, and more important, the access to local satellite tracking systems that have been operational for several years and are not shared with GFW. The present spatial analysis, the first for this region and for this species showing the distribution of the different fisheries within the EEZ, can be used as an initial tool for improving current management and mitigation measures (sensu Pikesley et al., 2013; Wallace et al., 2013), that can include but not be limited to the creation of protected seaways or corridors void of fisheries across the region.

Previous studies of olive ridley turtles within the ETP (Luschi et al., 2003; Polovina et al., 2004; Plotkin, 2010) have indicated an absence of common foraging areas with turtles generally distributed throughout the pelagic marine region performing wandering movements as an oceanic nomad. Whilst many of the turtles tagged within the study indeed followed this established pattern, others instead demonstrated different types of foraging behaviors with common use of a number of localized areas such as the gulfs of Tehuantepec, Fonseca and Guayaquil. Although fidelity to specific foraging areas has been observed in other oceanic regions (Whiting et al., 2007; Da Silva et al., 2011), the foraging behavior observed in the present study for olive ridleys of the ETP is novel. This may indicate a higher behavioral plasticity for this population than previously thought. As noted previously (Plotkin, 2010), such an ability to adapt to environmental changes in the marine ecosystem suggests that ETP olive ridleys may be less vulnerable to the effects of climate change than other sea turtle species in the area.

Further studies on olive ridley movements in relation to oceanographic conditions would support our results and be beneficial to furthering our understanding, especially because the behaviors described in this study were identified by a model based on coordinate locations alone, with no other behavioral data, such as diving behavior (e.g., Chambault et al., 2016). In the current study, no thermocline information was included, which can be highly dynamic in the region, and provide further clues to their foraging behavior (Hochscheid et al., 2010). Perhaps most importantly, the ability to monitor turtle movements over longer time periods to determine the time spent in certain areas and whether there exists fidelity between individuals to specific sites, both nesting and foraging. A large variety of tracking durations have been demonstrated from other studies of olive ridleys with

averages ranging from 77 days (Whiting et al., 2007) to 113 days (Da Silva et al., 2011) and 236 days (Plotkin, 2010). Further research is dependent upon the technological development of the transmitters and the improvement of anchoring systems.

As the oceanic climate continues to change due to human activities, the influence it exerts on sea turtle movements is unpredictable. Thus, we strongly recommend the continual monitoring of their movements and behaviors to ensure the efficacy of current protective legislation both regionally and internationally, especially in foraging areas identified by the present study, the Gulf of Guayaquil, Pampanal de Bolivar (Ecuador), Gorgona Island (Colombia), Gulf of Fonseca (Salvador and Honduras border), and the Gulf of Tehuantepec (Mexico).

DATA AVAILABILITY STATEMENT

Tracking data obtained in this study will be made available by the authors to any qualified researcher upon request.

ETHICS STATEMENT

The animal study was reviewed and approved by the Smithsonian Tropical Research Institute.

AUTHOR CONTRIBUTIONS

HG led the research project and tagged the turtles. CG performed the statistical analyses, models, and figures. HG, CG, and GR drafted the manuscript.

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