

Article

Genetic Evidence for Indo-Western Pacific Olive Ridley Sea Turtles in Mexican Waters

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Abstract: The olive ridley sea turtle is predominantly an epipelagic species with no apparent migration corridors. Research in feeding areas in other sea turtle species has identified aggregations of individuals from diverse backgrounds; however, no specific feeding areas have been identified for the olive ridley. We used mtDNA control region sequencing to identify the haplotype composition of 85 olive ridley turtles (adult and immature turtles from both sexes) captured and released in Central Mexican Pacific waters. Amplified fragments of the control region (751 bp) revealed the presence of 17 haplotypes ($h = 0.5877 \pm 0.0622$ and $\pi = 0.001698 \pm 0.001185$), and 16 of them were phylogenetically grouped within the lineage of the Eastern Pacific, but the haplotype Lo37 showed close evolutionary relationships with the lineage of the East Coast of India. Lagrangian drifter data showed that West–East transport from the Indo-Pacific to the tropical Eastern Pacific might be possible through passive drift. These results highlight the importance of more genetic studies offshore and the role of the ocean currents in the migratory behavior of olive ridleys, as well as the need to establish multinational strategies for the conservation and management of the species in international waters.

Keywords: olive ridley turtle long-distance migrations; mtDNA; genetic diversity; ocean currents; Lagrangian drifters; *Lepidochelys olivacea*; endangered species; Eastern Tropical Pacific



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1. Introduction

The olive ridley sea turtle (*Lepidochelys olivacea*) is predominantly an epipelagic pantropical species [1] that nests in tropical waters worldwide (except the Gulf of Mexico) [2]. It is the most abundant sea turtle in the world [3], but information on its population status is scarce and information on its ecology is unevenly distributed across regions [4]. Although listed as Vulnerable in the IUCN Red List since 2008 [4], substantial populations remain on the eastern border of the Pacific and at scattered sites at the Indian, Western and Central Pacific.

Studies using mitochondrial DNA (mtDNA) on olive ridley nesting colonies show a strong population structure at a global scale with four distinct lineages: Eastern Pacific, Western Pacific, Atlantic, and east coast of India [5–7]. However, within regions, the structure is modest [8]. In the Eastern Pacific, this species appears to form a panmictic

population with no structure, showing basin-wide connectivity and a shallow population structure mainly between Mexican and Central American populations [9]. Even the Baja California Sur rookery exhibited low but significant genetic differences compared to nesting turtles in mainland beaches of Mexico [10].

In marked contrast to other sea turtles, the olive ridley presents irregular migratory behavior [1,8]; satellite tracking on post-nesting females show migration to be complex, with no clear patterns and no evident migratory corridors [1,11]. Nonetheless, they transit hundreds or thousands of miles over large oceanic areas [1]. After the mating season, both males and females head toward the open ocean to continue their nomadic foraging behavior [1,11]. In the Eastern Pacific, migratory displacements greater than 2000 km from Mexico to Colombia and Ecuador have been identified, as well as migrations from nesting beaches in Costa Rica north- and southward, where they remain in waters of more than 3000 m deep [11]. Similar movements have been identified for Eastern Indian stocks [12]. In the Western Pacific, satellite tracking studies on adult females from northern Australia revealed migrations to various feeding areas, in coastal, continental shelf, and continental slope habitats [13].

With very few exceptions, the olive ridley turtle is not known to traverse entire ocean basins [4]. However, finding haplotypes from the Eastern Pacific lineage at nesting beaches in Madras, India [6,7], and in Flinders Beach, Australia, in the Western Pacific [14] indicates that not only are they capable but also that they can adopt new breeding sites. Nevertheless, for this species, no evidence of movement from the Western to the Eastern Pacific has been found. There are reports of transoceanic displacement for different marine species, but these have mainly been associated with the prevailing westward current patterns in the Northern Hemisphere [15].

Eastward trans-oceanic transport of pelagic organisms across the Pacific, by means of the North Pacific Current (NPC), has been well documented [15], but studies of transport associated with tropical currents, such as the North Equatorial Counter Current (NECC), are scarce. Mitochondrial DNA markers have been crucial in tracing marine turtle movements. For example, this technique demonstrated that juvenile loggerhead turtles (*Caretta caretta*) traverse about one-third of the planet from their natal beaches in Japan across the Pacific to foraging areas off Baja California, Mexico [8,15], or that green sea turtles (*Chelonia mydas*) from unknown rookeries in the Western Pacific reach developmental habitats off Colombia in South America [16] (see Supplementary File S1 for complete list). Combining genetics and telemetry, leatherback turtles (*Dermochelys coriacea*) with Western Pacific origins have been shown to converge in different marine currents [17]: the East Equatorial Pacific Current, the Kuroshio extension, the Eastern extension of the Australian Current, as well as the North Equatorial Current (NEC) flowing westward and the North Equatorial Countercurrent flowing eastward.

The pattern of oceanic currents plays a critical role for successful transoceanic transport, and different species and stocks have been associated with distinct oceanic habitats [18]. Both the NECC and the NPC have significant fluctuations in the Western Pacific with synchronic variations, both are strong in the Autumn and weak in the Spring [19]; however, the NPC is too cold for sea turtle species whose distribution is essentially tropical and subtropical [20,21]. More importantly, eastward transport by the NECC between 10° N and 5° S intensifies during major oceanographic events, such as the El Niño-Southern Oscillation (ENSO) [22,23]. The southern edge of the Kuroshio extension, the NEC, and the NECC all represent important foraging and migratory habitats for both loggerheads and olive ridleys; loggerheads primarily associate with the first, olive ridleys from the Western Pacific with any of them, while those from the Eastern Pacific stocks do not appear to have a preference with strong currents [18].

The power of molecular markers to identify sea turtle stocks has been instrumental in establishing that at many foraging sites or migratory routes, individuals from multiple nesting colonies converge. While this has been widely demonstrated for most sea turtle species [8], the paucity of in-water genetic studies on olive ridley turtles greatly limits

our knowledge on the connectivity of this species. For example, the recent study by Vilaça et al. [7] reports the haplotypic composition at an olive ridley feeding ground in the Eastern Pacific, but with a very small sample size ($n = 6$), reporting a single mtDNA haplotype. In the central North Pacific (close to Hawaii), genetic evaluation of bycaught olive ridleys in pelagic zones indicated they originate from both the Eastern and Western Pacific sources [18,24] ($n = 9$ and $n = 11$, respectively). The results we present here is part of a larger effort designed to estimate the population abundance and the spatiotemporal distribution related to physical–chemical factors, the sex ratio of adults, and to infer the foraging ecology of olive ridley turtles from the Central Mexican Pacific. In this study, we characterized the genetic composition of olive ridley foraging aggregations off the central portion of the Mexican Eastern Pacific and searched for indications of rookery mixtures or the presence of long-distance trans-oceanic individuals.

2. Materials and Methods

2.1. Study Area and Sampling

The study was conducted in the Central Mexican Pacific (CMP), an area of 70,134 km² bounded in land by Maruata, Michoacan to Cabo Corrientes, Jalisco and 16°50'38" N, 104°13'21" W to 19°17'16" N, 107°18'34" W at sea (Figure 1). Surveys were divided into two zones with the 4000 m isobath as a boundary between the two zones: (1) continental and (2) oceanic. Each was, in turn, subdivided into North and South by the state boundary between Colima and Jalisco where major olive ridley nesting takes place (Figure 1). Olive ridley captures were covered by a permit for scientific collection PAGM/DGVS/62196/12 provided by the Dirección General de Vida Silvestre (Ministry of the Environment, SEMARNAT).

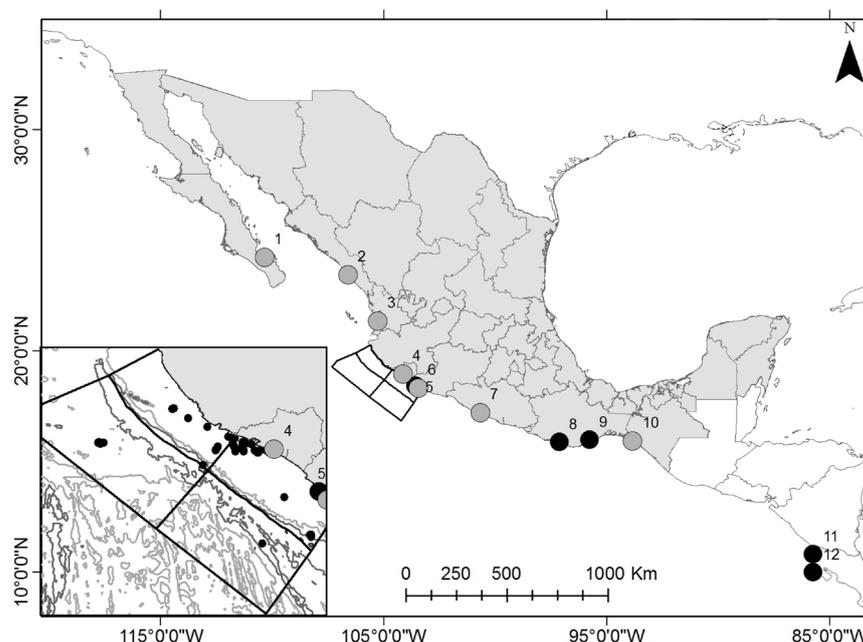


Figure 1. Location of olive ridleys caught in the Central Mexican Pacific between November 2011 and July 2012. The study area was divided into 4 strata: northern continental, southern continental, northern oceanic, and southern oceanic. Gray and black circles indicate locations of solitary and arribada nesting beaches, respectively. Major olive ridley nesting beaches in the Eastern Tropical Pacific outside our study area are included. 1: Punta Colorada, BCS; 2: El Verde Camacho, Sinaloa; 3: Platanitos, Nayarit; 4: Cuyutlán, Colima; 5: Ixtapilla, Michoacán; 6: Colola, Michoacán; 7: Piedra de Tlacoyunque, Guerrero; 8: La Escobilla, Oaxaca; 9: Morro Ayutla, Oaxaca; 10: Puerto Arista, Chiapas; 11: Nancite, Costa Rica; 12: Ostional, Costa Rica.

From November 2011 to July 2012, 3 research surveys in the coastal and oceanic region of the CMP and 14 surveys in coastal waters of Colima, Mexico were performed.

Search for turtles was carried out from a large vessel using binoculars (Fujinon®FMTRC-SX 7 × 50, Sendai, Japan) with reticle and integrated compass. When a large aggregation of turtles was detected, (i.e., 30 individuals or more in less than 10 min), a 16-foot boat with a 30 hp outboard was used to capture turtles. Steering towards the turtle aggregation was guided by radio communication with the large vessel to the turtles' locations. Most turtles caught were those with dry carapace at the water surface, which were easier to capture, since once they noticed our presence while resting and sunbathing, it was more difficult for them to submerge than if they were completely wet. Turtles were approached from the rear to avoid disturbance (otherwise they would submerge) and then captured by hand. Once on board, the turtle's head was covered with a cloth to minimize stress; the number of lateral scutes was counted and photographs were taken to confirm species [25]. A total of 85 turtles were captured and measured for curved carapace length (CCL) and total tail length (TTL), measurements that were used to identify sex in adult turtles, since the tail of males is significantly longer and thicker [26]. Individuals with CCL < 59 cm were classified as immatures and not separated by sex, as it was impossible to infer sex from morphological characters. A 0.5 cm³ tissue biopsy from each captured individual was extracted with a scalpel directly from the right anterior flap and preserved in a saturated NaCl solution with 20% DMSO [27] for processing at the Genetics Laboratory at the Institute of Marine Sciences and Limnology, UNAM. The location for each capture zone was recorded by a geo-positioning Garmin GPS map76CS.

2.2. Characterization of mtDNA Haplotypes

DNA was extracted by a modification of the common salt precipitation method [28] and visually evaluated for quality through agarose gel electrophoresis. We amplified an 880 bp segment of the mtDNA control region beginning at the rRNA-Pro locus using primers LTEi9 (5'-GGGAATAATCAAAAAGAGAAGG-3') and H950 (5'-GTCTGGATTTGGGGTTT-3') [29]. PCR products were verified by gel electrophoresis and purified with 20% polyethylene glycol (PEG 8000, 2.5 M NaCl; https://openwetware.org/wiki/PEG_purification_of_PCR_products (accessed on 10 July 2012)) for subsequent sequencing at Macrogen Inc. (Seoul, Republic of Korea).

The mtDNA sequences were edited using BioEdit Sequence Alignment Editor v 7.0.9 and aligned in Multalin [30]. Haplotype identification and relative frequencies were obtained using DNAsp 6 [31]. Haplotypes were matched against previously reported mtDNA control region sequences for *Lepidochelys olivacea*, available at GenBank (www.ncbi.nlm.nih.gov/genbank/ (accessed on 7 November 2022)), and against the most recent and complete list of haplotypes (653 bp) from the global phylogeography work by Vilaça et al. [7]. We named the haplotypes following the NO AA nomenclature in Vilaça et al. [7].

2.3. Molecular Analysis

Genetic diversity was calculated as haplotype diversity (h) and nucleotide diversity (π) [32] using Arlequin v 3.5 [33]. The genetic distance among mtDNA haplotypes was calculated using Arlequin v 3.5 [33]. The best model for our sequences was derived using the model test module in MEGA v 11 [34]. To estimate the genetic structure between turtle size categories (male and female adults, and immatures) and between capture zones (northern continental, southern continental, northern oceanic, and southern oceanic) we performed an analysis of molecular variance (AMOVA) using Arlequin v 3.5 [33,35]. We tested the null hypothesis of panmixia (absence of gene-geographic structure) using Wright's fixation index, F_{st} [36,37], using the available haplotype frequency profiles for olive ridley rookeries in the Eastern Pacific [7,9,38,39].

A Minimum Spanning Network for haplotype evolutionary relationships was constructed by the TCS method [40] and the PopART software (<http://popart.otago.ac.nz> (accessed on 15 December 2022)) using a ~751 bp segment shared by all sequences in this study and the most representative haplotypes reported worldwide. Additionally, a phylogenetic tree was built based on the best model for nucleotide substitutions using the

UPGMA method [34,41] with bootstrap (1000 replicates). *Lepidochelys kempii* and *Caretta caretta* mtDNA sequences (GenBank Access JX454981 and AB063118, respectively) were used as outgroups.

2.4. Trajectories of Satellite-Tracked Lagrangian Drifter Buoys

To complement the genetic results and identify possible routes of current-mediated transport of early-stage olive ridleys from Western Pacific habitats, we explored plausible pathways of transoceanic dispersal using the trajectories of satellite-tracked Lagrangian drifter buoys. We selected the buoys with an initial position of 0° < lat < 25° N and 100° E < lon < 180° E (<http://www.aoml.noaa.gov> (accessed on 7 December 2022)).

3. Results

3.1. Haplotype Composition

Of the 85 sampled olive ridley turtles, 25 were captured in the northern continental region, 40 in the southern continental region, 12 in the northern oceanic region, and 8 in the southern oceanic region (Figure 1). Of these, 27 were adult females, 31 adult males, and 27 immatures.

The 85 aligned sequences were truncated at 751 bp, resolving a total of 17 haplotypes with 30 variable sites (20 transitions, 3 transversions, and 8 indels). GenBank accession numbers for the nucleotide sequences are OP821911-OP821927. The most common haplotype was Lo46 (haplotype N by [5]) found in 65% of the samples, followed by Lo54 (haplotype O by [5]) in 9% of the samples. Other haplotypes occurred at low frequencies (Table 1). We recovered 51 olive ridley haplotypes publicly available, 35 in GenBank and 16 in Vilaça et al. [7]. Of the haplotypes in our samples, three were novel (Table 1).

Table 1. mtDNA control region haplotype frequencies (751 pb) identified for olive ridleys sampled in the Central Mexican Pacific. In brackets, for each life stage, shows the number of individuals per sampling zone (northern continental-southern continental-northern oceanic-southern oceanic). * Indicates new haplotypes.

Haplotype	Maturity Stages				Total
	Females	Males	Immatures		
Lo46	18 (8-3-5-2)	19 (4-14-0-1)	17 (6-6-3-2)		54 (18-23-8-5)
Lo54		4 (0-3-0-1)	4 (1-2-1-0)		8 (1-5-1-1)
Lo59	2 (1-1-0-0)		2 (1-0-0-1)		4 (2-1-0-1)
Lo52	1 (0-1-0-0)	1 (0-1-0-0)	1 (1-0-0-0)		3 (1-2-0-0)
Lo60	2 (1-0-0-1)	1 (0-1-0-0)			3 (1-1-0-1)
Lo27		1 (0-1-0-0)	1 (0-1-0-0)		2 (0-2-0-0)
Lo28	1 (1-0-0-0)				1 (1-0-0-0)
Lo31	1 (0-0-1-0)				1 (0-0-1-0)
Lo57		1 (0-0-1-0)			1 (0-0-1-0)
Lo61		1 (0-1-0-0)			1 (0-1-0-0)
Lo62		1 (0-1-0-0)			1 (0-1-0-0)
Lo71		1 (0-1-0-0)			1 (0-1-0-0)
Lo34			1 (1-0-0-0)		1 (1-0-0-0)
Lo35	1 (0-1-0-0)				1 (0-1-0-0)
Lo37 *			1 (0-1-0-0)		1 (0-1-0-0)
Lo53 *		1 (0-1-0-0)			1 (0-1-0-0)
Lo87 *	1 (0-0-1-0)				1 (0-0-1-0)
	27 (11-6-7-3)	31 (4-24-1-2)	27 (10-10-4-3)		85 (25-40-12-8)

3.2. Genetic Diversity and Lack of Genetic Differentiation

The olive ridley genetic diversity in the CMP sample was $h = 0.5877 \pm 0.0622$, nucleotide diversity $\pi = 0.001698 \pm 0.001185$ with a total of 17 haplotypes. Similar values were found when separating by maturity stages and sex (immatures, adult males, and adult females), and sampling areas (Supplementary File S2). Pairwise F_{st} were non-significant

for both between maturity stages and sampling areas ($F_{st} = 0$; n.s). Regarding studies reporting on nesting beaches in the Eastern Pacific, no differences were identified either (Supplementary File S2).

3.3. Phylogenetic Relationships

The best model for our sequences was Tamura 3 parameters [42] with gamma = 0.16. Evolutionary relationships among haplotypes (including those from published studies) grouped into three main clades: Clade I—East coast of India, Clade II—Western Pacific and Atlantic, and Clade III—Eastern Pacific (Figure 2; Supplementary File S3, Figure S1). Of the 17 haplotypes identified, 16 clustered within Clade III (Figure 2), but haplotype Lo37 unexpectedly exhibited clear affinity within Clade I (Clade K by [6]). This unique relationship suggests that this individual may have been subjected to a trans-oceanic transport from Indo-Western Pacific rookeries. This individual was an immature (CCL = 57 cm; CCW = 61 cm) and was found in a continental transect about 60 km from the coast; it was not possible to identify the sex from morphological characteristics.

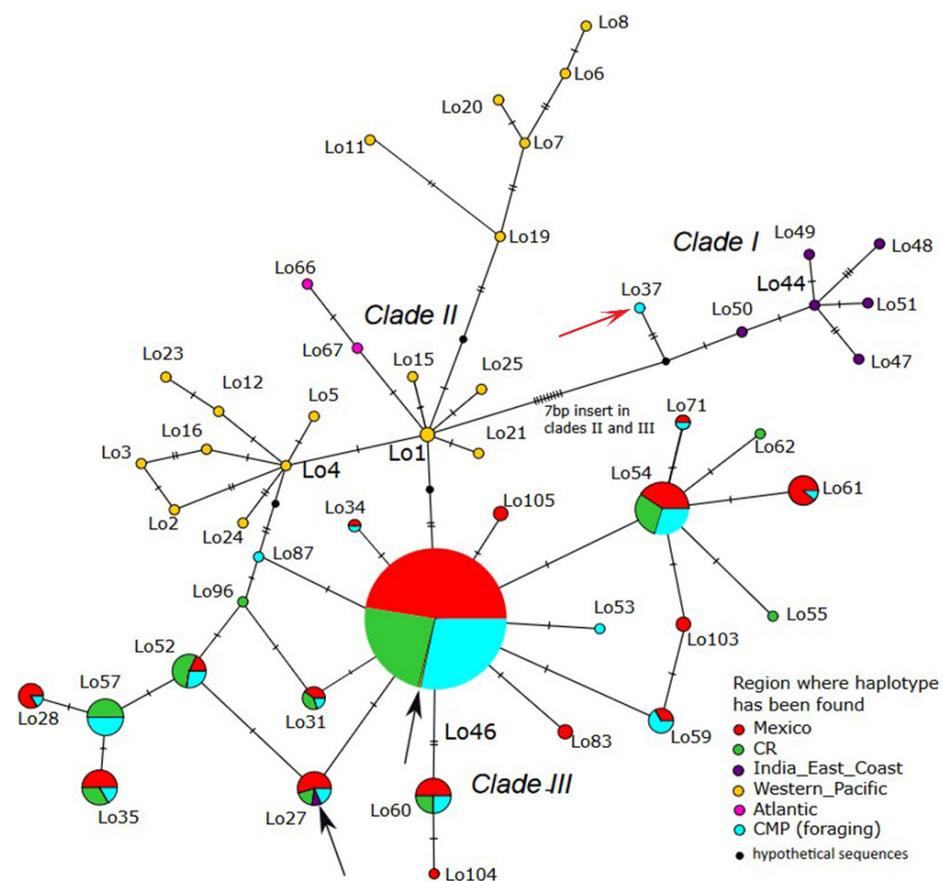


Figure 2. Minimum spanning network (MSN) for mtDNA control region haplotypes of olive ridleys sampled in the Central Mexican Pacific (CMP) and reported worldwide. Haplotypes from the CMP (in turquoise) were grouped in Clade III and Clade I. Clade I: East coast of India; Clade II: Western Pacific and Atlantic; Clade III: Eastern Pacific. Circles indicate haplotypes with sizes proportional to their relative frequency in Supplementary File S2. Black arrows indicate haplotypes of Eastern Pacific origin found on nesting beaches of the Western Pacific and East coast of India; red arrow indicates the single Clade I haplotype also exhibiting the 7 bp deletion characteristic of this clade.

3.4. Potential Current-Driven Trans-Oceanic Displacement

Information from Lagrangian drifter tracks indicated that trans-oceanic transport from western Pacific habitats could be possible on the NECC or the NPC. Transport of young olive ridley

turtles on the latter was discarded as being too cold. NECC has a pronounced seasonal cycle in the Pacific, reaching maximum strength in summer and autumn (Supplementary File, Figure S2a) and a minimum in winter and spring (Supplementary File S3, Figure S2b).

As the trajectories for individual drifters were discontinuous and very variable, we analyzed multiple buoys selecting those with drifts from the Indian Ocean towards the Eastern Pacific (Supplementary File S3, Figure S3). Buoys with origins in the Eastern Indian Ocean could reach the Western Pacific near the island of Bali (Java Sea) in a period between 92 and 829 days, although changes in direction (e.g., for buoy #60492; Supplementary File S3, Figure S4) shifting between eastward and westward bearings were frequently found, coinciding with the high variability in current direction known for the NECC. Some buoys originating in the South China Sea reached the Celebes Sea and the Sea Java, covering about 2000 km in less than 200 days (Supplementary File S3, Figure S5). Drifter buoys initiating in the Western Pacific, near the Philippines and Papua New Guinea, were transported by the NECC to the Central Pacific, beyond the Hawaiian longitude; one of them (buoy #7709278) released in 28 February, 1991, even reached the Eastern Tropical Pacific near the Dome of Costa Rica in almost two years and covered more than 11,000 km (Figure 3), probably associated with the very strong ENSO event of 1991-1992 (also reported by [16]).

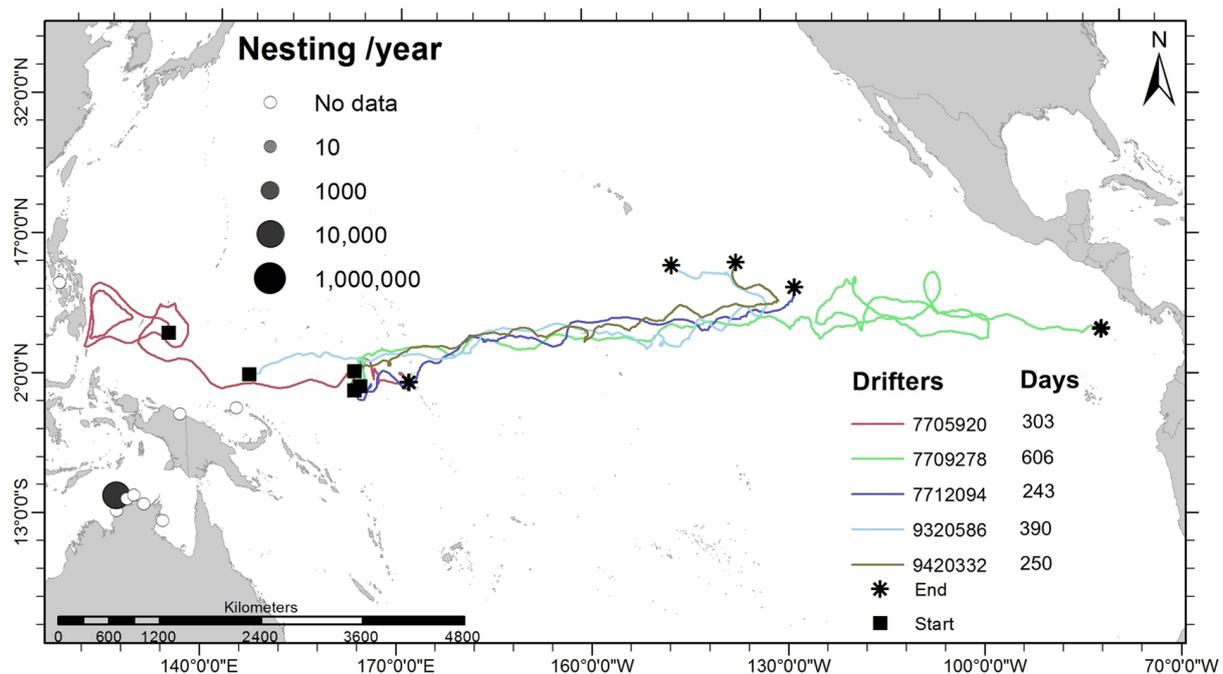


Figure 3. Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways linking olive ridley turtle breeding areas in the Western Pacific with the Central Pacific and Eastern Pacific. Olive ridley rookery locations and abundances derived from [6] olive ridley IUCN Database. Drifter data from NOAA/AOML Global Lagrangian Drifter Data (http://www.aoml.noaa.gov/envids/gld/krig/parttrk_id_temporal.php (accessed on 7 December 2022)).

Once the buoys from the Western Pacific were transported to the Eastern Pacific via the NECC, displacement on surface currents to the area of our study may also be possible. In the Eastern Pacific, buoys #7703173 and #7711029 drifted for 200 and 300 days from the NECC to the Costa Rica Current near the Costa Rica Dome (Supplementary File S3, Figure S6). Another buoy (#9102230) drifted 1500 km over a year on the NECC but with a north-east direction towards the Mexican Tropical Pacific, and another (#118579 buoy) for more than 100 days over 1500 km reaching the latitudes of our study (Supplementary File S3, Figure S6).

Transport in a West–East direction in the Pacific Ocean was also found associated with the NPC. Some drifters were found to move from the South China Sea to the Central Pacific, between 6000 and 7000 km in a span of one to two years (buoys #56439, #114991,

and #71351) (Supplementary File S3, Figure S7), and one (#7716198) from the NECC to the NPC, moving more than 6000 km in about three years (Supplementary File S3, Figure S7). Another set of buoys were tracked from the Central Pacific to the Eastern Pacific, reaching latitudes between 30° N and 50° N, latitudes where the sea surface temperature is too low for olive ridleys (Supplementary File S3, Figure S8).

In summary, of the 1837 Lagrangian drifters analyzed, although a minority, 41% moved in a West–East direction, most buoys took a NE direction reaching latitudes >10° N (influenced by the Kuroshio extension), and of these, only 11.4% of the buoys drifted to zones between 0° and 10° N (associated with NECC) and 7% to latitudes <0. The drifters transported by the NPC were displaced a greater distance than those influenced by the NECC, yet both moved from the Western to the Eastern Pacific (~12,000 km). Drifters carried by the NPC exhibited higher speeds (max. vel. 90 km/day) than those moving with the NECC (max. vel. 60 km/day). Transoceanic transport from the Western to the Eastern Pacific is less frequent and slower by the NECC than by the NPC but reaches more tropical latitudes, which would make this a more likely transport route for olive ridleys.

4. Discussion

4.1. Genetic Diversity and Haplotype Composition

Using a relatively large sample size ($n = 85$) compared to previous studies [7], seventeen mtDNA haplotypes were resolved from the sampled olive ridley marine aggregations in the CMP. Although, the haplotype diversity in these aggregations closely resembled those reported for Eastern Pacific rookeries ($h = 0.587$) [7,9,38,39,43] (Supplementary File S2), it was lower than in Western Pacific rookeries ($h > 0.70$) and higher than in Atlantic rookeries ($h = 0.19$) [7,14,44]. Nucleotide diversity was within the levels recognized as typical within populations (from 0.0005 to 0.020; [45]). Nonetheless, while the haplotype and nucleotide diversity values were within the range of those reported for rookeries in the Eastern Pacific (Supplementary File S2), the number of observed haplotypes is the maximum reported for a single sample, higher than any found in individual rookeries or even for the entire Pacific Mexican or Costa Rican regions. This can be interpreted as resulting from a mixture of various regional sources not statistically differentiated but containing multiple and distinct haplotypes.

Most of the sampled individuals (94%) exhibited of the 14 haplotypes reported previously for the species. The most common haplotype at the oceanic surveys was Lo46 (>60%), which corresponds to haplotype N by Bowen et al. [5] or haplotype K by Briseño-Dueñas [46] and represents the most frequent haplotype in all surveyed rookeries from Mexico and Costa Rica [9,10,38,46]. The rest of the haplotypes also were previously reported in low frequencies [10,38,46], indicating that they may be recent haplotypes.

4.2. Absence of Genetic Spatial Structure

Molecular analysis of variance on CMP samples showed values of $F_{st} = 0$ (n.s.), indicating no genetic differentiation between geographic zones, between sexes, as well as when contrasting with rookeries from the Eastern Pacific. This lack of population structure is consistent with the notion of panmixia for the olive ridley in the Eastern Tropical Pacific [9]. However, an alternative explanation is an incomplete lineage sorting due to recent colonization [5]. This latter scenario was corroborated by Vilaça et al. [7] who estimated colonization to have occurred ~30,000 years ago and described a star-like topology for the Minimum Spanning Network centered and dominated by haplotype Lo46. In addition, López-Castro and Rocha-Olivares [10] compared the mainland breeding rookeries of Mexico with those of Baja California Sur and found an incipient but significant genetic differentiation, which they suggested to be the consequence of a recent colonization by a few individuals. Thus, in general, olive ridleys exhibit a marked genetic structure on a larger geographic scale, with differences between but not within ocean basins [8].

4.3. Phylogenetic Relationships

As expected, most of the haplotypes found in the CMP grouped within the Eastern Pacific lineage, Clade III (Figure 2). On the other hand, since haplotype Lo37 shared a characteristic 7 bp deletion with the other Clade I sequences, we hypothesized that single sample to represent a vagrant turtle belonging to a distant rookery, most likely from the eastern coast of India or the Indo-Pacific because of its close phylogenetic relationship. Trans-Pacific transport of Western Pacific turtles has been reported for other species [15,16] but not for the olive ridley. Amorocho et al. [16] proposed a possible transport of green turtle individuals from the Western Pacific to the Eastern Pacific associated with the NECC, possibly lasting about two years. Westward transoceanic transport and even nesting translocation has occurred as haplotypes from Eastern Pacific olive ridleys have been reported in nesters from East coast of India [6] and Flinders Beach, Australia [14]. Nevertheless, there is a report indicative of the potential eastward transport of East India stocks: an olive ridley female was found nesting in Rushikulya, India, bearing a tag placed probably as a juvenile in Philippine waters [47]. However, until now, there have been no reports of Indo-Pacific haplotypes in any Eastern Pacific habitats. It is possible that sporadic translocation between nesting sites, probably mediated by ocean currents, is part of a complex phenomenon that may result in olive ridleys colonizing new areas [47].

Unfortunately, the suspected origin of the Lo37 individual would be somewhere in the Indo-Pacific, where genetic monitoring of olive ridley rookeries is still scarce [48]. Furthermore, the movement of olive ridley sea turtles in the Indian Ocean appears to be dynamic with no defined patterns [49]. Based on the known nesting distributions [4,48] and the available geographic distribution of haplotypes, this turtle would most likely originate from unsampled areas on the eastern coast of India or Sri Lanka or from the Western Pacific: Australia, Malaysia, Brunei, Cambodia, Indonesia, Papua New Guinea, Philippines, or Thailand. Previous Australian and Malaysian olive ridley mtDNA studies [14] found haplotypes that are phylogenetically very different from Lo37.

4.4. Role of Ocean Currents

Very little is known about how the olive ridley uses ocean currents during its life cycle. Hatchlings are believed to depend on ocean currents to reach their pelagic habitats [50]. During the juvenile stage, which is the least known for all sea turtles, they remain in the pelagic realm, are displaced long distances, and at times swim against the prevailing currents [51]. After sexual maturation, the pattern of migratory behavior for hawksbill, green, and loggerhead sea turtles has been well documented, shuttling between the breeding sites and specific foraging habitats to which they imprint and utilize for their entire inter-reproductive period. In contrast, the migratory patterns of adult leatherbacks and olive ridleys are primarily influenced by oceanographic mesoscale features of major ocean currents, where they appear to remain for prolonged stays in vast feeding areas [51,52]. For olive ridleys, Carr [50] proposed that they use ocean currents to move and converge in large marine expanses for foraging and protection, and Plotkin [11] reported a constant nomadic post-nesting behavior for olive ridleys in the Eastern Tropical Pacific, with no differences between sexes.

Analyses of Lagrangian drift trajectories [53] have revealed that the pattern of post-nesting dispersion of adult sea turtles from the breeding areas reflects the extent of passive dispersion that would have been experienced during the hatchling and juvenile stages. Thus, the prevailing oceanography around nesting areas provides key elements for the selection of foraging sites to be used by future adult sea turtles. Feeding sites might not be the product of an innate behavior or social facilitation, but rather a reflection of past experiences during earlier stages while being carried by ocean currents. Some flexibility and variability in post-nesting migratory behavior for olive ridleys have been observed even for turtles of the same genetic origin [11,39]. In the Central North Pacific, olive ridleys from western origins appear to spend time in association with major ocean currents, such as the Kuroshio extension, the NEC, and the NECC, while olive ridleys from eastern Pacific

sources do not [18]. Thus, the preference of the NECC by western Pacific olive ridley turtles would favor eastward displacements during strong and persistent ENSO years.

4.5. Implications for Conservation

With such a scanty presence of a Western Pacific olive ridley in a sample size of 85 in the present study, it is statistically impossible to reach robust conclusions on the occurrence of this lineage in Eastern Pacific habitats, which will remain as a critical unanswered question. Finding this turtle in the Central Mexican Pacific does highlight this zone as a potential migratory and foraging area [54]. Nevertheless, considering the latitudinal range of the potential trans-oceanic corridor (the NECC), it is most likely that the main zone where Western Pacific olive ridleys would be found is further south. The results presented here should encourage future surveys in offshore habitats (e.g., [55]) and the use of additional molecular markers to verify our findings. Also, stored samples from previous studies pursuing other issues (e.g., foraging ecology) [56] could be re-assayed with molecular markers to evaluate the possible presence of Western Pacific olive ridleys.

Finding olive ridleys from both East and West Pacific sources in pelagic areas of the North Central Pacific [18,24] demonstrated that even for this species, mixtures from opposite ends of the ocean basin may be more common than previously known, and for whose journey, ocean currents play an important role. Surveys of olive ridleys in epipelagic habitats are expensive and logistically challenging. Nevertheless, studies on the influence of oceanic currents in the Central Pacific and the contrasting preferences for these by Western and Eastern Pacific olive ridley populations coupled with satellite tracking [11,18] are needed to provide the necessary insight to understand the dynamics and frequency of the periodic trans-oceanic displacements by olive ridleys, such as what is reported here.

For instance, strong episodes of NECC lead to an accumulation of warm water in the Eastern Pacific during ENSO [22], a phenomenon that if strong and persistent enough, could promote the westward interoceanic transport of individuals. Under these scenarios, an increased presence of olive ridley from Western Pacific rookeries in latitudes where this current occurs (around Panama and Costa Rica) would be expected. The reason this has not been reported could be due to the scarce sampling effort for the species in oceanic habitats. Increased attention is warranted since future climate warming will likely increase the frequency and intensity of ENSO events [57], which should affect the strength and location of the NECC and thus transoceanic events. This could become relevant if increased contact between distant populations leads to the successful translocation of Western Pacific individuals into Eastern Pacific rookeries.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15030430/s1>. Supplementary File S1: Summary of reports on trans-oceanic transport of sea turtles; Supplementary File S2: Haplotype profiles for analyzed populations, Arlequin pairwise results; Supplementary File S3: Figures S1–S8. Figure S1: UPGMA tree describing the relationships among olive ridley haplotypes from the Central Mexican Pacific and from worldwide ocean basins constructed under the Tamura 3 parameters model of nucleotide substitution; Figure S2: Mean surface ocean currents in the Pacific region 40° N–40° S 60° E–70° W from the NOAA Ocean Surface Current Analyses Real Time program; Figure S3: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways linking olive ridley turtle breeding areas in the Indian Ocean and Western Pacific with the Eastern Pacific (i.e., a net eastward transport). Figure S4: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways linking olive ridley turtle breeding areas in the Indian Ocean and the Java Sea (transport from west to east); Figure S5: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways linking olive ridley turtle breeding areas in the Western Pacific (South China Sea) with the Celebes Sea and Java Sea. Figure S6: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways from NECC in the Eastern Tropical Pacific to the Costa Rica Dome and Mexican Tropical Pacific. Figure S7: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways from NPC in the Eastern Tropical Pacific to the Central Pacific. Figure S8: Satellite-tracked drifter buoy trajectories demonstrating potential ocean current pathways

via the NPC in the Central Tropical Pacific to the Eastern Pacific. References [58–74] are cited in Supplementary Materials.

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