Repeated sampling adds to the genetic diversity of *Lepidochelys olivacea* (Eschscholtz 1829) olive ridley sea turtle

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**ABSTRACT**

First sampled in the late 1990s, Campamento Tortuguero La Gloria, in Jalisco, Mexico, was resampled for olive ridley sea turtle (*Lepidochelys olivacea*) diversity 10 years later. A comparison with all previously reported mitochondrial sequences revealed that these new samples added to the known genetic diversity for this species, and revealed unexpectedly high genetic diversity among turtles nesting on this beach. The results highlight the importance of systematic resampling in known nesting rookeries to verify the genetic diversity of study populations. Three new olive ridley haplotypes are reported, all more closely related to Baja Californian haplotypes than to Australian haplotypes. Significant genetic divergence is reported within populations, within ocean basins (Atlantic, Pacific, Indian and Indo-Pacific), and between ocean basins. Furthermore, this is the first study that integrates satellite tagging data to demonstrate diverse post-nesting migration patterns of turtles with identical haplotypes, and it demonstrates flexibility in post-nesting migratory behaviour for olive ridley sea turtles of the same genetic provenance.

**INTRODUCTION**

The collapse of olive ridley sea turtle, *Lepidochelys olivacea*, populations throughout the 1960s and 1970s is attributed to hunting, egg poaching and habitat destruction (López-Castro and Rocha-Olivares 2005; Maulany et al. 2012; Salleh et al. 2012). These actions resulted in the death of at least two million *L. olivacea* in the eastern Pacific region within two decades. As a result of this mortality, in 2012, the Mexican population was listed as endangered, and all other populations were listed as threatened (U.S. Fish and Wildlife 2012). Despite the large reduction in number of *L. olivacea*, it remains the most abundant...
sea turtle species worldwide with populations in the Pacific, Atlantic and Indian Oceans (Plotkin 2010; U.S. Fish and Wildlife Service 2012). After the Indian Ocean, the eastern Pacific is the second most important nesting area with reproduction known to mainly take place in Mexico and Costa Rica (López-Castro and Rocha-Olivares 2005). Since 2012, the Mexican government has implemented several sea turtle conservation efforts on olive ridley sea turtles. Increased nesting on protected Mexican beaches suggests that these policies help to increase population sizes, yet species-wide molecular studies reveal that genetic diversity is extremely low among females in nesting populations, with four lineages currently recognized: Indian, Western Pacific, Atlantic and Eastern Pacific (Bowen et al. 1998; Abreu-Grobois 1999; Shanker et al. 2004; López-Castro and Rocha-Olivares 2005). Some studies recognize the olive ridley sea turtles from Baja California as a unique fifth lineage (López-Castro and Rocha-Olivares 2005).

Olive ridley sea turtles are of conservation concern across much of their range, but laws enforcing their protection vary, resulting in variable levels of concern by region (Wallace et al. 2010, 2011). Some populations are increasing in the eastern Pacific, but they are decreasing in other areas: olive ridley Regional Management Units are listed as ‘most endangered’ in the west Indian and northeast Indian Ocean basins, and ‘of great concern’ in the western Pacific (Bowen and Karl 2007; Wallace et al. 2010; Jensen et al. 2013) due to low genetic diversity.

On some beaches, olive ridley sea turtles are known to emerge from the ocean once a month, en masse, with as many as 150,000 turtles nesting (Plotkin et al. 1995). These mass nesting events are commonly termed ‘arribadas’. However, olive ridley sea turtles can also emerge independently, without large groups. These turtles are considered solitary nesters. The reasons for the varied nesting behaviour is unknown, but olive ridley sea turtles are flexible in their inter-nesting behaviour, and may respond to environmental cues that can result in nomadic solitary, or synchronized arribada behaviour. Differences in genetic structuring between arribada and solitary nesting turtle populations are also unknown. Sea turtle sampling for genomic work typically comes from nesting females. Hence, the flexible behaviour of olive ridley sea turtles may support greater than expected genetic diversity (Plotkin et al. 1995, 1997; Hamel et al. 2008; Rees et al. 2012). Unless researchers are continuously collecting samples, they may be missing clandestine species variability. Furthermore, longitudinal studies that resample individuals in populations offer insight into population-level changes in genetic diversity that may be occurring after significant periods of time, and permit the validation of previously reported genetic sequences.

This study tests the hypothesis that continuous field sampling efforts may change the known genetic diversity of sea turtle species. This might occur for two reasons. The first is that solitary nesters may be undersampled because fewer will nest in a given amount of time. Hence, researchers limited by collecting timeframes on their permits, may be more likely to sample during peak nesting events when they can maximize the number of samples they can collect given the amount of time and resources they have available to collect samples. If solitary nesting olive ridley sea turtles are genetically distinct from arribada nesting turtles, or certain environmental cues prevent nesting of particular nomadic individuals, then greater sampling efforts will help to illuminate this difference. A second reason new genetic variation might be discovered is because olive ridley population numbers are increasing in the eastern Pacific, from 1.1 million to 2.9 million in 10 years (Eguchi et al. 2007; Plot et al. 2012). This suggests that there might be
bottleneck recovery, and further sampling might reveal orphan olive ridley haplotypes that may have existed previously but were at such low frequency that they were undetected. Both scenarios suggest that our knowledge of genetic diversity of olive ridley turtles is currently incomplete due to constrained sampling practices.

To test this hypothesis, in 2008 we resampled olive ridley solitary nesters on Campamento Gloria, Jalisco, Mexico, a beach initially sampled by Abreu-Grobois and his research team between 1994 and 1996, and the genetic diversity of olive ridley sea turtles was analysed by his student Briseño-Dueñas (1998). We put the genetic diversity of this beach into the context of all known diversity of *L. olivacea* by studying the mitochondrial D-loop control region, and combining our data with all known D-loop sequences from olive ridley sea turtles to validate the genetic diversity of olive ridley sea turtles previously reported nesting on this beach, and for this sea turtle species. Genetic diversity measurements for four arribada beaches (Oaxaca, Mexico; Nancite and Escobilla, Costa Rica; Orissa, India) and 11 solitary nesting beaches were compared. Furthermore, we report the post-nesting migration patterns of four olive ridley sea turtles that were satellite tagged after nesting on Campamento Tortuguero La Gloria to compare the post-nesting migration patterns of sea turtles with identical and differing haplotypes. Satellite tracking studies of olive ridley sea turtles have suggested that there is no post-nesting spatial association for olive ridley sea turtles nesting on the same beach (Plotkin et al. 1995; Plotkin 2010), but these studies did not include genetic information that may explain the association between nomadic post-nesting behaviours and genetic provenance. A combined analysis of genetics and behaviour may provide insight into the pattern of gene flow and help to explain the observed genetic diversity for this species.

**Materials and methods**

**Sampling**

Campamento Tortuguero La Gloria, Tomatlán Jalisco Mexico (19.8981°N, −105.4232°W) maintains a marine turtle conservation programme on a 2400 m² site. The protected site includes a 1 km stretch of beach for *in situ* nests. Further, the University of Guadalajara supports an egg relocation programme there. The egg relocation programme protects as many as 5000 nests in a season (https://www.facebook.com/Programa-de-Conservacion-de-Tortugas-Marinas-Cucsur-UDG-169726823071035/). The Campamento also engages in an active community outreach programme, and facilitates nest conservation programmes and sea turtle biology programmes for the local schoolchildren, the local fishing village, the university community and the international community.

Genetic samples were collected at Campamento Tortuguero La Gloria in August 2008 under Mexico Permit number SGPA/DGVS/04102/08. Olive ridley sea turtles nesting on this beach are solitary nesters. Cloacal fluids, including blood, were collected in 50 ml centrifuge tubes during oviposition from female *L. olivacea* turtles as described by Bowen et al. (1998), and modified from Owens and Ruiz (1980). Samples were centrifuged, separated and stored in liquid nitrogen. In the laboratory they were ultracentrifuged to separate serum and red blood cells. Metal tags were typically attached to right flippers as part of the established CUCBA programme, and used as an identifier for the samples. Red blood cell samples were exported to the USA under US CITES Permit 10US234773/9, and used for DNA extraction.
**DNA extraction, amplification and purification**

DNA was extracted from the dried tissue using a DNeasy Kit (Qiagen 2011; Qiagen, Hilden, Germany) following the manufacturer's protocol. Polymerase chain reaction (PCR) amplification of an 875 bp D-loop mitochondrial DNA fragment was carried out with the primers LCM15382 (5’-GCTTAACCCTAAAGCATTGG-3’) and H950 (5’GTCTCGGATTAGGGTTT-3’) using methods described by Naro-Maciel et al. (2012). Each 20 µl reaction consisted of 1 µl DNA template, 10 µl distilled H$_2$O, 1.5 µl MgCl$_2$, 0.8 µl bovine serum albumin, 0.5 µl of each primer and 0.2 µl GoTaq DNA Polymerase (Promega, Madison, WI). PCR conditions were: 95°C for 5 min; 35 cycles of 95°C for 30 s, 57°C for 45 s and 72°C for 60 s; final extension at 72°C for 10 min followed by a 4°C hold. Eight microlitres of each product was visualized in 2% agarose gel to check for size and purity.

The PCR products were cleaned for sequencing using 0.5 µl 10× AP Buffer, 0.6 µl Antarctic Phosphatase (New England Biolabs, Ipswich, MA), 0.6 µl Exonuclease I (New England Biolabs) and 4 µl PCR product under the following conditions: 37°C for 15 min; 80°C for 15 min. Gel extraction using the Qiaquick Gel Extraction Kit (Qiagen 2011) was used to purify and isolate the proper fragment in any samples that had non-specific amplification. All amplified products were sequenced in both directions using Sanger sequencing at the DNA Analysis Facility on Science Hill, Yale University (http://dna-analysis.yale.edu). Table 1 lists field number and sea turtle flipper tag (when available), and associated D-loop sequence GenBank accession number, and indicates if the animal was satellite tagged.

**Sequence editing and alignment**

Forward and reverse D-loop sequences were obtained from 14 olive ridley sea turtle samples. The sequences were edited and compiled into consensus sequences using Geneious (version 6.1.6). To compare the sequences obtained in this study with those of other *L. olivacea* individuals (Table 2 in supporting material), the sequences were aligned with all *L. olivacea* D-loop sequences in GenBank (Bowen et al. 1998; Shanker et al. 2004; López-Castro and Rocha-Olivares 2005; Jensen et al. 2013) as well as

| Adopted name     | Identification number (this study) | GenBank accession number | Haplotype represented |
|------------------|-----------------------------------|--------------------------|-----------------------|
| Gloria           | 21 VA381                           | KY091840                 | MLK                   |
| Esperanza        | 22 VA383D                          | KY091841                 | MLN                   |
| No transmitter   | 24                                 | KY091842                 | MLK                   |
| No transmitter   | 25                                 | KY091843                 | MLN                   |
| No transmitter   | 26                                 | KY091844                 | MLK                   |
| No transmitter   | 27C                                | KY091845                 | MLK                   |
| No transmitter   | 28                                 | KY091846                 | MLK                   |
| No transmitter   | 29 VA382                           | KY091847                 | MLK                   |
| Carmen           | 30 VA395                           | KY091848                 | MLK                   |
| No transmitter   | 32 VA399                           | KY091849                 | MB32_L                |
| No transmitter   | 33 VA393                           | KY091850                 | MB33_L                |
| Shadowdancer     | 34 VA378                           | KY091853                 | MLK                   |
| No transmitter   | 35 VA394                           | KY091851                 | MB35_L                |
| Buttercup        | VA398                              | KY091852                 | MLK                   |
Table 2. Relative frequencies of each haplotype in each population and GenBank accession number.

| Jalisco | Chiapas | Oaxaca | Guerrero | Sinaloa | Baja California | Costa Rica | Surinam | Brazil | Guinea Bissau | Australia | Sri Lanka | Malaysia | India | GenBank Accession | Citation(s)          |
|---------|---------|--------|----------|---------|----------------|------------|---------|--------|---------------|-----------|-----------|----------|-------|----------------|---------------------|
| (26)    | (20)    | (20)   | (18)     | (15)    | (48)          | (23)       | (11)    | (15)   | (4)           | (154)     | (13)      | (5)      | (81)  |                  |                     |
| KSK_1L  | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.025 AF513542.1 | Shanker et al. 2004  |
| KSK_2L  | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.012 AF314654.1 | Shanker et al. 2004  |
| KSK_3L  | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.049 AF513543.1 | Shanker et al. 2004  |
| KSK_4L  | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.012 AF513545.1 | Shanker et al. 2004  |
| KSK_5L  | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.012 AF513546.1 | Shanker et al. 2004  |
| BBF     | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.615 0.852     | Bowen et al. 1998    |
| BBK     | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.617 0.231 1 | Bowen et al. 1998, Shanker et al. 2004 |
| MB32_L  | 0.038   | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.025 AF513542.1 | Shanker et al. 2004  |
| MB33_L  | 0.038   | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.012 AF314654.1 | Shanker et al. 2004  |
| MB35_L  | 0.038   | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.049 AF513543.1 | Shanker et al. 2004  |
| MJLo1_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.038 AF513545.1 | Shanker et al. 2004  |
| MJLo10_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513546.1 | Shanker et al. 2004  |
| MJLo11_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.019 AF513546.1 | Shanker et al. 2004  |
| MJLo12_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513544.1 | Shanker et al. 2004  |
| MJLo13_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513545.1 | Shanker et al. 2004  |
| MJLo14_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513546.1 | Shanker et al. 2004  |
| MJLo16_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.019 AF513545.1 | Shanker et al. 2004  |
| MJLo17_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513545.1 | Shanker et al. 2004  |
| MJLo19_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513546.1 | Shanker et al. 2004  |
| MJLo20_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513544.1 | Shanker et al. 2004  |
| MJLo21_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513546.1 | Shanker et al. 2004  |
| MJLo22_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513545.1 | Shanker et al. 2004  |
| MJLo23_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513544.1 | Shanker et al. 2004  |
| MJLo27_L| –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.043 AF513545.1 | Shanker et al. 2004  |
| MJLo3_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.065 AF513543.1 | Shanker et al. 2004  |
| MJLo4_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.032 0.154 0.065 | Shanker et al. 2004  |
| MJLo5_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513544.1 | Shanker et al. 2004  |
| MJLo6_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513544.1 | Shanker et al. 2004  |
| MJLo7_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.013 AF513546.1 | Shanker et al. 2004  |
| MJLo8_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513543.1 | Shanker et al. 2004  |
| MJLo9_L | –       | –      | –        | –       | –              | –          | –       | –      | –             | –         | –         | –        | –     | 0.006 AF513543.1 | Shanker et al. 2004  |

(Continued)
| Population | Jalisco | Chiapas | Oaxaca | Guerrero | Sinaloa | Baja California | Costa Rica | Surinam | Brazil | Guinea | Bissau | Australia | Sri Lanka | Malaysia | India |
|------------|---------|---------|--------|----------|--------|----------------|------------|---------|--------|--------|--------|-----------|-----------|----------|-------|
| GenBank Accession | | | | | | | | | | | | | | | | |
| MLE | – | – | – | – | – | 0.021 | – | – | – | – | – | – | – | – | – | AY920522.1 López-Castro and Rocha-Olivares 2005 |
| MLK | 0.346 | – | – | – | – | 0.917 | 0.304 | – | – | – | – | – | – | – | – | 0.012 AY920519.1 This study, and López-Castro and Rocha-Olivares 2005, Jensen et al. 2013, Bowen 1998 |
| MLM | – | – | – | – | – | 0.021 | – | – | – | – | – | – | – | – | – | AY920520.1 López-Castro and Rocha-Olivares 2005 |
| MLN | 0.077 | – | – | – | – | 0.021 | – | – | – | – | – | – | – | – | – | AY920521.1 This study, and López-Castro and Rocha-Olivares 2005 |
| MLO | – | – | – | – | – | 0.021 | – | – | – | – | – | – | – | – | – | AY920523.1 López-Castro and Rocha-Olivares 2005 |
| RBLo_B | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_C | – | – | 0.05 | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_E | 0.038 | – | 0.05 | – | 0.133 | 0.13 | – | 0.13 | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_F | – | – | – | – | 0.111 | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_G | – | 0.05 | – | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_I | – | – | 0.05 | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_K | 0.269 | 0.7 | 0.65 | 0.611 | 0.6 | – | 0.261 | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_M | 0.038 | – | 0.05 | 0.222 | 0.067 | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_N | 0.038 | 0.2 | 0.15 | 0.056 | 0.2 | – | 0.217 | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_O | 0.038 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_P | – | 0.05 | – | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |
| RBLo_Z | 0.038 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | na Abreu-Grobois 1999 |

Population sample size is indicated below the name of the population. Synonyms for each haplotype name are listed in Table 3, and ocean basin, and citation are listed for each collection site in Table 4.
sequences manually extracted from the literature (Briseño-Dueñas 1998; Abreu-Grobois 1999). Haplotypes from each source were given unique names for clarity, alternative names used by various authors for each haplotype name are included in Table 3 for clarity, and Table 4 includes a summary of sampled ocean basins and associated citations. A Clustal alignment was executed using MEGA version 6.06 (Tamura et al. 2013). The alignments were checked by hand using Mesquite version 3.02 (Maddison and Maddison 2016).

Arlequin version 3.5 (Excoffier and Lischer 2010) was used for all genetic analyses. To determine the amount of genetic diversity within each population, nucleotide diversity and mean number of pairwise differences between haplotypes were calculated for each population. To determine whether populations were genetically distinct from each other, linearized pairwise $F_{ST}$ (Slatkin 1995) was calculated between populations. Values of $p$ are determined by permutation tests. To determine the scale at which

### Table 3. The name used for a haplotype in this paper, published synonyms, citations for the original haplotype name, and citation for the synonym.

| Haplotype name | Synonym | Original citation | Citation for synonym |
|----------------|---------|-------------------|----------------------|
| BBF            | Bowen F | Bowen et al. 1998 | Bowen et al. 1998    |
| BBK            | Bowen K | Bowen et al. 1998 | Shanker et al. 2004  |
| MJLo1_L        | MJLo_15_L | Jensen et al. 2013 | Jensen et al. 2013   |
| MJLo1_L        | Bowen J | Jensen et al. 2013 | Bowen et al. 1998    |
| MJLo14_L       | MJLo18_L | Jensen et al. 2013 | Jensen et al. 2013   |
| MJLo2_L        | Bowen G | Jensen et al. 2013 | Bowen et al. 1998    |
| MJLo27_L       | Bowen M | Jensen et al. 2013 | Bowen et al. 1998    |
| MJLo4_L        | Bowen H | Jensen et al. 2013 | Bowen et al. 1998    |
| MLK            | Bowen N | López-Castro and Rocha-Olivares 2005 | Bowen et al. 1998 |
| MLK            | MB 34   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 24   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 26   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 398  | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 21   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 27   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 28   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 29   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLK            | MB 30   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLN            | MB 22   | López-Castro and Rocha-Olivares 2005 | this study          |
| MLN            | MB 25   | López-Castro and Rocha-Olivares 2005 | this study          |

### Table 4. Ocean basin and original citation for samples collected at each site.

| Collection site | Ocean basin    | Citation                                                                 |
|-----------------|----------------|--------------------------------------------------------------------------|
| Jalisco         | Pacific        | Lazo-Wasem et al. 2011, Abreu-Grobois 1999, Briseño-Dueñas 1998          |
| Chiapas         | Pacific        | Abreu-Grobois 1999, Briseño-Dueñas 1998                                  |
| Oaxaca          | Pacific        | Abreu-Grobois 1999, Briseño-Dueñas 1998                                  |
| Guerrero        | Pacific        | Abreu-Grobois 1999, Briseño-Dueñas 1998                                  |
| Sinaloa         | Pacific        | Abreu-Grobois 1999, Briseño-Dueñas 1998                                  |
| Baja California | Pacific        | López-Castro and Rocha-Olivares 2005                                    |
| Costa Rica      | Pacific        | Bowen et al. 1998, Briseño-Dueñas R. 1998                                |
| Surinam         | Atlantic       | Bowen et al. 1998                                                        |
| Brazil          | Atlantic       | Bowen et al. 1998                                                        |
| Guinea Bissau   | Atlantic       | Bowen et al. 1998                                                        |
| Australia       | Indo-Pacific   | Jensen et al. 2013, Bowen et al. 1998                                   |
| Sri Lanka       | Indo-Pacific   | Bowen et al. 1998                                                        |
| Malaysia        | Indian         | Bowen et al. 1998                                                        |
| India           | Indian         | Shanker et al. 2004                                                      |
most genetic differentiation occurs, an analysis of molecular variance (AMOVA) (Excoffier 1992) was performed. For the AMOVA, genetic differentiation was partitioned into the following scales, between ocean basin; Pacific (Jalisco, Chiapas, Oaxaca, Guerrero, Sinaloa, Baja California, Costa Rica), Atlantic (Surinam, Brazil, Guinea Bissau), Indian (Malaysia, India) and Indo-Pacific (Australia, Sri Lanka); between populations within ocean basin; and within populations. A minimum spanning network of all haplotypes (Kruskal 1956; Prim 1957) was also estimated in Arlequin and visualized with HapStar (Teacher and Griffiths 2011). This network was then modified in Adobe Illustrator (Figure 1) so that the area of each circle was proportional to the frequency of that haplotype (common haplotypes have larger circles). Haplotypes were coloured according to the

![Haplotype network derived from 704 bp mitochondrial D-loop fragment. Circle sizes are proportional to the frequency of each haplotype. The black circles are hypothetical haplotypes not sampled. Each colour represents the ocean basin where the sample was taken: blue is Pacific Ocean, yellow is Indian Ocean, red is Atlantic Ocean, and green is Indo-Pacific Ocean.]

Figure 1.
region in which they were found (Pacific in blue, Indian in yellow, Atlantic in red and Indo-Pacific in green). The haplotypes that were shared between the regions are shown proportionally to the number found in each region using a pie chart.

**Satellite tag attachment**

Between 4 August and 8 August 2008, five of the sampled female olive ridley sea turtles were satellite tagged under Mexico Permit number SGPA/DGVS/04102/08 (Table 1). Sea turtles were selected during evening patrols, which began at 22:00. Once an animal was encountered its body condition was assessed as healthy, underweight or emaciated. Solitary nesting females in healthy condition were opportunistically selected for tagging after they deposited their eggs and covered their nest. Once the nesting was completed the sea turtle was secured and shielded from the water to attach the satellite tag. The satellite tags used for this project were four SPLASH tags (time–depth recorders) Wildlife Computers, Redmond, WA and one wildlife computer SPOT tag (position-only tags). Initial tag weight and the weight of the 5-minute epoxy and fibreglass were estimated. These weights were summed and compared with to the animal’s body weight to reduce drag. The carapace was cleaned and abraded with 60 grit sand paper, and then cleaned with acetone or ethanol. The tags were attached to the animal’s carapace with a two-part 5-minute Devcon epoxy. The liquid epoxy hardened through an exothermic reaction, which took between 3 and 5 minutes. The epoxy hardened to full strength within 1 hour of attachment. The mixed two part epoxy was brushed on an area approximately 3 cm larger than the footprint of the tag and allowed to cure for 30 seconds. The remaining epoxy resin was added to the bottom of the tag before it was placed on the animal with the antenna facing forward. Fibreglass strips were placed on the seam between the tag and the carapace to add strength. Once the epoxy had glazed over, the animal was released at the tagging site to return to the surf.

All tags were programmed to sample for data every 10 seconds and signal up to 500 times per day for the first 3 months after deployment. Once the tag reached the 3 month mark the signalling rate was switched to every other day to save battery life. Splash tags were programmed to sample every 10 seconds and collect data on dive duration, dive depth, and time at temperature. Data were logged into one of 14 bins set to predetermined values to collect dive, depth, duration, and temperature from Splash Tags (DiGiovanni et al., in preparation). These data were summarized over a 4 hour period and transmitted via satellite link whenever the sea turtle surfaced long enough to transmit a signal. Histograms started collecting data at 01:00 GMT for Splash tags and 00:00 GMT for SPOT 5 tags.

These bins and periods were separated into the following GMT periods, 02:00, 06:00, 10:00, 14:00 and 22:00 for the Splash tags. The SPOT 5 tag had data transmitted in the following bins 00:00, 04:00, 08:00, 12:00, 16:00 and 22:00. Tags were programmed to sample position data every 10 seconds and were programmed to signal daily for up to 90 days. These data were internally processed by the ARGOS system and run through location filters (Least Squares or Kalman filters) to remove locations that were well outside logical possibilities. Locations were assigned a class code (3, 2, 1, 0, A and B) and assigned an estimated error < 250 m, > 250 < 500 m, > 500 m < 1500 m, > 1500. For this study we used only the class code 3, which had the smallest error estimate. These
data were sufficient to give us estimated post-nesting migration movements on a broad scale.

Results

Population genetics

A 699 bp segment of the mitochondrial D-Loop control region was successfully obtained from 14 females from Campamento Tortuguero La Gloria in Jalisco, Mexico. These 14 samples were assigned to one of five haplotypes. Three haplotypes are new to this species, and were present in one turtle each (MB32_L, MB33_L, and MB35_L; Table 2 in supporting material). One (MLN) was present in two of our turtles and was also found in the Baja California samples reported by López-Castro and Rocha-Olivares (2005) (Table 2 in supporting material). The fifth haplotype, (MLK), was present in nine of our turtles, the majority of the Baja California samples (López-Castro and Rocha-Olivares 2005), as well as in Costa Rican and Indian populations (Bowen et al. 1998; Shanker et al. 2004) (Table 2 in supporting material). Although our alignment shows that none of our haplotypes are shared with a previous study of the same beach (Abreu-Grobois 1999, Table 2 in supporting material), López-Castro and Rocha-Olivares (2005) reports that MLN and MLK are identical to Abreu-Grobois (1999) RBLOn and RBLOk haplotypes from turtles sampled at Campamento La Gloria in Jalisco 10 years earlier than our sampling. These sequences differ at four nucleotides.

Across all of the populations for which genetic data are available, nucleotide diversity is low (Table 5). Most loci in the mitochondrial region that was sequenced are invariable within populations. The mean numbers of pairwise differences between haplotypes within populations are also fairly low, with values varying between about one nucleotide, and about four nucleotides, with the exception of the Sri Lankan population in which haplotypes vary by about nine nucleotides on average. Haplotypes in Jalisco vary by three nucleotides on average.

Table 5. Summary statistics of genetic diversity in each population.

| Population (sample size) | Number of haplotypes | Nucleotide diversity ± SD | Mean no. of pairwise differences between haplotypes ± SD |
|--------------------------|----------------------|---------------------------|--------------------------------------------------------|
| Jalisco (n = 26)         | 11                   | 0.0052 ± 0.0031           | 3.6462 ± 1.9078                                         |
| Chiapas (n = 20)         | 4                    | 0.002 ± 0.0016            | 0.9947 ± 0.7                                           |
| Oaxaca (n = 20)          | 6                    | 0.002 ± 0.0016            | 0.9579 ± 0.6818                                         |
| Guerrero (n = 18)        | 4                    | 0.003 ± 0.0021            | 1.4706 ± 0.9335                                         |
| Sinaloa (n = 15)         | 4                    | 0.0023 ± 0.0018           | 1.1048 ± 0.7645                                         |
| Baja California (n = 48) | 5                    | 0.0004 ± 0.0005           | 0.2899 ± 0.3124                                         |
| Costa Rica (n = 23)     | 6                    | 0.0068 ± 0.0041           | 3.3202 ± 1.7695                                         |
| Surinam (n = 11)         | 1                    | 0 ± 0                     | 0 ± 0                                                  |
| Brazil (n = 15)          | 1                    | 0 ± 0                     | 0 ± 0                                                  |
| Australia (n = 154)      | 22                   | 0.003 ± 0.0019            | 2.1002 ± 1.1787                                         |
| Sri Lanka (n = 13)       | 3                    | 0.0203 ± 0.0112           | 9.5128 ± 4.6693                                         |
| Malaysia (n = 5)         | 1                    | 0 ± 0                     | 0 ± 0                                                  |
| India (n = 81)           | 8                    | 0.0035 ± 0.0023           | 1.6306 ± 0.9732                                         |
| GuineaBissau (n = 4)     | 1                    | 0 ± 0                     | 0 ± 0                                                  |

Columns represent the number of haplotypes found, the average nucleotide diversity, and the mean number of pairwise differences between haplotypes.
The AMOVA (Table 6) shows that there is significant genetic differentiation at all organizational levels. Approximately 57% of the variation found is a result of differences between ocean basins, but there is also considerable genetic variation among populations within the ocean basins (~26%), and within populations (~16%).

The pairwise $F_{ST}$s (Table 7) show that the Jalisco population is significantly genetically differentiated from all other populations with the exception of the Costa Rican population. Across all populations, pairwise $F_{ST}$s were relatively high (often > 0.5), reflecting the very few shared haplotypes between populations, and suggesting low gene flow between populations. Likewise, the Baja California population is genetically distinct from all other eastern Pacific populations (Table 7). However, some populations are not significantly genetically differentiated from each other, probably reflecting high gene flow between those populations. For example, in the Pacific region, the pairwise $F_{ST}$s between the Sinaloan, Oaxacan and Guerrero populations are not significantly different from zero (Table 6). Further, the Chiapas population is not genetically distinct from the Oaxacan or Sinaloan populations. The Atlantic populations show the most similarity; all three populations are genetically identical to each other. In the eastern India and Indo-Pacific regions the pattern is more complex, some of the populations in the two regions are not significantly genetically distinct from each other. For example, Malaysia and Australia are in the Indian and Indo-Pacific regions, respectively, but are not significantly genetically isolated from each other. Sampling, however, was extremely low in some of these populations, so these results may not reflect the complete genetic diversity within these populations or precise estimates of allele frequencies within populations.

The haplotypes clustered into three main groups (Figure 1): the haplotypes found in India (KSK1-5) differed from all others by 16 mutational steps, those found by Briseño-Dueñas (1998) and Abreu-Grobois (1999) in Mexico and Costa Rica differed from all others by three mutational steps, and the remainder clustered loosely between them. Most of the haplotypes were found only in one region (Figure 1). However, four were found in two regions (i.e. MJLo1_L, MLK, BBK, and MJLo27_L). MJLo1_L was found in both the Indian and Indo-Pacific regions, MLK was found in the Pacific and Indian regions, BBK was found in both the Indian and Indo-Pacific regions, and MJLo27_L was found in both the Pacific and Indo-Pacific regions. The haplotypes found in this study fall in the centre of this network. Both the MLK and MLN haplotypes were found in olive ridley sea turtles nesting in Jalisco and in Baja California, suggesting greater than expected gene flow between the two populations.

### Table 6. Analysis of molecular variance, partitioning genetic variance between hierarchical levels.

| Source of variation          | dF | Sum of squares | Variance component | Percentage of variation |
|------------------------------|----|----------------|--------------------|------------------------|
| Between regions (Ocean Basins) | 3  | 1316.836       | 3.333*             | 57.19                  |
| Among populations within regions | 10 | 309.942        | 1.559***           | 26.75                  |
| Within populations           | 439| 410.977        | 0.936***           | 16.06                  |
| Total                        | 452| 2037.755       | 5.829              |                        |

All variance components are significantly different from zero: * $p < 0.05$, *** $p < 0.0001$

Populations are grouped into four ocean basins, Atlantic, Pacific, Indian, and Indo-Pacific.
Table 7. Slatkin’s linearized pairwise $F_{ST}$ between populations.

| Population          | Jalisco (P) | Chiapas (P) | Oaxaca (P) | Guerrero (P) | Sinaloa (P) | Baja California (P) | Costa Rica (P) | Australia (IP) | Sri Lanka (IP) | Malaysia (I) | India (I) | Surinam (A) | Brazil (A) | Guinea Bissau (A) |
|---------------------|-------------|-------------|------------|--------------|-------------|---------------------|----------------|----------------|----------------|--------------|------------|-------------|------------|------------------|
| Jalisco             | 0           | –           | –          | –            | –           | –                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Chiapas             | 0.35        | 0           | –          | –            | –           | –                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Oaxaca              | 0.348       | −0.028      | 0          | –            | –           | –                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Guerrero            | 0.332       | 0.069       | 0.012      | 0            | –           | –                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Sinaloa             | 0.322       | −0.025      | −0.044     | 0.002        | 0           | –                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Baja California     | 0.423       | 0.911       | 0.912      | 0.894        | 0.913       | 0                   | –              | –              | –              | –            | –          | –           | –          | –                |
| Costa Rica          | 0.02        | 0.196       | 0.194      | 0.2          | 0.165       | 0.633               | 0              | –              | –              | –            | –          | –           | –          | –                |
| Australia           | 0.615       | 0.782       | 0.781      | 0.777        | 0.777       | 0.652               | 0.67           | –              | –              | –            | –          | –           | –          | –                |
| Sri Lanka           | 0.594       | 0.698       | 0.699      | 0.674        | 0.664       | 0.808               | 0.605          | 0.714          | –              | –            | –          | –           | –          | –                |
| Malaysia            | 0.512       | 0.895       | 0.898      | 0.854        | 0.89        | 0.918               | 0.602          | 0.403          | 0.451          | 0            | –          | –           | –          | –                |
| India               | 0.89        | 0.922       | 0.922      | 0.918        | 0.92        | 0.942               | 0.895          | 0.894          | 0.437          | 0.914        | –          | –           | –          | –                |
| Surinam             | 0.545       | 0.885       | 0.889      | 0.846        | 0.887       | 0.943               | 0.604          | 0.51           | 0.58           | 1            | 0.92       | –           | –          | –                |
| Brazil              | 0.575       | 0.898       | 0.901      | 0.863        | 0.901       | 0.947               | 0.634          | 0.519          | 0.624          | 1            | 0.923      | 0           | 0          | –                |
| Guinea Bissau       | 0.464       | 0.852       | 0.856      | 0.798        | 0.844       | 0.936               | 0.523          | 0.477          | 0.455          | 1            | 0.913      | 0           | 0          | –                |

Values in bold type indicate significant $F_{ST}$ showing genetic isolation between populations. Italicized values indicate non-significant $F_{ST}$s, pairs of populations that are genetically indistinguishable. Coloured cells are population comparisons within the same ocean basin. Within-Pacific comparisons are shown in blue, within-Indo Pacific comparisons are in green, within-Indian comparisons are in yellow, and within-Atlantic comparisons are in red.
**Satellite tracking**

From the five tagged animals, we received telemetry data over periods ranging from 22 to 89 days (Table 8, median was 60 days). Movement data were evaluated by looking at the distance displaced from the tagging site. The satellite positional data were used to build a post-nesting migration map using ArcGISv10.4 for the four turtles exhibiting post-nesting migration behaviour (Figure 2). The satellite tracking of the fifth animal, Carmen, lost signal during inter-nesting 22 days after tagging (Table 8). Although sample size is small, two patterns emerge. Three of the five animals travelled approximately 570 nautical miles offshore in a south-southwest direction into the pelagic zone after nesting. Two of these animals had the MLK haplotype, and one animal had the MLN haplotype. The remaining two animals moved north and south along the coast, and had the MLK haplotype (Figure 2). Animals with the MLK haplotype are indicated with a solid line, and the animal with the MLN haplotype is represented with a dotted line. The satellite data demonstrate that turtles of identical provenance can have different post nesting migration behaviours and hence different feeding and mating grounds.

**Discussion**

This study reports new genetic diversity in Campamento Tortuguero La Gloria, and confirms the reported genetically distinct populations within and between regions studied, as well as illustrating the relationship among mitochondrial haplotypes for *L. olivacea*. The study suggests greater than expected genetic diversity for olive ridley sea turtles nesting at Campamento Tortuguero La Gloria, and supports the need for genetic resampling of protected wildlife species that can reveal greater than expected diversity. Furthermore, this paper supports the conservation priority status of the Campamento Tortuguero La Gloria because of the rich genetic diversity represented by the solitary nesting females, which was similar to the level of genetic diversity observed in the arribada samples of Costa Rica, and significantly higher than the genetic diversity observed in arribada samples from Oaxaca, Mexico and Orissa, India (Table 5).

**Table 8.** Summary of olive ridley satellite tag data on Campamento Tortuguero La Gloria.

| Tag PTT # | Adopted name and GenBank accession number and haplotype | Deploy date | Last position | At large (days) | Distance displace (km) |
|-----------|---------------------------------------------------------|-------------|---------------|----------------|------------------------|
| 62,154    | Gloria KYO91840 MLK                                      | 8/4/2008    | 10/25/2008    | 82             | 1072                   |
| 86,301    | Shadowdancer KYO91853 MLK                                | 8/6/2008    | 10/19/2008    | 74             | 206                    |
| 86,302    | Carmen KYO91848 MLK                                      | 8/8/2008    | 8/30/2008     | 22             | 16                     |
| 86,303    | Buttercup KYO91852 MLK                                   | 8/6/2008    | 11/3/2008     | 89             | 1519                   |
| 86,306    | Esperanza KYO91841 MLN                                   | 8/7/2008    | 10/12/2008    | 66             | 1075                   |
|           | Median                                                   |             |               | 70             | 639                    |

Turtles were named by local schoolchildren as part of *Project Migration*, a programme that helps school children to learn science through turtle tracking.
The three newly reported haplotypes (MB32_L, MB33_L, MB35_L) for *L. olivacea* support our hypothesis that repeated sampling can increase the known genetic diversity for the species. The genetic data also support bottleneck recovery models postulated by Plot et al. (2012) that predict greater than expected genetic diversity over time for protected species whose population sizes are increasing.

The other two haplotypes detected in this study were MLN and MLK. MLN had been previously detected in Baja California, and MLK in Baja California, Costa Rica and India. The presence of these two haplotypes in the beach we studied are surprising and increase our understanding of population structure and gene flow in this species between eastern Pacific and Indian Ocean basins. Although populations in Baja California share these haplotypes with those in Jalisco, the Baja population is significantly genetically distinct from all other eastern Pacific populations, suggesting that

![Figure 2. Map of sea turtle migration for five tagged olive ridley sea turtles nesting on Campamento Tortuguero La Gloria, Jalisco, Mexico. Sea turtles with haplotype MLK are observed swimming into the pelagic zone in a south-southwest direction, and along the coast (solid line). The single sea turtle with the haplotype MLN also swam in a south-southwest direction (dotted line).](image)
gene flow between them is rare. The Jalisco population is also genetically distinct from all other eastern Pacific populations (Table 7). Increased sampling at other eastern Pacific beaches might change this finding.

The four haplotypes that are shared between basins suggest that there is some limited gene flow between the Pacific, Indo-Pacific and Indian populations. Haplotypes were found shared between all combinations. Further, most of the turtles sampled in this study shared the MLK haplotype with turtles from India (Table 2, Bowen et al. 1998; López-Castro and Rocha-Olivares 2005). This suggests that there is greater trans-Pacific migration of olive ridley sea turtles than previously known. However, the Atlantic populations appear to be genetically isolated from the remaining populations, with no shared haplotypes between the Atlantic populations and other populations. Further, all of the individuals sampled in the Atlantic basin are genetically identical, suggesting a bottleneck event in the past and barriers to gene flow between Atlantic and Pacific basins.

Post-nesting satellite tracking revealed that MLK females travel north and south along the coast supporting potential gene flow between Jalisco and Baja California, as well as long-distance offshore migration behaviour that supports a trans-Pacific exchange. This provides evidence that post-nesting migration behaviour for closely related individuals is diverse and supports flexible behavioural strategies that may increase the opportunity for gene flow across ocean basins. It suggests that the MLK haplotype, which is found across much of the range of the olive ridley sea turtle, is probably an ancestral haplotype, and the ability to access diverse post-migration feeding grounds can increase gene flow across the species range and distribution. Our results also show that post-nesting migration behaviour does not characterize or define maternal lineages. Female turtles with the same haplotype can exhibit different post-nesting migration patterns. In the case of haplotype MLK, turtles can migrate north and south along the coast as well as off shore into the pelagic zone.

Although our study illustrates the importance of resampling populations to accurately measure genetic diversity in populations, it does not support sampling bias between olive ridley arribada and solitary nesting populations. Our study included samples from four arribada beaches (i.e. La Escobilla, Oaxaca Mexico; Orissa, India; and Costa Rican Beaches, Nancite and Ostional), and 10 solitary nesting beaches. There was no significant difference in genetic diversity observed between solitary and arribada beaches, suggesting that both groups may benefit from repeated sampling.

Figure 1 represents the analysis of all aligned olive ridley D-loop sequences. Although haplotypes MLN and MLK may be shared with turtles previously sampled at Campamento Tortuguero La Gloria of the Jalisco Coast, Mexico, our analysis suggests that our sequences are not identical to the D-loop sequences reported by Abreu-Grobois (1999) 10 years earlier. In an attempt to disambiguate the data, haplotype synonyms were tracked in the literature as they tend to be renamed with every new data set (Table 3 and Table 4). López-Castro and Rocha-Olivares (2005) reported that their Baja California haplotypes had all been previously reported by Briseño-Dueñas (1998) or Shanker et al. (2004). However, our analysis of their GenBank data did not support their claim.

In summary, our study adds to the genetic diversity of the olive ridley sea turtle species by at least three new haplotypes, and by as many as five new haplotypes for Campamento Tortuguero La Gloria. More sampling is necessary for all previously
sampled beaches to accurately estimate the current population structure of this species as its population size increases.

**The importance of small-scale fisheries and local community action in sea turtle conservation**

In our study, we found that genetic diversity is highest in Campamento Tortuguero La Gloria (Table 5), suggesting that this beach deserves greater recognition, conservation support and resources than it currently receives for olive ridley sea turtle protection and conservation. The beach is a success story, because although significant threats to sea turtle populations due to coastal small-scale, passive net fisheries, and discarded ghost nets continue to receive global attention (Gilman et al. 2009, Alfaro-Shigueto et al. 2010, 2011; Gunn et al. 2010; Jensen et al. 2013), less is reported on the sea turtle conservation successes of small community resource management programmes (Hickey and Johannes 2002).

Campamento Tortuguero La Gloria provides regular conservation education programmes to children and families in the immediate villages, as well as to university students and guests agreeing to work as volunteers. They include regular overnight education programmes for teachers and children, and work in collaboration with the neighbouring small-scale fishermen and their families to protect the viability and sustainability of local resources to keep the coastline clean and safe for all community partners. It is not unusual to see families of the small fisheries involved in the protection of the nesting turtles, releasing turtles caught in nets, and cleaning waters by physically removing trash and plastic from the sand and water (Pinou, personal observation).

This mutual relationship between the small-scale fishery community and sea turtle conservation camp maintains a respectful, reciprocally sustainable environment that can improve sea turtle survivorship by decreasing mortality caused by beach trash, egg poaching and consumption of turtle meat. Furthermore, it improves water quality and beach habitat for a sustainable small-scale fishery. The collaboration provides a sustainable income for fishing families as small-scale community businesses, and in return fishermen and their families monitor their fishing gear closely for trapped turtles that they release, and facilitate successful sea turtle nesting as they help simultaneously to conserve beaches and water quality.

Our study adds to the list of exemplary cases of community solidarity, and strongly advocates for the increased recognition and support of Campamento Tortuguero La Gloria as an olive ridley sea turtle beach of special attention. Strong grass roots education programmes in coastal communities are effective in teaching those communities the importance of conserving coastal resources (Macrovaldi and Macrovaldi 1999; Campbell 2007; Campbell et al. 2007; Gjertsen and Niesten 2010). Such successful community-based conservation practices provide opportunities for alternative income to sea turtle consumption and egg poaching, contribute to community beach clean-up that reduces coastal waste and dumping of items such as abandoned fishing gear, and can result in voluntary temporary closures of local fisheries that are self-managed by the local communities and indirectly result in increased sea turtle nesting, cleaner coastlines, and improved sense of community empowerment and cultural independence. Furthermore, small-scale fishery education that focuses on practices that improve the
handling and release of sea turtles captured in the water minimized injury and risk of mortality by increasing the turtles’ post-hooking survival prospects (Gilman et al. 2006, 2009). Such successes reinforce the position of increasing local control of conservation practices often debated in the wider conservation community (Campbell 2007).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Geolocation Information

Campamento Tortuguero La Gloria, Tomatlán Jalisco Mexico (19.8981°N, −105.4232°W).

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