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Tracing the origin of olive ridley turtles entangled in ghost nets in the Maldives: A phylogeographic assessment of populations at risk



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ABSTRACT

Abandoned, lost or discarded fishing nets, (ghost nets) represent a major threat to marine vertebrates. However, thorough assessments of their impact on threatened species are largely missing. In the Maldives, olive ridley sea turtles (*Lepidochelys olivacea*) are frequently caught in ghost nets however the archipelago does not support a significant nesting population. Our aim in this study was to determine the origin of olive ridleys entangled in ghost nets found in the Maldives and evaluate potential impacts on respective source populations.

Based on a citizen science and conservation program, we recorded 132 olive ridley turtles entangled in ghost nets in just one year. Genetic analyses (mtDNA) of entangled individuals and of potential source populations revealed that most captured olive ridleys originated from Sri Lanka and eastern India. Oman could be excluded as source population, even during the prevalence of the south west monsoon. Based on our results and already available published literature, we were able to estimate that the recorded ghost net entanglements accounted for a relatively small amount (0.48%) of the eastern Indian population. However, the entangled turtles accounted for a much larger percentage (41%) of the Sri Lankan population. However, it should be noted that our estimates of population-level mortality are linked to substantial uncertainty due to the lack of reliable information on population dynamics. Consequently, any precautionary protection measures applied should be complemented with improved quantification of turtle recruitment and life-stage specific mortalities.

1. Introduction

Over 1 million species are globally threatened with extinction, a result largely attributed to changes in land and sea use and direct exploitation of organisms (UN, 2019). One group under severe threat includes marine reptiles (Gibbons et al., 2000; Fuentes et al., 2012). Some of the main threats for marine reptiles and turtles, in particular, are incidental capture or bycatch during active fishing practices (Lewison and Crowder, 2007; Cuevas et al., 2018; Alfaro-Shigueto et al., 2018), unregulated coastal development (Harewood and Horrocks, 2008; Mazaris et al., 2009; Dimitriadis et al., 2018), predation from humans (both on nests and adults; Allen et al., 2001; Mancini et al., 2011; Engeman et al., 2006; Koch et al., 2006; Garcuía et al.,

2003) and entanglement in abandoned, lost or discarded fishing gear (ALDFG) (Jensen et al., 2013; Wilcox et al., 2013; Stelfox et al., 2016; Duncan et al., 2017). The quantitative evaluation of these threats must be a focal point of research in order to support the development of conservation strategies and prevent further local and global species extinctions.

Despite the widely acknowledged importance of ghost fishing (Wilcox et al., 2016; Stelfox et al., 2019), its effect on sea turtles and other marine vertebrate populations is substantially understudied (Nelms et al., 2015; Stelfox et al., 2016). Current knowledge gaps may be a direct result of methodological difficulties in quantifying ghost net entanglements. Ghost nets can travel long distances (Wilcox et al., 2013), even across entire oceans (Sayer and Williams, 2015). However,

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travel paths of ghost nets represent a major uncertainty. Moreover, the often-stochastic distribution of ghost nets substantially complicates the quantification of these nets and its impact on marine life.

An accurate impact assessment of ghost nets requires continuous screening over different seasons coupled with quantitative records of turtle entanglement events. Further, genetic analyses of entangled individuals would be ideally acquired in order to identify their potential source populations (population defined in a conservation context, see Moritz, 1994). In the Maldives, olive ridleys appear to be particularly susceptible to entanglement in ghost nets and have been recorded in high numbers throughout the year (Stelfox et al., 2015). While other turtle species are reported to be more threatened by entanglement in other areas of the world, the high frequency of olive ridley turtle entanglements in the Maldives (Stelfox et al., 2019) provide an opportunity to assess the impact of ghost nets on the viability of turtle populations. We also hypothesise that since records of nesting olive ridleys in the Maldives are extremely rare (Stelfox pers. comm), the majority of entanglements are likely to be affecting non-local source populations. Determining the origin of the turtles entangled therefore requires data on their genetics. Importantly, one of the largest gatherings of nesting olive ridleys annually occurs a little north east of the Maldives. These arribadas (Spanish for arrival; Shanker et al., 2004) have been well documented along several beaches off the east coast of India., The genetic structure of these eastern Indian populations has also been relatively well investigated, just as the ones in northern Australia and Sri Lanka (Bowen et al., 1997; Shanker et al., 2004; Jensen et al., 2013). In contrast, however little is known about haplotype composition and frequency of nesting populations in other areas of the Indian Ocean such as Oman and on the southern and eastern African coasts (Rees et al., 2012). This data gap could be especially critical as seasonal switches in ocean currents occur between the South-West (SW) and North-East (NE) monsoon is likely to be important with regard to untangling where the ghost net turtles in the Maldives are coming from. Further, the importance of so called 'orphan haplotypes' i.e. turtles with a genetic structure not linked to a known nesting population has been shown in a previous study (Jensen et al., 2013). Indeed, in this study focused around northern Australia (Jensen et al., 2013), 45% of the turtles assessed belonged to this category. Knowledge of such orphans obviously complicates the design and implementation of management plans of these turtles and the threats they face but is none the less important if we are to effectively limit the effect ghost nets has on this species.

Our aim, therefore, was to assess the impact ghost nets (recorded in the Maldives) had on known olive ridley nesting populations (i.e. source populations) and determine the origin of the entangled individuals. To achieve this goal, we first built on existing knowledge of phylogenetics of nesting olive ridleys' across the Indo Pacific (Shanker et al., 2004; Bowen et al., 1997; Jensen et al., 2013). These were then compared to mitochondrial haplotypes of entangled individuals in the Maldives (i.e. mixed stock analysis). We then attempted to identify if previously reported 'orphan' haplotypes (Jensen et al., 2013) originated from our nesting stock and/or were captured in the genetics of the entangled turtles. Finally, we wanted to explore if season (north east (NE) or south west (SW) monsoons) impacted where the turtles were originating from (Shankar et al., 2002). This was undertaken using a citizen science approach to monitor ghost net catches over a 12 month period across the archipelago. It was hypothesised that those entangled during the NE monsoon would stem from Sri Lanka and eastern Indian genetic stocks. Whilst those entangled during the SE monsoon would originate from turtles nesting in sites such as Oman.

2. Materials and methods

2.1. Monitoring of ghost nets in the Maldives

We used a citizen science approach applied by the Olive Ridley

Project (ORP registered charity no. 1165905) to document ghost nets drifting into the Maldives over a 12-month period (February 2017–February 2018). Since 2013, ORP have run scientific workshops throughout the Maldives, explaining how people (citizen scientists) can safely rescue sea turtles and, where possible collect data on ghost net findings and entanglement cases. Participants were also encouraged to propagate their knowledge to other members of their communities, which allowed ORP to capitalise on multiplication effects and increase the network of data collectors. It should be noted however, that the majority of resorts (where the ORP citizen scientists are predominantly based) are situated in only two of the 26 atolls; North Male and Baa atoll. The data provided in this study therefore only reflects a relatively small portion of the Maldivian archipelago and is likely an underrepresentation of the true number of ghost net and entanglement events.

Data on net characteristics (e.g. mesh size, twine diameter and colour), presence or absence of turtles (species verified by the authors through photo identification), GPS coordinates and date found were recorded via an online portal hosted on the ORP website (https:// oliveridleyproject.org/report-a-ghost-net). When entangled turtles were encountered by our citizen scientists, the turtles were sent to the ORP rehabilitation facility in Baa atoll. Once at the centre, small tissue samples (Permit no. EPA/2017/PSR-T02) were collected from the front left flipper by ORP veterinarians. If this flipper was damaged or missing, alternative flippers were used. In some cases, tissue samples were collected in situ by marine biologists (trained in this task during our workshops) before going to the ORP rehabilitation centre. All samples were immediately stored in 100% ethanol and placed in the refrigerator at -4°c. Accompanying each sample was information on the 'incident', which included: turtle species, sex (if known), curved carapace length (cm), injuries sustained from entanglement, GPS coordinates of where found and date of rescue.

2.2. Genetic characterisation of source populations

Initially, we performed an extensive literature search to identify what previous genetic analysis had been undertaken of olive ridley turtles across the Indian Ocean. First, key word searches on Google Scholar and Science Direct were performed using the search terms "genetics", "mtDNA", "haplotypes", "haplotype network", "Indian Ocean", "bycatch", "population", "phylogenetics", "ghost nets" and "ALDFG" in combination with "olive ridley" or "Lepidochelys olivacea" to identify relevant literature. The resulting articles were used as a starting point to identify additional references providing further data. Our search identified only three articles providing haplotype composition and frequency data for olive ridley sea turtles in the Indian Ocean or wider Indo-Pacific region. These included rookeries along the east coast of India (n = 65 turtles, excluding offshore capture; Shanker et al., 2004), Sri Lanka (n = 17 turtles; Bowen et al., 1997) and Northern Australia (n = 102 turtles; Jensen et al., 2013) (Fig. 1.). Additional data from Peninsular Malaysia and Andaman and Nicobar Islands were excluded because of either low replicate numbers (\leq 5) or lack of sequence data (Bowen et al., 1997; Shanker et al., 2011). All studies were based on sequences of the mtDNA control region, however, studies differed in the length of amplified fragments. For example, the Australian samples were longer (770 bp fragments), whilst the available sequences from turtle populations across eastern India and Sri Lanka were considerably shorter (410 bp or 470 bp).

We complemented the available (previously published) data by analysing additional samples from Oman and eastern India. In Oman, samples from females nesting along a 4 km stretch of beach in Masirah island (n = 33 turtles) were provided to us by the Environment Society of Oman (ESO) (CITES No. 34/2016, 40/2018). These samples were collected during the peak nesting season (February–April) between 2013 and 2017 along with turtle measurements and Photo-ID to ensure repeat nesters were not sampled twice in this study. Samples from



Fig. 1. Nesting sites (triangles), sampling locations of turtles entangled in ghost nets in the Maldivian Archipelago (circles) and bycatch recorded in coastal waters off Madagascar (diamonds). Samples include rookeries in Oman (n = 33; sampled in this study), India (n = 74, including 9 sampled in this study), Sri Lanka (n = 17), Australia (n = 102) as well as ghost net samples from the Maldives (n = 45) and bycatch from Madagascar (n = 9), both sampled in this study.

nesting females in Rushikulya, India (n = 9 turtles), were collected by K. Shanker to give us the larger 770 bp fragment data for this region (Fig. 1). Additionally, a small sample of turtles caught as fisheries by-catch (collected by Kelonia) off the coast of Madagascar (reportedly by French longline fisheries) were also included (n = 9), in order to extend our data collection and potentially identify additional haplotypes.

All samples were collected as small (2–4 mm) tissue biopsies from the flippers as was the case for those entangled in ghost nets. After collection, samples were preserved in 100% molecular grade ethanol and kept at -4 °C until extraction.

2.3. mtDNA extraction and amplification

DNA was extracted from turtle tissue using the DNeasy® Blood & Tissue Kit and following manufactures recommendations. First, DNA quantity and quality were checked by running 1 µl through a spectroptometer (NanoDrop 2000) before being prepared for amplification. Extracted samples were amplified by polymerase chain reaction (PCR) using the forward primer LTEi9 (5'-AGC GAA TAA TCA AAA GAG AAG G-3') and reverse H950 (5'-GTC TCG GAT TTA GGG GTT TA-3') (Abreu-Grobois et al., 2006). These primers target the 880 bp fragment of the mtDNA region. PCRs were run at a 25 µl volume which included, 12.5 µl of PCRBIO Ultra Mix Red (PCRBIO Ultra Polymerase, 6 Mm MgCl₂, 2 Mm dNTP), 1 µl of each primer, 9.5 µl of SIGMA H₂O and 1 µl of template DNA. PCRs were performed on a GeneAmp® 9700 PCR system following a denaturation step of 95 °C for 5 min followed by 45 cycles of denaturation (45 s at 94 °C), annealing (45 s at 56 °C), extension (45 s at 72 °C) and a final extension for 5 min at 72 °C. Analyses of PCR products were performed by gel electrophoresis and imaged using Thermo Scientific. Unsuccessful PCR amplifications went through a second PCR and if still unsuccessful the original tissue was re-extracted. Sequencing of forward and reverse reactions was carried out by Eurofins Scientific and at the Centre for Cellular and Molecular Platforms (C-CAMP, NCBS), Bangalore, India.

2.4. Data analyses

All sequences obtained in this study and from previously published literature were aligned using Clustal W within the Geneious (v11.1.5) software. Newly sequenced samples were manually checked for ambiguity of base-pair identification using an electropherogram and ambiguous sequences from the Maldives (n = 7), Oman (n = 4) and eastIndia (n = 2) were excluded from further analyses.

After quality control, we identified the number of haplotypes in DNAsp V 6.12 (Rozas et al., 2003). A haplotype was defined as a unique sequence differing from other sequences at any nucleotide site. These differences may be described as one or a combination of nucleotide transitions, transversions or INDELS.

Common indices of biodiversity including haplotype richness and evenness (Pielou, 1966) and both weighted and unweighted phylogenetic diversity (Faith, 1992) were computed in R (v 1.1.3; R Core Team, 2013). Rarefaction was performed before analyses on all above-mentioned indices (except haplotype evenness). However, as the population with lowest sequenced individuals (Sri Lanka; n = 17) had much fewer individuals than other populations, we excluded Sri Lanka from rarefaction. Hence, comparisons between the diversity of olive ridley populations in Sri Lanka and other populations must be treated with caution as the different sampling efforts could affect the results. For the above, analyses were performed using the shorter 410 bp segments in order to maximise the number of available individuals.



Fig. 2. Minor injuries across the right and left anterior flipper as a result of ghost net entanglement in the Maldives (left), Picture credit: Olive Riley Project. Complete amputation of right flipper as a result of entanglement in ghost nets in the Maldives (right), Photo Credit: Claire Petros.

We then investigated differences in population structure and composition. We generated two medium joining networks (haplotype networks) using the software NETWORK (Network version 4.5.1.6, 2009). One was undertaken on the short sequences (410 bp) as above and was constructed to show the relationship between haplotypes from published rookeries and those collected in this study. The second version was run on longer sequences up to 770 bp and was constructed to uncover haplotype divergence from the shorter fragment and to potentially identify the origin of orphan haplotypes collected in ghost nets in Australia (i.e. a haplotype not recorded from any source populations) (Jensen et al., 2013). We followed the software user guidelines and applied a double weighting to characters that had deletions or insertions for both networks.

Moreover, we tested whether different nesting sites showed significant differences in their haplotype composition (defined by the shorter 410 bp fragment lengths) in a Discriminate Analyses of Principal Components (DAPC) following Jombart et al. (2010). In brief, mismatches in nucleotide bases (A, C, T and G) of aligned mtDNA were vectorised into a binary matrix (every allele was coded as one variable; 1 s and 0 s indicated presence/absence of alleles in individual haplotype). Further, we used a Principle Component Analyses (PCA) to reduce the number of variables (alleles). The PCA allowed us to use 10 principle components (95% of variance explained) as input for the discriminate analyses (DA), which is limited by the number of allowed input variables (Jombart et al., 2010). The DA was performed using the different rookeries (Fig. 1). After the completion of the DA, we used a Permutational Multivariate Analyses of Variance (PERMANOVA) to test for significant differences between rookeries and identify genetic structuring between populations. Because multiple pairwise comparisons were performed, we applied a Holm-correction to adjust p-values (Holm, 1979). DAPCA and PERMANOVA were implemented in R using the 'MASS' package (Ripley et al., 2013).

Finally, we assessed the contributions of different source populations to entangled turtles found in Maldivian ghost nets using a 'mixstock' analysis (Bolker et al., 2007). Mixstock relies on a 'winBUGS'based Bayesian algorithm that uses Monte Carlo Markov Chain (MCMC) procedures and a hierarchical model structure (Bolker et al., 2007) aimed at estimating the contribution of different sources to a mixed sample. In order to achieve this, we first divided our samples into two groups according to season (NE: n = 21, and SW: n = 15). The results of the two analyses were very similar (Supplementary information S1a) therefore we reran our analysis with all samples pooled (n = 38); this allowed us to include samples that had no date recorded (n = 2). Again, we used 410 bp fragments to maximise the power of our analysis.

Mixstock provides the option to include the different sizes of source populations into calculations (Bolker et al., 2007). Therefore, we compiled estimates of population sizes for all rookeries (Supplementary information S2) and used these estimates as additional input for a second mix-stock analysis using all ghost net samples.

For each analysis, five chains were run at 20,000 steps, each with 10,000 used as burn in. To ensure correct chain convergence with the posterior probabilities, we used the Gelman-Rubin diagnostic (Gelman and Rubin, 1992) and ensured shrink factors remained below 1.2 (Pella and Masuda, 2001). Individuals with orphan haplotypes (haplotypes only found in ghost nets but in no source population) were removed before the final mixed stock analysis (n = 1).

3. Results

Between February 2017 and February 2018, 177 ghost net fragments (incomplete and damaged fishing nets) were recorded (see Stelfox et al., 2019 for more detailed information about net types and responsible fisheries). In these nets, a total of 137 turtles were entangled, including 1 green (curved carapace length not available), 4 hawksbills (curved carapace length range; 30-40 cm) and 132 olive ridley turtles (curved carapace length range; 13–70 cm). Most net fragments entangled only one turtle; however, 20 net fragments entangled multiple turtles (between two-seven) and four turtles were found dead. Net fragments varied in size from large mono-specific gear (in excess of two tonnage) to small football sized fragments. Due to limitations in the field (e.g. sample transport), immediate release upon rescue by volunteers without collection of tissue, and removal of sequences after quality control, we were only able to attain 38 high quality olive ridley sequences in this study. Entangled olive ridleys were found during both monsoons, NE (n = 21) and SW (n = 15) (exact sampling time records missing for two individuals). The olive ridleys which were sequenced (n = 38) ranged in size from between 13 and 69 cm in curved carapace length with 74% (n = 26) being classed as 60 cm or smaller, i.e. sub adults or juveniles. Entangled turtles displayed a wide variety of injuries ranging from shallow lacerations around the flippers and neck to deeply embedded entangling wounds and complete flipper amputations (Fig. 2). In some cases, severe dehydration and death were also reported.

3.1. Diversity and genetic structure of source populations

Four populations (according to nesting country) were assessed in this study. For the shorter sequences (including those truncated from this study), the different populations were characterised by a relatively similar haplotype richness (Fig. 3A). That is except for Oman, which showed a lower value (two haplotypes compared to four found in Australian, Sri Lankan and east Indian populations). The two haplotypes occurring in Oman showed the same relative abundances to each other, resulting in an evenness of 1 (Fig. 3B). In comparison, Indian



Fig. 3. The genetic diversity of olive ridley turtles (*Lepidochelys olivacea*) at different nesting sites and of individuals entangled in ALDFG in the Maldives. Displayed are (A) haplotype richness, (B) evenness of haplotype frequency (C) unweighted phylogenetic diversity and (D) weighted phylogenetic diversity. Phylogenetic diversities were calculated using the faith indices (Faith, 1992). All data for these analyses were based on 410 bp fragments of mtDNA. Prior to calculations for A, C and D, data has been rarefied. The rookeries from Sri Lanka were excluded from rarefaction (indicated by *) due to lower sample numbers (n = 17). Consequently, comparisons to other sites need to be applied with caution.

rookeries (although comprised of four haplotypes), were dominated by one Lo44 (Accession # MN342241), which was reflected in a comparatively lower evenness of 0.34 (Fig. 3B). Interestingly, genetic diversity was lower within Australian rookeries, indicated by low unweighted as well as weighted faith indices (Fig. 3 C–D). This suggests a close relationship among these Australian haplotypes. While unweighted phylogenetic diversity was similar among all other rookeries, Sri Lanka showed the highest weighted genetic diversity (Fig. 3D). Despite lower sample size, Sri Lanka was the only rookery excluded from rarefaction due to the lower sampling effort and number of sequences therefore available to us.

Our haplotype network (created from the 410 bp fragments -Fig. 4A), provides a general overview of genetic structuring between nesting sites from Australia (n = 102), eastern India (n = 72), Sri Lanka (n = 17) and Oman (n = 29). Broadly, this network highlights the separation of two major haplotype groups that are separated by a large genetic distance (7 bp INDEL, one transversion and nine transitions). Within each of the two groupings, a relatively low degree of divergence is observed and haplotypes cluster around the two dominating haplotypes Lo44 ('K' in Shanker et al., 2004 and Bowen et al., 1997) and Lo1 ('J' in Shanker et al., 2004 and Bowen et al., 1997). Haplotype Lo44 was predominately found in eastern Indian rookeries and the majority of other Indian samples belonged to closely related haplotypes. Lo1 was dominated by Australian samples and again, other Australian samples were attributed to relatively closely related haplotypes (Fig. 4A). In contrast, samples from Sri Lankan and Omani rookeries contained haplotypes belonging to both Lo1 and Lo44 haplotype clusters. Consequently, turtles from these nesting populations illustrate relatively large genetic distances between the individuals assessed. Likewise, Maldivian ghost nets and French fishery bycatch samples included individuals from both haplotype groups.

We also constructed a second haplotype network based on the larger 770 bp fragment. This was including a lower number of samples but it allowed us to analyse divergence from the shorter fragments (Fig. 4B). This second network also allowed us to attempt the identification of orphan haplotypes previously identified in a study from northern Australia (Jensen et al., 2013). By using these primers (resulting in the longer bp fragments) we were able to extend sequence length for three existing haplotypes (Lo44 and Lo50 - Accession # MN342242) initially documented from east Indian rookeries by Shanker et al. (2004) as 'K' and K4 respectively, and haplotype Lo42 (Accession # MN342240) described by Bowen et al. (1997) as haplotype 'I' in Sri Lankan rookeries. The additional genetic resolution (stemming from the larger fragment length analysed) resulted in a subdivision of Lo1 (central among Australian populations) and indicated a few haplotypes (n = 7)which diverged from Lo1 into Lo15 (see Jensen et al., 2013). Similarly, haplotype Lo44 (the primary haplotype associated with Indian rookeries) diverged into haplotype Lo97 (Accession # MN342235 - Supplementary information S3ab). In total, our study revealed the existence of four 'new' haplotypes, one from east Indian rookeries (Lo97), one from the Omani rookery (Lo99 - Accession # MN342236) and two 'orphans' which were from entangled turtles collected in the Maldives (Lo98 and Lo100 - Accession # MN342237, MN342238 respectively). Interestingly, over 50% of the Omani turtles analysed were shown to have a unique, previously unidentified haplotype (the Lo99 - see above) which differed from others by only one mutation from the more common Lo44 which itself is shared across the eastern Indian rookeries (Fig. 4B).

3.2. Difference between source populations

Some of the nesting populations (Australia and eastern India) included data from several rookeries. Utilising this (and by conducting a PCA and DA), we assessed whether different rookeries show significant differences in their haplotype composition (Table 1). Not surprisingly, we found no significant differences between the eastern Indian rookeries (Table 1), a result confirming earlier findings by Shanker et al. (2004). Subsequently east Indian rookeries were therefore able to be pooled as one population and treated as a separate but single genetic stock. Australian rookeries, however, showed significant differences



Fig. 4. Olive ridley (*L. olivacea*) haplotype networks based on a medium joining algorithm for the 410 bp fragment (A; n = 269) and 770 bp fragment (B; n = 229). Circles represent individual haplotypes and circle size reflects the relative abundance of each haplotype across all samples. Colours represent the relative contribution of different nesting populations, ALDFG and bycatch samples to individual haplotypes. Cross lines along connections between haplotypes represent a nucleotide mutation between haplotypes. Medium vectors (mv) are hypothesised ancestral links or missing rookeries between nodes required to link the shortest connection with maximum parsimony represented here by grey lines. B includes haplotypes found in ALDFG in Australia recorded by Jensen et al., 2013.

Table 1

Pairwise comparisons between different rookeries following DAPC analyses. Displayed are F-values (below diagonal) and *p*-values (above diagonal) of pairwise comparisons between rookeries (FB = Flinders beach, MG = McCluer Group, TI = Tiwi islands, MAD = Madras, GN = Gahirmatha, DVM = Devi River Mouth, RU = Rushikulya, SL = Sri Lanka). All test were based on the 410 bp sequence fragment of the control region of the mtDNA. Non-significant values are highlighted in bold and holm correction of multiple tests are shown in parenthesis.

	FB	MG	TI	MAD	GN	DVM	RU	OMAN	SL
FB		0.423(0.423)	0.001(0.008)	0.001(0.008)	0.001(0.008)	0.001(0.008)	0.001(0.008)	0.001(0.008)	0.001(0.008)
MG	1.134		0.496(0.496)	0.001(0.007)	0.001(0.007)	0.001(0.007)	0.001(0.007)	0.002(0.007)	0.013(0.026)
TI	6.022	0.474		0.001(0.006)	0.001(0.006)	0.001(0.006)	0.001(0.006)	0.001(0.006)	0.001(0.006)
MAD	22.653	16.233	50.932		0.144(0.288)	0.249(0.288)	0.066(0.198)	0.001(0.005)	0.002(0.008)
GN	25.372	16.73	55.734	1.595		0.858(0.861)	0.503(0.826)	0.001(0.004)	0.003(0.004)
DVM	33.43	55.336	69.12	1.548	0.564		1.000(1.000)	0.001(0.003)	0.003(0.006)
RU	46.665	53.461	98.092	2.343	0.877	0.032		0.001(0.002)	0.001(0.002)
OMAN	17.955	11.19	28.46	34.793	38.886	53.291	72.735		0.001(0.001)
SL	7.159	6.641	16.037	5.793	5.086	9.567	12.604	20.284	



Fig. 5. Haplotype frequency chart comparing mixed stock (Total) and seasonal variation (South West (SW) and North East (NE) Monsoon) of the nesting olive ridley populations identified by our PCA and DA; Sri Lanka, Oman, Northern Australia (NTAus), Cape York Australia (CYPAus) and the east coast of India.

between Flinders beach and Tiwi Island (F = 6.022, p = .008). This again supported findings by Jensen et al. (2013), who grouped rookeries into two populations, those from the Northern Territory (NTAus), i.e. McCluer group and Tiwi islands, and those from the Cape York Peninsula (CYPAus), i.e. Flinders beach. These two genetic stocks were therefore retained for future analyses (Supplementary information S4). Omani and Sri Lankan populations remained separate from the two Australian and the single east Indian genetic stocks and so were both considered as two separate genetic stocks (source populations).

3.3. Genetic structure and origin of ghost net samples

A total of seven haplotypes (Lo1 n = 4, Lo4 n = 1, Lo42 n = 1, Lo44 n = 23, Lo97 n = 6, Lo98 n = 1 and Lo100 n = 1) were detected across the 770 bp fragment (n = 38) found in turtles entangled in ghost nets in the Maldives. Haplotypes Lo44 and Lo97 accounted for 79% of all ghost nets and represented haplotypes that are common in the east Indian population (Fig. 5). 11% of all individuals caught in ghost nets belonged to haplotype Lo1, which is found in populations from east India, Sri Lanka, Australia and Oman. Two 'orphan haplotypes' (Lo98 and Lo100), which have not yet been reported from any population in the Indian Ocean, were found in our ghost net samples. In our bycatch samples from Madagascar, a total of four haplotypes (Lo1, Lo44, Lo97 and Lo67) were detected in the nine samples assessed. One of these haplotypes (Lo67 – Accession # MN342239) differed by one nucleotide mutation from the common Lo1 haplotype (Fig. 4) and accounted for > 50% (n = 5) of the individuals tested.

We then utilised a mixed-stock analysis to determine the origin of olive ridley turtles caught in ghost nets throughout the Maldives (Fig. 6). After excluding one orphan haplotype (Lo100; found in our ghost net samples but not the source populations), we ran a mixed stock analysis based on ghost nets found during the NE and SW monsoon seasons. The analysis resulted in very small and non-significant seasonal variations (Supplementary information S1a) and we therefore compiled all our data to increase the overall robustness of our analysis (Fig. 6A). Our results revealed a substantial contribution from east Indian (73%) and Sri Lankan stocks (23%). Contrary to our expectations, entangled turtles showed no evidence of originating from Oman as the common Omani haplotype Lo99 was not present in the ghost net samples (Fig. 5). When we included population estimates (Supplementary information S2) as a prior in our mixed stock analyses (Supplementary information S1b), the contribution of the relatively small Sri Lankan population substantially reduced (n = 0.002%). This result suggests that the majority of entangled turtles found in the Maldives archipelago originate from east Indian populations (Fig. 6B).

4. Discussion

Drifting ghost nets represent a major threat to marine life but quantifying its impact on mortality rates of endangered species such as turtles remains a challenge. Here, we used a citizen science monitoring program to record ghost net turtle entanglements throughout the Maldives archipelago. In just one year (2017–2018), a total of 177 nets were recorded, which had 132 olive ridley turtles entangled within them. We analysed the mtDNA of 38 of these turtles and illustrated that entangled individuals originated predominantly from eastern Indian and Sri Lankan populations.

4.1. Impact of ghost nets on olive ridley populations

In contrast to a previous study, which found that 45% of all entangled turtles assessed could not be assigned to a known nesting population i.e. characterised as being 'orphan haplotypes' (Jensen et al., 2013), we only identified two orphans (equating to 5.3% of our entangled turtles). This therefore allowed us to trace (with high reliably) the origin of the majority of the entangled turtles found in the Maldives during the survey period. The result of the respective mixed stock analysis reveals that a large proportion (73% of the individuals assessed) originated from east India and 23% of the turtles from Sri Lanka. Australian and Omani source populations are relatively less impacted. Interestingly, if 'source population size' was included into our model calculations, the relative importance of the east Indian population increased to 99% (Fig. 6). This highlights the importance of standardising such models when exploring estimations and assigning risk of given threats to certain populations. Currently, there is no consensus on how strongly population size should be weighted, and factors such as geographic distance may affect this decision. We therefore present the two extreme approaches (i.e. disregarding population size or giving it a strong weight) and the true relative contributions of each source population is likely to lie somewhere between the two.

Surprisingly, we found no seasonal variation in the contribution of



Fig. 6. Mean relative contribution of 5 genetically distinct olive ridleys (*L. olivacea*) populations which are being found entangled in ALDFG drifting into the Maldives - estimated using a mix-stock analysis (Bolker et al., 2007). Curves represent density probability functions. Panel (A) and (B) display results when estimations are based only on haplotype composition (A) or both, haplotype composition and population size (included as priors) (B). Abbreviations represent Australia Cape York (Australia CYP) and Australia Northern Territory (Australia NT).

source populations but a decrease in the percentage of entangled turtles recorded during the SW monsoon (SW - 23%, NE - 55%). Ocean currents across the Maldivian archipelago change seasonally and are strongly associated with the monsoons. Therefore, we expected that different populations of turtles may be affected during different times of the year. One possible explanation for the lack of seasonal impact on relative haplotype frequencies is that olive ridley turtles (from east Indian and Sri Lankan rookeries) are using the Maldives as a foraging ground. This hypothesis is supported by the occasional observation of free-swimming olive ridleys in the Maldives (Anderson et al., 2009). Further support comes from the relative minor injuries found on a number of the turtles entangled, a result indicative of short time spans between entanglements and ghost net retrievals. Further still, neighbouring areas (Gulf of Mannar, Sri Lanka and the Arabian Sea) are known to be important foraging grounds for olive ridleys, findings based on bycatch data and satellite telemetry of adult turtles (Kannan, 2008; Behera et al., 2018; Rees et al., 2012). Interestingly where juveniles and sub adults forage remain largely unknown. If the Maldives is indeed an important foraging ground, and possibly one for juveniles and sub adults (based on the recorded size class distributions of the entangled turtles - see supplementary information S5) urgent action should be implemented to try and manage this important habitat. However future research is needed to confirm that such grounds indeed exist.

Although it is difficult to exactly quantify the impact of ghost nets on regional populations, trying to estimate the impact can assist with management directives.

As discussed above, the population of olive ridleys nesting in eastern India and Sri Lanka were most at risk of entanglement in the nets found adrift in the Maldives. The average number of olive ridleys nesting annually in eastern India has been estimated at ~200,000 (Manoharakrishnan and Swaminatha, 2018), with a further 770 nesting in Sri Lanka (Rajakaruna et al., 2018). Indian and Sri Lankan nests hold on average 120 and 105 eggs, respectively (Manoharakrishnan and Swaminatha, 2018; Rajakaruna et al., 2018). If we assume a hatching success rate of ~80% (Manoharakrishnan and Swaminatha, 2018), an estimated ~19,200,000 'new' turtles are born every year in east India and ~64,600 in Sri Lanka. It has been established as a rule of thumb that 1 in every 1000 hatchling survives to a reproductive age (Frazer, 1983), so that would imply an annual net recruitment of around 19,200 turtles for east Indian and 64 for Sri Lankan populations. In this study, we found in only one year (2017-2018) 132 olive ridley turtles entangled in ghost nets in the Maldives alone. Based on our mixed stock analyses, we assumed that about 70% of these turtles originate from east Indian and 20% from Sri Lankan populations. Entanglement in

ghost nets would therefore reduce yearly recruitment by 0.48% for the eastern Indian populations and by 41% for the Sri Lankan population. However, these estimates are only based on the recorded ghost nets, the majority from only two out of the 26 atolls and therefore neglect the fact that a large proportion of net entanglements were certainly missed by our team. Indeed, a recent study estimated that between 3400 and 12,200 entangled turtles may have gone undetected in the Maldives over a 51 month period (Stelfox et al., 2019). Moreover, better estimates on the levels of nest survivorship along the east coast of India and Sri Lanka may improve our impact assessment of ghost nets. Additionally, we do not consider ghost net entanglements close to Sri Lanka or the east Indian coast for which no data exists. Therefore, although our calculations above should only be read as rough estimates of the impact ghost nets have on olive ridley populations, they are likely underestimates of the true scale of the issue. Regardless of the accuracy, the threat is clear, an urgent need for more reliable population-ecological data is evident, which would allow for the improvement of ghost net impact assessments and support regional turtle conservation across the Indo-Pacific.

4.2. The importance of improving our phylogeography knowledge of olive ridleys (L. olivacea)

Our assessment of olive ridley phylogeography conformed to earlier analyses (Bowen et al., 1997; Shanker et al., 2004; Jensen et al., 2013), highlighting the existence of two distinct haplotype clusters (around Lo44 and Lo1, which are central to east India and Australia genetic stocks, respectively). The current line of thought gives two hypotheses explaining which of these haplotype clusters is the ancestral lineage. The first (Bowen et al., 1997; Jensen et al., 2013) suggests that all Indo-Pacific rookeries evolved from haplotype Lo1 (found in all populations in this study, including ghost net and bycatch samples) and that radiation of Lo44 subsequently happened in India. The alternative hypothesis states that the east Indian haplotype Lo44 is the ancestral linage and that Lo1 represents a successful descendent (Shanker et al., 2004). The latter hypothesis is supported by the presence of a signature 7 bp INDEL in haplotype Lo44 that is also found in Kemp ridleys (Lepidochelys kempii) and many other species of sea turtles (loggerhead, green, hawksbill and leatherback). Our analysis points to Lo1 being the ancestral haplotype giving further support to hypothesis one above, as the cluster surrounding this haplotype show greater deviation from a star-shaped pattern, an indication in itself of a longer evolutionary history (Slatkin and Hudson, 1991). However, it is beyond the scope of this study to determine which of the hypotheses are true.

Interestingly, our study did however identify that haplotype

composition found in the Omani population were unique to this genetic stock. Both Lo1 and a derivative of Lo44 were present in equal frequencies. It is highly unlikely that both of these haplotypes evolved in parallel in Oman, because both the phylogeographic hypotheses highlighted above require some sort of dispersal event. Consequently, the current genetic structure of the Omani population strongly suggests that there were two distinct colonisation events. This is also supported by an analysis of genetic and geographic distances of different populations (Supplementary information S6). While there is a clear positive relationship for Australian and eastern Indian populations, indicating that distance affects the degree of genetic similarity, no such relationship was found for the Oman population. The same is true for Sri Lanka, suggesting that both locations were colonised by at least two different haplotypes, perhaps from distant populations.

Such long-distance migrations have recently been hypothesised, based on the detection of eastern Pacific haplotypes in Australian and east Indian populations (Shanker et al., 2004; Jensen et al., 2013). In our study, we also found one orphan haplotype from a female individual (Lo100), which differs by only one mutation from rookeries in Birdshead Peninsular, Papua, Indonesia (Jensen et al., 2013). This indicates one of two possibilities. Either, this individual drifted entangled in a ghost net from Indonesia, or it represents a migrant visitor implying a low-volume influx of haplotypes from distant populations. Recent sighting of an olive ridley turtle off the south coast of the UK is further evidence for migrancy or individuals simply losing their way (https:// www.bbc.co.uk/news/uk-england-sussex-51167213).

Finally, we want to highlight the urgency to investigate uncharacterised rookeries, e.g. along the west coast of India (Shanker et al., 2004), Kenya (Frazier, 1975; Okemwa et al., 2004), Yemen (Frazier, 1980) and Andaman and Nicobar Islands (Andrews et al., 2006). Such data would be crucial to define population structure in the region. For example, our 'random' analysis of bycatch data from French longliners (collected off the coast of Madagascar), revealed a haplotype previously described by Bowen et al. (1997) from rookeries in the Atlantic (Lo67). In order to interpret such findings and to determine the importance of long-distance migrations for conservation, it would be crucial to fill these gaps in the map of olive ridley phylogeography.

5. Conclusions

Here we highlight that ghost nets may threaten the existence of small turtle populations and its quantification and management should be a major focus of the Northern Indian Ocean Marine Turtle Task Force of the Indian Ocean, South East Asia Marine turtle Memorandum of Understanding (NIO-MTTF IOSEA-MoU). Specifically, we identify Sri Lankan rookeries, which are genetically distinct from other neighbouring rookeries and have relatively small nesting numbers to be at high risk from ghost nets in the Indian Ocean.

We also show that citizen scientist is an invaluable asset to research and highlights the crucial contribution that citizen science projects can play in conservation and academic research. The Olive Ridley Project have a network of informed citizens scientist that are able to report ghost gear and entanglement events over a broad geographical region and respond quickly to entanglement reports using minimal resource. Citizen science can be a useful tool to help inform conservation practitioners and should be included in methodological designs where appropriate.

Managing the impacts of ghost gear in the Indian Ocean will require a multifaceted approach. First, all ghost nets reported in this study were unidentified, damaged fragments and therefore had no clear link to a specific fishery. Therefore, regional fishery managers, such as the Indian Ocean Tuna Commission (IOTC), need to improve compliance where appropriate and/or implement gear marking and gear loss reporting by its country members. Second, the development of incentivised deposit return schemes (in ports or landing sites) would undoubtedly encourage/improve appropriate disposal of end of life and/or damaged fishing gear. Finally, educational workshops must run in parallel to any management strategy in order to better outline reasons for gear loss and prevent loss in the future. Informed fishers are more likely to abide by new or existing policies when information is available about the impact of ghost gear to their livelihoods.

We end by highlighting that ghost gear drifting into the Maldives impacts a number of source populations (i.e. genetic stocks) of olive ridleys from different countries. Further the gear lost may originate from even more countries in the region and beyond. Therefore, it is imperative that future conservation and research efforts which aim to tackle this issue involves a close collaboration between NGOs, regional fisheries managers and governments from all countries within the Northern Indian Ocean and ideally even further.

CRediT authorship contribution statement

Martin Stelfox:Conceptualization, Data curation, Investigation, Writing - review & editing.Alfred Burian:Investigation, Writing review & editing.Kartik Shanker:Data curation.Alan F. Rees:Data curation.Claire Jean:Writing - review & editing.Maïa S. Willson:Data curation.Nashwa Ahmed Manik:Data curation.Michael Sweet:Investigation, Writing - review & editing.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

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References

- Abreu-Grobois, F.A., Horrocks, J., Formia, A., Dutton, P.H., LeRoux, R., Vélez-Zuazo, X., Soares, L., Meylan, P., 2006. New mtDNA Dloop primers which work for a variety of marine turtle species may increase the resolution of mixed stock analyses. In: Proceedings of the 26th Annual Symposium on Sea Turtle Biology. ISTS, Island of Crete, Greece, pp. 179 March.
- Alfaro-Shigueto, J., Mangel, J.C., Darquea, J., Donoso, M., Baquero, A., Doherty, P.D., Godley, B.J., 2018. Untangling the impacts of nets in the southeastern Pacific: rapid assessment of marine turtle bycatch to set conservation priorities in small-scale fisheries. Fish. Res. 206, 185–192.
- Allen, C.R., Forys, E.A., Rice, K.G., Wojcik, D.P., 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatching turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. Fla. Entomol. 250–253.
- Anderson, R.C., Zahir, H., Jauharee, R., Sakamoto, T., Sakamoto, I., Johnson, G., 2009. Entanglement of Olive Ridley turtles Lepidochelys olivacea in ghost nets in the equatorial Indian Ocean. In: IOTC Proceedings. IOTC, Mombasa, Kenya, pp. 12–14.

- Andrews, H.V., Tripathy, A., Aghue, S., Glen, S., John, S., Naveen, K., 2006. The status of sea turtle populations in the Andaman and Nicobar Islands of India. In: Towards an Integrated and Collaborative Sea Turtle Conservation Programme in India: A UNEP/ CMS-IOSEA Project Report, pp. 71–82.
- Behera, S., Tripathy, B., Sivakumar, K., Choudhury, B.C., Dutta, S.K., Pandav, B., 2018. Nesting space dynamics and its relationship with the Arribada of Olive Ridley Turtles at Gahirmatha Rookery, East Coast of India. J. Herpetol. 52 (4), 381–386.
- Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B., 2007. Incorporating multiple mixed stocks in mixed stock analysis: 'many-to-many' analyses. Mol. Ecol. 16 (4), 685–695.
- Bowen, B.W., Clark, A.M., Abreu-Grobois, F.A., Chaves, A., Reichart, H.A., Ferl, R.J., 1997. Global phylogeography of the ridley sea turtles (Lepidochelys spp.) as inferred from mitochondrial DNA sequences. Genetica 101 (3), 179–189.
- Cuevas, E., Guzmán-Hernández, V., Uribe-Martínez, A., Raymundo-Sánchez, A., Herrera-Pavon, R., 2018. Identification of potential sea turtle bycatch hotspots using a spatially explicit approach in the Yucatan Peninsula, Mexico. Chelonian conservation and biology 17 (1), 78–93.
- Dimitriadis, C., Fournari-Konstantinidou, I., Sourbès, L., Koutsoubas, D., Mazaris, A.D., 2018. Reduction of sea turtle population recruitment caused by nightlight: evidence from the Mediterranean region. Ocean & Coastal Management 153, 108–115.
- Duncan, E.M., Botterell, Z.L., Broderick, A.C., Galloway, T.S., Lindeque, P.K., Nuno, A., Godley, B.J., 2017. A global review of marine turtle entanglement in anthropogenic debris: a baseline for further action. Endanger. Species Res. 34, 431–448.
- Engeman, R.M., Martin, R.E., Smith, H.T., Woolard, J., Crady, C.K., Constantin, B., Groninger, N.P., 2006. Impact on predation of sea turtle nests when predator control was removed midway through the nesting season. Wildl. Res. 33 (3), 187–192.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61 (1), 1–10.
- Frazer, N.B., 1983. Survivorship of adult female loggerhead sea turtles, Caretta caretta, nesting on Little Cumberland Island, Georgia, USA. Herpetologica 436–447.
- Frazier, J.G., 1975. Marine turtles of the Western Indian Ocean. Oryx 13, 164-175.
- Frazier, J.G., 1980. Exploitation of marine turtles in the Indian Ocean. Hum. Ecol. 8 (4), 329–370.
 Fuentes, M.M., Hamann, M., Lukoschek, V., 2012. Marine Reptiles. CSIRO Marine and
- Atmospheric Research. Garciía, A., Ceballos, G., Adava, R., 2003. Intensive beach management as an improved
- Garcha, A., Cebailos, G., Adaya, K., 2003. Intensive beach management as an improved sea turtle conservation strategy in Mexico. Biol. Conserv. 111 (2), 253–261.
 Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple se-
- quences. Stat. Sci. 7 (4), 457–472.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, Déjà Vu amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50 (8), 653–666.
- Harewood, A., Horrocks, J., 2008. Impacts of coastal development on hawksbill hatchling survival and swimming success during the initial offshore migration. Biol. Conserv. 141 (2), 394–401.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scand. J. Stat. (6), 65–70.
- Jensen, M.P., Limpus, C.J., Whiting, S.D., Guinea, M., Prince, R.I., Dethmers, K.E., Adnyana, I.B.W., Kennett, R., FitzSimmons, N.N., 2013. Defining olive ridley turtle Lepidochelys olivacea management units in Australia and assessing the potential impact of mortality in ghost nets. Endanger. Species Res. 21 (3), 241–253.
- Jombart, T., Devillard, S., Balloux, F., 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet. 11 (1).
- Kannan, P., 2008. Studies on the green turtle (Chelonia mydas) in the Gulf of Mannar biosphere reserve, Tamil Nadu, India. In: Indian Ocean Turtle Newsletter. vol. 7. pp. 12–15.
- Koch, V., Nichols, W.J., Peckham, H., De La Toba, V., 2006. Estimates of sea turtle mortality from poaching and bycatch in Bahia Magdalena, Baja California Sur, Mexico. Biol. Conserv. 128 (3), 327–334.
- Lewison, R.L., Crowder, L.B., 2007. Putting longline bycatch of sea turtles into perspective. Conserv. Biol. 21 (1), 79–86.
- Mancini, A., Senko, J., Borquez-Reyes, R., Póo, J.G., Seminoff, J.A., Koch, V., 2011. To

poach or not to poach an endangered species: elucidating the economic and social drivers behind illegal sea turtle hunting in Baja California Sur, Mexico. Hum. Ecol. 39 (6), 743–756.

- Manoharakrishnan, M., Swaminatha, A., 2018. India. In: Phillott, A.D., Rees, A.F. (Eds.), Sea Turtles in the Middle East and South Asia Region: MTSG Annual Regional Report 2018. Draft Report of the IUCN-SSC Marine Turtle Specialist Group.
- Mazaris, A.D., Matsinos, G., Pantis, J.D., 2009. Evaluating the impacts of coastal squeeze on sea turtle nesting. Ocean & Coastal Management 52 (2), 139–145.
- Moritz, C., 1994. Defining evolutionary units for conservation. Trenndsin ecology and evolution 9, 373–375.
- Nelms, S.E., Duncan, E.M., Broderick, A.C., Galloway, T.S., Godfrey, M.H., Hamann, M., Godley, B.J., 2015. Plastic and marine turtles: a review and call for research. ICES J. Mar. Sci. 73 (2), 165–181.
- Network version 4.5.1.6, 2009. Fluxus Technology Ltd. http://www.fluxus-engineering. com/netwinfo.htm.
- Okemwa, G.M., Nzuki, S., Mueni, E.M., 2004. The status and conservation of sea turtles in Kenya. Mar Turtle Newsletter 105, 1–6.
- Pella, J., Masuda, M., 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fish. Bull. 99 (1), 151.
- Pielou, E.C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. 10 (2), 370–383.
- R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria3-900051-07-0. http://www. R-project.org/.
- Rajakaruna, R.S., Ekanayake, E.M.L., Suraweera, P.A.C.N.B., 2018. Sri Lanka. In: Phillott, A.D., Rees, A.F. (Eds.), Sea Turtles in the Middle East and South Asia Region: MTSG Annual Regional Report 2018. Draft Report of the IUCN-SSC Marine Turtle Specialist Group.
- Rees, A.F., Al-Kiyumi, A., Broderick, A.C., Papathanasopoulou, N., Godley, B.J., 2012. Conservation related insights into the behaviour of the olive ridley sea turtle Lepidochelys olivacea nesting in Oman. Mar. Ecol. Prog. Ser. 450, 195–205.
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package 'Mass'. CRAN Repos. Httpcran R-Proj. OrgwebpackagesMASSMASS Pdf.
- Rozas, J., Sánchez-DelBarrio, J.C., Messeguer, X., Rozas, R., 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19, 2496–2497.
- Sayer, S., Williams, K., 2015. Ghost gear in Cornwall, UK 2014 to 2015. In: World Animal Protection Commissioned Report.
- Shankar, D., Vinayachandran, P.N., Unnikrishnan, A.S., 2002. The monsoon currents in the north Indian Ocean. Prog. Oceanogr. 52 (1), 63–120.
- Shanker, K., Ramadevi, J., Choudhury, B.C., Singh, L., Aggarwal, R.K., 2004. Phylogeography of olive ridley turtles (Lepidochelys olivacea) on the east coast of India: implications for conservation theory. Mol. Ecol. 13 (7), 1899–1909.Shanker, K., Choudhury, B.C., Aggarwal, R.K., 2011. Conservation Genetics of Marine
- Shanker, K., Choudhury, B.C., Aggarwal, R.K., 2011. Conservation Genetics of Marine Turtles on the Mainland Coast of India and Offshore Islands. Final Project Report. Wildlife Institute of India, Dehradun and Centre for Cellular and Molecular Biology, Hyderabad.
- Slatkin, M., Hudson, R.R., 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129 (2), 555–562.
- Stelfox, M.R., Hudgins, J.A., Ali, K., Anderson, R.C., 2015. High mortality of Olive Ridley Turtles (Lepidochelys olivacea) in ghost nets in the central Indian Ocean. BOBLME-2015. Ecology 14, 1–23.
- Stelfox, M., Hudgins, J., Sweet, M., 2016. A review of ghost gear entanglement amongst marine mammals, reptiles and elasmobranchs. Mar. Pollut. Bull. 111 (1–2), 6–17.

Stelfox, M., Bulling, M., Sweet, M., 2019. Untangling the origin of ghost gear within the Maldivian archipelago and its impact on olive ridley (Lepidochelys olivacea) populations. Endanger. Species Res. 40, 309–320.

- United Nations, 2019. Global assessment on biodiversity. Retrieved from. https://www. ipbes.net/news/Media-Release-Global-Assessment, Accessed date: 25 May 2019.
- Wilcox, C., Hardesty, B.D., Sharples, R., Griffin, D.A., Lawson, T.J., Gunn, R., 2013. Ghostnet impacts on globally threatened turtles, a spatial risk analysis for northern Australia. Conserv. Lett. 6 (4), 247–254.
- Wilcox, C., Mallos, N.J., Leonard, G.H., Rodriguez, A., Hardesty, B.D., 2016. Using expert elicitation to estimate the impacts of plastic pollution on marine wildlife. Mar. Policy 65, 107–114.