

# Defining olive ridley turtle *Lepidochelys olivacea* management units in Australia and assessing the potential impact of mortality in ghost nets

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**ABSTRACT:** In Australia, the olive ridley sea turtle *Lepidochelys olivacea* has received little research attention and monitoring. The Australian populations are relatively small and their distribution is limited to remote areas in the northern part of the country. Previous global genetic studies of olive ridley populations showed that the Australian breeding population at the McCluer Group of islands, Northern Territory, is genetically distinct from other olive ridley populations breeding in the Indo-Pacific. However, nothing is known about the genetic stock structure among Australian olive ridley rookeries found across northern Australia. High predation of eggs by feral pigs, dogs and monitor lizards *Varanus* spp. is believed to have severely impacted the number of nesting females at some rookeries. Of particular concern is the small nesting population on the western Cape York Peninsula, and without immediate conservation action this population could face extinction. The results presented here establish that there are at least 2 independent management units (stocks) of olive ridley turtles nesting in Australia and emphasise the importance of conserving the genetically distinct small breeding population nesting along the western Cape York Peninsula. In addition, results from 44 turtles caught in ghost nets across the Gulf of Carpentaria revealed that 45% of the haplotypes (32% of all ghost net samples) had not been observed at any rookery in Australia or SE Asia. This research highlights the need for better information on olive ridley population structure in the region and for urgent conservation action for the western Cape York population.

**KEY WORDS:** Genetics · By-catch · Population structure · Phylogeography · mtDNA

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## INTRODUCTION

Although the olive ridley sea turtle *Lepidochelys olivacea* is one of the most abundant species of sea turtles in the world, it is under threat in many regions, with smaller populations in the western Pacific showing some of the strongest declining trends (Abreu-Grobois & Plotkin 2008). This species has a circumtropical global distribution and is best known for its mass nesting events, called arribadas, which occur at only a few locations in India, Mexico and Costa Rica (Pritchard & Plotkin 1995, Hamann et al. 2003, Plotkin 2007, Pritchard 2007a). Less is known about the populations at the numerous locations where this turtle nests in low density, often at remote beaches around the world (Pritchard & Plotkin 1995, Bernardo & Plotkin 2007, Plotkin 2007). This is particularly true for the western Pacific and SE Asia where information about their distribution and abundance is limited (Bernardo & Plotkin 2007, Plotkin 2007, Pritchard 2007b). In this region, olive ridley turtles are known to nest in Myanmar and Brunei (each with ~300 nests per year; Thorbjarnarson et al. 2000), Indonesia (~800 to 1000 nests per year; Limpus 1997, I. B. W. Adnyana & C. Hitipeuw pers. comm.), Papua New Guinea (Ulaiwi 1997), Malaysia and Thailand (each with <50 nests per year; Chan 2001), Vietnam (tens of nests per year; Hamann et al. 2006) and Australia (few thousand females per year; Whiting et al. 2007b, Limpus 2008).

Olive ridleys used to be abundant in Myanmar, Thailand and Peninsular Malaysia, but several decades of intense egg harvest have driven this species to low numbers in most parts of the region (Limpus 1997). Olive ridley turtles generally migrate long distances and forage both in shallow coastal waters and in the open sea (Polovina et al. 2004, Morreale et al. 2007, da Silva et al. 2011). For example, olive ridley turtles are frequently caught accidentally in Hawaiian longline fisheries operating in the central Pacific, thousands of kilometres from major nesting areas (Moore et al. 2009). In contrast, Australian olive ridley turtles forage over the Australian continental shelf and appear to have narrower dispersal ranges, based on bycatch data from a coastal fishery (Guinea & Chatto 1992) and from satellite tagging of post-nesting females (McMahon et al. 2007, Whiting et al. 2007a). Our knowledge of olive ridley populations and how they use the marine environment has increased recently due to additional field studies of smaller populations (da Silva et al. 2007, Whiting et al. 2007b), the application of satellite tagging (McMahon et al. 2007, Whiting et al. 2007a, da Silva et al.

2011, Maxwell et al. 2011) and genetic studies (Bowen et al. 1997, Shanker et al. 2004, López-Castro & Rocha-Olivares 2005, Jensen et al. 2006).

For marine turtles and many other species, molecular markers have provided a rapid assessment of many aspects of population biology. They have been used extensively in marine turtle research to investigate population structure (Bowen et al. 1992, Encalada et al. 1996, Dethmers et al. 2006), the origin of turtles in mixed foraging areas (Bowen et al. 1996, Velez-Zuazo et al. 2008, Dethmers et al. 2010), global phylogeography (Bowen et al. 1992, 1997, Dutton et al. 1999), and mating systems (FitzSimmons 1998, Ireland et al. 2003, Jensen et al. 2006). In particular, the control region of the mitochondrial DNA (mtDNA) has proven useful for identifying genetic stock structure and in mixed stock analysis of foraging animals (Bowen 1995, Lee 2008). Two important applications of molecular markers that are directly relevant to the conservation and management of sea turtle species are (1) the identification of genetic stocks or management units (MUs) (Moritz 1994) and (2) the ability to determine the origin of turtles at feeding grounds, in fisheries bycatch or in harvests. (Jensen et al. 2013).

Previous genetic studies of olive ridley rookeries investigated the broader global phylogeography and historical colonisation patterns leading to the current distribution of the species and only looked at fine scale ( $\leq 2000$  km) population structure in India and Mexico (Bowen et al. 1997, Shanker et al. 2004, López-Castro & Rocha-Olivares 2005). These studies indicate that the Indo-Pacific rookeries in India, Sri Lanka, Malaysia, Australia, Mexico and Costa Rica are distinct from each other and from Atlantic populations (Bowen et al. 1997, Shanker et al. 2004). In the eastern Pacific, olive ridley turtles appear to form 1 large panmictic population with no genetic differences observed among turtles nesting in Costa Rica and several rookeries in Mexico along a coastline stretching approximately 3000 km (Bowen et al. 1997). However, there is some evidence of differentiation of the most northern rookeries in Baja California, Mexico (López-Castro & Rocha-Olivares 2005). While studies of population structure within regions have rapidly advanced for other species of marine turtles in recent years, including green turtles *Chelonia mydas* (Chassin-Noria et al. 2004, Bass et al. 2006, Dethmers et al. 2006), hawksbill turtles *Eretmochelys imbricata* (Bass 1999, Browne et al. 2010, LeRoux et al. 2012), flatback turtles *Natator depressus* (Pittard 2010), loggerhead turtles *Caretta caretta* (Shamblin et al. 2011) and leatherback turtles *Der-*

*mochelys coriacea* (Dutton et al. 2013), the finer-scale population structure of olive ridley turtles has received little attention. This lack of information is hindering not only sound management decisions for the species, but also the ability to conduct mixed-stock analyses of turtles in foraging areas or those caught as bycatch in fisheries.

In Australia, olive ridley nesting is scattered across many rookeries throughout the Northern Territory (Chatto & Baker 2008), with an estimated few thousand females nesting annually (Pritchard & Plotkin 1995, Whiting et al. 2007b). In 1999, the Australian Government upgraded the threatened status of olive ridley turtles from Vulnerable to Endangered, indicating recognition of the risk of extinction within Australian waters. While the number of nesting females in Australia is relatively small compared to populations in other regions (e.g. India, Mexico and Costa Rica) (Hamann et al. 2003, Plotkin 2007), it appears to be the largest in SE Asia and the eastern Indian Ocean. Low density nesting is found along 350 km of the western coast of Cape York Peninsula, Queensland, between Rutland Plains (15° 43' S) and Cape York (10° 42' S), with an estimated tens of turtles per season at any one beach (Limpus 2008). There are only 3 records of olive ridley clutches laid in Western Australia (Prince et al. 2010). Throughout their distribution in Australia, olive ridley eggs are subject to high levels of predation by feral pigs, dogs, monitor lizards *Varanus* spp. and Indigenous harvest at several locations (Whiting et al. 2007b, Chatto & Baker 2008, Limpus 2008), and all other life stages face additional threats once turtles enter the marine habitat. This is of particular concern for the western Cape York rookery, as there are low numbers of nesting turtles and a history of high levels of egg and hatchling predation (C. J. Limpus unpubl. data).

One of the significant threats to foraging or migrating olive ridley turtles in northern Australia is the occurrence of large quantities of lost and discarded fishing gear, known as 'ghost nets' (Kiessling 2003, Gunn et al. 2010, Wilcox et al. 2013). These nets are lost or discarded by open-ocean fisheries or from coastal waters near towns in the Arafura and Timor Seas and SE Asia and, as they drift, they entangle and kill several marine species including olive ridley turtles (White 2006, Drysdale et al. 2009, Gunn et al. 2010). Some of these nets can be several kilometres long and form a ball floating at the surface that provides a structure for attachment by a variety of marine organisms and thus attracts many grazers and browsers including juvenile and adult turtles. While unquantified, the number of turtles killed in ghost nets within

the Gulf of Carpentaria (GoC) appears to be hundreds and possibly thousands annually (Limpus 2008). Given the estimate of only a few thousand nesting olive ridley females annually, the Australian rookeries are unlikely to withstand an annual mortality of many hundreds of turtles over the long term (Limpus 2008).

In this study we used mtDNA control region sequences to examine the genetic relationships among 3 olive ridley rookeries in Australia and compared those rookeries to global populations. Secondly, we examined the composition of mtDNA haplotypes from turtles caught in ghost nets to investigate their population origin and to help set conservation priorities for this species.

## MATERIALS AND METHODS

### Sample collection

Tissue samples were collected from 102 nesting olive ridley females at 3 Australian rookeries: the Tiwi Islands (n = 64) and the McCluer Group islands (n = 11) in the Northern Territory and Flinders Beach (n = 27) on the western Cape York Peninsula (CYP) in Queensland (Fig. 1). Samples were taken from turtles nesting at 4 islands in the McCluer Group, from Cape Van Diemen, Melville Island, in the Tiwi Island Group and along the 24 km Flinders Beach, at Mapoon on the CYP (see Table 1). Samples were preserved in absolute alcohol or in 20% dimethyl sulfoxide (DMSO) in a saturated NaCl solution. In addition, to investigate the origins of olive ridley turtles caught in ghost nets, available samples from turtles recovered from ghost nets were collected along the western edge of the GoC by the Dhimurru rangers (n = 21) and by the Mapoon Indigenous Land Council along the eastern GoC (n = 23) (see Table 1). The size of measured turtles from the ghost nets ranged from 30 to 78 cm (curved carapace length) and the turtles were classified as either alive, dead or decomposed. Unpublished sequences from rookeries in Indonesia were kindly made available for comparison with unknown ghost net haplotypes and for use in the phylogenetic analysis (I. B. W. Adnyana unpubl. data).

### Characterisation of mtDNA haplotypes

DNA was extracted from tissue samples using a salting-out procedure. First, tissue was digested by Proteinase K (0.55 mg ml<sup>-1</sup>) at 55°C overnight in

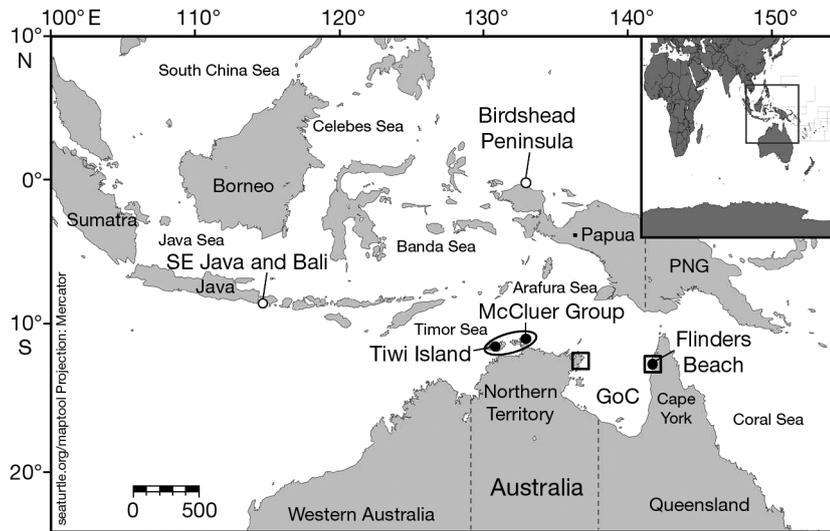


Fig. 1. (●) The 3 olive ridley rookeries in Australia sampled for this study, (○) the origins of the additional sequences used from nesting sites in SE Java/Bali and the Birdshead Peninsula, Papua in Indonesia, and (□) sites for ghost net samples in the eastern and western Gulf of Carpentaria (GoC). Ellipse encloses Tiwi Island/McCluer Group management unit

lysis buffer (300  $\mu$ l; 40 mM Tris/HCl, 20 mM EDTA, 100 mM NaCl, pH 7.2) and 15  $\mu$ l of 10% sodium dodecyl sulphate (SDS). This was followed by precipitation of the fractionation with ammonium acetate (150  $\mu$ l; 7.5 M) and ethanol precipitation (100%, 2 $\times$  volume) of the DNA from the supernatant. DNA pellets were dried and resuspended in 50  $\mu$ l ddH<sub>2</sub>O. Extractions were checked for DNA quality and quantity by running 4  $\mu$ l through a 1.2% agarose gel and visualising with SYBR<sup>®</sup> Safe (Invitrogen) stain under UV light. Samples were amplified via polymerase chain reactions (PCR) using the primers LTEi9 (5'-AGC GAA TAA TCA AAA GAG AAG G-3') and H950 (5'-GTC TCG GAT TTA GGG GTT TA-3') (Abreu-Grobois et al. 2006). These primers amplify an ~880 bp fragment of the mtDNA control region. For the genetic analysis, sequences were truncated to ~780 bp to ensure good quality sequence. This region overlaps the 470 bp segment used by Bowen et al. (1997) in a previous study that included 7 of the same samples from the McCluer Group. PCRs were set up in 25  $\mu$ l reactions containing 1 $\times$  reaction buffer, 0.25 mM of each deoxynucleoside triphosphate, 1.5 mM MgCl<sub>2</sub>, 10  $\mu$ M of each primer, 1.25 U of *Taq* polymerase and ~40 ng of template DNA. The PCRs were carried out on an Eppendorf Mastercycler<sup>®</sup> ep thermocycler using an initial denaturing step at 94°C for 5 min, followed by 35 cycles of 45 s at 94°C (denaturing), 45 s at 52°C (annealing) and 45 s at 72°C (extension), and a final extension step of 5 min at 72°C. PCR products were

analysed for quality and quantity on agarose gels (as above), and all successfully amplified samples were purified prior to sequencing using a polyethylene glycol (PEG) procedure described by T. Glenn ([www.mcdb.lsa.umich.edu/labs/olsen/files/PCR.pdf](http://www.mcdb.lsa.umich.edu/labs/olsen/files/PCR.pdf)).

Sequencing of the forward and reverse reactions was carried out by MacroGen (Korea). Sequences were aligned using Clustal W (Thompson et al. 1994) as implemented within the software Geneious (V5.6.5) (Drummond et al. 2011). Haplotypes were matched against published haplotypes by doing a BLAST search on GenBank ([www.ncbi.nlm.nih.gov/genbank/](http://www.ncbi.nlm.nih.gov/genbank/)) and against available unpublished sequences from Australasia. All sequences were identified by the original name from published shorter sequences and/or given a new coding identification for Indo-Pacific olive ridley turtles using the prefix Lo (e.g. Lo1, Lo2, etc.) and submitted to GenBank.

### Molecular analysis

Genetic diversity was calculated as haplotype ( $h$ ) and nucleotide ( $\pi$ ; Nei 1987) diversities using the software Arlequin (v. 3.5) (Excoffier & Lischer 2010). Haplotype diversity takes into account the number of haplotypes in a population and their frequency within that population. Nucleotide diversity additionally considers the mean number of nucleotide differences (mutations) among all pairs of haplotypes in the population. Higher levels of nucleotide diversity indicate higher levels of haplotype divergence within a population. Estimates for both measures of diversity vary between 0 and 1. The genetic distance among mtDNA haplotypes was calculated as a corrected percent sequence divergence among haplotypes in the program MEGA (version 5.03) (Tamura et al. 2007). The program Modeltest 3.0 (Posada & Crandall 1998) was used to find the best model for nucleotide substitution, and this identified the model HKY85 + G ( $\alpha = 0.1256$ ) (Hasegawa et al. 1985) as appropriate for olive ridleys. The HKY85 + G model was then used to correct for multiple substitutions per site and different substitution rates between transitions and transversions. Genetic differentiation among sampling locations was tested using 2 different measures of popula-



Group (G and J), 2 from Sri Lanka (J and H), 1 from Malaysia (J), 1 from India (J) and 1 from Costa Rica (M) (Bowen et al. 1997, Shanker et al. 2004). Of the longer haplotypes we found, Lo1 was the most common haplotype (66%) and it was found at all 3 rookeries sampled. Lo2 was also found at all 3 rookeries but at low frequency at Flinders Beach (7%) and the Tiwi Islands (11%), and a higher frequency at the McCluer Group (27%). Lo3 was found at a low frequency (<2%) at the Tiwi Islands rookery and at a higher frequency (33%) at the Flinders Beach rookery. Lo4 and Lo5 were only found at the Tiwi Islands rookery and only at low frequencies (<4% and <2%, respectively). Lo15 was found at the McCluer Group (10%, 1 individual) and Flinders Beach (22%) rookeries. One haplotype, Lo27, was only found at Flinders Beach at a low frequency (4%).

Genetic diversity in the sampled rookeries was low to moderate. Haplotype diversity varied between 0.39 and 0.75, and estimates of nucleotide diversity were low and ranged from 0.0012 to 0.0033 (Table 1). The low level of nucleotide diversity was reflected in the shallow divergence among the 7 haplotypes, with sequence divergence ranging from 0.1 to 0.8%. Construction of a haplotype network showed that these rookery haplotypes varied by 1 to 8 mutations (Fig. 2).

### Population differentiation

The neighbouring Tiwi Islands and McCluer Group rookeries, which are separated by just 200 km, were not genetically differentiated using either the conventional  $F_{ST}$  ( $F_{ST} = 0.0056$ ,  $p = 0.307$ ) or the sequence-

based  $\phi_{ST}$  ( $\phi_{ST} = 0.004$ ,  $p = 0.303$ ) distance estimates. In contrast the Flinders Beach and Tiwi Islands rookeries, which are 1200 km apart, were genetically differentiated under both methods of analysis ( $F_{ST} = 0.244$ ,  $p < 0.001$  and  $\phi_{ST} = 0.168$ ,  $p = 0.0009$ ). The Flinders Beach and McCluer Group rookeries, which are 1000 km apart, were significantly differentiated when using  $F_{ST}$  ( $F_{ST} = 0.109$ ,  $p = 0.039$ ) but not when using  $\phi_{ST}$  ( $\phi_{ST} = 0.017$ ,  $p = 0.274$ ). However, when combining the 2 neighbouring (and genetically indistinguishable) Tiwi and McCluer rookeries, they were highly differentiated from Flinders Beach under both methods of analysis ( $F_{ST} = 0.236$ ,  $p < 0.001$  and  $\phi_{ST} = 0.157$ ,  $p < 0.0007$ ).

### Genetic composition of captures by ghost nets

The genetic composition of turtles caught in ghost nets varied between the eastern GoC ( $n = 23$ ) and western GoC ( $n = 21$ ). The genetic diversity in the eastern GoC ghost net samples was similar or slightly higher than that of the rookery samples for haplotype ( $h = 0.73$ ) and nucleotide ( $\pi = 0.0039$ ) diversity, while the western GoC showed a much greater genetic diversity than the rookery samples for both haplotype ( $h = 0.97$ ) and nucleotide ( $\pi = 0.0048$ ) diversity (Table 1). A total of 17 mtDNA haplotypes were identified among western GoC samples in comparison to the 9 haplotypes found in the eastern GoC samples (Table 1). The randomised chi-square test indicated low but significant variation in the haplotype frequencies of turtles sampled from the 2 regions ( $p = 0.035$ ). The common rookery haplotype Lo1 was also

the most common haplotype found in the eastern GoC (52%) and the western GoC (19%) ghost net samples. An additional 3 Australian rookery haplotypes were identified among the western GoC samples (Lo2, Lo4 and Lo21), but at low frequency. Eight haplotypes from the ghost net samples matched unpublished haplotypes recently identified at 2 rookeries in Indonesia (Table 1, Figs. 1 & 3) (I. B. W. Adnyana unpubl. data), 7 of which were not found among the Australian rookeries. The remaining 9 haplotypes found across the 2 ghost net locations were each present at low frequency (<7%), but together made up 32% of the total ghost net sample and are 'orphan' haplotypes that have not been found in any nesting

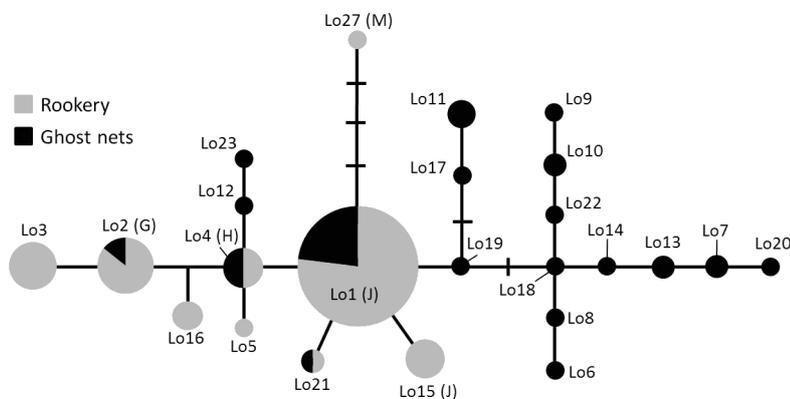


Fig. 2. *Lepidochelys olivacea*. Haplotype network based on maximum parsimony of 780 bp of the mtDNA control region. Vertical and horizontal bars represent 1 extra mutational step connecting 2 haplotypes. Pie charts represent the distribution of the haplotypes at either 1 of the 3 Australian rookeries (grey) or samples from ghost nets (black). The size of the circles represents the relative frequency of the haplotypes out of the total sample

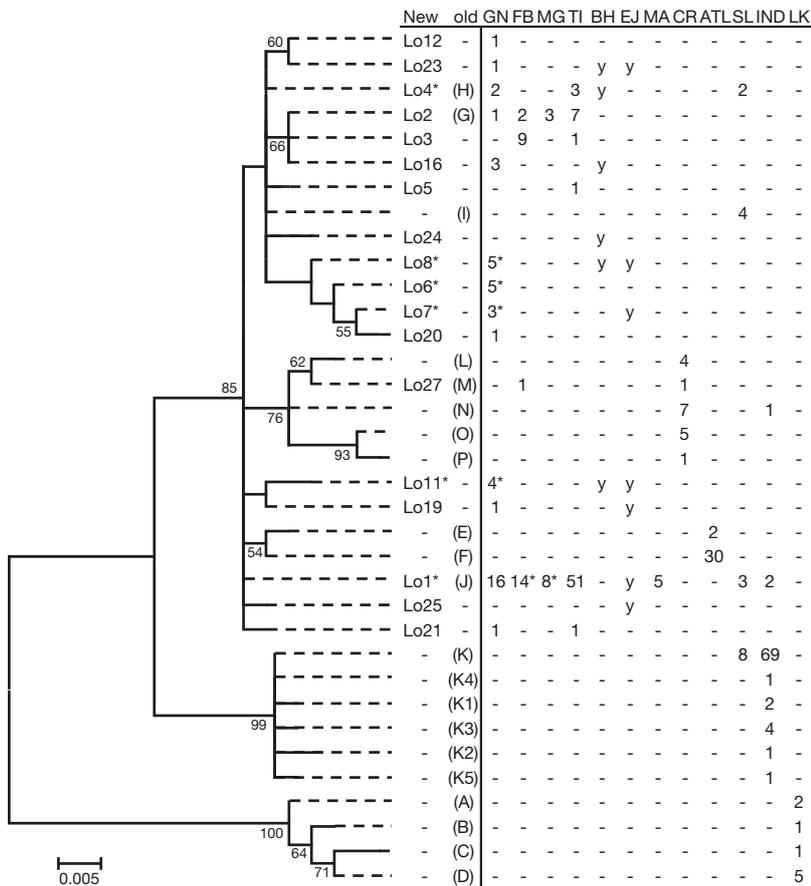


Fig. 3. *Lepidochelys olivacea*. Evolutionary relationships of haplotypes based on 470 bp mtDNA sequence. The evolutionary history was inferred using the maximum likelihood method. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (only values above 50% are shown). Haplotypes and their frequencies are shown for samples collected in the ghost nets (GN), and at rookeries at Flinders Beach (FB), McCluer Group (MG) Islands, Tiwi Islands (TI) (this study), Birdshead Peninsula (BH) and East Java (EJ) (I. B. W. Adnyana pers. comm.), Malaysia (MA), Costa Rica (CR), Atlantic Ocean (ATL), Sri Lanka (SL) (Bowen et al. 1997) and India (IND) (Shanker et al. 2004). *L. kempyii* (LK) was used as an outgroup (Bowen et al. 1997). y (for BH and EJ): haplotypes found in those rookeries but no frequency data is available. Haplotypes marked with an asterisk are different at the 780 bp but identical at the 470 bp used for the tree: Lo1 = Lo15, Lo7 = Lo9, Lo6 = Lo10 and Lo13, Lo8 = Lo14, Lo18 and Lo22, Lo4 = Lo26, and Lo11 = Lo17 (see Table 1)

population to date. These orphan haplotypes showed slightly more divergence (sequence divergence range from 0.1 to 1.0%) than the Australian rookery samples (sequence divergence range from 0.1 to 0.8%). The haplotype network indicated greater complexity among ghost net samples than that found within the rookery samples (Fig. 2). To consider whether the orphan haplotypes may be due to low sample size in our nesting samples we created a rarefaction curve (Fig. 4). The visibly asymptotic curve for the Northern Territory indicates that the most of the diversity

in the population is represented within the sample, but the curve for Cape York is still increasing, although starting to level off. This suggests that increased sampling could reveal additional haplotypes at low frequency in Cape York. It is unlikely, however, that this would account for the large number of orphan haplotypes found in the ghost net samples.

### Phylogeography

There were 2 ambiguous loops in the haplotype network (Fig. 2) that were resolved using Pfenninger & Posada's (2002) criteria. Overall, the haplotype network reflected the low divergence among all nesting samples. The common Haplotype Lo1 (J) is also found in Indonesia, India, Sri Lanka and Malaysia. This haplotype is central in the network and is likely an ancestral haplotype from which other haplotypes in the Indo-Pacific were derived, thus suggesting that this haplotype was central to the (re-)colonisation of the Atlantic and Pacific Oceans. Most of the haplotypes found in samples from ghost nets form their own cluster of closely related haplotypes that include the orphan haplotypes that have not been identified at any rookery to date. The phylogenetic tree showed poor bootstrap support for most branches due to the low sequence divergence among olive ridley haplotypes (Fig. 3). There were, however, some clear patterns in the tree. The K haplotypes found only in India and Sri Lanka had high support as a distinct and divergent clade relative to all other olive ridley haplotypes. There was some support (>60% bootstrap) for the grouping of eastern Pacific haplotypes (L, M, N, O, P). It is worth noting that 1 turtle from Flinders Beach had Haplotype Lo27, which is identical to the eastern Pacific Haplotype M for the 470 bp fragment. A similar scenario was found in India, where an eastern Pacific haplotype (N) was found

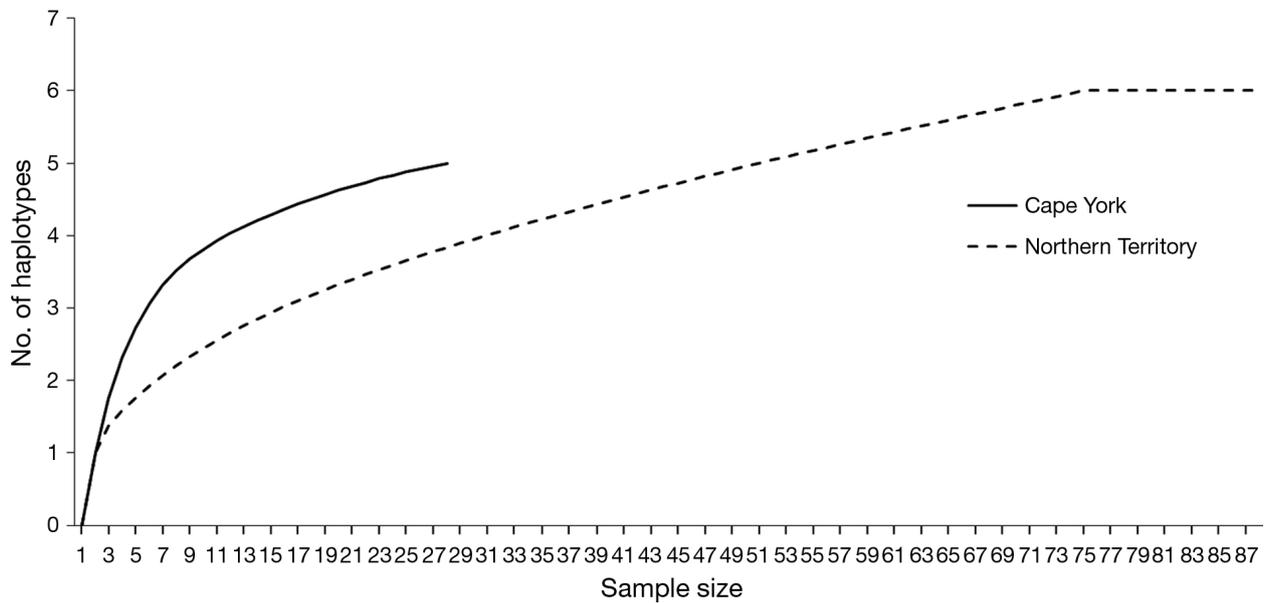


Fig. 4. *Lepidochelys olivacea*. Rarefaction curve of samples collected from the 2 genetic stocks (Cape York and the Northern Territory). The 2 curves plot the number of haplotypes as a function of the number of samples

at low frequency (Shanker et al. 2004). Future long sequencing of East Pacific olive ridleys with Haplotype M and N could help determine if they are identical for the longer fragment. There was little genetic distance between Atlantic and Pacific haplotypes, but some support (52% bootstrap) grouping the Atlantic haplotypes (E and F). There was also low support (61% bootstrap) for a clade containing a mix of haplotypes from throughout SE Asia (including Australia) and many of the 'orphan' haplotypes from the ghost net samples.

## DISCUSSION

This study indicates that the critically small olive ridley population nesting along western Cape York is genetically isolated from the larger population in the Northern Territory that nests around the Tiwi Islands and the McCluer Group (Limpus 2008), and should thus be regarded as a separate MU. The genetic results are also consistent with the notion that insufficient numbers of turtles from the Northern Territory nest along western Cape York and that connectivity is so low that it is unlikely for the former to recolonise the area in the event of population extirpation. Additionally, it appears that entanglement of olive ridley turtles by ghost nets is impacting not only the Australian rookeries, but also more distant rookeries in the region.

## Genetic diversity and phylogeography

Genetic diversity within Australian rookeries is moderate, with closely related haplotypes that appear to have diverged from 2 common haplotypes (Lo1 [J] and Lo4 [H]), similar to observations of divergent haplotypes from Atlantic and eastern Pacific rookeries. All haplotypes observed in the rookery and ghost net samples come from the lineage of Indo-Pacific and Atlantic haplotypes that are separated from the previously observed K clade of India, which is thought to be the ancestral source for the contemporary distribution of olive ridley turtle populations (Bowen et al. 1997, Shanker et al. 2004). Haplotype J, which we have identified as 2 haplotypes, Lo1 and Lo15 (using 780 bp), has been observed at rookeries in India (Shanker et al. 2004), Sri Lanka, Malaysia (Bowen et al. 1997), Indonesia (I. B. W. Adnyana unpubl. data), the Tiwi Islands, the McCluer islands and western Cape York (Fig. 3), and in stranded turtles caught in ghost nets. The splitting of the common J haplotype when using longer sequences was helpful in characterising population boundaries of the Australian populations and will prove useful once additional samples are sequenced from throughout the region. Tests for genetic divergence between rookeries in Australia and Sri Lanka verify the separation of these populations (Sri Lanka and Northern Territory  $F_{ST} = 0.508$ ; Sri Lanka and western Cape York  $F_{ST} = 0.281$ ).

Unfortunately, sample sizes from Malaysia were too small for comparisons, but all 5 samples had the J haplotype (Bowen et al. 1997). Comparisons with green turtles, which share the same nesting regions, suggest that populations in neighbouring countries will be genetically distinct (Dethmers et al. 2006, Jensen 2010), but the geographic spread of olive ridley haplotypes in the Atlantic and eastern Pacific (Bowen et al. 1997, Shanker et al. 2004, López-Castro & Rocha-Olivares 2005) suggests that the divergent haplotypes in Australia will be observed at other rookeries within the region. Previous analyses suggest that there has been a range expansion in olive ridley turtles between Sri Lanka and Australia, and long-distance colonisation, likely from west to east across the Indian Ocean (Shanker et al. 2004), which is consistent with the observed new rookery haplotypes that have little genetic divergence. Similar to the findings of Shanker et al. (2004) in India, the presence of an eastern Pacific haplotype in Australia supports the hypothesis that infrequent, long-distance dispersal of this species occurred at some time in the past.

Estimates of genetic divergence and diversity have provided insights into marine turtle colonisation histories (Shanker et al. 2004, López-Castro & Rocha-Olivares 2005), including within the study area (Dethmers et al. 2006). The Arafura Sea-GoC areas of the Australian-New Guinea continental shelf were terrestrial habitat during the Pleistocene lower sea levels. Colonisation by nesting marine turtles was only possible following sea level rises towards the end of the last ice age, with flooding of the western Arafura Sea into the GoC sometime after 12 000 yr BP (Yokoyama et al. 2001). Gillieson (2005) summarised sand dune geomorphology for the coastal areas of western CYP near Mapoon, concluding that postglacial sea level rise in northern Australia ceased by about 5500 yr BP and was associated with widespread coastal dune formation and periodic reworking of Pleistocene sand masses. In green turtles, colonisation of beaches in the western and southern GoC from the west, and subsequent genetic divergence, is indicated by larger mtDNA genetic divergence found between the populations in the GoC and northern Great Barrier Reef ( $F_{ST} = 0.65$ ) in comparison to that between the GoC and Northwest Shelf (Western Australia) ( $F_{ST} = 0.26$ ) populations (FitzSimmons et al. 1997). Additionally, the prevalence of haplotypes that are shared between the GoC population and populations from Western Australia and SE Asia, rather than from populations in the Pacific, further suggests colonisa-

tion from the north or west, followed by genetic isolation (Dethmers et al. 2006). A similar scenario may have occurred during olive ridley colonisation of the GoC, given the sharing of the 3 most common haplotypes, in addition to possibly having unique haplotypes in each population. It appears that genetic divergence has occurred between olive ridley populations in the Northern Territory and western Cape York ( $F_{ST} = 0.24$ ) since the colonisation of this area from the western Indian Ocean (Shanker et al. 2004). In contrast, a lower level of genetic divergence was observed among flatback rookeries in the Northern Territory and GoC (mean  $F_{ST} = 0.05$ ; Pittard 2010), and no divergence was observed between hawksbill turtle rookeries in the Northern Territory and northern Queensland (Broderick et al. 1994), suggesting either a delayed colonisation by these species or ongoing gene flow.

#### Ghost nets and conservation issues

The nesting distribution and densities of olive ridley turtles throughout SE Asia, the eastern Indian Ocean and the western Pacific Ocean have been poorly documented, and even less is known of foraging populations in the region. The high number of orphan haplotypes found in ghost net samples highlights the need for a more extensive sampling of olive ridley rookeries in SE Asia and the western Pacific. Outside of Australia, adult and immature olive ridley turtles are both known to make long-distance migrations to forage in distant pelagic areas in the open ocean (Polovina et al. 2004, Morreale et al. 2007, Plotkin 2007). In contrast, satellite telemetry studies of adult olive ridley turtles breeding in the Northern Territory indicate that they disperse to a range of different foraging areas but appear to remain over the northern Australian continental shelf where they forage on benthic communities (Conway 1994, McMahon et al. 2007, Whiting et al. 2007a, Conway & Guinea 2009). Flipper tag recoveries and genetic studies of green turtles in foraging grounds around northern Australia (Limpus 2007, Dethmers et al. 2010, Jensen 2010) have indicated that these foraging populations are composed of turtles from various rookeries throughout the region, including Indonesia and Malaysia (Limpus 2007, Dethmers et al. 2010). Foraging olive ridley turtles in the region are also likely to include at least a significant proportion of adult and immature turtles from rookeries outside Australia (particularly Indonesia and Papua New Guinea). However, it is becoming less likely that for-

aging turtles in the Arafura Sea have come from Malaysian rookeries as they had severely declined to a few turtles by the mid-1990s (Chan 2006, Abreu-Grobois and Plotkin 2008) and the estimated age to maturity in this species is only 10 to 18 yr (Zug et al. 2006).

Every year, thousands of abandoned or lost fishing nets (ghost nets) are found along the beaches of the GoC and the northern coast of the Northern Territory. While a few of these are from the Australian prawn fishery, most (>90%) are thought to be of foreign origin, probably from fisheries operating in Indonesian waters (Kiessling 2003, White 2006). It is unknown where these nets are discarded, but many enter the GoC where they entangle and kill many fish, sharks, and turtles while drifting (White 2006, Limpus 2008, Gunn et al. 2010). The majority of these nets are found on the eastern side of the GoC from Cape York to south of Weipa during the wet season when the northwest monsoon winds blow, and on the western side of the GoC from Cape Arnhem to Groote Eylandt during the dry season when the southeast trade winds blow (Gunn et al. 2010). Our haplotype results from stranded turtles caught in ghost nets revealed that 45% of the haplotypes (32% of all 'ghost net' samples) have not been observed at any rookery and their nesting origin is therefore not traceable at present. The remaining 11 haplotypes matched those found in the Australian rookeries or in 2 rookeries in Indonesia, but low sample numbers prevent any meaningful mixed stock analysis. These findings do however suggest that Australian rookeries in the Northern Territory as well as within the GoC are losing turtles to the ghost nets. This conclusion is corroborated by satellite tracking data of a turtle tagged while nesting at the Tiwi Islands that subsequently foraged along the western GoC (Whiting et al. 2007a). While our sample sizes are small and any conclusions have to be interpreted with caution, the difference in haplotype composition between the eastern and western GoC ghost net samples indicate that nets stranding along the western GoC are catching a genetically more diverse group of turtles, which presumably have more diverse origins than those caught in nets found in the eastern GoC. Overall, the presence of 16 orphan haplotypes in the ghost net samples indicates that these turtles likely originate from several rookeries. Given the placement of the unknown haplotypes in the neighbour-joining tree (Fig. 3), it would not be surprising to find that ghost nets are impacting rookeries that span a large geographical area. The neighbour-joining tree places many of the

orphan haplotypes in their own clade, suggesting that there remain significant unsampled rookeries in the Indo-Pacific.

At this point, it remains unclear whether the diverse mixture of haplotypes found in the ghost nets result from entanglement within the GoC of a diverse mixed stock of turtles foraging within the GoC or from turtles foraging at more distant locations that were captured by ghost nets that subsequently drifted into the GoC. The presence of several (8 of 16 recorded) turtles that were still alive in the ghost nets in the western GoC, suggests that these turtles could have drifted in from no further away than the adjacent Arafura Sea. In contrast, all 8 ghost net entangled turtles from the western GOC that were classed as either 'dead' or 'decomposed' either had orphan haplotypes, or those found only in Indonesia, suggesting support for longer transport distances. Future work on ghost nets should attempt to document the relative amount of time a ghost net has drifted based on epibionts, as well as collecting data on the size and condition of entangled turtles.

This study adds to the growing body of evidence that concerted conservation action is needed to manage the Australian olive ridley populations, particularly those from the western Cape York beaches, to guarantee the survival of this threatened population into the future. Decades of high depredation of eggs by feral pigs, feral dogs and varanids, previous incidental bycatch in prawn trawl nets (Poiner & Harris 1996) and other fisheries, Indigenous harvest, and unknown numbers of turtles killed in ghost nets have put olive ridley populations in Australia under risk of extinction (Limpus 2008). To better understand the status of the Australian populations, it is important to increase the genetic sampling throughout their range. Sporadic and low-density nesting occurs within the western GoC at the Sir Edward Pellew Islands and Groote Eylandt in the Northern Territory. Sampling of these beaches will help determine whether these turtles belong to the Arnhem Land or to the western Cape York stock. More broadly, additional sampling of other olive ridley rookeries in the region, including in southern Papua New Guinea, are needed to determine population boundaries and allow a better evaluation of the origin of turtles caught in ghost nets. Field studies aimed at increasing nesting success are being conducted in western Cape York in conjunction with Indigenous ranger groups, and new studies on ghost nets have been initiated that will aid in our understanding and the conservation of the olive ridleys in Australia.

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