

ARTICLES



MARINE TURTLE GENETIC STOCKS OF THE INDO-PACIFIC: IDENTIFYING BOUNDARIES AND KNOWLEDGE GAPS

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INTRODUCTION

Effective management of marine species has been challenging in part because of the cryptic nature of diverse life stages and the complexity of aquatic dispersal that is mediated by oceanographic features. This makes it difficult to define population boundaries or to understand population dynamics, particularly for marine migratory species where knowledge of migratory routes and population interactions during different life stages can be difficult to elucidate. Because of this, management for conservation of marine species has often taken place without the knowledge of exactly what is being managed. Are aggregations of individuals part of a single isolated population, a complex metapopulation, or do they come from a collection of independent populations that only share foraging habitats or migratory corridors? As our ability to define marine populations has improved through linking mark-recapture techniques, population genetics, satellite telemetry and isotope studies to oceanographic data, so too has the need to apply these findings to conservation management.

Conservation of marine turtle populations relies on being able to define populations and understand the geographic extent of habitat use throughout individual life history phases that may include oceanic or benthic developmental habitats, and extensive individual, population and species-level variation in the size and location of foraging home ranges and subsequent adult breeding migrations. To understand and manage populations requires determining whether a population nests at a single beach or island, or nests at multiple beaches. From an ecological perspective, populations are considered to be functionally independent, such that demographic processes are mostly independent of other populations and there is limited gene flow among different populations (Palsbøll *et al.*, 2007). Populations are often comprised of sub-populations that

are typically recognised as different spatial or temporal groupings of individuals. Examples of this include the many distinct rookeries that comprise the Northwest Shelf green turtle population (Dethmers *et al.*, 2006) or the western Pacific leatherback population that nests across sites in Indonesia, Papua New Guinea, and the Solomon Islands, and shows behavioural differences in foraging behaviour among summer and winter nesting groups (Dutton *et al.*, 1999; Benson *et al.*, 2011). Continued gene flow among sub-populations is at a high enough level that sub-populations share demographic features and are not distinguished genetically.

From the perspective of conservation management, populations are also considered to be groupings of animals that function independently in the near term (tens or hundreds of years) and can thus be thought of as 'Management Units' (MU) or 'genetic stocks' (Moritz, 1994). Use of these terms, as well as the terms 'population' and 'sub-population', can be problematic due to different usage, thus it is necessary to clarify what is meant. In the IUCN Red List process, 'population' is defined to mean the entire taxon (species) and, more specifically, the definition only considers adults that are contributing to future generations (IUCN, 2010). What ecologists would consider as populations are instead defined as 'sub-populations' within the IUCN Red List assessments (IUCN, 2010). The term 'stock' can be problematic as it is often used in fisheries management to represent different geographic aggregations of fish that are commercially fished, without regard to whether they constitute a single population or mixed populations that share a feeding ground (Carvalho & Hauser, 1994). With regard to marine turtle populations, the term 'Regional Management Unit' (RMU) has been introduced for the purpose of setting conservation priorities (Wallace *et al.*, 2011), yet the units that are defined are often inconsistent with a Management Unit (Moritz, 1994) approach (FitzSimmons, In Press). For the purposes of this paper,

the terms population, Management Unit, and genetic stock are considered to be synonymous and the basis for effective marine turtle conservation management.

Several Management Units have been defined for marine turtles within the Indo-Pacific (e.g., Dethmers *et al.*, 2006; Bourjea *et al.*, 2007; Pittard, 2010). The location of foraging grounds and migratory routes are known for some genetic stocks (e.g., Benson *et al.*, 2011), but many knowledge gaps remain. Because of limited tissue sampling for genetic studies, there are genetic stocks yet to be identified and additional sampling is needed to determine the geographic range of rookeries used by each genetic stock. For example, the defined green turtle genetic stock for Papua New Guinea, was based on a single location in the northeast at Long Island (Dethmers *et al.*, 2006), but further research by Velez-Zuazo *et al.* (2006) showed that this stock extended a further 2000 kms westward to include rookeries off the northwest coast of Papua, Indonesia. Mark-recapture tagging studies have provided considerable information on the habitat range of genetic stocks (Limpus, 1997) and the use of satellite telemetry has been a valuable source of data on populations, particularly where there are limited mark-recapture records (e.g., Lushci *et al.*, 2006; Benson *et al.*, 2011). Genetic analyses of foraging aggregations of turtles have added to this knowledge by providing estimates of the proportional representation of genetic stocks at different foraging areas (Dethmers *et al.*, 2010; Jensen, 2010; Nishizawa *et al.*, 2013), but the efforts required to sample sufficient numbers of turtles at foraging grounds means that few studies have been conducted to date. These studies are particularly valuable if there are substantial levels of mortality at foraging areas as it allows the proportional assignment of mortality to the different genetic stocks that share the feeding ground (Jensen *et al.*, 2010).

This paper aims to summarise the present state of knowledge for all species of marine turtle populations within the Indo-Pacific in terms of the distribution of rookeries, the relative size of rookeries, and how rookeries are grouped into genetic stocks. Information on the international extent of foraging areas or migratory routes is provided from mark-recapture data, satellite telemetry data, or genetic studies that indicate a genetic stock uses habitat across international borders. Data are provided as species-specific maps to show the locations of genetic stocks and to identify areas where there are knowledge gaps. This paper has been also been provided to the secretariat of the Indian Ocean South East Asia Memorandum of Understanding (IOSEA) to be included on the website (<http://www.ioseaturtles.org/>) and updated periodically with input from IOSEA affiliates.

METHODS

Rookery location and estimated rookery size were taken from the published literature, unpublished reports, theses, conference proceedings, and personal communications from researchers throughout the Indo-Pacific. These data have been generated using GIS software (ArcView) and used to construct the maps shown in Figures 1-6. In these Figures, nesting locations are shown as dots that denote recorded nesting sites. The size of the dot is scaled, with the smallest dots representing 1-10 nesting females per year to the largest dots representing tens of thousands of females per year for *Caretta caretta*, *Chelonia mydas* and *Lepidochelys* spp., or thousands of females per year for *Dermochelys coriacea*, *Eretmochelys imbricata* and *Natator depressus*. Crosses denote recorded nesting sites for which the size of the nesting population has not been quantified. Nesting sites demonstrated to be a part of the same genetic stock are encircled and the abbreviated name of the genetic stock is identified (see Table 1).

Designations of genetic stocks were taken from the published literature, unpublished reports, theses and conference proceedings. In all cases, these studies used a definition of genetic stocks following the Management Unit (MU) concept as provided by Moritz (1994). Following Moritz (1994), marine turtle MUs are recognised by having significant allele frequency differences, such as observed in mitochondrial (mt) DNA haplotype frequencies (e.g., Dethmers *et al.*, 2006), nuclear microsatellite allele frequencies (e.g., FitzSimmons *et al.*, 1997b), or SNPs (single nucleotide polymorphisms) allele frequencies (e.g., Roden *et al.*, 2013). If the null hypothesis that sampled rookeries have the same mtDNA haplotype frequencies cannot be rejected, then they are considered as being grouped into the same genetic stock. If the null hypothesis is rejected when comparing two rookeries, or groups of rookeries, then they are designated as separate genetic stocks. This is done on the basis that significant genetic differentiation indicates limited gene flow and that populations are thus expected to function with demographic independence (Moritz, 1994; Palsbøll *et al.*, 2007). Data from mtDNA are particularly useful for conservation management of marine turtle populations because the matrilineal inheritance of the mtDNA means that the data reflect the history and relationships among rookeries (Aulsebrook, 1995). Application of nuclear genetic markers (microsatellites and SNPs) can be beneficial for understanding male-mediated gene flow among populations and male migratory behaviour relative to females. When used in regional studies, they have contributed to the designation of genetic stocks, mostly with similar results (FitzSimmons

et al., 1997b; Pittard, 2010; Roden *et al.*, 2013).

RESULTS

In total, 57 genetic stocks have been identified for all species of marine turtles within the Indo-Pacific, but many regional or species-specific gaps remain (Tables 1-2, Figures 1-6). For 37 (65%) of these stocks, some habitat use outside of the country(s) where the rookeries are located have been identified through tag recovery data, satellite telemetry data, or genetic stock analyses. International habitat use by various genetic stocks was recorded for all species, emphasising the need for international cooperation in marine turtle conservation efforts. The designated genetic stocks represent not only the demographically independent marine turtle populations within the Indo-Pacific, they also represent unique combinations of genetic diversity within the region.

Caretta caretta

Five genetic stocks of loggerhead turtles have been identified (Table 1, Figure 1) in the Indo-Pacific (Hatase *et al.*, 2002; Shamblin *et al.*, 2014). At present, genetic studies of the southwest Pacific stock do not uncover any differences between rookeries in eastern Australia and New Caledonia (FitzSimmons *et al.*, unpubl. data), although tagging of females suggests that these regions function as independent populations (Limpus, 2008a). Frequency differences among mtDNA haplotypes distinguish rookeries in Japan, eastern and western Australia as forming three unique populations, though the level of divergence among mtDNA haplotypes in the eastern Indian Ocean and western Pacific Ocean is low. Only one shared haplotype, found in one turtle in Japan, has been observed in both Australia and Japan (Hatase *et al.*, 2002). In contrast, there is high genetic divergence between the Japan/Australia/New Caledonia genetic lineages and the highly divergent Oman and South Africa lineages (Shamblin *et al.*, 2014). Additional sampling is needed for the southwest Pacific Ocean and to determine whether the Sri Lanka rookeries form an additional genetic stock, and to clarify whether rookeries in Yemen are part of the northwest Indian Ocean stock.

Genetic analyses have been conducted on some loggerhead turtle feeding ground samples, stranded turtles and turtles caught by fisheries. This includes feeding grounds in Western Australia and Queensland (Pacioni *et al.*, 2012, unpubl. data), stranded turtles in Australia (FitzSimmons *et al.*, unpubl. data), and fisheries bycatch samples in Peru (Boyle *et al.*, 2009). The latter study confirmed an hypothesis that loggerhead turtles from rookeries in eastern Australia and New

Caledonia are traversing the south Pacific and are caught by long-line fisheries off the coast of Peru.

Chelonia mydas

Green turtles have the largest number of genetic stocks identified within the Indo-Pacific, with 30 different stocks designated to date (Figure 2). This reflects a high level of genetic diversity found in the region, including at least five divergent genetic lineages (Dethmers *et al.*, 2006; Bourjea *et al.*, 2007). Dethmers *et al.* (2006) analysed 27 rookeries and determined there were 17 management units among sample sites in the western Indian Ocean, SE Asia and western Pacific. The Scott Reef genetic stock (Dethmers *et al.*, 2006) has been expanded to include Browse Island (Jensen, 2010) and the genetic stock identified from Long Island in northeast Papua New Guinea has been expanded to include all of northern New Guinea (Velez-Zuazo *et al.*, 2006). Research by Mahardika *et al.* (2007) suggests that the northeast Borneo and east Borneo genetic stocks, identified by Dethmers *et al.* (2006) as the SE Sabah and Berau Islands management units, may constitute a single genetic stock, although work by Arshaad & Kadir (2009) supports the designation of at least two stocks. In the southwestern Indian Ocean, Bourjea *et al.* (2007) identified four genetic stocks that include the Arabian Peninsula, the northern Mozambique Channel, Europa and Juan de Novo. There is some evidence that there may be additional genetic differentiation within the genetic stock of the northern Mozambique Channel, but further sampling in the region is required (Bourjea *et al.*, 2007).

Regional genetic studies have identified additional genetic stocks in the Indo-Pacific. These include genetic stocks at Coburg Peninsula in the Northern Territory, Australia and the Cocos (Keeling) Islands (Jensen, 2010). In the northwestern Pacific and South China Sea, three genetic stocks have been identified to exist in Japan, southeast Taiwan and southwest Taiwan (Cheng *et al.*, 2008; Nishizawa *et al.*, 2011). Genetic differentiation identified two stocks in Taiwan, which was somewhat unexpected, given the two island rookeries are only ~250 km distant from each other. However, a similar result of genetic differentiation was found between the Ashmore Reef and Scott/Browse genetic stocks in the Arafura Sea, which are comprised of island rookeries ~225 km distant (Dethmers *et al.*, 2006; Jensen, 2010). Most surprisingly, there was a high level of genetic differentiation (no haplotypes were shared between the sites) between the Taiwan stocks, although the sample size was small (n = 14) for one site and additional sampling is needed. The most striking result was found by Nishizawa *et al.* (2011), who uncovered mtDNA genetic differentiation between

rookeries on two islands in Japan where sample sites were located only 40 – 60 kms apart. They recommended further study to confirm this, so these rookeries are considered a single stock at present. In contrast to these geographically limited genetic stocks, the North West Shelf stock in Western Australia encompasses over 1000 kms between the furthest rookeries sampled (Dethmers *et al.*, 2010) and the northern New Guinea stock includes rookeries over 2000 kms apart (Velez-Zuazo *et al.*, 2006).

Genetic studies of rookeries in Thailand did not find significant genetic divergence between rookeries at Khram Island in the Gulf of Thailand and Huyon Island in the Andaman Sea (Kittiwattanawong *et al.*, 2003), even though these are separated by >2300 km of coastline. It was suggested that these results could be due to low levels of gene flow through the Malacca Straits after colonisation by a common ancestor (Kittiwattanawong *et al.*, 2003). This explanation is problematic given that each of the rookeries is genetically divergent from the intermediately located Peninsular Malaysia stock. Satellite telemetry of post-nesting turtles shows behavioural differences between the two rookeries in the location of their foraging grounds (Kittiwattanawong *et al.*, 2002, 2003; Kittiwattanawong & Manansap, 2009), suggesting demographic independence of the two rookeries, although additional telemetry data are needed. As suggested, a lack of genetic differentiation can occur when populations are colonised from the same ancestral population, and too few generations have occurred to develop differentiation through genetic drift and new mutations (Avice, 2000). Alternatively, genetic similarities may reflect the random nature of colonisation from multiple source populations that result in demographically separate populations appearing to be similar. The most common haplotype in Thailand rookeries is shared among all rookeries throughout the region, the second most common haplotype is observed in several Malaysian stocks and none of the other six haplotypes observed at lower frequencies are shared between the two Thailand rookeries. Colonisation of the Sunda Shelf in the last 8,000 years as sea levels dropped would have occurred from multiple source populations, which could have led to the Thailand rookeries appearing to be similar, as suggested for loggerhead populations on the east and west coast of Florida (Encalada *et al.*, 1998). A similar situation of no observed genetic divergence occurs between two hawksbill populations in Australia (nQLd, nEA; Table 1), but due to differences in nesting seasonality, they are considered as separate genetic stocks (Limpus, 2009a). We provisionally consider the two rookeries sampled in Thailand as separate stocks based on behavioral differences in foraging locations (Kittiwattanawong & Manansap, 2009) and their

differentiation from the Peninsular Malaysia stock.

Mixed stock analyses of mtDNA data have been conducted for several green turtle foraging grounds in the Indo-Pacific to determine the proportional contribution of different genetic stocks to shared foraging grounds. Foraging grounds have been analysed in the southwest Pacific Ocean (Jensen, 2010; Read *et al.*, In Press), northwest Pacific Ocean (Nishizawa *et al.*, 2013), western Indian Ocean (Jensen, 2010), Arafura and Timor seas (Dethmers *et al.*, 2010), South China Sea (Jensen, 2010) and the Celebes Sea (Mahardija *et al.*, 2007). Considerable variation in results exists, with some foraging ground aggregations being composed mostly of turtles from the nearest genetic stock (i.e., Aru, Gulf of Capentaria, nGBR; Dethmers *et al.*, 2010; Jensen, 2010) while other aggregations include significant numbers of turtles from genetic stocks over 1,000 km distant (i.e., New Caledonia and Japan; Nishizawa *et al.*, 2013; Read *et al.*, In Press). Unfortunately, the presence of a high proportion of shared mtDNA haplotypes in the Indo-Pacific often precludes firm conclusions about the origins of turtles at foraging grounds. Instead, most knowledge on the international dispersal of post-nesting turtles has come from tag recovery data (Table 1 references). Genetic analyses have been conducted on green turtles harvested in Bali and Australia (Moritz *et al.*, 2002), demonstrating that the Bali harvest harvests turtles from a broad geographic region and includes turtles originating from other countries, whereas the nGBR harvest primarily has a local impact (Moritz, 2002; Jensen, 2010).

Important knowledge gaps remain, with several large, isolated rookeries not yet analysed, and regions where additional sampling of rookeries would help clarify stock boundaries (see Figure 2). Additional green turtle genetic stocks are likely to be found in the Indo-Pacific, particularly if the rookeries are located more than 500 km from rookeries used by other genetic stocks (Dethmers *et al.*, 2006). Mixed stock analyses of feeding grounds will require large sample sizes (Jensen, 2001) and will be most effective if conducted as regional transects (e.g., Dethmers *et al.*, 2010; Jensen, 2010) that incorporate knowledge of the complex ocean currents of the region.

Dermochelys coriacea

Population genetic studies have identified three genetic stocks in the Indo-Pacific, but many gaps remain in the sampling of low-density rookeries throughout the region. Stocks are identified in the southwest Indian Ocean, northeast Indian Ocean (Malaysia, Nicobar Islands) and western Pacific Ocean (Dutton *et al.*, 1997, 2007; Shanker *et al.*, 2011) (Table 2, Figure 3). The

grouping of Malaysia and Nicobar is tentative as it is based on only nine samples from Malaysia (Dutton *et al.*, 1999) and there is some evidence that they forage in different areas (Limpus, 1997; Shanker, pers. comm. 2014, data at seaturtle.org/stat/). Additional sampling is needed in many areas to determine the boundaries of the nesting regions for each stock. Satellite telemetry has revealed the extensive foraging range of the western Pacific Ocean stock, with differential migratory behaviour observed between austral summer and winter nesting turtles (Benson *et al.*, 2011). Although it is speculated that demographic differences may exist between austral summer and winter nesting turtles, nesting throughout the year among western Pacific Ocean turtles would allow for sufficient gene flow such that the stock is considered a meta-population (Benson *et al.*, 2011). Ongoing satellite telemetry of post-nesting females from the northeast Indian Ocean stock is similarly demonstrating a wide dispersal of individuals to foraging areas in several countries (Shanker, pers. comm. 2014, data at atseaturtle.org/stat/) and suggests the origins for at least some of the stranded leatherback turtles along the western Australia coast (Prince, 2004).

Eretmochelys imbricata

Population genetic studies of hawksbill turtles in the Indo-Pacific have revealed the presence of at least nine genetic stocks (Mortimer & Broderick, 1999; FitzSimmons, 2010; Arshaad & Kadir, 2009, Tabib *et al.*, 2011, 2014). Interesting results include the possible separation of stocks within the Arabian Gulf and the grouping of distant rookeries in Seychelles and Chagos (FitzSimmons, 2010; Tabib, 2014). The Gulf of Thailand stock is proposed, but additional samples are needed to confirm this (Arshaad & Kadir, 2009). The north Queensland and northeast Arnhem Land stocks could not be differentiated with genetic analyses, but are separated on the basis of that the turtles in those populations nest at different times of year (Limpus, 2009a). There are severe knowledge gaps in the genetic study of hawksbill turtle rookeries throughout the Indo-Pacific (Figure 4). Foraging ground mixed stock analyses have been conducted for some areas (FitzSimmons, 2010), but most data on the use of foraging grounds across international borders comes from limited tag recovery data of post-nesting females (Table 1 references).

Lepidochelys olivacea

Separate genetic stocks have been identified in six regions that include the eastern India coast, Sri Lanka, Andaman and Nicobar Islands (India), Peninsular

Malaysia, western Northern Territory (Australia) and western Cape York Peninsula (Australia) (Bowen *et al.*, 1998; Shanker *et al.*, 2004; Jensen *et al.*, 2013; Shanker *et al.*, 2011). Preliminary data from nesting turtles in Indonesia have been provided that suggest substantial variation from the Australian rookeries (I. B. W. Adnyana *et al.*, unpublished data, reported in Jensen *et al.*, 2013). Many important sampling gaps exist, particularly in Africa, Oman, western India, northeast Indian Ocean, the South China Sea, Arafura Sea and Timor Sea (Figure 5). As observed in other species, the geographic extent of genetic stocks is highly variable, such as the grouping of many rookeries along the eastern India coast into a single genetic stock, whereas turtles nesting in nearby in Sri Lanka are genetically differentiated into a separate stock (Shanker *et al.*, 2004).

Information on the use of internationally dispersed foraging grounds by particular stocks is limited, given there are no published genetic studies of olive ridley turtles sampled at feeding grounds in the Indo-Pacific and few tag recovery records of turtles found outside of the countries they were tagged in. Jensen *et al.* (2013) analysed mtDNA variation in olive ridley turtles that had become entangled in discarded fishing nets (ghost nets) that drifted ashore in the Gulf of Carpentaria. It appears that the nets are entangling turtles from Australian and Indonesian stocks at shared feeding grounds in the Arafura Sea, and thus have a broad impact. Satellite tagging of post-nesting females from Northern Australia supports the hypothesis of shared feeding grounds, given that some tracked females entered Indonesian waters (Whiting *et al.*, 2007). Considerably more genetic, tagging and satellite telemetry studies are needed to better understand the dynamics of olive ridley populations within the Indo-Pacific.

Natator depressus

Five genetic stocks of flatback turtles have been identified (Pittard, 2010), all of which nest only within Australia (Table 1, Figure 6). Some of these stocks use feeding grounds in Indonesia and Papua New Guinea (Limpus, 2007). Within the eastern Queensland and Arafura Sea genetic stocks there is evidence of restricted gene flow among at least some pairs of rookeries that have been sampled (Pittard, 2010). Some rookeries may be more independent than can be uncovered by genetic studies at present. Additional sampling along the northwest coast of Western Australia Kimberley region will help determine the boundary between the winter nesting genetic stock sampled at Cape Domett (Joseph Bonaparte Gulf stock) and the summer nesting stock sampled at Eco Beach (southwest Kimberley stock).

Several satellite telemetry studies of post-nesting females are being conducted and reveal extensive migrations, mostly within Australian waters (see seaturtle.org/stat/).

DISCUSSION

Considerable progress has been made to define population boundaries and understand migratory behaviour of marine turtles within the Indo-Pacific, which has supported international efforts in conservation management. Genetic studies have led to the identification of 57 genetic stocks that are considered as separate management units in that the loss of nesting females in one stock will not be replaced readily by nesting turtles from another stock. Over two-thirds (68%) of the genetic stocks have turtles that either breed in more than one country, or breed and forage in different countries, thus international cooperation is critical for understanding and protecting marine turtle populations in the Indo-Pacific.

One important conclusion from population genetic studies is the inability to predict which rookeries are grouped together as a genetic stock, unless tagging efforts have been extensive and cover a large number of rookeries in a region. Stock boundaries have varied hugely, separating rookeries <60 kms distant, to the grouping of rookeries >2000 kms apart; thus filling in knowledge gaps needs to be quantitative, and cannot be assumed. Similarly, tagging and satellite telemetry studies of migratory turtles have provided important data on the broader geographic range of a stock at foraging locations and migratory pathways, but unless studies are extensive, it is not possible to quantify the extent to which stocks use different locations. Genetic studies using mixed stock analyses have provided quantification of how stocks are distributed in benthic as well as pelagic habitats. These studies have been particularly important in allowing quantification of stock-specific impacts from human disturbance, such as incidental capture in fisheries or directed take (Bowen *et al.*, 1995; Jensen *et al.*, 2012). One of the largest remaining gaps is the lack of understanding about the pelagic phase of post-hatchling and juvenile turtles in the Indo-Pacific, and genetic studies can provide important insights if samples can be obtained (e.g., Boyle *et al.*, 2009).

Genetic stocks/Management Units versus Regional Management Units

Most of the designations of genetic stocks have been based upon rejecting a hypothesis that sampled rookeries share the same mtDNA haplotype frequencies. Palsbøll *et al.* (2011) argue that a more effective approach would be to

set a threshold level of dispersal as the criteria for defining management units. For marine turtle genetic stocks, dispersal would relate to the number of females that migrate between two rookeries, or groups of rookeries, being analysed. From a genetic perspective, the question becomes not just whether two populations are genetically divergent, but by how much. The authors acknowledge however, that empirical links between dispersal and demographic independence are poorly known for most species (Waples & Gaggiotti, 2006), and that species-specific models linking demographic parameters and population genetic estimations are needed. Setting a threshold level of dispersal has been done for the identification of salmon stocks by the IUCN Salmon Specialist Group, who determined the appropriate threshold level to be less than one migrant per year. Theoretical analyses are needed to link a threshold level of dispersal to the equivalent level of genetic divergence as observed in genetic studies. For sockeye salmon (*Onchorhynchus nerka*) the threshold of one migrant per year was determined to equate to a genetic divergence of $F_{ST} = 0.04$ using nuclear microsatellite data (IUCN, 2014), where $F_{ST} = 0$ for identical populations and $F_{ST} = 1$ for populations that do not share any of the same alleles. If the same approach is taken for defining marine turtle stocks, then rookeries known to have (on average) one female per year that has switched between two rookeries, then these rookeries can be defined as part of the same genetic stock. To determine an F_{ST} threshold for defining marine turtle stocks requires establishing the relationships among dispersal, gene flow, generation time and genetic divergence using empirical data. At present, the designation of genetic stocks based upon rejecting a null hypothesis of no genetic divergence is likely to be a valid, and probably conservative, approach for defining marine turtle populations.

An alternate approach for defining 'units' for management, known as Regional Management Units (RMUs), was proposed by Wallace *et al.* (2010) and used for setting global conservation priorities (Wallace *et al.*, 2011). In general, this approach does not take a population level perspective, but instead groups populations into regional constructs, largely based upon the sharing of foraging areas. While the RMU process aims to be informative by incorporating a variety of data sources and provides distribution maps of habitat use (Wallace *et al.*, 2010), the resultant RMUs may comprise a single population, multiple populations, or unknown populations, thus it is not clear what is being managed. Within the Indo-Pacific 31 RMUs have been defined, which include eight putative RMUs where data were lacking (Wallace *et al.*, 2010). In comparison to the 57 genetic stocks identified to date within the Indo-Pacific,

and with the expectation that more will be defined, the RMU approach is clearly different. Olive ridley turtle populations are reduced from six genetic stocks (with more expected) to four RMUs, with a west Pacific RMU that includes the western Pacific, all of southeast Asia, Australia and the western Indian Ocean. Additionally, there are two northeast Indian RMUs that separate turtles based on whether or not they nest in arribadas (Wallace *et al.*, 2010). Most of the seven hawksbill turtle RMUs are putative so do not bear scrutiny, but the five flatback turtle genetic stocks have been reduced to three RMUs (Wallace *et al.*, 2010), one of which includes geographically distant stocks that nest at different times of the year. The biggest discrepancy is for green turtle populations in the Indo-Pacific; with 30 genetic stocks reduced to eight RMUs (Wallace *et al.*, 2010). One RMU that stands out as inappropriate is the southwest Pacific RMU, which includes the New Caledonia, Coral Sea, southern Great Barrier Reef, northern Great Barrier Reef and northern New Guinea genetic stocks (Wallace *et al.*, 2010). This includes stocks (sGBR, nGBR) that are highly genetically divergent and known to function with complete demographic independence, other than the sharing of feeding grounds in some locations (Limpus, 2008b). Because leatherback turtle genetic stocks tend to use several nesting beaches within a large region, and loggerhead turtle genetic stocks are quite isolated from each other, the RMU approach for these two species in the Indo-Pacific does not differ from a genetic approach, with the exception that the RMU approach presents putative stocks.

Rather than benefitting the local or regional management of marine turtle populations, the RMU approach has the potential in some areas and for some species to de-emphasise the importance of monitoring and managing from an ecologically sound population perspective. We argue for the need to maintain the focus of management at the level of the genetic stock because critically, nesting habitats used by a specific population (genetic stock, MU) would not readily be recolonised by migrants from other genetic stocks in the near term if local extinction occurs (Moritz, 1994; Palsbøll *et al.*, 2007). Additionally, the distribution of genetic divergence in the Indo-Pacific emphasises the importance of prioritizing the conservation of genetic stocks, not simply based on the size of the stock, but also by the unique combination of genetic diversity found within genetic stocks. For example, some genetic stocks are known to only support tens of females per year while other stocks support tens of thousands of females, but from a biodiversity perspective they may be equally significant. For example, the much smaller non-arribada olive ridley populations of the Indo-Pacific contain more

genetic diversity than the large arribada population in India (Shanker *et al.*, 2004, 2011; Jensen *et al.*, 2013).

Management for turtle conservation at a genetic stock level involves a two-step process of first identifying which rookeries group together to form a genetic stock, and then identifying the nearshore and oceanic habitat used by each population with a combination of genetic, tagging and telemetry data. This combined approach provides managers with the information needed to prioritise actions based on threats to nesting beaches and feeding grounds for each population. It also provides more specific information to be used when negotiating internationally regarding these shared populations. Rather than relying on the RMU maps given in Wallace *et al.* (2010), countries should develop maps for each genetic stock indicating rookery locations and habitat use in pelagic and benthic environments. This has recently been done in Australia for incorporation into a revised marine turtle recovery plan. For the advancement of marine turtle conservation and management in the Indo-Pacific, we urge the continued progress in delineating marine turtle genetic stocks in the Indo-Pacific and using that information as the basis for targeting further research, monitoring and international collaboration to achieve better management outcomes for marine turtles.

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Table 1. Marine turtle genetic stocks found within the geographic region included within the Indian Ocean-South-East Asian Marine Turtle Memorandum of Understanding, shown by species, stock and country, with known links between nesting and foraging populations across international borders. Countries shown in italics are those with rookeries presumed to be a part of a particular stock but this has not been confirmed by tagging or genetic studies. Genetic stocks identified with an asterisk show evidence of some genetic differentiation among some rookeries within the stock.

Species/Genetic Stock	Country-nesting	Other Countries- feeding grounds	Other countries-post-hatchling/juvenile pelagic	References
<i>Caretta caretta</i>				
northwest Pacific Ocean (nwPac)	Japan	Philippines	Mexico, USA	deVeyra, 1994; Bowen <i>et al.</i> , 1995; Hatase <i>et al.</i> , 2002; Limpus, 2008a
southwest Pacific Ocean (swPac)	Australia, New Caledonia	Indonesia, Papua New Guinea, Solomon Islands	Peru	Limpus <i>et al.</i> , 1992; FitzSimmons <i>et al.</i> , 1996; Kelez <i>et al.</i> , 2003; Alfaro-Shigueto <i>et al.</i> , 2004; Boyle <i>et al.</i> , 2009; Limpus, 2008a; Limpus <i>et al.</i> , database ¹
southeast Indian Ocean (seInd)	Australia	Indonesia		FitzSimmons <i>et al.</i> , 1996; Pacioni <i>et al.</i> , 2012; Limpus <i>et al.</i> , database ¹
northwest Indian Ocean (nwInd)	Oman	Bahrain, Iran, Pakistan, Qatar, Saudi Arabia, Somalia, United Arab Emirates, Yemen		Baldwin <i>et al.</i> , 2003; Limpus, 2008a; Rees <i>et al.</i> 2010; Hamann <i>et al.</i> 2013; Shamblyn <i>et al.</i> , 2014
southwest Indian Ocean (swInd)	South Africa	France, Kenya, Madagascar, Mozambique, Seychelles, Somalia, Tanzania		Baldwin <i>et al.</i> , 2003; Lushci <i>et al.</i> , 2006; Limpus, 2008a; Shamblyn <i>et al.</i> , 2014
<i>Chelonia mydas</i>				
western New Caledonia (wNC)	New Caledonia	Australia, Papua New Guinea		Deithmers <i>et al.</i> , 2006; Limpus, 2008b; Read <i>et al.</i> , 2014; Limpus <i>et al.</i> , database ¹
Coral Sea Platform (CS)	Australia	Papua New Guinea		Deithmers <i>et al.</i> , 2006, Limpus, 2008b; Limpus <i>et al.</i> , database ¹
Southern Great Barrier Reef (sGBR)	Australia	Fiji, New Caledonia, Papua New Guinea, Vanuatu		Limpus <i>et al.</i> , 1992; Norman <i>et al.</i> , 1994; FitzSimmons <i>et al.</i> , 1997a,b; Deithmers <i>et al.</i> , 2006; Limpus, 2008b; Read <i>et al.</i> , 2014; Limpus <i>et al.</i> , database ¹
Northern Great Barrier Reef (nGBR)	Australia	Indonesia, New Caledonia, Papua New Guinea, Vanuatu		Limpus <i>et al.</i> , 1992; Norman <i>et al.</i> , 1994; FitzSimmons <i>et al.</i> , 1997a,b; Deithmers <i>et al.</i> , 2006; Limpus, 2008b; Limpus <i>et al.</i> , database ¹
Gulf of Carpentaria (GoC)	Australia			Norman <i>et al.</i> , 1994; FitzSimmons <i>et al.</i> , 1997a,b; Deithmers <i>et al.</i> , 2006
Cobourg Peninsula (CP)	Australia			Jensen, 2010
Ashmore Reef (AR)	Australia			Deithmers <i>et al.</i> , 2006; Jensen, 2010
Scott-Browse (SB)	Australia			Deithmers <i>et al.</i> , 2006; Jensen, 2010
North West Shelf (NWS)	Australia	Indonesia		Norman <i>et al.</i> , 1994; FitzSimmons <i>et al.</i> , 1997a, b; Deithmers <i>et al.</i> , 2006, Limpus 2008b, Limpus <i>et al.</i> database ¹
Cocos (Keeling) Islands (CK)	Australia			Jensen, 2010
northern New Guinea (nNG)	Indonesia, Papua New Guinea	Australia, Japan, Malaysia		Norman <i>et al.</i> , 1994; Deithmers <i>et al.</i> , 2006; Velez-Zuazo <i>et al.</i> , 2006; Limpus, 2008b; Nishizawa <i>et al.</i> , 2013; Limpus <i>et al.</i> , database ¹

Micronesia (FSM)	Micronesia	Indonesia, Japan, Marshall Islands, Palau, Philippines	deVeyra, 1994; Norman <i>et al.</i> , 1994; Dethmers <i>et al.</i> , 2006; Nishizawa <i>et al.</i> , 2013; Limpus <i>et al.</i> , database
Aru (Aru)	Indonesia		Dethmers <i>et al.</i> , 2006
West Java (wJ)	Indonesia	Australia	Norman <i>et al.</i> , 1994; Dethmers <i>et al.</i> , 2006; Limpus, 2008b; Limpus <i>et al.</i> , database ¹
east Borneo (eB)2	Indonesia	Malaysia, Philippines	Sagun, 2003; Dethmers <i>et al.</i> , 2006; Mahardika <i>et al.</i> , 2007; Adnyana <i>et al.</i> , 2008; Arshaad <i>et al.</i> , 2008
West Borneo (wB)	Malaysia	Philippines	Norman <i>et al.</i> , 1994; Bali <i>et al.</i> , 2002; Dethmers <i>et al.</i> , 2006; Arshaad <i>et al.</i> , 2008
Sulu Sea (SS)	Philippines, Malaysia	Indonesia, Palau, Papua New Guinea	De Silva, 1982; Dethmers <i>et al.</i> , 2006; de Veyra, 1994; Sagun, 2004; Arshaad <i>et al.</i> , 2008; Isnain, 2009; Limpus <i>et al.</i> , database ¹
southwest Japan (swJ)*	Japan	Philippines	Sagun, 2003; Cheng <i>et al.</i> , 2008; Nishizawa <i>et al.</i> , 2011
east Taiwan (eT)	Taiwan		Cheng <i>et al.</i> , 2008; Nishizawa <i>et al.</i> , 2011
west Taiwan (wT)	Taiwan		Cheng <i>et al.</i> , 2008; Nishizawa <i>et al.</i> , 2011
Vietnam (V)	Vietnam	Indonesia, Malaysia, Philippines	Arshaad & Kadir, 2009; Dung, 2009
east Peninsular Malaysia (ePM)	Malaysia	Indonesia, Philippines, Singapore, Vietnam	Dethmers <i>et al.</i> , 2006; Arshaad <i>et al.</i> , 2008; van de Merwe <i>et al.</i> , 2009; Lau <i>et al.</i> , 2009; Limpus <i>et al.</i> , database ¹
Gulf of Thailand (GT)	Thailand	Cambodia, Malaysia, Philippines, Singapore, Vietnam	Kittiwattanawong <i>et al.</i> , 2002, 2003; Arshaad & Kadir, 2009; Kittiwattanawong & Manansap, 2009; Limpus <i>et al.</i> , database ¹
Adaman Sea (AS)	Thailand	India	Kittiwattanawong <i>et al.</i> , 2002, 2003; Arshaad & Kadir 2009; Kittiwattanawong & Manansap, 2009; Limpus <i>et al.</i> , database ¹
Myanmar (M)	Myanmar		Arshaad & Kadir, 2009
east Arabian Peninsula (eAP)	Saudi Arabia, Oman	Eritrea, Maldives, United Arab Emirates, Yemen	Ross, 1984; Miller, 1989; Gasperetti <i>et al.</i> , 1990; Bowen <i>et al.</i> , 1992; Broderick, 1998; Limpus <i>et al.</i> , database ¹
north Mozambique Channel (nMC)*	Seychelles, Comoros, France3, Madagascar	Mozambique, Tanzania, Somalia	Le Gall & Hughes, 1987; Mortimer & Broderick, 1999; Formia <i>et al.</i> , 2001; Bourjea <i>et al.</i> , 2007; Limpus <i>et al.</i> , database ¹
south Mozambique Channel (i.e., Europa) (sMC)	France3	Comoros, Madagascar, Mozambique, Seychelles	Le Gall & Hughes, 1987; Bourjea <i>et al.</i> , 2007
Central Mozambique Channel (i.e., Juan de Novo) (cMC)	France3	Comoros, Madagascar, Mozambique, Seychelles	Bourjea <i>et al.</i> , 2007
<i>Dermochelys coriacea</i>			
western Pacific Ocean (wPac)	Indonesia (Papua), Papua New Guinea, New Ireland, New Britain, Solomon Islands, Vanuatu	Australia, Federated States of Micronesia, Japan, Korea, Malaysia, Marshall Islands, New Caledonia, New Zealand, Palau, Philippines, United States of America	Dutton <i>et al.</i> , 1999, 2007; Adnyana, 2009; Limpus, 2009b; Minami <i>et al.</i> , 2009; Benson <i>et al.</i> , 2011; Limpus <i>et al.</i> , database ¹

southwest Indian Ocean (swInd)	South Africa India ⁴ , Malaysia, Sri Lanka	Mozambique, Namibia Australia, France ³ , Indonesia, Madagascar, Seychelles, United Kingdom ⁵	Dutton <i>et al.</i> , 1999; Luschi <i>et al.</i> , 2006 Dutton <i>et al.</i> , 1999; Shanker <i>et al.</i> , 2011; Shanker, pers. comm.
<i>Eretmochelys imbricate</i>			
Solomon Islands (Sol)	Solomon Islands	Australia, Papua New Guinea	Limpus, 2009a; Limpus <i>et al.</i> , database ¹
north Queensland (nQld)	Australia	Indonesia, Papua New Guinea	Limpus, 2009a; FitzSimmons, 2010; Limpus <i>et al.</i> , database ¹
northeast Arnhemland (neAl)	Australia	Indonesia, Philippines	Limpus, 2009a; FitzSimmons, 2010
Sulu Sea (SS)	Malaysia	Indonesia, Singapore	De Silva, 1982; Adnyana <i>et al.</i> , 2008; Arshaad & Kadir, 2009; Isnain, 2009
western Peninsular Malaysia (wPM)	Malaysia		Lau <i>et al.</i> , 2009
Gulf of Thailand (GoT)	Thailand		Arshaad & Kadir, 2009
eastern Indian Ocean (eIO)	Australia		FitzSimmons, 2010
western/central Indian Ocean (wIO)	Seychelles, Chagos		Mortimer & Broderick, 1999; FitzSimmons, 2010
Arabian/PersianGulf* (AG)	Iran, Saudi Arabia		FitzSimmons, 2010; Tabib <i>et al.</i> , 2011, 2014
<i>Lepidochelys olivacea</i>			
western Cape York (wCYP)	Australia	Indonesia	Jensen <i>et al.</i> , 2013; Limpus <i>et al.</i> , database ¹
Northern Territory (wNT)	Australia	Indonesia	Jensen <i>et al.</i> , 2013; Whiting <i>et al.</i> , 2007
Peninsular Malaysia (PM)	Malaysia		Bowen <i>et al.</i> , 1998
Andaman Sea (AS)	India ⁴		Shanker <i>et al.</i> , 2011
Sri Lanka (SL)	Sri Lanka		Bowen <i>et al.</i> , 1998; Shanker <i>et al.</i> , 2004
eastern India (eI)	India	Sri Lanka	Kapurusinghe & Cooray, 2002; Shanker <i>et al.</i> , 2004; Frazier, 2007
<i>Natator depressus</i>			
eastern Australia (eAust)*	Australia		Pittard, 2010
Aratura Sea (AS)*	Australia	Papua New Guinea, Indonesia	Limpus, 2007; Pittard, 2010; Limpus <i>et al.</i> , database ¹
Joseph Bonaparte Gulf (BG)	Australia		Pittard, 2010
southwest Kimberley (swKim)	Australia		Pittard, 2010
Pilbara Coast (PI)	Australia		Pittard, 2010

¹This is a global database focused on the Indo-Pacific that is curated by C. J. Limpus. It includes records of nesting locations, tag recoveries and satellite telemetry data based on published literature, reports, conference and workshop presentations, government and personal databases and pers. comm. information from people throughout the region.

²see Dethmers *et al.* (2006), Mahardika *et al.* (2007) and Arshaad & Kadir (2009) for different interpretations of stock boundaries.

³Western Indian Ocean islands

⁴Andaman and/or Nicobar Islands

⁵British Indian Ocean Territory; Chagos Archipelago

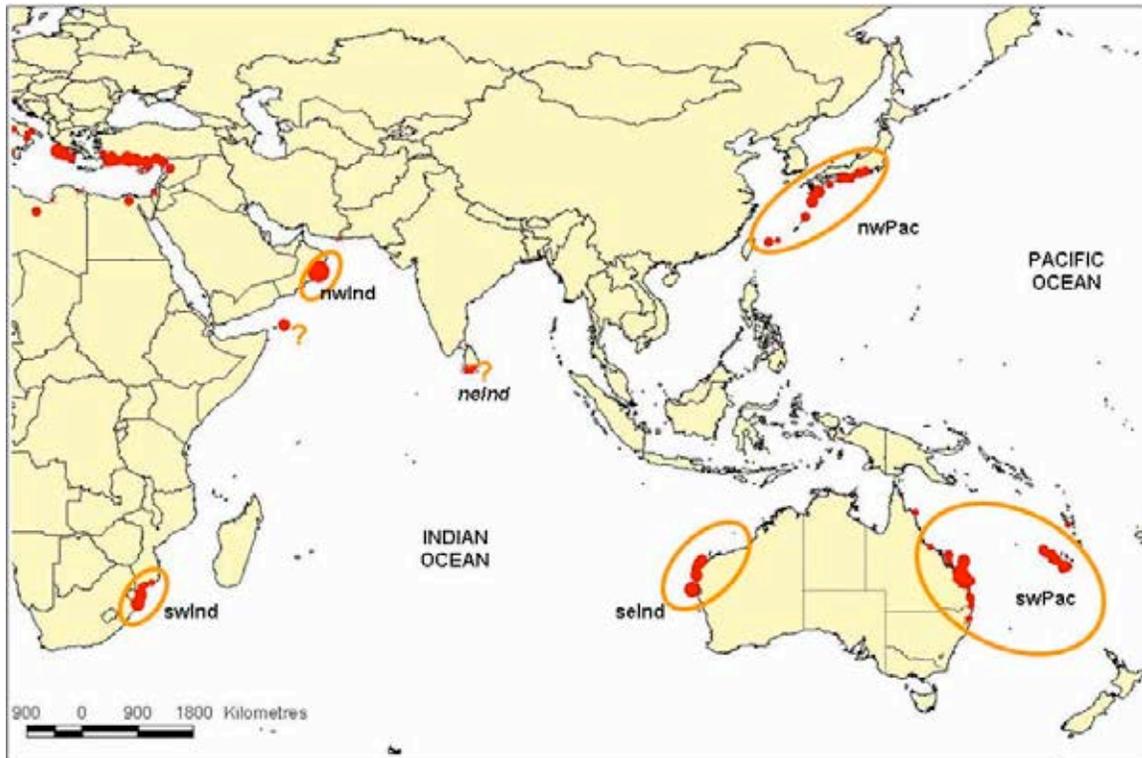


Figure 1. Location of *Caretta caretta* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.

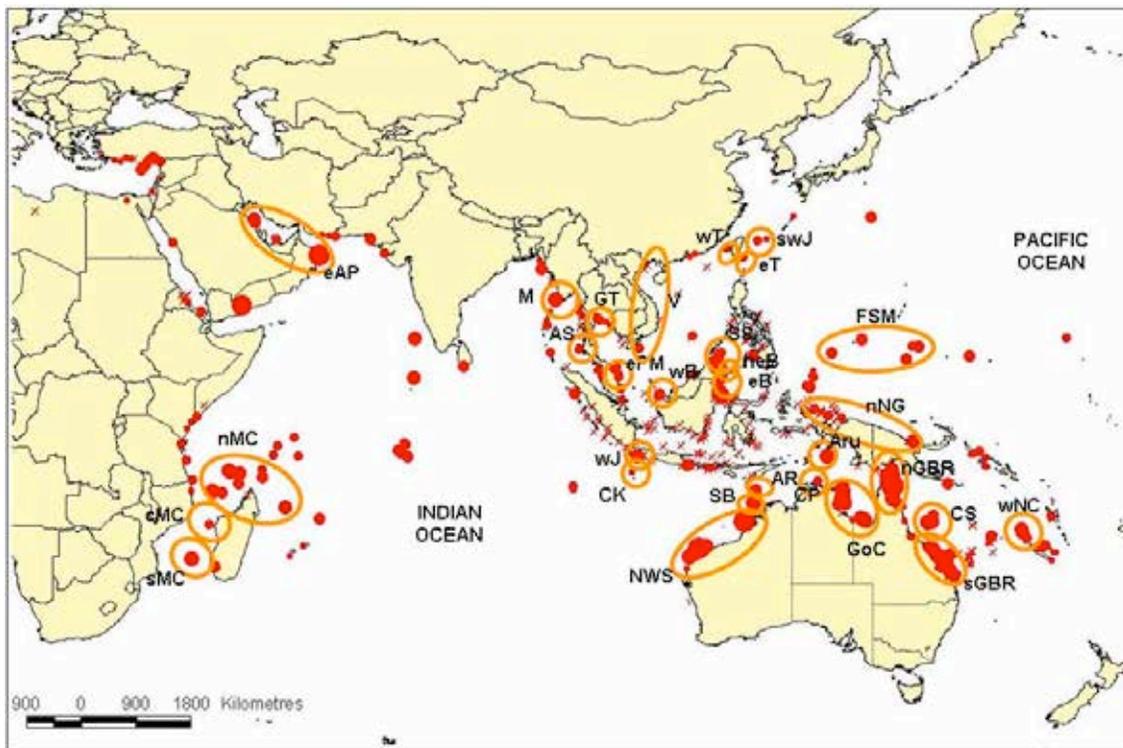


Figure 2. Location of *Chelonia mydas* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.

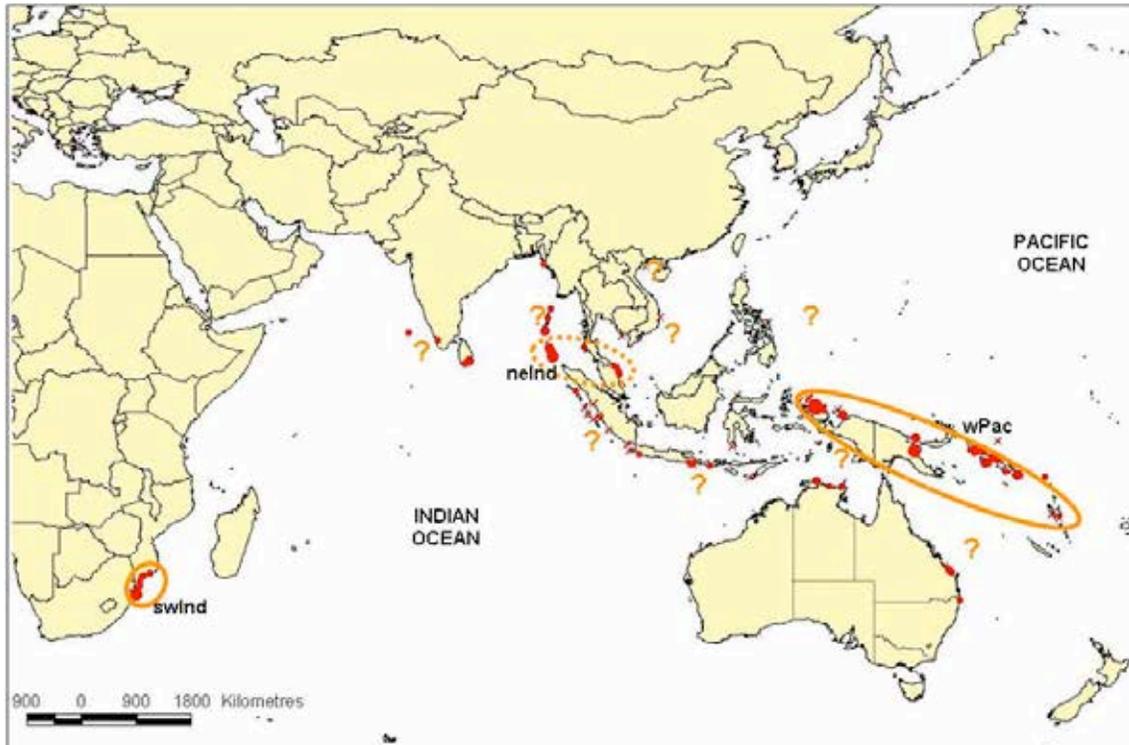


Figure 3. Location of *Dermochelys coriacea* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.

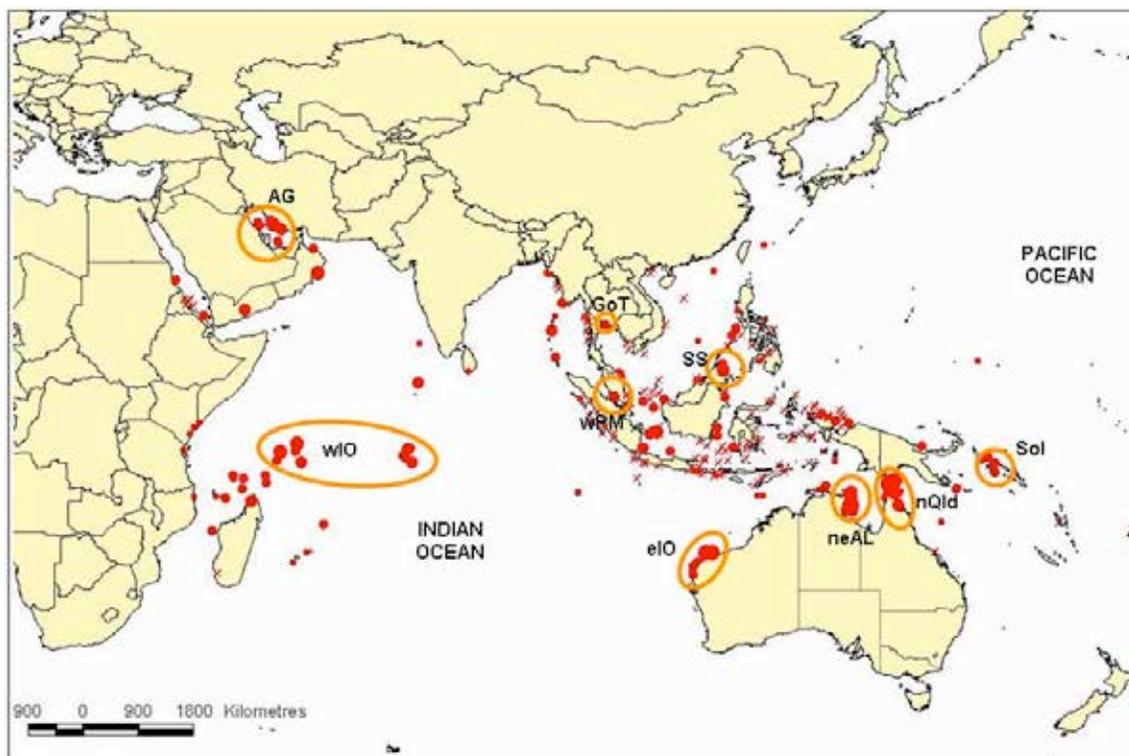


Figure 4. Location of *Eretmochelys imbricata* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.

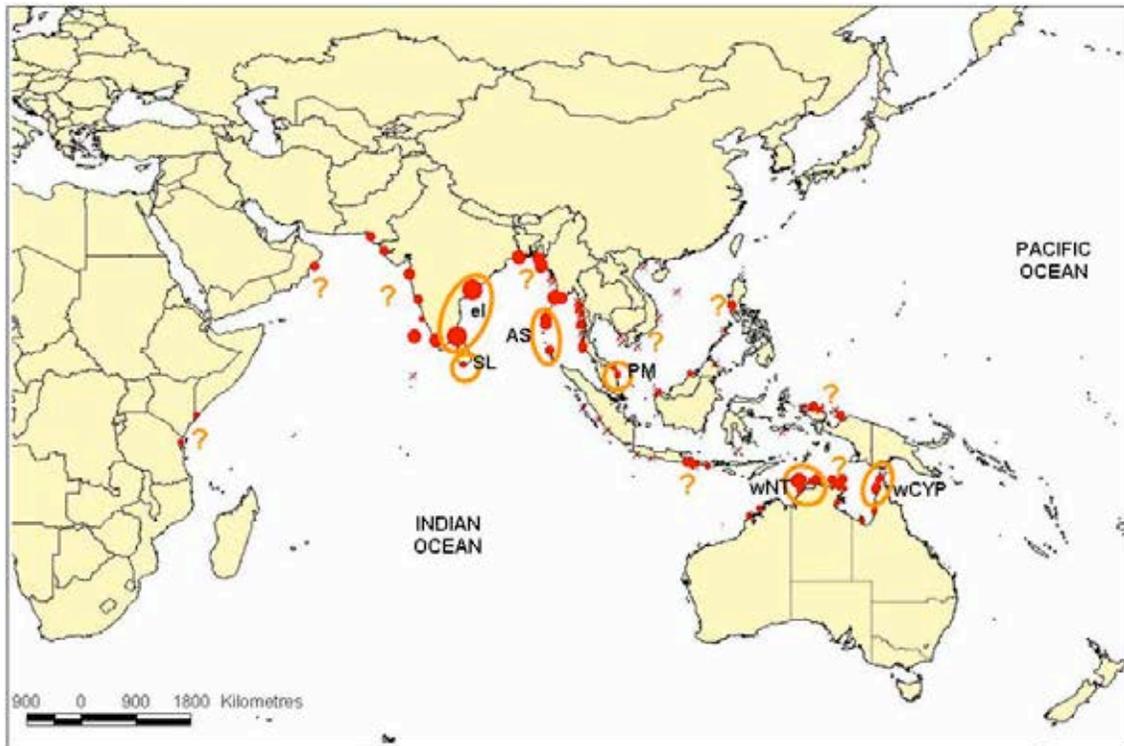


Figure 5. Location of *Lepidochelys olivacea* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.

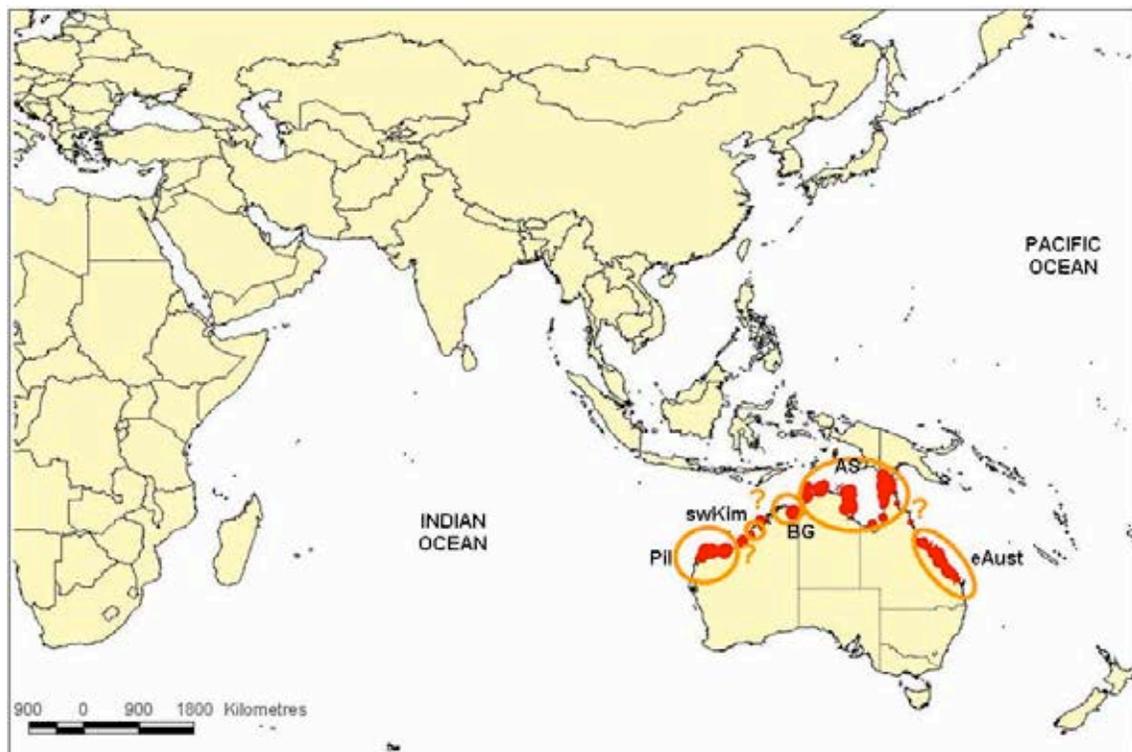


Figure 6. Location of *Natator depressus* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks.