



**MEMORANDUM OF UNDERSTANDING
ON THE CONSERVATION AND
MANAGEMENT OF MARINE TURTLES
AND THEIR HABITATS OF THE INDIAN
OCEAN AND SOUTH-EAST ASIA**

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



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The following paper, which addresses an action point identified by the Sixth Meeting of IOSEA Signatory States, is reproduced in the form in which it was submitted by the co-authors, Dr. Nancy FitzSimmons and Dr. Colin Limpus, without substantive editing by the Secretariat.

Action requested / Expected outcome

Signatory States are invited to make use of this document to draw conclusions and recommendations about the conservation of marine turtle genetic stocks, particularly shared populations, as well as additional research that may be required to fill knowledge gaps. The paper will be relevant to other deliberations concerning the overall review of IOSEA implementation, as well as sub-regional group discussions.

Marine Turtle Genetic Stocks of the Indo-Pacific: identifying boundaries and knowledge gaps

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Introduction

1. 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 and to understand population dynamics. It is additionally complicated 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 or sustainable use of marine species has often taken place without the knowledge of what exactly 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, population genetics, satellite telemetry and isotope studies to oceanographic data, so too has the need to apply these findings to conservation management.

2. Conservation of marine turtle populations relies on being able to define populations and to understand the geographic extent of habitat use throughout consecutive life history phases that may include pelagic 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 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 often comprise 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). In these cases, continued gene flow among sub-populations is at a high enough level such that sub-populations share demographic features and are not distinguished genetically.

3. From the perspective of conservation management, populations are also considered as those groupings of animals that function independently in the near term (10s or 100s of years) and can thus be thought of as 'Management Units' (MU) or 'genetic stocks' (Moritz 1994). However, use of these terms, as well as the terms 'population' and 'sub-population' can be problematic due to different usages. 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 (Wallace *et al.* 2010) 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 or genetic stock are considered to be synonymous and to be the basis for effective marine turtle conservation management.

4. Several Management Units have been defined for marine turtles within the Indo-Pacific (e.g. for green turtles, 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. for leatherback turtles, 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, for many years, the defined green turtle genetic stock for Papua New Guinea, was based on a single location in the northeast at Long Island (Norman *et al.* 1994; Dethmers *et al.* 2006), but further research by Velez-Zuazo *et al.* (2006) showed that this stock extends a further 2000 km 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, in recent years, 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). However the efforts required to sample sufficient numbers of turtles at a reasonably representative series of foraging grounds means that few studies have been completed to date. These latter studies are necessary when there are substantial levels of mortality at foraging areas as they allow proportional assignment of mortality to the different genetic stocks that share the feeding grounds (Jensen *et al.* 2010).

5. This paper summarises 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 extent of foraging areas or migratory routes is provided from mark-recapture data, satellite telemetry data, or genetic studies. These studies also identify genetic stock habitat use 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 can be updated periodically with input from IOSEA affiliates.

METHODS

6. 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, dots 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 10s of thousands of females per year for *Caretta*, *Chelonia* and *Lepidochelys* or thousands of females per year for *Dermochelys*, *Eretmochelys*, and *Natator*. 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). A question mark denotes that the genetic identity has not been resolved.

7. Designations of genetic stocks were taken from 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 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 to be grouped into the same genetic stock. If the null hypothesis is rejected when comparing turtles at 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, with matrilineal inheritance of the mtDNA, the data reflect the history and relationships among rookeries (Awise 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

8. In total, 57 genetic stocks have been identified for the six species of marine turtles within the Indo-Pacific, but many regional or species-specific gaps remain (Table 1; Figures 1-6). For 37 (65%) of these stocks, some habitat use outside of the country(s) of origin (i.e., 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

9. 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 Australia and western Australia as forming three unique populations. Only one shared haplotype, found in one turtle in Japan, has been observed in both Australia and Japan (Hatase *et al.* 2002) and the level of divergence among mtDNA haplotypes in the eastern Indian Ocean and western Pacific Ocean is low. 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.

10. 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 later study confirmed the hypothesis that loggerhead turtles from rookeries in eastern Australia and New Caledonia are traversing the south Pacific and being caught by long-line fisheries off the coast of Peru.

Chelonia mydas

11. 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 those sample sites in the western Indian Ocean, south east 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 western 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).

12. 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 km apart. They recommended further study to confirm this and turtles at 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 km between the furthest rookeries sampled (Dethmers *et al.* 2010) and the northern New Guinea stock includes rookeries over 2000 km apart (Velez-Zuazo *et al.* 2006).

13. Studies 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 8000 years as sea levels changed 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 behavioural differences in foraging locations (Kittiwattanawong & Manansap 2009) and their differentiation from the Peninsular Malaysia stock.

14. 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 1000 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), showing that the Bali harvest is widespread and includes turtles originating from other countries, whereas the nGBR harvest primarily has a more localised impact (Moritz 2002; Jensen 2010).

15. 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 where rookeries are located more than 500 km from rookeries used by identified 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 (i.e., Dethmers *et al.* 2010; Jensen 2010) that incorporate knowledge of the complex ocean currents of the region.

Dermochelys coriacea

16. 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 seaturtle.org/stat/) and suggests the origins for at least some of the stranded leatherback turtles along the western Australia coast (Prince 2004).

Eretmochelys imbricate

17. 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 Persian Gulf and the grouping of distant rookeries in Seychelles and Chagos Archipelago (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

18. 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.* unpubl. 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).

19. Information on the use of internationally dispersed foraging grounds by particular stocks is very limited. There are few 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 where they were tagged. 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 support the hypothesis of shared feeding grounds, given that some tracked females entered Indonesian waters (Whiting *et al.* 2007; C. Limpus, unpubl. data). 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

20. 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 EcoBeach (southwest Kimberly 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

21. Considerable progress has been made to define population boundaries and understand migratory behaviour of marine turtles within the Indo-Pacific. This has supported international efforts in turtle conservation management. Genetic studies have led to the identification of 57 genetic stocks that are considered as separate management units for which 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. These results emphasise that international cooperation is critical for understanding and protecting marine turtle populations in the Indo-Pacific.

22. 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 km distant, to the grouping of rookeries >2000 km apart. Therefore filling knowledge gaps needs to be quantitative, and should not be assumed. Similarly, flipper tagging and satellite telemetry studies of migratory turtles have provided important data on the broader geographic range of stocks 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. The initial genetic studies using mixed stock analyses have quantified how stocks are distributed in benthic as well as pelagic habitats. These studies have been particularly important in 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 paucity of understanding of the pelagic phase of post-hatchling and juvenile turtles in the Indo-Pacific. Genetic studies can provide important insights regarding these early life history phases if samples can be obtained (e.g., Boyle *et al.* 2009).

Genetic stocks/Management Units versus Regional Management Units

23. Most of the designations of genetic stocks have been based upon rejecting the 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 the null hypothesis of no genetic divergence is likely to be a valid, and probably conservative approach for defining marine turtle populations.

24. 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. For example:

- 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.
- 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 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.

25. Rather than benefiting 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 maintaining the focus of management at the level of the genetic stock because critical nesting areas used by a specific population (genetic stock, MU) would not be readily 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 conservation of genetic stocks, not simply based on the size of the stock, but also by the unique combinations of genetic diversity found within genetic stocks. For example, some genetic stocks are known to only support 10s of females per year while other support 10s 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).

26. Managing 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 near-shore 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 at nesting beaches and feeding grounds for each population. It also provides the more specific information required during international negotiations regarding 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 and using that information as the basis for targeting further research, monitoring and international collaboration to improve management outcomes for marine turtles.

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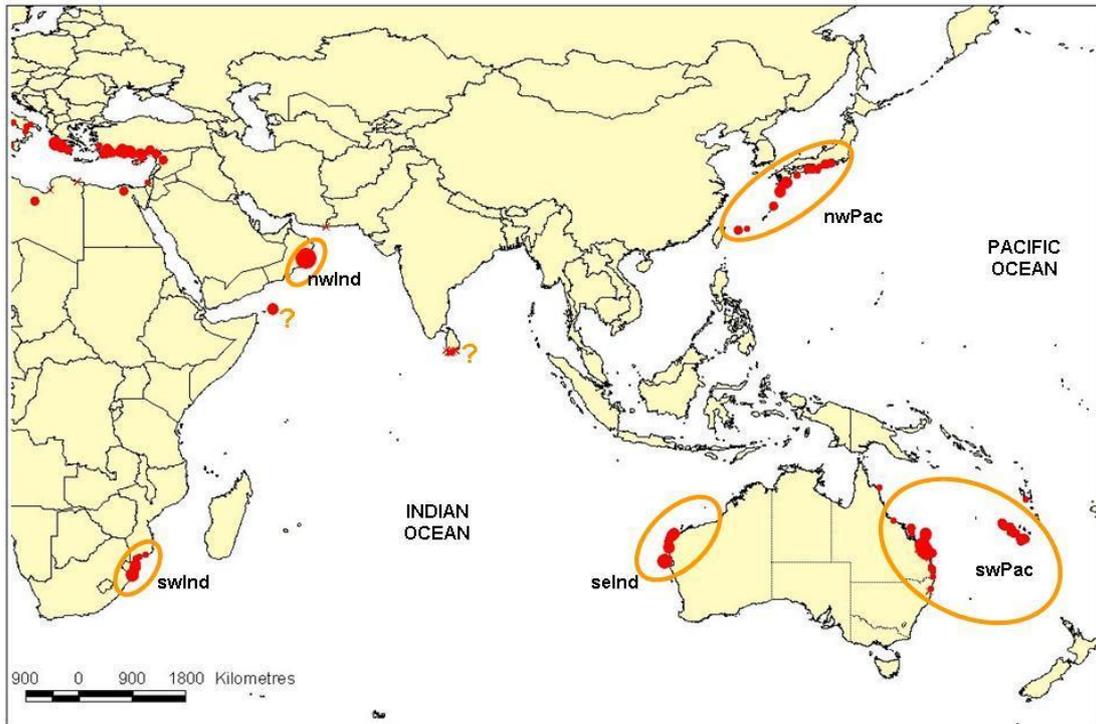


Figure 1. Location of *Caretta caretta* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

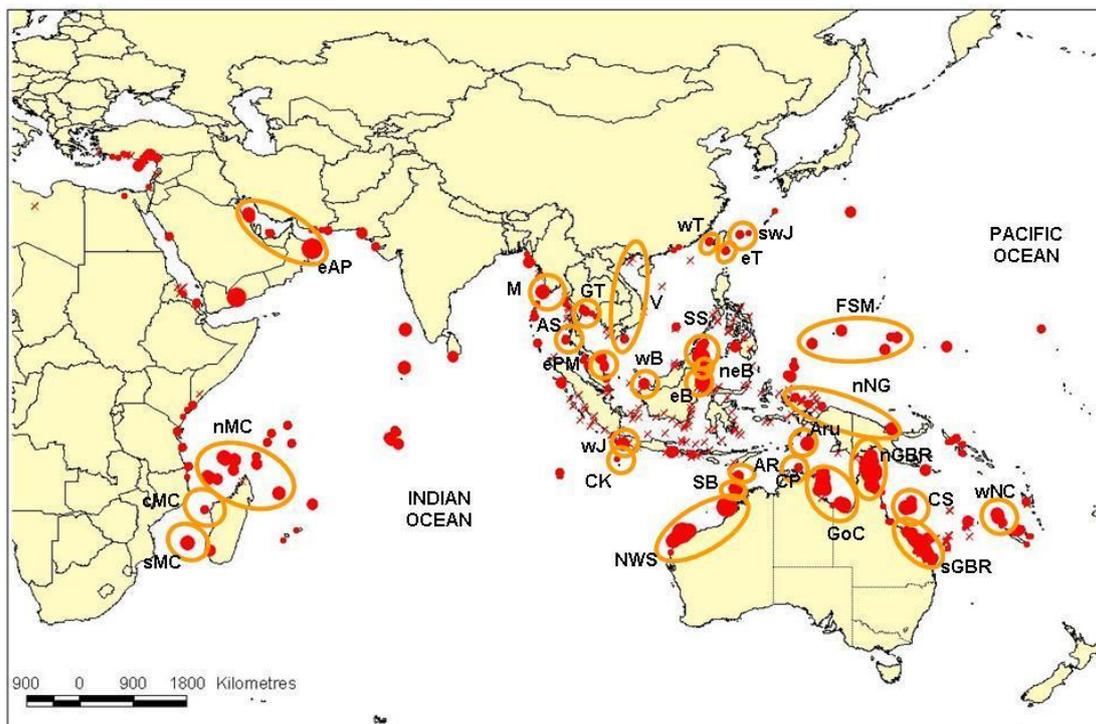


Figure 2. Location of *Chelonia mydas* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

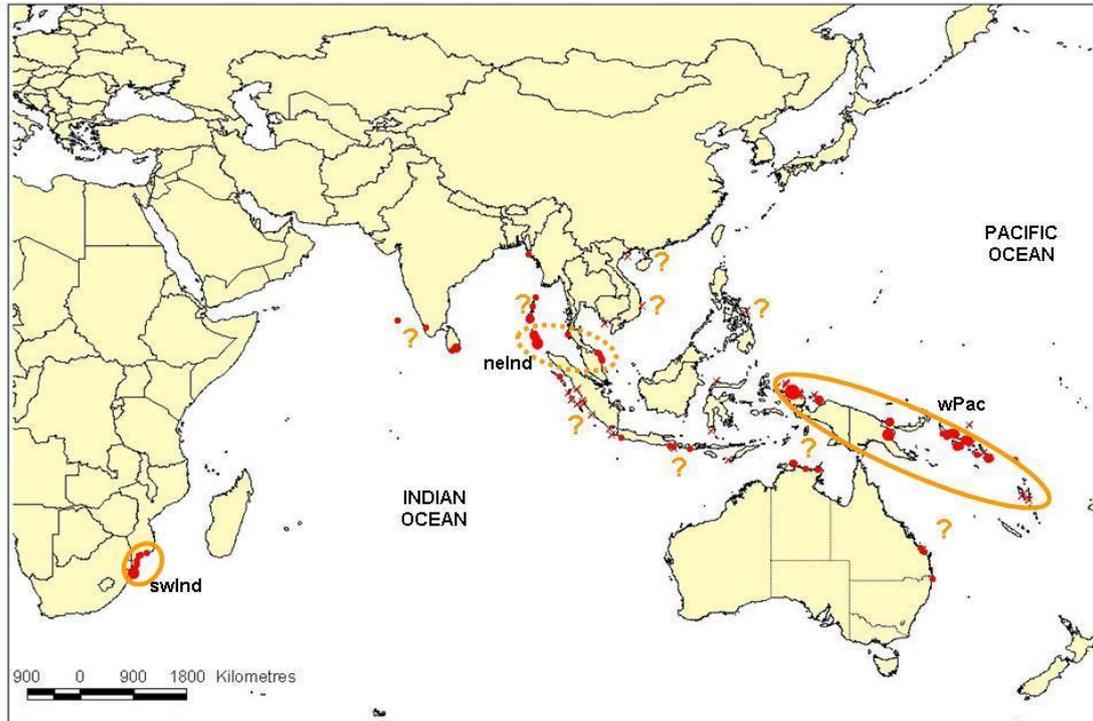


Figure 3. Location of *Dermochelys coriacea* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

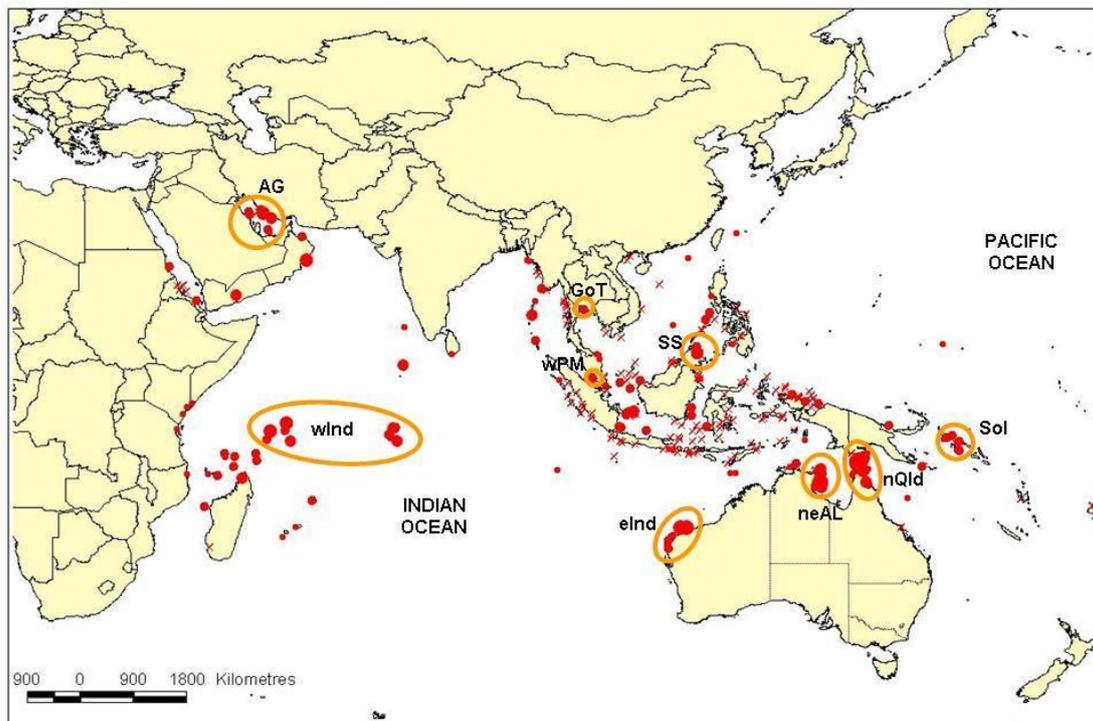


Figure 4. Location of *Eretmochelys imbricata* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

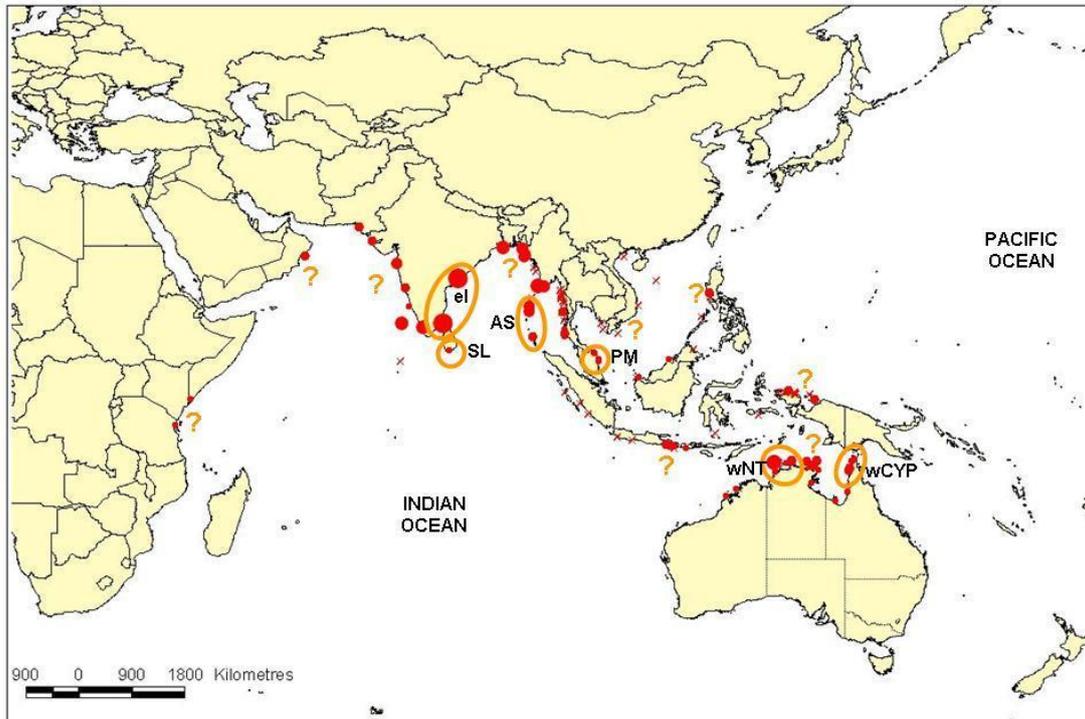


Figure 5. Location of *Lepidochelys olivacea* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

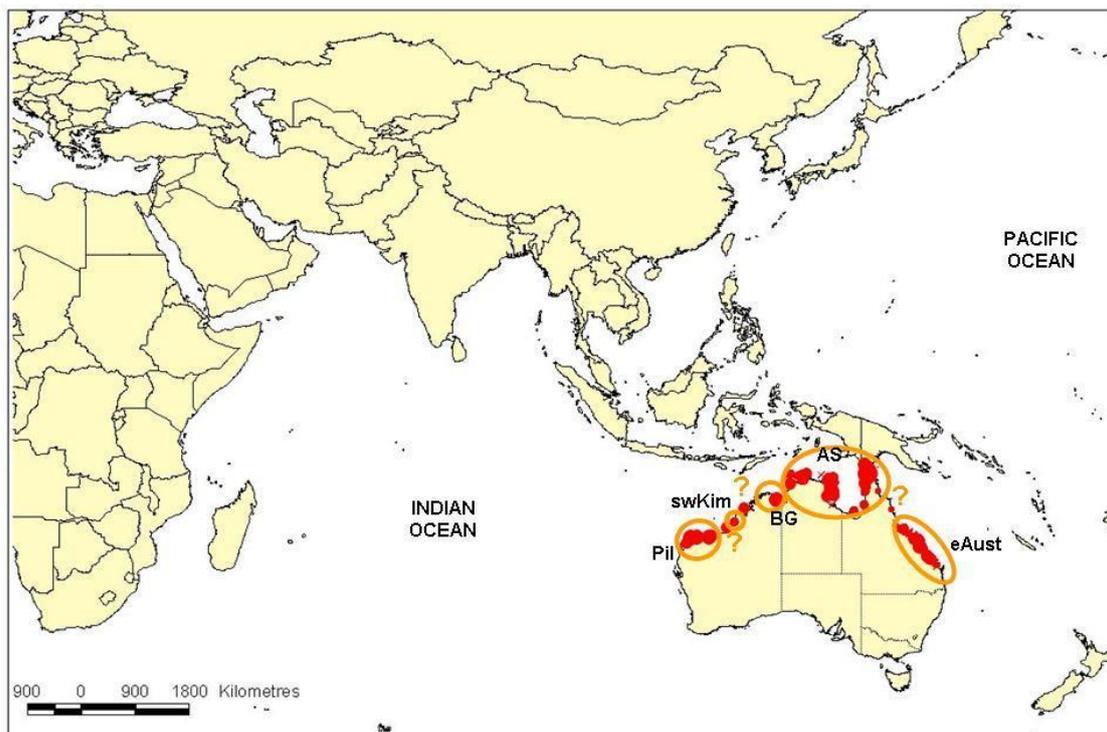


Figure 6. Location of *Natator depressus* rookeries throughout the Indo-Pacific showing the relative size of rookeries and the grouping of rookeries into identified genetic stocks. See methods section for description of the map.

Table 1. Marine turtle genetic stocks found within the geographic region bounded by the IOSEA 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 stocks 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	de Veyra 1994, Bowen et al. 1995, Hatase <i>et al.</i> 2002, Limpus 2008a
southwest Pacific Ocean (swPac)	Australia, New Caledonia (France)	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 et al. 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, Islamic Republic of Iran, Pakistan, Qatar, Saudi Arabia, Somalia, United Arab Emirates, Yemen		Baldwin <i>et al.</i> 2003, Limpus 2008a, Rees et al. 2010, Hamann <i>et al.</i> 2013, Shamblin <i>et al.</i> 2014
southwest Indian Ocean (swInd)	South Africa	France, Kenya, Madagascar, Mozambique, Seychelles, Somalia, United Republic of Tanzania		Baldwin <i>et al.</i> 2003, Lushci <i>et al.</i> 2006, Limpus 2008a, Shamblin <i>et al.</i> 2014

<i>Chelonia mydas</i>				
western New Caledonia (wNC)	New Caledonia (France)	Australia, Papua New Guinea		Dethmers <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		Dethmers <i>et al.</i> 2006, Limpus 2008b, Limpus <i>et al.</i> database ¹
Southern Great Barrier Reef (sGBR)	Australia	Fiji, New Caledonia (France), Papua New Guinea, Vanuatu		Limpus <i>et al.</i> 1992, Norman <i>et al.</i> 1994, FitzSimmons <i>et al.</i> 1997a, b, Dethmers <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 (France), Papua New Guinea, Vanuatu		Limpus <i>et al.</i> 1992, Norman <i>et al.</i> 1994, FitzSimmons <i>et al.</i> 1997a, b, Dethmers <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, Dethmers <i>et al.</i> 2006
Cobourg Peninsula (CP)	Australia			Jensen 2010
Ashmore Reef (AR)	Australia			Dethmers <i>et al.</i> 2006, Jensen 2010
Scott-Browse (SB)	Australia			Dethmers <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, Dethmers <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, Dethmers <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		de Veyra 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 ¹
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, Province of China			Cheng <i>et al.</i> 2008, Nishizawa <i>et al.</i> 2011
west Taiwan (wT)	Taiwan, Province of China			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
<i>Gulf of Thailand</i> (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
<i>Adaman Sea</i> (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, France ³ , Madagascar	Mozambique, United Republic of 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)	France ³ ,	Comoros, Madagascar, Mozambique, Seychelles		Le Gall & Hughes 1987, Bourjea <i>et al.</i> 2007
Central Mozambique Channel (i.e., Juan de Novo) (cMC)	France ³ ,	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	Mozambique, Namibia		Dutton <i>et al.</i> 1999, Luschi <i>et al.</i> 2006
northeast Indian Ocean (neInd)	India ⁴ , Malaysia, <i>Sri Lanka</i>	Australia, France ³ , Indonesia, Madagascar, Seychelles, United Kingdom ⁵		Dutton <i>et al.</i> 1999, Shanker <i>et al.</i> 2011, Shanker pers. comm. (telemetry data at seaturtle.org)
<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			Limpus 2009a, FitzSimmons 2010
Sulu Sea (SS)	Malaysia	Indonesia, Philippines		De Silva 1982, Adnyana <i>et al.</i> 2008, Arshaad & Kadir 2009, Isnain 2009
western Peninsular Malaysia (wPM)	Malaysia	Indonesia, Singapore		Lau <i>et al.</i> 2009
Gulf of Thailand (GoT)	Thailand			Arshaad & Kadir 2009
eastern Indian Ocean (eInd)	Australia			FitzSimmons 2010
Western/central Indian Ocean (wInd)	Seychelles, Chagos Archipelago			Mortimer & Broderick 1999, FitzSimmons 2010
Persian Gulf* (PG)	Islamic Republic of 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
Arafura 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 (Pil)	Australia			Pittard 2010

¹This is a global database currently 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