# Population genetics of Southeast Asian and Western Pacific green turtles, *Chelonia mydas*

**Final Report to UNEP/CMS**



Lady Musgrave Island, southern Great Barrier Reef, Australia



**Green turtle, Sarawak Turtle Islands, Malaysia**

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# EXECUTIVE SUMMARY

- The broad aim of this project is to identify Management Units (MU) as the focal point for regional management, with particular emphasis on Southeast Asia, but drawing also on broader studies through the Indo-Pacific. In this report we focus on results from analysis of green turtles in Southeast Asian and Western Pacific region, including samples from breeding and feeding populations and also major regional harvests.

- We screened 670 nesting turtles from 27 breeding aggregations throughout Southeast Asia and the Western Pacific and 339 turtles from 3 feeding populations and 2 harvests in northern Australia, Papua New Guinea and Indonesia. These samples were assayed for variation in mitochondrial DNA (mtDNA) using gradient gel and sequencing methods.

- We have identified 25 mtDNA variants shared among several rookeries with each rookery typically being characterised by a subset of 3-4 mtDNA variants.

- A characteristic feature of green turtles in this region is strong divergence in frequencies of variants among breeding aggregations despite the widespread distribution of, and close relationships among many variants.

- Based on evidence for significant genetic divergence we recognise the following 17 genetically discrete breeding units (Management Units) in the South East Asian and Western Pacific region:

|  |  |
|---|---|
| **Coral Sea Platform:** | Several cays |
| **New Caledonia:** | Eastern mainland coast |
| **PNG:** | Long Island |
| **Micronesia:** | Elato, Ngulu and Ulithi Atolls |
| **Aru:** | Enu Island |
| **SE Sabah:** | Sipidan Island |
| **Berau Islands:** | Sangalaki Island |
| **Sulu Sea:** | Malaysia and Philippines Turtle Islands |
| **Sarawak :** | Sarawak Turtle Islands |
| **Peninsular Malaysia:** | Paka and Redang Island |
| **West Java:** | Pangumbahan |
| **Gulf of Carpenteria:** | Bountiful Island, Groote Eylandt and Port Bradshaw |
| **Ashmore Reef:** | Ashmore Reef islands |
| **Scott Reefs:** | Sandy Island |
| **North West Shelf:** | North West Cape and Lacepede Island |
| **NGBR:** | Raine Island, No. 8 Sandbank and Bramble Cay |
| **SGBR:** | Heron, Lady Musgrave and North West Islands |

- Two emergent properties of green turtles in the Indo-Pacific are **i)** that groups of adjacent rookeries that are isolated from other rookeries by more than a few hundred kilometres can be expected to support a genetically distinct Management Unit, and **ii)** where a chain of adjacent rookeries extends over a large geographical area, the entire assemblage can be expected to represent a single Management Unit.

- Extrapolating from the findings above we can begin to make predictions about the genetic affinities of some genetically unsampled but regionally significant rookeries. Rookeries in the following two regions are likely to comprise of new Management Units based on their size and proximity to other Management units; north west coast of Irian Jaya and the coastal areas from Thailand thru to Vietnam and China. Rookeries off the West Kalimantan coast in the South China Sea are likely to be included within the Sarawak Management Unit and would benefit from a multinational management approach similar to that covering the Sulu Sea Management Unit.

- The genetic markers we have characterised for each Managment Unit are suitable for assessing stock composition in regional harvested and resident populations of green turtle. The assessment of multiple harvests and feeding assemblages has enabled us to better understand the likely geographic extent of threatening processes that impact on green turtle populations. Initial observations are;

    i. Each feeding assemblage includes turtles from multiple MUs and, conversely, the Management Area for each MU is much greater than the rookeries and immediately adjacent waters.
    ii. Analysis of these foraging populations suggests that significant contributions from some, but not all, adjacent rookeries is typical and that large contributions from distant rookeries are rare.
    iii. The adjacent NGBR MU rookeries dominate the Torres Strait harvest of Papua New Guinea and Australia.
    iv. The Bali-centred harvest draws on multiple MUs, with major contributions from both Indonesia (Aru) and at least several adjacent nations including the Gulf of Carpentaria MU, Australia; PNG MU, Papua New Guinea and Sulu Sea MU, Malaysia/Phillipines).

**AIMS**

The general aims of the present study are:
- To sample major rookeries of marine turtles not yet characterised by our group or international collaborators.
- To identify the number and distribution of separate management units (breeding populations or "stocks") of marine turtles in the Indo-Pacific.
- To identify genetic markers, or combinations thereof, that can be used to estimate the migratory range of different management units.
- To apply these markers to major harvests, by-catch and feeding grounds in the region allowing, in combination with available tagging evidence, estimation of which stocks may be adversely affected by human activities.

**BACKGROUND**

The green turtle, *Chelonia mydas*, is a large, long lived, herbivorous reptile that grazes on marine macrophytes in shallow tropical and temperate waters throughout the world (Lanyon *et al.* 1989, Limpus *et al.* 1994a, Limpus and Chaloupka 1997). The tropical waters of Southeast Asian and Western Pacific Region support many breeding locations (Figure 1) and are of global significance. The adults migrate long distances from feeding to breeding sites to lay eggs on traditional nesting beaches (Limpus *et al.* 1992; Figure 2). They show great fidelity to both nesting (Meylan 1982) and feeding grounds (Limpus *et al.* 1992) even though they may be separated by thousands of kilometres (Mortimer & Carr 1987). Multiple clutches are laid within a season with many years between breeding seasons (Limpus *et al.* 1994b, Limpus *et al.* 2001). Seasonal variability in breeding rates is regulated by regional El Niño climate events that are thought to affect the quality of foraging pasture (Limpus and Nicholls, 2000). Available evidence indicates that post-hatchling turtles undertake passive migrations drifting in oceanic gyre systems for several years before they take up residence in shallow water habitat (Muzick & Limpus 1996) and may involve the circumnavigation of entire ocean basins (Carr 1987). Fossil records indicate long term use of traditional breeding sites (>1000 years bp at Raine Island; Limpus 1987) despite these sites being transient over geologic time due to sea level changes and through the natural process of coastal erosion and accretion. Over ecological time scales, genetic studies have demonstrated that green turtles return to their natal areas to lay eggs (Meylan *et al.* 1989).

The success of wildlife management strategies is contingent on understanding the evolutionary and demographic underpinning of contemporary biodiversity. Knowledge of the genetic structure among marine turtle rookeries in the Indian Ocean and Western Pacific enables us to define demographically discrete breeding populations ("Stocks" or "Management Units") on which sound management decisions can be based. Although flipper tagging or telemetry provides much useful information about the demography, site fidelity and migrations of individual animals, the available data are strongly biased towards adult females and intensively surveyed locations, mostly nesting beaches. In contrast, genetic studies provide information on populations rather than individuals. Thus, they complement tagging studies and have the potential to rapidly elucidate the geographical boundaries of breeding populations and their migrations through feeding and developmental ranges (Bowen and Avise, 1996).

Mitochondrial DNA is particularly valuable because it tracks genetic exchange mediated by females. The maternal inheritance and consequent small effective population size of mtDNA

also tends to accentuate genetic differences among populations, so that frequencies of variants diverge. This provides strong discrimination among sites that exchange few females and creates potential for population specific markers or combinations thereof that can be used to assess the natal composition of samples taken from feeding grounds or harvests. The perspective on female movements provided by mtDNA is of particular relevance to management as females are responsible for the colonisation of nesting beaches. For marine turtles in particular, large variances in reproductive success among females are likely to further enhance differentiation among populations and hence the utility of mtDNA as a marker.

Several studies have successfully used mtDNA variants to resolve population boundaries in breeding aggregations of marine turtles (Bowen *et al*. 1992; Bowen *et al*. 1994, Broderick *et al*. 1994, Norman *et al*. 1994 and Bass *et al*. 1996). Typically, such studies find that rookeries, often separated by hundreds of kilometres, combine to form genetically discrete populations or Management Units (*sensu* Moritz 1994), a conclusion supported by tagging evidence from intensively studied archipelagos (Table 1 and C. Limpus, unpubl. data). Other studies have used mtDNA variants as genetic tags to determine the stock composition of foraging populations (Broderick *et al*. 1994, Bowen *et al*. 1996, Sears *et al*. 1995, Lahanas *et al*.1998) or the origin of turtles taken in fisheries bycatch (Bowen *et al*. 1995).

Southeast Asian and Western Pacific waters are a strong-hold for several species of marine turtle, with populations existing as feeding assemblages and as nesting populations. Tagging studies have demonstrated that many adult females migrate long distances from feeding areas to breeding sites, with migrations often extending to neighbouring nations (Figure 2: Turtles living in Indonesia, Philippines and Malaysia migrate to breed at the Sulu Sea Turtle Islands. Turtles living in New Caledonia, Vanuatu, Fiji, Solomon Islands, Papua New Guinea and eastern Indonesia migrate to breed at the Great Barrier Reef rookeries along with turtles that live in Australian waters). These tagging studies also show that adult turtles resident in local feeding grounds are drawn from local rookeries as well as those from neighbouring nations.

Green turtles are highly significant culturally and as a source of nutrition and income in local communities throughout Southeast Asia and the Western Pacific but many populations have declined. Conservation management of these internationally significant populations needs to consider threatening processes operating within national waters as well as in the broader geographic range across which turtles migrate. These factors include substantial commercial and subsistence harvests in especially PNG (Limpus and Parmenter 1985), Solomon Islands (Broderick 1997), Indonesia (Dethmers 1999), Philippines (R. Cruz, *pers. Comm.*) and Australia (Kennet *et al*. 1997), by-catch in fisheries and local impacts on feeding and nesting areas. Management of each of these factors would benefit from an understanding of the nature and extent of independent breeding populations (Management Units) and on the stock composition within feeding grounds.

Our previous work (Norman *et al*.1994) demonstrated the utility of molecular markers to identify green turtle MUs in the Australasian region. However significant gaps in our sampling (Arafura, Celebes and South China Sea) precluded us from using these markers to assess stock contributions in regional harvested and resident populations. We have now filled these sampling gaps with the addition of key rookeries from the Arafura (Port Bradshaw, Groote Eylandt and Enu Island) and Celebes Seas (Sangalaki Island). We still lack samples from key rookeries in Thailand, Vietnam and China to complete our sampling of the South China Sea. In this report we seek to integrate this new genetic data with

observations from regional tagging programs. We focus on the green turtle, as this is the species most intensively studied by our group and for which new data have been generated with funding from CMS/UNEP.
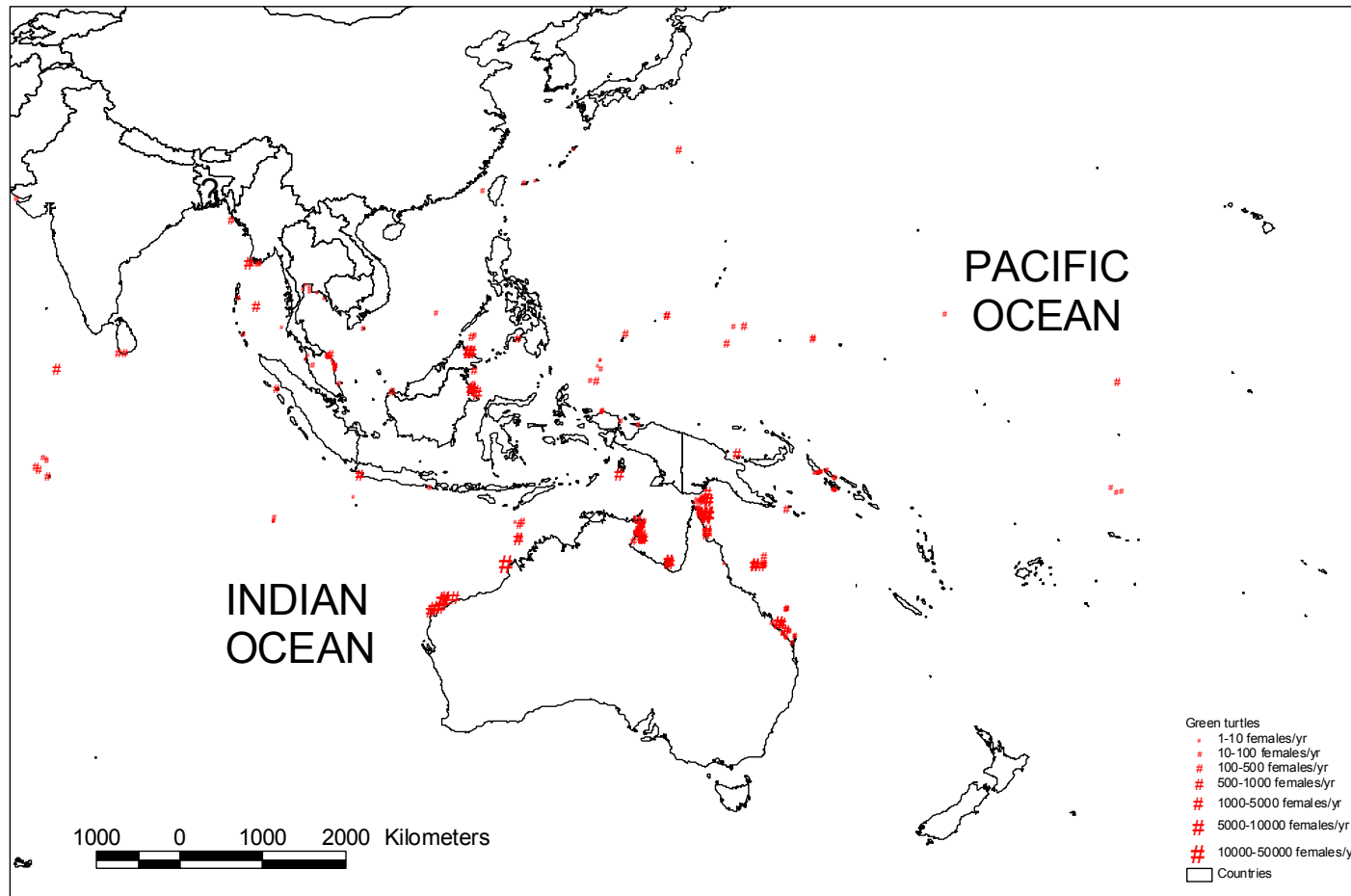
Figure 1. Distribution of green turtle nesting populations within the Southeast Asia – Western Pacific region. Data compiled from published reports and unpublished regional reports into a database maintained by C.J.Limpus.

Table 1. Green turtle, *Chelonia mydas*, fidelity to individual rookeries between successive breeding seasons illustrated by data from the extensive combined State and Federal tagging program in eastern Australia during the 1999-2000 Australian summer nesting season. Saturation tagging of the total nesting population only occurred at Heron Island, Milman Island and Mon Repos. Other rookeries were sampled at mid season only.

Total number of green turtles recorded in eastern Australia = 8156. These included 2720 remigrants to the same rookery plus 172 remigrants that changed rookeries between seasons. 133 green turtles were recorded changing rookery within the same breeding season.

| ROOKERIES WHERE TURTLES WERE ORIGINALLY TAGGED | | MM | D/S | PC | RI | N8 | N7 | CSC | SW | CI & FI | NW | WI | HI | HO | LM | LE | WR | RB | MP | MR | FR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Milman Is | MM | 96 | | 1 | 3 | | | | | | | | | | | | | | | | |
| Douglas & Sinclair | D/S | 1 & 1 | - | | | | | | | | | | | | | | | | | | |
| Moulter Cay | PC | | | 1 | 7 | | | | | | | | | | | | | | | | |
| Raine Is | RI | | | 7+(3) | 847 | | | | | | | | | | | | | | | | |
| No8 Sandbank | N8 | | | | 1 | - | | | | | | | | | | | | | | | |
| No7 Sandbank | N7 | | | | 3 | | - | | | | | | | | | | | | | | |
| Coral Sea cays | CSC | | | | | | | 133 +(2) | | | | | | | | | | | | | |
| Swain Reefs cays (4 cays) | SW | | | | | | | | 3 | | | | | | | | | | | | |
| Curtis + Facing Is | CI & FI | | | | | | | | | 1 | | | | | | | | | | | |
| Northwest Is | NW | | | | | | | | | 1 | 344 | 1+(5) | 10+(9) | | 0+(1) | | | | | | |
| Wreck Is | WI | | | | | | | | | | 9+(6) | 382 | 8+(12) | | 2 | 1 | | | | | 1 |
| Heron Is | HI | | | | | | | | | | 74+(42) | 16+(34) | 501 | | 4+(2) | | | | | | |
| Hoshyn Is | HO | | | | | | | | | | | | | 0 | | | | | | | |
| Lady Musgrave Is | LM | | | | | | | | | | 2 | 4 | 4+(3) | 3 | 383 | 1 | 1 | | | | |
| Lady Elliott Is | LE | | | | | | | | | | | | | | 1+(4) | 0 | | | | | |
| Wreck Rock | WR | | | | | | | | | | 2 | | | | 1 | | 12 | | | | 1+(1) |
| Rules Beach | RB | | | | | | | | | | | | | | | | | 0 | | | |
| Moore Park | MP | | | | | | | | | | | | | | | | | | 1 | | |
| Mon Repos | MR | | | | | | | | | | | | | | | | | | | 1 | |
| Fraser Island | FR | | | | | | | | | | 1 | | | | 0+(5) | 0+(2) | | | | | 15 |
| Total tagged turtles | | 271 | 0 | 144 | 2069 | 0 | 0 | 1095 | 27 | 6 | 805 | 766 | 1801 | 76 | 740 | 99 | 65 | 4 | 4 | 3 | 181 |

ROOKERIES EXAMINED IN 1998-1999 SEASON. Values are given as number of interseasonal remigrants + (number of within season change of colony)

Northern Great Barrier Reef Rookeries

Southern Great Barrier Reef Rookeries
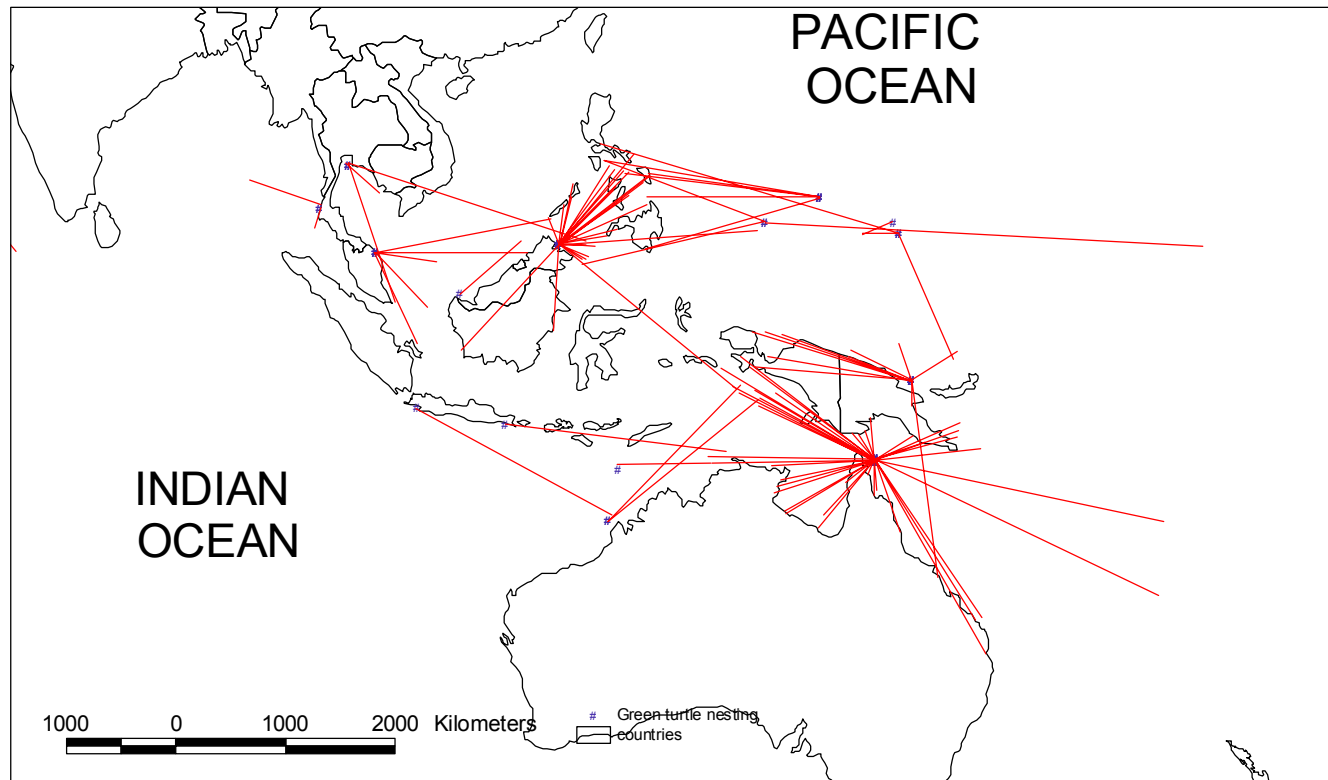
Figure 2. Linkage between feeding and nesting areas for green turtles in Southeast Asia – Western Pacific region. Lines link tagging and recapture sites for individual turtles and are not intended to portray individual migratory paths. Data compiled from published reports and unpublished regional reports into a database maintained by C.J.Limpus.

## SAMPLING AND METHODS

*Breeding populations*

We have sampled to encompass all major (known) green turtle nesting populations throughout Southeast Asia, Australia, Western Pacific and Eastern Indian Ocean, with the exception of some South China Sea rookeries (Thailand, Vietnam and China) for which samples have not been forthcoming.  We have analysed 670 nesting green turtles from 27 rookeries throughout Australia, Malaysia, Philippines, Indonesia, Micronesia, New Caledonia and Papua New Guinea (Figure 3: Green turtle sampling locations).

The large number of green turtle breeding populations extant in the study area, together with the widespread distribution of feeding grounds in tropical waters has necessitated a major sampling effort throughout the region and has involved many collaborators.  Genetic distinctiveness of these populations is determined by the presence of significant differences in the frequency of DNA variants.  A longer-term perspective on connectivity among populations is provided from the geographic locations of these variants in relation to their phylogeny.



Figure 3.  Geographic location of the 27 rookeries sampled and analysed from Southeast Asia and the Western Pacific.

*Molecular methods*

The major tool used here is mitochondrial DNA (mtDNA), although we have analysed more variable markers, nuclear microsatellite loci (FitzSimmons *et al*. 1995, 1997a; FitzSimmons *et al.* 1998), for the more intensively studied Australian populations. The most sensitive approach for mtDNA analysis is to examine directly and difference in the mtDNA sequence; we focus on a c.384 base pair, highly variable segment called the "control region" (Norman

*et al.* 1994). However, direct sequencing is relatively expensive and slow where large numbers of individuals need to be screened as is the case for this project (N>1000).

Thus, we (Norman *et al.* 1994; Broderick unpub. data) have developed an approach that allows screening of large numbers of samples but retains the sensitivity of sequencing. This uses heteroduplex analysis on gradient (DGGE) gels (Dowling *et al.* 1996) and, combined with targeted sequencing, provides the level of resolution we require (usually able to detect one change in 384 bp of sequence). This technique uses the melting behaviour of DNA fragments to detect genetic site substitutions. The standard application of this technique detects some, but not all, single base pair changes. The sensitivity of this technique was increased by using heteroduplex analysis that hybridises candidate DNA variants with known sequence variants in a process of heating and cooling. When hybrids are re-run on a DGGE gel, any differences in genetic composition between the control and test DNA will produce multiple fragments (heteroduplexes) of differing mobilities. An advantage of this method over PCR-RFLP analysis (but see Abreu-Grobois *et al.*, 1996) lies in its ability to detect, with greater sensitivity, new as well as known mtDNA variants. The strategy now used is to (i) survey samples for each rookery using DGGE against a control lane combining known sequence variants, (ii) confirm identification of samples of similar mobility using heteroduplex analysis, and (iii) to sequence representatives from each genotype/locality combination for final verification and to test sensitivity.

The DGGE approach is again being employed in the second phase of the project wherein >1000 samples of green turtles from harvests and feeding grounds are being analysed to determine which stocks are represented and to what extent. This uses mixed stock analysis as applied in fisheries management and rests on the assumption that all of the potentially contributing stocks have been typed. Briefly, a maximum likelihood model is fitted to identify the mixture of contributing stocks that best explain the distribution of variants in the feeding ground or harvest. We have tested this approach using mtDNA markers for green and hawksbill turtles and found it to yield useful qualitative and quantitative information, subject to thorough surveys of breeding populations (Norman 1996; Broderick & Moritz 1996).

*Statistical Analysis*

Sequences were aligned using Clustal X (Thompson *et al.* 1997) and estimates of nucleotide diversity and divergence were calculated using MEGA2.0 (Kumar *et al.* 2001) and Arlequin 2000 (Schneider *et al.* 2000) based on Kimura 2P distance measures. Phylogenetic trees were constructed using MEGA2.0 to visualise the relationships among the observed mtDNA variants. AMOVA (10000 replicates; Excoffier *et al.* 1992), Exact tests of population differentiation (100000 replicates; Raymond & Rousset 1995) and pairwise Fst tests (10000 replicates; Slatkin 1991) implemented in the population genetics package Arlequin 2000 were used to examine genetic structure among surveyed populations. Both nucleotide (Kimura 2P) and conventional $F_{ST}$ distance measures were used to calculate within and among population diversity.

## RESULTS

### Sensitivity of molecular methods

Our screening of mtDNA variation at major rookeries throughout southeast Asia and western Pacific has revealed genetic heterogeneity among most regional sets of rookeries and, where

analysed, a lack of heterogeneity among rookeries from the same region.  The initial survey of mtDNA RFLP variation (Norman *et al.* 1994; Norman 1996) determined that different rookeries within each of the southern and northern Great Barrier Reefs were statistically homogeneous, a result supported by evidence for a high frequency of exchange of tagged breeding females and males among rookeries within the northern and southern Great Barrier Reefs respectively but very low frequency of interchange between the northern and southern rookeries (Table 1; Limpus *et al.,* unpubl. data).  These studies revealed statistically significant differences between the southern and northern Great Barrier Reefs and between these and Gulf of Carpentaria (Bountiful Island) and west Australian locations.  In the west, the two north-west shelf locations (Lacepedes & North-West Cape) could not be distinguished.  Analyses of nuclear gene (microsatellite variation, FitzSimmons *et al.* 1997a) confirmed that the NW shelf rookeries are statistically indistinguishable, but confirmed that these are distinct from the Bountiful Island rookery and that each of these is different from the east coast populations.  In contrast to the mtDNA, the southern Great Barrier Reefs rookeries are indistinguishable from northern Great Barrier Reefs for nuclear genes, an observation that we attribute to mating between southern and northern Great Barrier Reefs turtles when the former migrate through Torres Strait *en route* to their breeding grounds. The RFLP analyses of mtDNA variants in the SE Asian rookeries (Norman 1996; Moritz *et al.,* unpubl. data) revealed that all rookeries analysed, except for the two from Peninsula Malaysia (Paka, Pulau Redang) and those from the Malaysia/ Philippines Turtle Islands, were genetically distinct.

The current DGGE method has been found to approach the accuracy of direct sequencing while retaining the efficiency of RFLPs.  Most alleles could be distinguished on the DGGE in a straightforward manner however for one class of alleles (C3, C1 and Caru) and additional RFLP test was required.  While C3 and Caru can be distinguished using outgroup heteroduplex DGGE it is a rather laborious procedure and cutting these fragments with the restriction enzyme *Sau*96A provided an expedient solution.

**Molecular diversity**

Our screening of samples from 27 breeding population identified 25 variants, the frequencies of which are shown in Table 2.  The sequences for these variants are shown in Appendix 1 and the molecular relationships among them is summarised in a Neighbour-Joining tree (Figure 4).  These mtDNA variants fall into five major clades each separated by an average of 4.45% ($\pi = 0.028 - 0.056$) sequence divergence.  MtDNA variants found within each of these major clades are closely related ($\pi = 0.0 - 0.016$, mean = 0.001) and typically differ by only one or two mutations.

While some mtDNA variants described here are widespread and others have highly restricted distributions, they can be broadly grouped into three categories.  Those that are i) widespread occurring in the majority of rookeries and often in high frequency (eg A2, C1 and C3), ii) found among several adjacent rookeries (eg Caru, A1, C9, D2, B5, B1, B3, C9, C4, C8, C5) and iii) found only in one rookery (eg C12, C13, J1, J2, J14212, B4, C7, C2). Despite being comprised of geographically widespread and often genetically divergent mtDNA variants, a characteristic feature of green turtles in this region is marked divergence in frequency of variants among breeding aggregations (Table 2).

Table 2.  Frequencies of mtDNA variants (A1 through C5) among 27 locations. Note that some locations (eg. southern and northern Great Barrier Reefs, Peninsula Malaysia, Phillipine/Malaysian turtle islands) represent multiple rookeries between which there is no significant genetic difference.

| Country | Region | Location | A1 | A2 | A3 | A4 | B1 | B3 | B4 | B5 | C1 | C2 | C3 | C4 | C5 | C7 | C8 | C9 | C12 | C13 | Caru | D2 | E1/E2 | J1 | J2 | J14212 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Australia | Central WA | North West Cape | | | | | | | | | 11 | 1 | 1 | | | | | 1 | | | 1 | | | | | | 15 |
| Australia | Coral Sea | Coral Sea | | 30 | | | | 9 | | | 1 | | 1 | | | | | | | | | | | | | | 41 |
| Australia | GOC | Bountiful Island | | | | | | | | | 10 | | 8 | 1 | | | 1 | | | | | | | | | | 20 |
| Australia | NE Arnhem Land | Groote Eylandt | | | | | | | | | 14 | | 7 | | | | 1 | | | | 1 | | | | | | 23 |
| Australia | NE Arnhem Land | Port Bradshaw | | | | | | | | | 19 | | 16 | 7 | | | 1 | | | | | | | | | | 43 |
| Australia | Nth Great Barrier Reef | Several | | 2 | | | 42 | 2 | | | | | | 1 | | | | 2 | | | | | | 2 | 1 | | 52 |
| Australia | NW Western Australia | Lacepedes | | 1 | | | | | 1 | | 25 | | 2 | | | | | 1 | | | | | | | | | 30 |
| Australia | Sth Great Barrier Reef | Several | | 94 | | | | 8 | | | | | | | | | | | | | | | | | | | 102 |
| Australia | Timor Sea | Ashmore Reef | | 1 | 9 | | | | | | | | 3 | 7 | | | | | | | | | | | | | 20 |
| Australia | Timor Sea | Sandy Island | | 1 | | | | | | | | | 5 | 11 | | | | 2 | | | | | | | | | 19 |
| Indonesia | Aru | Enu | | | 1 | | | | | | | | | | | | | | | | 27 | | | | | | 28 |
| Indonesia | Berau | Sangalaki | | | | | | | | | | | 7 | | 9 | | | | | | 5 | 7 | | | | 1 | 29 |
| Indonesia | West Java | Pangumbahan | | | | | | | | | | | 17 | | 6 | | | | | | | | | | | | 23 |
| Malaysia | Peninsular Malaysia | Paka, P. Redang | | | | | | | | 3 | | | 22 | 1 | | | | | | | 1 | | | | | | 27 |
| Malaysia | Sarawak | Turtle islands | | | | | | | | 2 | | | 2 | 18 | | | | | | | | | | | | | 22 |
| Malaysia | SE Sabah | Sipidan | | | | | | | | | | | 18 | | 3 | | | | | | 1 | 8 | | | | | 30 |
| Malaysia/Philippines | Turtle Islands | several | | | | | | | | | | | 13 | | 1 | | | | | | | 53 | | | | | 67 |
| Micronesia | Elato Atoll | | 4 | | 9 | | | | | | | | | | | | | | | | | | 2 | | | | 15 |
| Micronesia | Ngulu Atoll | | 2 | 1 | 11 | 1 | | | | | | | | | | | | | | | | | 11 | | | | 26 |
| Micronesia | Yap | Ulithi Atoll | 1 | 1 | 6 | 1 | | | | | | | | | | | | | | | | | | | | | 9 |
| New Caledonia | New Caledonia | eastern coastline | | 2 | | | 4 | 2 | | | | | 1 | | | | | | | 1 | | | | | | | 10 |
| Papua New Guinea | NE PNG | Long Island | | | 16 | | | | | | | | 1 | | | 1 | | | | | | | | | | | 18 |
| | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Total | | | 7 | 133 | 52 | 2 | 46 | 21 | 1 | 5 | 88 | 1 | 134 | 28 | 19 | 1 | 3 | 4 | 2 | 1 | 36 | 68 | 13 | 2 | 1 | 1 | 669 |
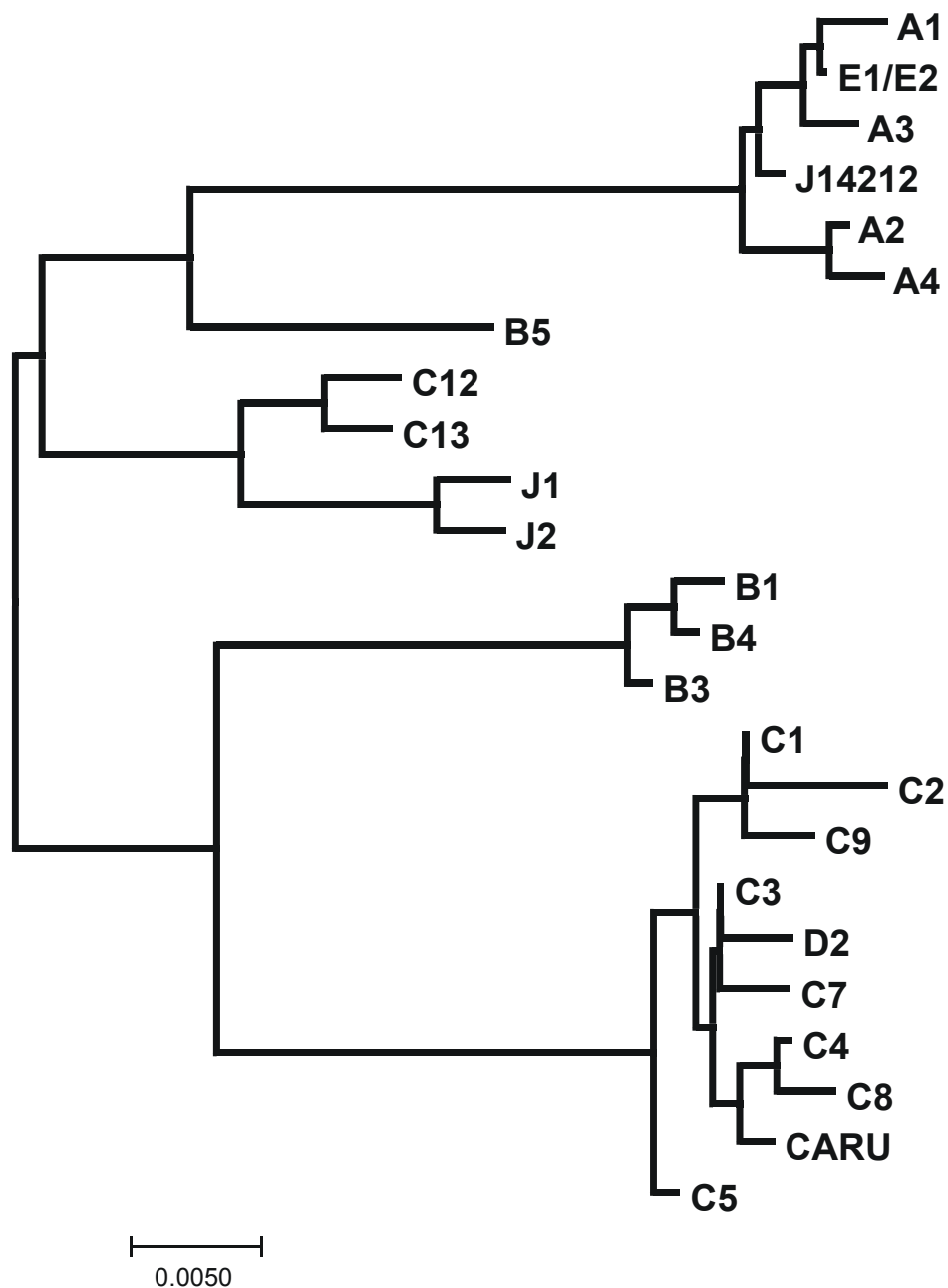
Figure 4. Molecular relationships of mtDNA variants detected among green turtle rookeries.

## Differentiation among green turtle breeding populations

Formal tests for population subdivision were done using Exact tests for population differentiation and comparisons of pairwise $F_{ST}$ tests (using haplotypic and nucleotide diversity) based on the frequencies of mtDNA variants shown in Table 2. The Exact test is broadly analogous to Fisher's exact and chi-square contingency tests and, unlike $F_{ST}$ tests, makes no underlying assumptions about past evolutionary relationships between two populations. We found that Exact tests for population differentiation had the most power to discriminate between surveyed rookeries, failing to differentiate only 18 pairwise comparisons from 27 rookeries tested. This is compared to 31 and 26 non-significant

comparisons when using $F_{ST}$ tests with and without nucleotide diversity, respectively (Appendix 2).

To identify genetically discrete stocks we have taken an iterative approach by pooling geographically adjacent and statistically undifferentiated rookeries first and then repeating the analysis. This process was continued until all pairwise comparisons became significant (P<0.05). We relied on Exact tests exclusively in these early stages to pool rookeries after which point within and among rookery comparisons were explored more exhaustively using other tests. In order to maximize power, as is appropriate for such management related questions (Baverstock and Moritz 1996; Taylor *et al*. 2000), we consider each pairwise comparison as a discrete hypothesis and thus do not reduce α levels for multiple tests.

Some rookeries have been pooled *apriori* due to either their limited sampling or close proximity to more extensively sampled rookeries. The following rookeries have been pooled and renamed as follows;

| | | |
|---|---|---|
| Raine Island and No.8 Sandbank | = | Far North Queensland |
| Gulisan and Selingan Islands | = | Turtle Islands/ Malaysia |
| Baguan, Langaan and Taganak Islands | = | Turtle Islands/ Philippines |

The first round of Exact tests compared 27 breeding assemblages and failed to discriminate (p > 0.05; Appendix 2) between the following rookeries:

| | | | |
|---|---|---|---|
| Bramble Cay | vrs. | Far North Queensland | p=0.51421+-0.0056 |
| Heron Island | vrs. | Lady Musgrave Island | p=0.32959+-0.0024 |
| Heron Island | vrs. | North West Island | p=0.64471+-0.0012 |
| Lady Musgrave Island | vrs. | North West Island | p=0.68758+-0.0015 |
| Lady Musgrave Island | vrs. | Coral Sea Platform | p=0.73769+-0.0048 |
| North West Island | vrs. | Coral Sea Platform | p=0.19848+-0.0071 |
| Paka | vrs. | Palau Redang | p=0.48117+-0.0052 |
| North West Cape | vrs. | Lacepedes | p=0.44656+-0.0100 |
| North West Cape | vrs. | Groote Eylandt | p=0.17353+-0.0072 |
| Bountiful Island | vrs. | Groote Eylandt | p=0.80882+-0.0037 |
| Bountiful Island | vrs. | Port Bradshaw | p=0.62023+-0.0038 |
| Bountiful Island | vrs. | Scott Reef | p=0.13158+-0.0069 |
| Groote Eylandt | vrs. | Port Bradshaw | p=0.09139+-0.0058 |
| Elato Atolls | vrs. | Ngulu Atolls | p=0.31437+-0.0035 |
| Elato Atolls | vrs. | Ulithi Atolls | p=0.41272+-0.0049 |
| Ngulu Atolls | vrs. | Ulithi Atolls | p=0.28111+-0.0056 |
| Ulithi Atolls | vrs. | Long Island | p=0.18419+-0.0104 |
| Turtle Islands/ Malaysia | vrs. | Turtle Islands/ Philippines | p=1.00000+-0.0000 |

The majority of these non-significant comparisons are among adjacent rookeries and/or those with smaller sample sizes. Based on these results we pooled rookeries into regional assemblages that were mutually non-significant across *all* pairwise comparisons. Thus Heron, Lady Musgrave and North West Islands comprise a homogenous genetic group, as all pairwise comparisons among them were insignificant. The significant differentiation among the Coral Sea Platform and Heron Island rookeries precludes the former rookery from

membership of a rookery assemblage comprising Heron, Lady Musgrave and North West Islands.

This logical approach above was applied throughout pooling rookeries into regional assemblages and renaming them as follows:

Peninsular Malaysia: Paka and Palau Redang
Sulu Sea: Turtle Islands/Malaysia and Turtle Islands/ Philippines
Micronesia: Ngulu, Ulithi and Elato Atolls

NGBR: northern Great Barrier Reef: Bramble Cay and Far North Queensland
SGBR : southern Great Barrier Reef: Heron Island, North West Island and Lady Musgrave
North West Shelf: North West Cape and Lacepedes, Western Australia
Gulf of Carpenteria: Groote Eylandt, Port Bradshaw and Bountiful Island, northern Australia

The second and final round of Exact tests compared 17 breeding groups and all pairwise comparisons were now significant (P<0.05; all but 7 < 0.001; Appendix 3) including comparisons among Scott Reef in NW Australia and those in the Gulf of Carpenteria which were previously indistinguishable. We therefore recognise 17 genetically discreet breeding units or "Management Units" (MUs) in southeast Asia and western Pacific (Figure 5). These MUs can be broadly grouped by the seas and oceans in which they occur and their genetic composition is described in detail below. The pooled frequencies for mtDNA variants for these 17 management units are given in Table 3.
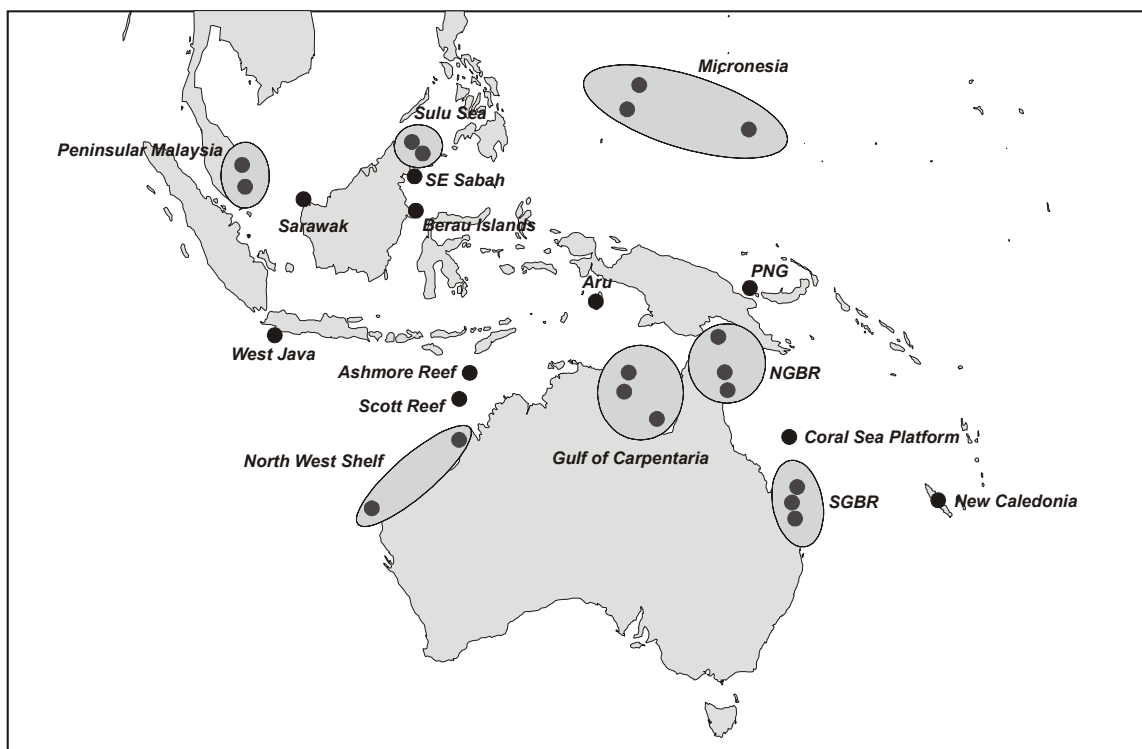


Figure 5. Locations of Management Units for green turtles in Southeast Asia and the western Pacific as inferred from analysis of geographic structure of mtDNA variants.

Circles encompass multiple sampled rookeries belonging to the same Management Unit.  See Table 3 for further details.

Table 3.  Frequencies of mtDNA variants across Management Units recognised for green turtles in southeast Asian and the western Pacific region.

| Sea/Ocean | Genetic Stock | A1 | A2 | A3 | A4 | B1 | B3 | B4 | B5 | C1 | C2 | C3 | C4 | C5 | C7 | C8 | C9 | C12 | C13 | Caru | D2 | E1/E2 | J1 | J2 | J14212 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Celebes Sea | Berau Islands | | | | | | | | | | | 7 | | 9 | | | | | | 5 | 7 | | | | 1 | 29 |
| | SE Sabah | | | | | | | | | | | 18 | | 3 | | | | | | 1 | 8 | | | | | 30 |
| South China Sea | Peninsular Malaysia | | | | | | | | 3 | | | 22 | 1 | | | | | | | 1 | | | | | | 27 |
| | Sarawak | | | | | | | | 2 | | | 2 | 18 | | | | | | | | | | | | | 22 |
| Sulu Sea | Sulu Sea | | | | | | | | | | | 13 | 1 | | | | | | | | 53 | | | | | 67 |
| Arafura Sea | Gulf of Carpentaria | | | | | | | | | 43 | | 31 | 8 | | | 3 | | | | 1 | | | | | | 86 |
| | Aru | | | 1 | | | | | | | | | | | | | | | | 27 | | | | | | 28 |
| Eastern Indian Ocean | North West Shelf | | 1 | | | | | 1 | | 36 | 1 | 3 | | | | | 2 | | | 1 | | | | | | 45 |
| | Ashmore Reef | | 1 | 9 | | | | | | 3 | | 7 | | | | | | | | | | | | | | 20 |
| | Scott Reef | | 1 | | | | | | | 5 | | 11 | | | | | 2 | | | | | | | | | 19 |
| | Java | | | | | | | | | | | 17 | | 6 | | | | | | | | | | | | 23 |
| NW Pacific Ocean | Micronesia | 7 | 2 | 26 | 2 | | | | | | | | | | | | | | | | | 13 | | | | 50 |
| | PNG | | | 16 | | | | | | | | 1 | | | 1 | | | | | | | | | | | 18 |
| SW Pacific Ocean | Coral Sea Platform | | 30 | | | | 9 | | | 1 | | 1 | | | | | | | | | | | | | | 41 |
| | NGBR | | 2 | | | 42 | 2 | | | | | | | 1 | | | | 2 | | | | | 2 | 1 | | 52 |
| | SGBR | | 95 | | | | 8 | | | | | | | | | | | | | | | | | | | 103 |
| | New Caledonia | | 2 | | | 4 | 2 | | | | | 1 | | | | | | | 1 | | | | | | | 10 |
| | | 7 | 134 | 52 | 2 | 46 | 21 | 1 | 5 | 88 | 1 | 134 | 28 | 19 | 1 | 3 | 4 | 2 | 1 | 36 | 68 | 13 | 2 | 1 | 1 | 670 |

## Genetic characterisation of Green turtle stocks

*North Western Pacific Ocean*

**PNG:** The Long Island rookery in northeast Papua New Guinea is dominated by the A3 allele, which is common throughout the Pacific and also has the C7 allele, which is only known to occur here, in low frequency.

**Micronesia:** This management unit comprises rookeries from a broad but remote expanse of the Pacific Ocean and includes rookeries from Elato, Ngulu and Yap. These rookeries are dominated by the E1/E2 and A3 alleles. The former allele is unusual in that it is characterised by an insertion of a 10bp repeat rather than the more common source of variation, point mutations.

*South Western Pacific Ocean*

**Coral Sea Platform:** These rookeries are also dominated by the A2 allele however the B3 allele is found at a higher frequency differentiating it from SGBR.

**SGBR:** These rookeries are dominated by the A2 allele and include the rookeries of the Capricorn-Bunker Group, southern Great Barrier Reef.

**NGBR:** These rookeries are dominated by the B1 allele though several other phylogenetically divergent alleles also occur in low frequency and include the rookeries of Raine Island and No8 Sandbank, northern Great Barrier Reef.

**New Caledonia:** The alleles found are common throughout the South Western Pacific Ocean but the population is unique in that all the alleles here are found in similar frequencies. This is one location that would benefit from an increased sample size.

*Eastern Indian Ocean*

**Scott Reef:** This rookery appears unique among the NW Australian rookeries in being dominated by both the C1 and C3 alleles. The same rookery was found to have statistically significant differences from the NW shelf rookeries at microsatellite loci (FitzSimmons *et al*. 1997a).

**Ashmore Reef:** This rookery appears to be distinct from the neighbouring Sandy Island and Pangumbahan rookeries based on the high frequency of the A3 allele, in combination with C1 and C3 alleles.

**NW Shelf:** This management unit spans geographically dispersed rookeries located on the shelf from North West Cape to Lacepede Island, these being dominated by the C1 allele and also having unique profiles for microsatellite loci.

**West Java:** The Pangumbahan rookery is characterised by the presence of the C5 allele and widespread C3 allele, both in high frequencies.

*Arafura Sea*

**Gulf of Carpentaria:** The rookeries in the Gulf of Carpentaria share few alleles with others from the adjacent Pacific rookeries; rather, they are dominated by the C1 and C3 alleles that characterise rookeries throughout SE Asian Archipelago and East Indian Ocean. The C4 allele in low frequency here is also widely distributed throughout the SE Asian Archipelago. This rookery is distinguished from the NW shelf and others by differences in frequencies of the dominant mtDNA variants and also by a unique profile for microsatellite alleles (FitzSimmons *et al*. 1997a).

**Aru:** This rookery is unique among rookeries in the region as it is nearly fixed for the Caru allele and the C3 allele, found in all other rookeries in the region, has not yet been detected here.

*Celebes Sea*

**Berau:** This rookery is characterised by four alleles, C3, C5, Caru and D2, in near equal frequencies. It is the only rookery outside Aru that has the Caru allele at moderate frequency.

**SE Sabah:** The Sipidan rookery is dominated by the widespread C3 allele but also has D2 and C5 alleles at moderate frequency.

*Sulu Sea*

**Sulu Sea:** The Malaysia and Philippines Turtle Islands also have the common C3 allele but are dominated by the D2 allele. No significant differences in allele frequency were found between the rookeries from Malaysia vs. Phillipines.

*South China Sea*

**Peninsular Malaysia:** This management unit comprises the rookeries at Paka and Palau Rendang and is dominated by the C3 allele but also has other alleles, including the B5 allele, in low frequency.

**Sarawak:** These rookeries located in south of the state are dominated by the C4 allele with the B5 and C3 alleles in low frequency.

**Distribution of genetic variation among green turtle stocks**

The distribution of diversity among populations is, in theory, correlated with the magnitude of dispersal among populations. Because we have information on both frequency of alleles and divergence among them, we can examine the distribution of diversity using frequency alone or both classes of information. Given recent fluctuations in population size, populations are unlikely

to be at equilibrium.  In this circumstance, the frequency only statistics (H in Table 4) will be most informative about recent dynamics and frequency plus divergence statistics (K, Table 4) about longer term biogeographic processes.

The results of the analysis are intriguing.  The partitioning of diversity among populations or among grouped populations is generally increased by including the sequence diversity, suggesting that there is a substantial contribution of long-term (phylogeographic) isolation to the genetic structure. This signature of long-term isolation is maximised when populations are grouped by either the seas or oceans in which they occur and is even greater when the more admixed SW Pacific populations (see Table 3; Figure 5) are excluded.  Our preliminary conclusions from this analysis are that the expansion of marine turtle populations across the SE Asian Archipelago after sea levels rose approximately 10,000 ybp occurred primarily from the Indian Ocean rather than the north Pacific sources.  This hypothesis will be explored more fully using alternative analyses.

| Comparison | | Among Groups | Among Populations in Groups | Within Populations | FCT | FSC | FST |
|---|---|---|---|---|---|---|---|
| Among Genetic Stocks | H | | 54.21 | 45.79 | | | 0.54 |
| | K | | 77.02 | 22.98 | | | 0.77 |
| Among Seas | H | 14.92 | 40.03 | 45.04 | 0.15 | 0.47 | 0.55 |
| | K | 48.76 | 29.49 | 21.75 | 0.49 | 0.58 | 0.78 |
| Among Oceans | H | 11.84 | 44.12 | 44.04 | 0.12 | 0.50 | 0.56 |
| | K | 59.90 | 21.57 | 18.53 | 0.60 | 0.54 | 0.81 |
| NW Pacific Ocean SW Pacific Ocean SE Asian Archepelago Eastern Indian Ocean | H | 17.10 | 39.12 | 43.78 | 0.17 | 0.56 | 0.47 |
| | K | 60.63 | 19.96 | 19.41 | 0.61 | 0.51 | 0.81 |
| NW Pacific Ocean SE Asian Archepelago Eastern Indian Ocean | H | 7.28 | 39.65 | 53.08 | 0.07 | 0.43 | 0.47 |
| | K | 73.32 | 9.23 | 17.45 | 0.73 | 0.35 | 0.83 |

| Oceans | Seas | Stocks |
|---|---|---|
| Pacific Ocean | NW Pacific Ocean | PNG |
| | | Micronesia |
| | SW Pacific Ocean | Coral Sea Platform |
| | | NGBR |
| | | New Caledonia |
| | | SGBR |
| Eastern Indian Ocean | | Ashmore Reef |
| | | North West Shelf |
| | | Scott Reefs |
| | | Java |
| SE Asian Archepelago | Arafura Sea | Gulf of Carpentaria |
| | | Aru |
| | Celebes Sea | SE Sabah |
| | | Berau Islands |
| | South China Sea | Peninsular Malaysia |
| | | Sarawak |
| | Sulu Sea | Sulu Sea |

Table 4. Diversity statistics for different combinations of geographic populations across Southeast Asia and the western Pacific.  The distribution of total diversity within and among groups/populations is calculated using allele frequencies only (H) or allele frequencies and molecular divergence (K; Kimura 2P distance measure).

**Resident foraging and harvested populations**

The second phase of the genetic analysis is to screen samples from resident (feeding ground) populations and harvests in the region to determine which management units are represented and to what extent. Information on which MUs are represented is necessary to predict the consequences of disturbance or management in feeding grounds and to estimate the impact of harvests in Australia and adjacent nations. We are currently completing our screening of foraging populations from northern (Fog Bay NT) and western Australia (Ashmore Reef) and eastern Indonesia (Aru) and for harvests from Indonesia (via Bali), PNG/Australia (Torres Strait) and northern Australia (NE Arnhem Land; Figure 6). The data and results we present here are preliminary and should be interpreted in a qualitative rather than quantitative fashion. However, the major trends and conclusions are unlikely to change.

Maximum likelihood algorithms (ML) have been the method of choice when trying to elucidate proportional stock contribution in mixed populations. ML has been applied in many fisheries (eg Smouse *et al*.1990; Millar 1987; Fournier *et al*. 1984, Brown *et al*. 1999) and several marine turtle populations (Norman 1996 for greens, Sears *et al*.1995 and Bowen *et al*. 1995 for loggerheads and Bowen *et al*. 1999 for Caribbean hawksbills). The degree of genetic differentiation between the contributing stocks greatly influences the accuracy of this approach as does sample size of both breeding and mixed populations (Chapman 1996, Broderick and Moritz 1996 and Epifanio *et al*. 1995). Stocks with slight differentiation of allele frequencies are harder to resolve than those with fixed differences. Little can be done about the inherent nature and distribution of genetic variation other than to select loci with maximum differentiation (eg. mtDNA) or to use multilocus approaches (Smouse *et al*.1990, Broderick and Moritz 1997, Paetkau *et al*. 1995). We have tried to maximize sample sizes where possible but unlike the former fisheries examples, sample sizes for marine turtles are often small and difficult to come by. However modest sampling (30-100) is usually sufficient to identify major contributors or to exclude individual stocks from having major contributions.

The primary assumption of mixed stock analysis (MSA) is that all of the potentially contributing stocks are known and adequately characterised. When this assumption is violated the utility of the stock analysis is greatly reduced. Our sampling of rookeries throughout the Australasian region is geographically extensive and incorporates all known major breeding aggregations. We cannot entirely rule out the presence of unsampled stocks among local feeding and harvested populations but we think it reasonable to assume that their presence is negligible given our extensive sampling and knowledge of green turtle rookeries throughout this region.

Our screening methodology for foraging and harvested populations was the same for nesting populations relying on DGGE and sequencing to uncover mtDNA variants. The vast majority of mtDNA variants were previously identified during our screening of the nesting populations (Table 5). The Bali harvest contained three new mtDNA variants at low frequency; had they been at high frequency, this would have been evidence of significant contributions from one or more unsampled stocks. Having satisfied the first condition of MSA, that all known contributors have been characterised, we feel that our data is robust enough to continue with the maximum likelihood analysis.

Proportional stock contributions of foraging and harvested populations were estimated using ML algorithms implemented in the program SPAM (Statistics Program for Analysing Mixtures, version 3.2; Alaska Department of Fish and Game 2000). Again, these results (Table 6) should be interpreted with caution, but are useful as a guide to which stocks are making a major contribution to a particular foraging or harvested population and which are not.

**Aru:** This foraging population is dominated by Caru and A3 alleles implying that Aru and PNG MUs are strongly represented in this population. The Micronesian MU also has the A3 allele in high frequency but the absence of the E1, E2 or A1 alleles precludes it as a likely contributor. The B1 allele occurs at low frequency (10%) but as this allele is essentially diagnostic for the NBGR stock, this stock is represented at that frequency. The MSA results confirm these observations indicating that Aru MU has the highest representation at 48% followed by PNG (19%) and NGBR (10%). The high proportion of Aru MU turtles among the foraging turtles is not surprising given that the harvest occurred in close proximity to the Aru rookeries.

**Ashmore Reef:** This foraging population is dominated by two widely distributed alleles, C1 and C3 and, curiously, the A3 allele common (45%) in the local breeding population is rare (3.2%). The C1 allele in this case is more informative as it is found in high frequency among the western Australian and Gulf of Carpentaria MUs. The MSA results indicate that the North West Shelf has the highest representation at 43% followed by the Gulf of Carpentaria (24%) and Scott Reefs (12%).

**Fogg Bay:** Only a small number (n = 24) of the available samples have been analysed so far and, like Ashmore Reef, turtles at this site had mostly C1 or C3 alleles. The MSA results indicate a large contribution from the North West Shelf MUs (36%), Scott Reefs (20%) and Sarawak (11%). Aru and other western Australian MUs may have a higher representation here but we clearly need to analyse more samples to clarify their contribution.

**Bali Harvest:** This is genetically the most diverse sample analysed so far indicating the presence of several stocks at high frequency. The high frequency of the Caru allele means that Aru MU is likely to be well represented here. The C3 allele is dominant here also but it is not particularly diagnostic given its wide distribution. The A3 and D2 alleles have a more restricted distribution, the former indicating the presence of PNG and Ashmore Reef MUs while the latter indicates the presence of MUs from the Sulu and Celebes seas. The MSA results indicate that the Aru MU has the highest contribution at 24% but that PNG (13%), Gulf of Carpentaria (13%) and Sulu Sea (11%) may also be represented in reasonable proportions. This wide representation of MUs is not unexpected given that turtles harvested from throughout Indonesia were imported for sale into Bali.

**Torres Strait:** This sample is dominated by the B1 allele and being diagnostic for the NGBR MU we expect this breeding population to make the major contribution. The MSA results confirm this indicating that this MUs contribution to the harvest is around 90%. Again this is not surprising given the proximity of the harvest site to the rookeries and the bias in harvest towards breeding females.

In many cases, the limitations posed by analysis of a single gene are evident. For example, where the feeding ground or harvest is dominated by alleles that have a broad geographic distribution but variable frequency (eg. C1, C3 in Fogg Bay and Ashmore reef feeding grounds) the confidence limits on estimates will be substantial. The only real solution to this problem is to increase the number of loci examined and to use multilocus assignment methods for individuals (Paetkau *et al.* 1995); with funding from Environment Australia, this is now being done for these and other populations by Dr. N.N. FitzSimmons.
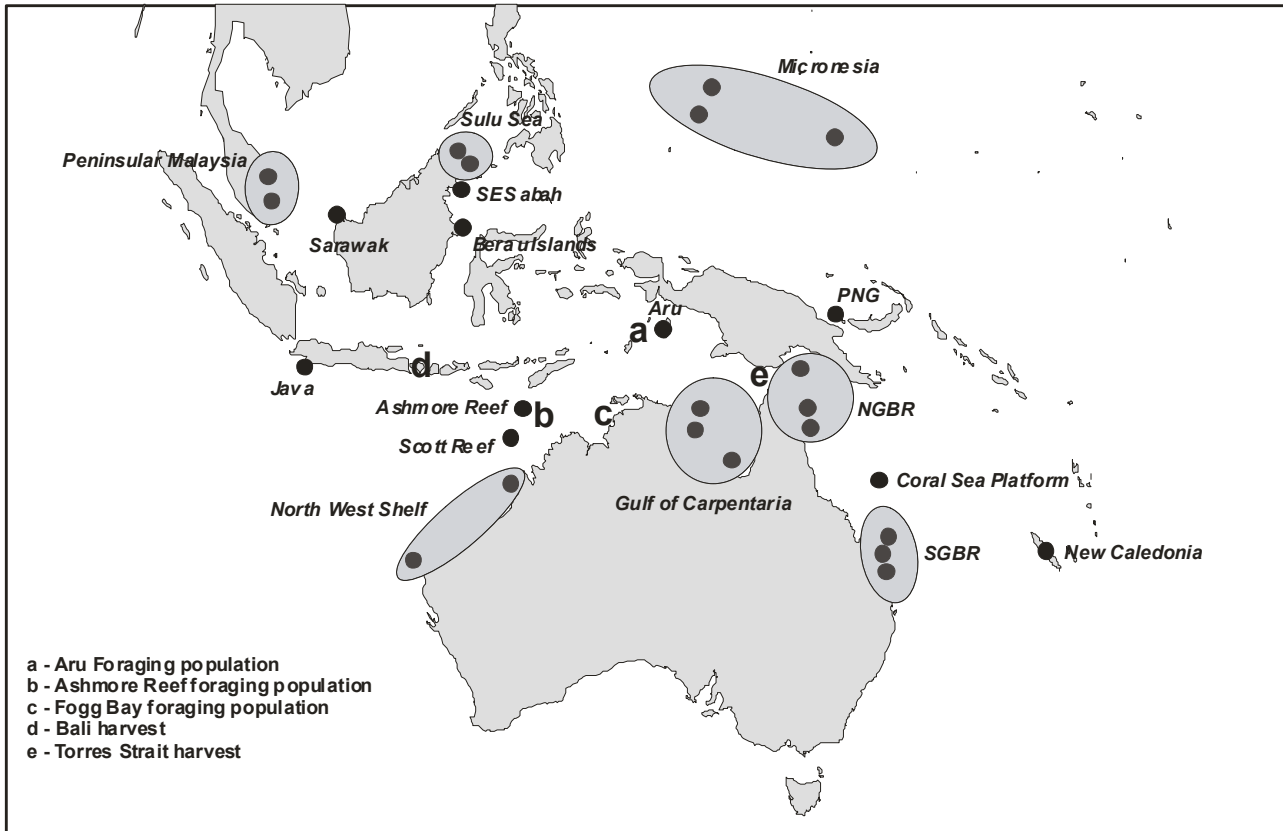
Figure 6: Locations of foraging and harvested populations considered for the MSA. Management Units recognised in this study are also shown for convenience.

Table 5: Relative frequencies of mtDNA alleles found among harvested and foraging populations.

| | n | A2 | A3 | B1 | B3 | C1 | C2 | C3 | C4 | C5 | C7 | C8 | C9 | Caru | D2 | J1 | J14191 | J1738 | J1764 | J2396 | J8002 | J8805 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fogg Bay | 35 | | 0.057 | 0.029 | | 0.371 | 0.029 | 0.229 | 0.114 | 0.029 | | | 0.086 | 0.057 | | | | | | | | |
| Ashmore Reef | 65 | 0.015 | 0.031 | 0.015 | | 0.569 | | 0.262 | 0.015 | 0.015 | 0.015 | | 0.015 | 0.015 | | | | | | | 0.015 | 0.015 |
| Aru | 40 | | 0.225 | 0.100 | | 0.075 | | 0.050 | | 0.025 | | | | 0.475 | 0.025 | | 0.025 | | | | | |
| Torres Strait | 109 | 0.083 | | 0.798 | 0.028 | | | | | | | | 0.055 | | | 0.037 | | | | | | |
| Bali | 90 | 0.011 | 0.178 | 0.022 | | 0.056 | | 0.211 | 0.056 | 0.044 | | 0.022 | | 0.244 | 0.122 | | | | 0.011 | 0.011 | 0.011 | |

Table 6: Maximum likelihood estimates of stock contributions among foraging and harvested populations.

| Seas | Stocks | Foraging Populations | | | | | | Harvested Populations | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Aru | | Ashmore Reef | | Fogg Bay | | Bali | | Torres Strait | |
| | | Estimate | S.E. | Estimate | S.E. | Estimate | S.E. | Estimate | S.E. | Estimate | S.E. |
| Celebes Sea | Berau Islands | 0.034 | 0.047 | 0.001 | 0.004 | 0.007 | 0.022 | 0.054 | 0.064 | 0.000 | 0.000 |
| | SE Sabah | 0.004 | 0.017 | 0.000 | 0.005 | 0.000 | 0.003 | 0.071 | 0.073 | 0.000 | 0.000 |
| South China Sea | Peninsular Malaysia | 0.002 | 0.010 | 0.014 | 0.044 | 0.012 | 0.043 | 0.006 | 0.020 | 0.000 | 0.000 |
| | Sarawak | 0.000 | 0.000 | 0.004 | 0.010 | 0.117 | 0.063 | 0.044 | 0.028 | 0.000 | 0.000 |
| Sulu Sea | Sulu Sea | 0.022 | 0.028 | 0.000 | 0.000 | 0.000 | 0.002 | 0.114 | 0.053 | 0.000 | 0.000 |
| Arafura Sea | Gulf of Carpentaria | 0.006 | 0.021 | 0.238 | 0.232 | 0.072 | 0.144 | 0.125 | 0.063 | 0.000 | 0.000 |
| | Aru | 0.493 | 0.091 | 0.009 | 0.013 | 0.050 | 0.041 | 0.243 | 0.052 | 0.000 | 0.000 |
| Eastern Indian Ocean | North West Shelf | 0.064 | 0.048 | 0.427 | 0.180 | 0.361 | 0.161 | 0.002 | 0.009 | 0.012 | 0.026 |
| | Ashmore Reef | 0.051 | 0.084 | 0.035 | 0.054 | 0.029 | 0.058 | 0.084 | 0.099 | 0.000 | 0.008 |
| | Scott Reefs | 0.003 | 0.015 | 0.124 | 0.141 | 0.197 | 0.169 | 0.002 | 0.009 | 0.047 | 0.036 |
| | Java | 0.020 | 0.035 | 0.069 | 0.072 | 0.077 | 0.084 | 0.062 | 0.057 | 0.000 | 0.000 |
| NW Pacific Ocean | Micronesia | 0.000 | 0.003 | 0.000 | 0.000 | 0.000 | 0.002 | 0.000 | 0.000 | 0.000 | 0.003 |
| | PNG | 0.187 | 0.092 | 0.030 | 0.033 | 0.044 | 0.042 | 0.131 | 0.070 | 0.000 | 0.000 |
| SW Pacific Ocean | Coral Sea Platform | 0.000 | 0.000 | 0.000 | 0.002 | 0.000 | 0.000 | 0.000 | 0.001 | 0.013 | 0.031 |
| | NGBR | 0.097 | 0.049 | 0.015 | 0.016 | 0.030 | 0.030 | 0.020 | 0.016 | 0.877 | 0.109 |
| | SGBR | 0.000 | 0.000 | 0.006 | 0.011 | 0.000 | 0.000 | 0.007 | 0.009 | 0.041 | 0.038 |
| | New Caledonia | 0.002 | 0.013 | 0.001 | 0.006 | 0.001 | 0.005 | 0.002 | 0.008 | 0.027 | 0.086 |
| | Other | 0.016 | | 0.027 | | 0.002 | | 0.033 | | 0.000 | |
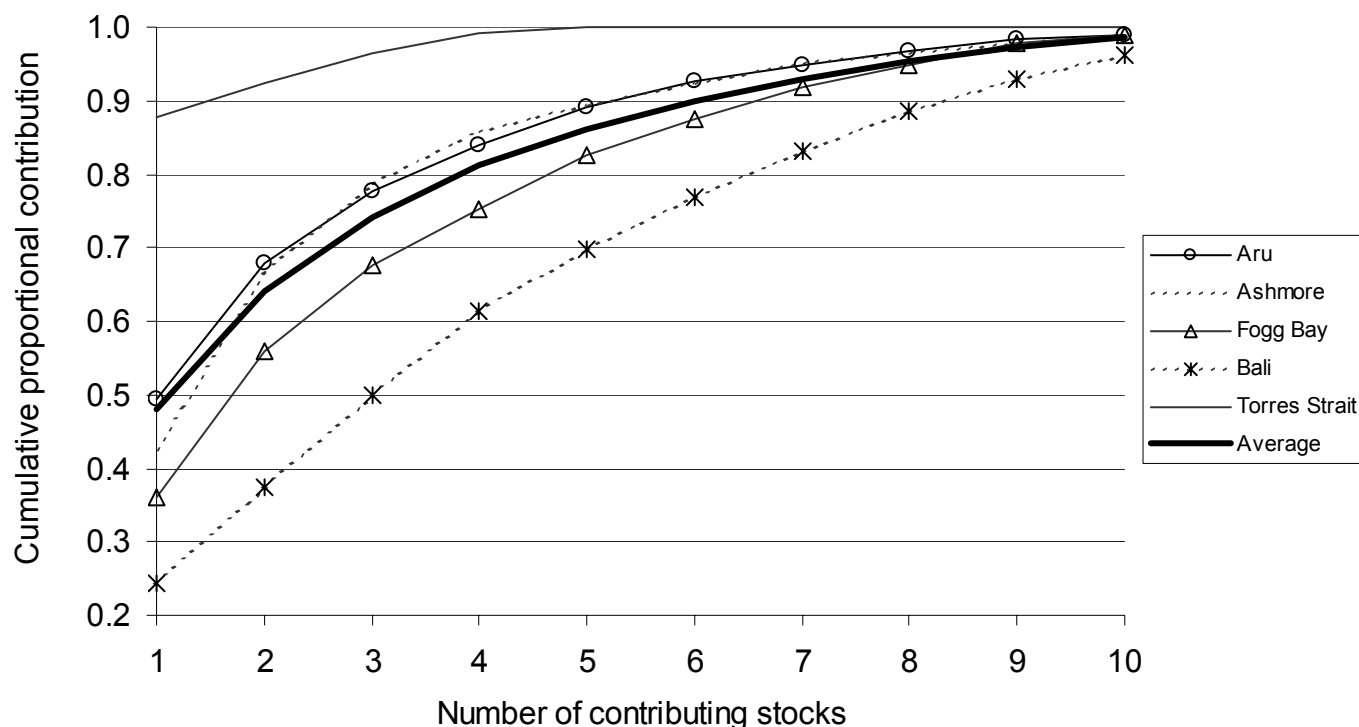


Figure 7: Contributing stock accumulation curves for MSA of three harvested and two foraging populations in the Australasian region.

Bearing in mind that the above analysis of the feeding populations and harvest is preliminary, some of the results are of considerable interest.  In keeping with tag returns from intensively studied populations (Figure 2: see for example tag recoveries from the Sulu Sea and from the northern Arafura Sea) each feeding assemblage analysed includes turtles from multiple MUs and, conversely, feeding grounds for some MUs are geographically dispersed, indicating that the geographic area of habitat supporting each MU is much greater than just the rookeries and immediately adjacent waters.   For example, despite the limited sample sizes, it is evident that the Aru and Ashmore reef feeding grounds support multiple MUs.  A second striking result is that the feeding range for the large but little studied Gulf of Carpentaria stock may be primarily to the west (Ashmore reef), rather than north (Aru) or east (Torres Strait).  Third, the Torres Strait harvest is dominated by the adjacent NGBR MU.  The  Bali-centred harvest draws on multiple MUs, with major contributions from both Indonesia (Aru) and at least several adjacent nations including the Gulf of Carpentaria MU, Australia; PNG MU, Papua New Guinea and Sulu Sea MU, Malaysia/Phillipines.  The impact may be broader than this because our limited sampling does not take into account seasonal or historical trends within the geographical extent of the fishery.

An alternative way to assess the relative composition of feeding and harvested populations is ask how many MUs are required to explain say, 90% of the composition.  By ranking the estimates and calculating cumulative totals we find that only 2 stocks are required to explain 90% of the data at Torres Strait, 6 MUs for Ashmore Reef and Aru, 7 MUs for Fogg Bay and 9 MUs for the Bali harvest (Figure 7).  This approach provides a relative measure of the geographic impact of each harvest or likely impact should a foraging population be subject to harvesting.  Not surprisingly, it is apparent that large harvests (like Bali) operating over expansive areas will have the greatest impact on the greatest number of MUs.  However given the high diversity of MUs represented in a typical foraging population, even harvests of limited geographic extent are likely to impact multiple MUs.   The Torres Strait harvest is dominated by migrating NGBR turtles, almost to the exclusion of all other MUs, a pattern consistent with tag return data (Limpus *et al.* 1992).  It is likely that fewer than expected MUs are impacted here because the majority of turtles harvested are transient adult migrants rather than from the local resident population.

# CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Using mtDNA analysis, we have identified 17 genetically divergent sets of populations of green turtles in the Southeast Asian and western Pacific region. These Management Units represent the logical focus for recovery actions. This is because breeding populations that are demonstrably different in their genetic make-up are likely to exchange few individuals and so will respond separately to threatening processes and management actions (Moritz 1994). Sets of recommendations and major findings have been developed through the integration of genetic and available tagging data and are presented below.

The genetic homogeneity across the Malaysian and Philippine Turtle Islands (Nth of Sabah; figure 3 and 5) indicates regular interchange of females and thereby supports their joint management; we recommend that this multinational initiative be continued (Palma 1997). The as yet genetically undescribed green turtle population nesting in the Indonesian islands of the South China Sea off West Kalimantan are expected to be genetically similar to the adjacent Sarawak MU and would benefit from a similar multinational management approach. There is no such evidence for joint Management Units between Australia and neighbouring nations (Indonesia, New Caledonia and PNG) with all nesting beaches for each MU contained within a single country. The larger countries are typically supporting multiple MUs within single countries, e.g. Malaysia, Indonesia and Australia.

The general pattern through Southeast Asian and the Western Pacific is one of heterogeneity among rookeries separated by more than a few hundred kilometres. This implies that restoration of recently depleted populations via natural colonisation is unlikely except over the very long-term (100 or 1000's of generations). Accordingly, management to restore these populations will require local effort to increase survivorship and reduce mortality, especially at nesting beaches and feeding areas.

It should be emphasised that "Management Units" refer to the geographic scope of connected breeding sites. The turtles from each of these MU's cover a much greater geographic area during development and migrations between nesting and feeding locations. Some clues as to the Management Area for each Management Unit or Stock recognised here can come from a combination of tag returns (see figure 2), satellite tracking and genetic analysis of feeding and harvested populations.

The mixed stock analysis clearly demonstrated that different fisheries impact multiple MU's and that the extent of that impact differs between fisheries. While there are substantial variances surrounding these estimates, they are useful to identify those MU's that are likely to be impacted by a particular fishery. The corollary, to identify those stocks that are not represented or barely so, is of perhaps equal management importance. Genetic analysis of three foraging populations suggests that significant contributions from some, but not all, adjacent rookeries is typical and that large contributions from distant rookeries is rare. Assessing the impact of harvested populations is likely to be much more complex. The Bali harvest, for example, comprises of turtles that have been collected over a vast geographic area (several seas) while the Torres Strait harvest comprises of turtles collected over several islands and reefs within the Torres Strait (~150km diameter area). The Bali harvest is a large harvest and is impacting several MUs, the Aru MU in particular, while the Torres Strait harvest is predominately impacting a single MU, the NGBR. To improve these estimates and recommendations from them it would be useful to more towards methods (assignment tests based on microsatellite loci) that permit estimation of the source of individual turtles (Paetkau *et al.* 1995) and to consider what rates of migration are needed to sustain particular MUs in the context of demographic trends and known management issues (Taylor *et al.* 2000).

As this current project reaches its conclusion, there is now a considerable understanding of the population genetic structure of green turtle breeding in the Southeast Asian and Western Pacific region and some generalities can be drawn.

Two properties of green turtle populations here are:
  i) Groups of adjacent rookeries that are isolated from other rookeries by more than a few hundred kilometres can be expected to support a genetically distinct Management Units.
  ii) Where a chain of adjacent rookeries extends over a large geographical area, the entire assemblage can be expected to represent a single Management Unit.

It is no longer necessary to genetically assess each individual rookery. Rookeries adjacent to stocks that have been genetically assessed can be managed as part of those MUs. Rookeries that are remote from identified management units will require representative breeding sites to be genetically assessed.

Extrapolating from the findings above we can begin to make predictions about the genetic affinities of some genetically unsampled but regionally significant rookeries. Rookeries in the following regions are likely to comprise new MU's based on their size and distance from other MUs;
  i) Northwest coast of Irian Jaya / South Eastern Philippines.
  ii) Coastal areas from Thailand thru to Vietnam and China.

Indonesian rookeries off the West Kalimantan coast in the South China Sea are likely to be part of the Sarawak MU and would benefit from multinational management approach similar to that covering the Sulu Sea MU.

In the absence of knowledge of the extent of green turtle nesting along the southern and Western coasts of Sumatra, Indonesia, we cannot predict whether or not they represent a distinct management from those in western Java. Or indeed, whether the Sumatran populations are genetically different to the green turtles that nest in the Andaman Sea of India and Thailand.

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Appendix 1.  Sequences from mtDNA control region for variants detected among Australasian populations of green turtles (*Chelonia mydas*)

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A1        TAGCATATGA CCAGTAATGT TAACAGTTGA TTTGGCCCTA AACATGAAAA TTATTGAGTT TACATAAA-C ATTTTAATAA CATGAATATT AAGCAGAGAA
A2        .......... .......... .......... .......... .......... .......A.. .G......-. .......... .......... ..........
A3        .......... .......... .......... .......... .......... .......... .G......-. .......... .......... ..........
A4        .......... .......... .......... .......... .......... .......A.. .G......-. .......... .......... ..........
B1        .......... .......... .......... .......... .......... .....A.A.. .G......-T G......... .......... ..........
B3        .......... .......... .......... .......... .......... .....A.A.. .G......-T G......... .......... ..........
B4        .......... .......... .......... .......... .......... .....A.A.. .G......-T G......... .......... ..........
B5        .......... .......... .......... .......... ......A... .....A.A.. .G.....AT .......... .......... .........G
C1        .......... .......... .......... .......... .......... .......A.C C.......-T .......... .......... ..........
C2        .......... .......C. .......... .......... .......... .......A.C C.......-T .......... .......... ..........
C3        .......... .......... .......... .......... .......... .......A.C C.......-T .......... .......... ..........
C4        .......... .......... .......... .......... .......... .......A.C C.......-T ......C.. .......... ..........
C5        .......... .......... .......... .......... .......... .......A.. C.......-T .......... .......... ..........
C7        .......... .......... .......... .......... .......... .......A.C C.......-T .......... .......... ..........
C8        .......... .......... .......... .......... .......... .......A.C C.......-T ......C.. .......... ..........
C9        .......... .......... .......... .......... .......... .......A.C C.......-T .......G .......... ..........
C12       .......... .......... .......... .......... ......A... .......A.. C.......-T ......GG .......... ..........
C13       .......... .......... .......... .......... ......A... .......A.. C.......-T ......GG .......... ..........
CARU      .......... .......... .......... .......... .......... .......A.C C.......-T .......... .......... ..........
D2        .......... .......... .......... .......... .......... .......A.C C.......-T ......G... .......... ..........
E1        .......... .......... .......... .......... .......... .......... ........-. .......... .......... ..........
E2        .......... .......... .......... .......... .......... .......... ........-. .......... .......... ..........
J1        .......... .......... .......... .......... ......A... .....A.A.. C.......-T ......GG .......... ..........
J2        .......... .......... .......... .......... ......A... .....A.A.. C.......-T ......GG .......... ..........
J14212    .......... .......... .......... .......... .......... .......A.. .G......-. .......... .......... ..........

A1        TTAAAAGTGA AATGATATAG GACATAAAAT TAAACCATTA TACTCAACCA TGAATATTGT CACAGTAATT GGTTATTTCT TAAATAGCTA TTCACGAGAA
A2        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
A3        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
A4        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
B1        .......... .......... .......... .......... .......... .......... T..G..... .......... ......A... ..........
B3        .......... .......... .......... .......... .......... .......... ...G..... .......... ......A... ..........
B4        .......... .......... .......... .......... .......... .......... T..G..... .......... ......A... ..........
B5        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
C1        .......... .......... .......... .......... .......... .......C.. ...G..... .......... ...G...... ..........
C2        .......... .......... .......... .......... .......... .......C.. ...G..... .......... ...G...... ..........
C3        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
C4        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
C5        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
C7        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
C8        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
C9        .......... .......... .......... .......... .......... .......C.. ...G..... .......... ...G...... ..........
C12       .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
C13       .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
CARU      .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
D2        .......... .......... .......... .......... .......... .......C.. .......... .......... ...G...... ..........
E1        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
E2        .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
J1        .......... .......... .......... .......... .......... .......... ...G..... ........C .......... ..........
J2        .......... .......... .......... .......... .......... .......... ...G..... ........C .......... ..........
J14212    .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
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A1      ATAAGCAACC CTTGTTAGTA AGATACAACA TTACCAGTTT CAAGCCCATT CAATTTGTGA CGTACATAAT TTGATCTATT CTGGCCTCTG GTTGTTCTTT
A2      .......... .......... .......... .......... .......... .........G .......... C......... .......... .......C..
A3      .......... .......... .......... .......... .......... .........G .......... .......... .......... .......C..
A4      .......... .......... .......... .......... .......... .........G .......... A......... .......... .......C..
B1      .......... ......G... .......... .......... .......... T.G...A.AG .......... .......... .......... .....CT...
B3      .......... ......G... .......... .......... .......... T.G...A.AG .......... .......... .......... .....CT...
B4      .......... ......G... .......... .......... ..G....... T.G...A.AG .......... .......... .......... .....CT...
B5      .......... .......... .......... .......... ..G.....G .........C .......... .......... .......... ..........
C1      .......... .......... .......... .......... ..G....... T.G...A.AG .........C C......... .......... .....CT...
C2      .......... .......... .......... .......... ..G....... T.G...A.AG ........GC C......... .......... .....CT...
C3      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
C4      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
C5      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
C7      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
C8      .......... .......... .......... .......... .......... T.G...A.AG ........C C......... .......... .....CT...
C9      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
C12     ........T. .......... .......... .......... ..G....... ..G.....G .......... .......... .......... .......T...
C13     .......... .......... .......... .......... ..G....... .G....G .......... .......... .......... .......T...
CARU    .......... .......... .......... .......... .......... T.G...A.AG ........C C......... .......... .....CT...
D2      .......... .......... .......... .......... ..G....... T.G...A.AG ........C C......... .......... .....CT...
E1      .......... .......... .......... .......... .......... .........G .......... .......... .......... ..........
E2      .......... .......... .......... .......... .......... .........G .......... .......... .......... ..........
J1      .......... .......... .......... .......... .G....... ..G....... .......... C......... .......... .......T...
J2      .......... .......... .......... .......... .G....... ..G....... .........C .......... .......... .......T...
J14212  .......... .......... .......... .......... .......... .........G .......... .......... .......... ..........

A1      CAGGCACATA TAAATAACGA CGTTCATTCG TTCCTCTTTA AAAGGCCTTT GGTTG----- -----AATGA -TTCTATACA TTAGATTTAT AACCT
A2      .......... .......... .......... .......... ....----- -----..... G......... .......... .....
A3      .......... .......... .......... .......... ....----- -----.-..... G......... .......... .....
A4      .......... .......... .......... .......... ....----- -----.-..... G......... .......... .....
B1      .......... C.....GTA. .......... .......... ....----- -----..... G......... ...A...... .....
B3      .......... C.....GTA. .......... .......... ....----- -----..... G......... ...A...... .....
B4      .......... C.....GTA. .......... .......... ....----- -----..... G......... ...A...... .....
B5      .......... C.....GTA. .......... ....C..... ....----- -----..... G......... ...A...... .....
C1      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C2      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C3      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C4      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C5      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C7      .......... C.....G.A. ...C...... .......... ....----- -----..... G......... ...A...... .....
C8      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C9      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
C12     .......... C.....GTA. .......... ....C..... ....----- -----..... G......... ...A...... .....
C13     .......... C.....GT.. .......... ....C..... ....----- -----..... G......... ...A...... .....
CARU    .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
D2      .......... C.....GTA. ...C...... .......... ....----- -----..... G......... ...A...... .....
E1      .......... .......... .......... .......... ....CCTTT GGTTGG.... G......... .......... .....
E2      .......... .......... .......... .......... ....CCTTT GGTTG..... G......... .......... .....
J1      .......... C.....GTA. .......... ....C..... ....----- -----..... G......... ...A...... .....
J2      .......... C.....GTA. .......... ....C..... ....----- -----..... G......... ...A...... .....
J14212  .......... .......... .......... .......... ....----- -----..... G......... .......... .....
```

Appendix 2: Pairwise tests for genetic differentiation among Marine Turtle rookeries.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Bramble Cay | * | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 Far North Queensland | 0.5142 | * | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3 Heron Island | 0.0000 | 0.0000 | * | | | | | | | | | | | | | | | | | | | | | | | | |
| 4 Lady Musgrave | 0.0000 | 0.0000 | 0.3296 | * | | | | | | | | | | | | | | | | | | | | | | | |
| 5 North West Island | 0.0000 | 0.0000 | 0.6447 | 0.6876 | * | | | | | | | | | | | | | | | | | | | | | | |
| 6 Paka | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | | | | | | | | | | | | | |
| 7 Palau Redang | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.4812 | * | | | | | | | | | | | | | | | | | | | | |
| 8 North West Cape | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | | | | | | | | | | | |
| 9 Coral Sea | 0.0000 | 0.0000 | 0.0076 | 0.7377 | 0.1985 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | | | | | | | | | | |
| 10 Bountiful Island | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0010 | 0.0030 | 0.0391 | 0.0000 | * | | | | | | | | | | | | | | | | | |
| 11 Groote Eylandt | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0008 | 0.1735 | 0.0000 | 0.8088 | * | | | | | | | | | | | | | | | | |
| 12 Port Bradshaw | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0011 | 0.0034 | 0.0000 | 0.6202 | 0.0914 | * | | | | | | | | | | | | | | | |
| 13 Lacepedes | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.4466 | 0.0000 | 0.0054 | 0.0214 | 0.0000 | * | | | | | | | | | | | | | | |
| 14 Ashmore Reef | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0004 | 0.0011 | 0.0000 | 0.0000 | 0.0013 | 0.0002 | 0.0000 | 0.0000 | * | | | | | | | | | | | | | |
| 15 Sandy Island | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0235 | 0.0242 | 0.0020 | 0.0000 | 0.1316 | 0.0240 | 0.0154 | 0.0001 | 0.0049 | * | | | | | | | | | | | | |
| 16 Elato Atoll | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0011 | 0.0000 | * | | | | | | | | | | | |
| 17 Ngulu Atoll | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.3144 | * | | | | | | | | | | |
| 18 Ulithi Atoll | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0002 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0441 | 0.0000 | 0.4127 | 0.2811 | * | | | | | | | | | |
| 19 Enu | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | |
| 20 Sangalaki | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0009 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | |
| 21 Pangumbahan | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0129 | 0.0099 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0005 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0004 | * | | | | | | |
| 22 Sarawak | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | |
| 23 SE Sabah | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0103 | 0.0137 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0002 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0142 | 0.0131 | 0.0000 | * | | | | |
| 24 Turtle Islands - Malaysia | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0006 | * | | | |
| 25 Turtle Islands - Philippines | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 1.0000 | * | | |
| 26 New Caledonia | 0.0347 | 0.0305 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0008 | 0.0001 | 0.0001 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.0018 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | |
| 27 Long Island | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0057 | 0.0000 | 0.0184 | 0.0026 | 0.1842 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * |

a) Exact Test of Rookery Differentiation Based on Haplotype Frequencies; insignificant comparisons are shaded.

## Appendix 2 Continued

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Bramble Cay | * | 0.7504 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0367 | 0.0000 |
| 2 Far North Queensland | -0.0185 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0377 | 0.0000 |
| 3 Heron Island | 0.7851 | 0.7788 | * | 0.3323 | 0.6402 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 4 Lady Musgrave | 0.6767 | 0.6580 | 0.0157 | * | 0.9999 | 0.0000 | 0.0000 | 0.0000 | 0.2754 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0002 | 0.0000 |
| 5 North West Island | 0.7187 | 0.7047 | -0.0087 | -0.0309 | * | 0.0000 | 0.0000 | 0.0000 | 0.0888 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 6 Paka | 0.6731 | 0.6651 | 0.8692 | 0.7662 | 0.8045 | * | 0.4061 | 0.0000 | 0.0000 | 0.0013 | 0.0001 | 0.0003 | 0.0000 | 0.0007 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0855 | 0.0000 | 0.0000 | 0.0000 | 0.0235 | 0.0000 | 0.0000 |
| 7 Palau Redang | 0.5504 | 0.5286 | 0.7919 | 0.6460 | 0.7047 | 0.0088 | * | 0.0000 | 0.0000 | 0.0135 | 0.0023 | 0.0068 | 0.0000 | 0.0107 | 0.1722 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0030 | 0.1465 | 0.0000 | 0.1540 | 0.0000 | 0.0025 | 0.0000 |
| 8 North West Cape | 0.5792 | 0.5627 | 0.8009 | 0.6690 | 0.7214 | 0.6217 | 0.4572 | * | 0.0000 | 0.0757 | 0.2170 | 0.0211 | 0.7852 | 0.0000 | 0.0022 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 9 Coral Sea | 0.5752 | 0.5523 | 0.1242 | 0.0102 | 0.0489 | 0.6308 | 0.5211 | 0.5474 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0011 | 0.0000 |
| 10 Bountiful Island | 0.5115 | 0.4903 | 0.7270 | 0.5895 | 0.6451 | 0.3237 | 0.1904 | 0.0966 | 0.4857 | * | 0.6289 | 0.7398 | 0.0041 | 0.0079 | 0.1586 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0005 | 0.0000 | 0.0003 | 0.0009 | 0.0000 |
| 11 Groote Eylandt | 0.5346 | 0.5169 | 0.7370 | 0.6096 | 0.6607 | 0.4354 | 0.2958 | 0.0236 | 0.5079 | -0.0257 | * | 0.2156 | 0.0368 | 0.0007 | 0.0349 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 |
| 12 Port Bradshaw | 0.4663 | 0.4453 | 0.6336 | 0.5241 | 0.5682 | 0.2759 | 0.1677 | 0.1184 | 0.4477 | -0.0235 | 0.0157 | * | 0.0002 | 0.0006 | 0.0880 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0005 | 0.0000 | 0.0000 |
| 13 Lacepedes | 0.6547 | 0.6468 | 0.8154 | 0.7203 | 0.7560 | 0.7000 | 0.5830 | -0.0198 | 0.6091 | 0.1847 | 0.0900 | 0.1946 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 14 Ashmore Reef | 0.4788 | 0.4555 | 0.6829 | 0.5360 | 0.5953 | 0.3180 | 0.1820 | 0.3233 | 0.4399 | 0.1720 | 0.2279 | 0.1685 | 0.4387 | * | 0.0108 | 0.0227 | 0.0074 | 0.0879 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0008 | 0.0000 | 0.0009 | 0.0039 |
| 15 Sandy Island | 0.5131 | 0.4914 | 0.7169 | 0.5736 | 0.6312 | 0.1252 | 0.0417 | 0.2800 | 0.4668 | 0.0344 | 0.1183 | 0.0495 | 0.3960 | 0.1403 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0218 | 0.0312 | 0.0000 | 0.0236 | 0.0000 | 0.0000 | 0.0227 |
| 16 Elato Atoll | 0.5279 | 0.5074 | 0.7602 | 0.6155 | 0.6740 | 0.5831 | 0.4619 | 0.5105 | 0.3916 | 0.4237 | 0.3670 | 0.5775 | 0.1185 | 0.3926 |  | * | 0.2544 | 0.7126 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 17 Ngulu Atoll | 0.4392 | 0.4158 | 0.6328 | 0.4918 | 0.5489 | 0.4751 | 0.3321 | 0.3730 | 0.4149 | 0.3159 | 0.3464 | 0.3038 | 0.4827 | 0.1049 | 0.3146 | 0.0180 | * | 0.2056 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0003 | 0.0012 |
| 18 Ulithi Atoll | 0.5480 | 0.5236 | 0.7807 | 0.6144 | 0.6806 | 0.6232 | 0.4290 | 0.4785 | 0.4824 | 0.3972 | 0.4328 | 0.3701 | 0.6044 | 0.0808 | 0.3949 | -0.0379 | 0.0247 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.0009 | 0.2927 |
| 19 Enu | 0.7725 | 0.7775 | 0.9191 | 0.8556 | 0.8754 | 0.8648 | 0.7429 | 0.7612 | 0.7260 | 0.6903 | 0.6904 | 0.5977 | 0.8068 | 0.6530 | 0.6965 | 0.7211 | 0.5971 | 0.7802 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 20 Sangalaki | 0.4149 | 0.3931 | 0.6141 | 0.4801 | 0.5347 | 0.3112 | 0.1697 | 0.3315 | 0.4060 | 0.2207 | 0.2659 | 0.2139 | 0.4475 | 0.1958 | 0.1825 | 0.2972 | 0.2346 | 0.2948 | 0.4834 | * | 0.0010 | 0.0000 | 0.0000 | 0.0089 | 0.0000 | 0.0008 | 0.0000 |
| 21 Pangumbahan | 0.6073 | 0.5950 | 0.7977 | 0.6857 | 0.7293 | 0.0798 | 0.0591 | 0.5426 | 0.5760 | 0.2805 | 0.3804 | 0.2541 | 0.6305 | 0.2713 | 0.1146 | 0.5107 | 0.4216 | 0.5321 | 0.7761 | 0.1913 | * | 0.0000 | 0.0591 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 22 Sarawak | 0.6414 | 0.6178 | 0.8280 | 0.7231 | 0.7631 | 0.6637 | 0.5043 | 0.6045 | 0.6122 | 0.4922 | 0.5426 | 0.3821 | 0.6807 | 0.4816 | 0.5087 | 0.5518 | 0.4552 | 0.5806 | 0.8131 | 0.4161 | 0.6070 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 23 SE Sabah | 0.5178 | 0.5007 | 0.7043 | 0.5850 | 0.6328 | 0.1159 | 0.0466 | 0.4411 | 0.4977 | 0.2168 | 0.3043 | 0.2050 | 0.5390 | 0.2056 | 0.0886 | 0.4134 | 0.3413 | 0.4207 | 0.6587 | 0.0984 | 0.0729 | 0.5094 | * | 0.0001 | 0.0002 | 0.0005 | 0.0000 |
| 24 Turtle Islands - Malaysia | 0.6561 | 0.6488 | 0.8262 | 0.7315 | 0.7671 | 0.6691 | 0.6233 | 0.6258 | 0.6258 | 0.5210 | 0.5525 | 0.4662 | 0.6901 | 0.4917 | 0.5069 | 0.5769 | 0.4813 | 0.6064 | 0.8122 | 0.2814 | 0.5962 | 0.6793 | 0.5094 | * | 0.7565 | 0.0000 | 0.0000 |
| 25 Turtle Islands - Philippines | 0.6211 | 0.6119 | 0.7773 | 0.6855 | 0.7207 | 0.6017 | 0.5831 | 0.5972 | 0.5972 | 0.4830 | 0.5170 | 0.4391 | 0.6506 | 0.4569 | 0.4632 | 0.5427 | 0.4598 | 0.5629 | 0.7569 | 0.2466 | 0.5402 | 0.6367 | 0.2954 | -0.0254 | * | 0.0000 | 0.0000 |
| 26 New Caledonia | 0.1333 | 0.1162 | 0.6389 | 0.4254 | 0.5105 | 0.4604 | 0.2647 | 0.3641 | 0.2850 | 0.2653 | 0.3119 | 0.2524 | 0.5054 | 0.2199 | 0.2423 | 0.2988 | 0.2148 | 0.2782 | 0.6905 | 0.1804 | 0.3829 | 0.4736 | 0.2815 | 0.5013 | 0.4633 | * | 0.0000 |
| 27 Long Island | 0.6867 | 0.6815 | 0.8739 | 0.7773 | 0.8127 | 0.7603 | 0.6228 | 0.6617 | 0.6502 | 0.5679 | 0.5928 | 0.5042 | 0.7281 | 0.2183 | 0.5678 | 0.1355 | 0.1900 | 0.0526 | 0.8666 | 0.4582 | 0.6686 | 0.7218 | 0.5608 | 0.7298 | 0.6795 | 0.5349 | * |

b) Rookery pairwise FSTs using haplotypic data (below diagonal) and their p values (above diagonal); insignificant comparisons are shaded.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Bramble Cay | * | 0.7514 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.1067 | 0.0000 |
| 2 Far North Queensland | -0.0248 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.3797 | 0.0000 |
| 3 Heron Island | 0.8387 | 0.7903 | * | 0.3380 | 0.6416 | 0.0000 | 0.0000 | 0.0000 | 0.0053 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 4 Lady Musgrave | 0.7276 | 0.6492 | 0.0157 | * | 0.9999 | 0.0000 | 0.0000 | 0.0000 | 0.2536 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0144 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 5 North West Island | 0.7713 | 0.7066 | -0.0087 | -0.0309 | * | 0.0000 | 0.0000 | 0.0000 | 0.0779 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0070 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 6 Paka | 0.7408 | 0.6548 | 0.9114 | 0.8253 | 0.8561 | * | 0.3653 | 0.0000 | 0.0000 | 0.0005 | 0.0003 | 0.0005 | 0.0000 | 0.0018 | 0.3756 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.1495 | 0.0883 | 0.0630 | 0.0206 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 7 Palau Redang | 0.6549 | 0.5512 | 0.8714 | 0.7536 | 0.7994 | -0.0149 | * | 0.0000 | 0.0000 | 0.0008 | 0.0004 | 0.0003 | 0.0042 | 0.0184 | 0.0657 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0231 | 0.0561 | 0.0430 | 0.1557 | 0.0096 | 0.0000 | 0.0007 | 0.0000 |
| 8 North West Cape | 0.7668 | 0.6820 | 0.9349 | 0.8611 | 0.8863 | 0.3172 | 0.2677 | * | 0.0000 | 0.0267 | 0.1323 | 0.0039 | 0.7373 | 0.0007 | 0.0081 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 9 Coral Sea | 0.5635 | 0.4836 | 0.1377 | 0.0180 | 0.0591 | 0.6655 | 0.5908 | 0.7005 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0007 | 0.0000 | 0.0000 | 0.0007 | 0.0000 | 0.0165 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0025 | 0.0013 |
| 10 Bountiful Island | 0.7852 | 0.7095 | 0.9355 | 0.8690 | 0.8907 | 0.1367 | 0.1860 | 0.1223 | 0.7126 | * | 0.6648 | 0.7049 | 0.0053 | 0.0000 | 0.3507 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 11 Groote Eylandt | 0.7928 | 0.7210 | 0.9377 | 0.8759 | 0.8955 | 0.2076 | 0.2323 | 0.0503 | 0.7223 | -0.0265 | * | 0.1590 | 0.0238 | 0.0001 | 0.0884 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0007 | 0.0000 |
| 12 Port Bradshaw | 0.8311 | 0.7788 | 0.9418 | 0.8980 | 0.9105 | 0.1533 | 0.2542 | 0.1866 | 0.7671 | -0.0236 | 0.0292 | * | 0.0000 | 0.0000 | 0.0898 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 13 Lacepedes | 0.7393 | 0.6670 | 0.9054 | 0.8366 | 0.8604 | 0.2266 | 0.2209 | -0.0165 | 0.6961 | 0.0721 | 0.0404 | 0.1403 | * | 0.0000 | 0.0593 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 14 Ashmore Reef | 0.5081 | 0.4065 | 0.5342 | 0.3565 | 0.4246 | 0.3578 | 0.2435 | 0.4329 | 0.2287 | 0.4500 | 0.4720 | 0.5567 | 0.4386 | * | 0.0012 | 0.0012 | 0.0000 | 0.0116 | 0.0001 | 0.0003 | 0.0001 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0188 | 0.0049 |
| 15 Sandy Island | 0.7291 | 0.6453 | 0.8994 | 0.8127 | 0.8440 | 0.0150 | 0.0567 | 0.6584 | 0.6584 | 0.0001 | 0.0249 | 0.0345 | 0.0627 | 0.3526 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0230 | 0.0005 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 16 Elato Atoll | 0.8142 | 0.7429 | 0.6593 | 0.4708 | 0.5201 | 0.9241 | 0.8564 | 0.9621 | 0.3290 | 0.9613 | 0.9633 | 0.9617 | 0.9115 | 0.4074 | 0.9047 | * | 0.3303 | 0.1041 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.1129 |
| 17 Ngulu Atoll | 0.8269 | 0.7679 | 0.6196 | 0.4615 | 0.4998 | 0.9194 | 0.8661 | 0.9498 | 0.3356 | 0.9501 | 0.9524 | 0.9540 | 0.9102 | 0.4484 | 0.9042 | 0.0050 | * | 0.1147 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0095 |
| 18 Ulithi Atoll | 0.7849 | 0.6977 | 0.5013 | 0.2908 | 0.3441 | 0.9078 | 0.8191 | 0.9547 | 0.2101 | 0.9551 | 0.9581 | 0.9582 | 0.8989 | 0.3385 | 0.8860 | 0.0955 | 0.0693 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0001 | 0.0000 | 0.0000 | 0.3284 |
| 19 Enu | 0.7753 | 0.7055 | 0.9167 | 0.8484 | 0.8707 | 0.3086 | 0.2106 | 0.5515 | 0.6928 | 0.4747 | 0.4969 | 0.5092 | 0.4457 | 0.4314 | 0.3073 | 0.9342 | 0.9274 | 0.9249 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 20 Sangalaki | 0.7527 | 0.6826 | 0.9010 | 0.8288 | 0.8537 | 0.0293 | 0.0596 | 0.3111 | 0.6841 | 0.1805 | 0.2277 | 0.2151 | 0.2594 | 0.4009 | 0.0689 | 0.9074 | 0.9058 | 0.8940 | 0.2543 | * | 0.0395 | 0.0000 | 0.0000 | 0.0403 | 0.0000 | 0.0001 | 0.0000 |
| 21 Pangumbahan | 0.8064 | 0.7370 | 0.9407 | 0.8796 | 0.8984 | 0.0356 | 0.1485 | 0.5948 | 0.7212 | 0.3376 | 0.4230 | 0.2809 | 0.3355 | 0.4637 | 0.0962 | 0.9711 | 0.9579 | 0.9675 | 0.4968 | 0.0405 | * | 0.0000 | 0.0081 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 22 Sarawak | 0.7348 | 0.6571 | 0.8959 | 0.8142 | 0.8438 | 0.1255 | 0.0875 | 0.3814 | 0.6719 | 0.2698 | 0.3327 | 0.3305 | 0.3906 | 0.1877 |  | 0.8952 | 0.8969 | 0.8766 | 0.3839 | 0.2075 | 0.2858 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 23 SE Sabah | 0.8205 | 0.7600 | 0.9409 | 0.8875 | 0.9033 | 0.0611 | 0.1815 | 0.5383 | 0.7411 | 0.3021 | 0.3813 | 0.2711 | 0.3508 | 0.5035 | 0.1171 | 0.9661 | 0.9556 | 0.9622 | 0.4765 | 0.0372 | 0.1236 | 0.3065 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 24 Turtle Islands - Malaysia | 0.8350 | 0.7768 | 0.9481 | 0.8972 | 0.9119 | 0.4051 | 0.3756 | 0.7529 | 0.7525 | 0.6400 | 0.6724 | 0.5797 | 0.5007 | 0.3718 |  | 0.9766 | 0.9644 | 0.9743 | 0.6404 | 0.2458 | 0.6768 | 0.4630 | 0.3829 | * | 0.7632 | 0.0000 | 0.0000 |
| 25 Turtle Islands - Philippines | 0.8518 | 0.8026 | 0.9506 | 0.9084 | 0.9198 | 0.3939 | 0.3964 | 0.7229 | 0.7749 | 0.6034 | 0.6394 | 0.5543 | 0.5109 | 0.3745 |  | 0.9753 | 0.9653 | 0.9734 | 0.6401 | 0.2362 | 0.6065 | 0.4785 | 0.3192 | -0.0220 | * | 0.0000 | 0.0000 |
| 26 New Caledonia | 0.0810 | -0.0021 | 0.7261 | 0.5115 | 0.5993 | 0.5697 | 0.4146 | 0.6246 | 0.3063 | 0.6631 | 0.6828 | 0.7600 | 0.6111 | 0.2033 | 0.5601 | 0.6551 | 0.6981 | 0.5656 | 0.6516 | 0.6157 | 0.6985 | 0.5796 | 0.7307 | 0.7546 | 0.7891 | * | 0.0004 |
| 27 Long Island | 0.7338 | 0.6533 | 0.4903 | 0.3108 | 0.3655 | 0.8229 | 0.7390 | 0.8656 | 0.2201 | 0.8741 | 0.8820 | 0.9040 | 0.8379 | 0.2653 | 0.8106 | 0.0682 | 0.0867 | 0.0028 | 0.8515 | 0.8278 | 0.8864 | 0.8092 | 0.8937 | 0.9045 | 0.9156 | 0.5150 | * |

c) Rookery pairwise FSTs using Kimura2P molecular distances (below diagonal) and their p values (above diagonal); insignificant comparisons are shaded.

Appendix 3: Pairwise tests for genetic differentiation among Marine Turtle Stocks.

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | North West Shelf | * | | | | | | | | | | | | | | | | |
| 2 | Coral Sea Platform | 0.0000 | * | | | | | | | | | | | | | | | |
| 3 | Gulf of Carpentaria | 0.0000 | 0.0000 | * | | | | | | | | | | | | | | |
| 4 | NGBR | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | | | | | |
| 5 | SGBR | 0.0000 | 0.0032 | 0.0000 | 0.0000 | * | | | | | | | | | | | | |
| 6 | Ashmore Reef | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | | | |
| 7 | Scott Reefs | 0.0000 | 0.0000 | 0.0078 | 0.0000 | 0.0000 | 0.0044 | * | | | | | | | | | | |
| 8 | Micronesia | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | | |
| 9 | Aru | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | | |
| 10 | Berau Islands | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | | | | |
| 11 | Java | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0002 | 0.0000 | 0.0000 | 0.0002 | * | | | | | | |
| 12 | Peninsular Malaysia | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0019 | 0.0000 | 0.0000 | 0.0000 | 0.0092 | * | | | | | |
| 13 | Sarawak | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | | | |
| 14 | SE Sabah | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0146 | 0.0188 | 0.0028 | 0.0000 | * | | | |
| 15 | Sulu Sea | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | | |
| 16 | New Caledonia | 0.0000 | 0.0000 | 0.0000 | 0.0164 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * | |
| 17 | PNG | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0089 | 0.0000 | 0.0193 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | * |

a) Exact Test of Rookery Differentiation Based on Haplotype Frequencies; insignificant comparisons are shaded.

Appendix 3 Continued

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | North West Shelf | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 2 | Coral Sea Platform | 0.5931 | * | 0.0000 | 0.0000 | 0.0049 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0010 | 0.0000 |
| 3 | Gulf of Carpentaria | 0.1396 | 0.4508 | * | 0.0000 | 0.0000 | 0.0020 | 0.0430 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 4 | NGBR | 0.6464 | 0.6017 | 0.4993 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0059 | 0.0000 |
| 5 | SGBR | 0.7755 | 0.0989 | 0.6313 | 0.7701 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 6 | Ashmore Reef | 0.4251 | 0.4399 | 0.1918 | 0.5261 | 0.7039 | * | 0.0098 | 0.0039 | 0.0000 | 0.0000 | 0.0000 | 0.0010 | 0.0000 | 0.0010 | 0.0000 | 0.0000 | 0.0039 |
| 7 | Scott Reefs | 0.3769 | 0.4668 | 0.0666 | 0.5557 | 0.7285 | 0.1403 | * | 0.0000 | 0.0000 | 0.0000 | 0.0205 | 0.0176 | 0.0000 | 0.0332 | 0.0000 | 0.0000 | 0.0000 |
| 8 | Micronesia | 0.4770 | 0.4256 | 0.3553 | 0.4886 | 0.6352 | 0.1027 | 0.3465 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0088 |
| 9 | Aru | 0.7527 | 0.7260 | 0.5677 | 0.7577 | 0.8724 | 0.6530 | 0.6965 | 0.5666 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 10 | Berau Islands | 0.4396 | 0.4060 | 0.2441 | 0.4659 | 0.6565 | 0.1958 | 0.1825 | 0.2734 | 0.4834 | * | 0.0010 | 0.0000 | 0.0000 | 0.0117 | 0.0000 | 0.0000 | 0.0000 |
| 11 | Java | 0.6037 | 0.5760 | 0.2773 | 0.6318 | 0.7917 | 0.2713 | 0.1146 | 0.4351 | 0.7761 | 0.1913 | * | 0.0430 | 0.0000 | 0.0654 | 0.0000 | 0.0000 | 0.0000 |
| 12 | Peninsular Malaysia | 0.6310 | 0.6065 | 0.2887 | 0.6577 | 0.8054 | 0.3021 | 0.1125 | 0.4685 | 0.7922 | 0.2958 | 0.0753 | * | 0.0000 | 0.0098 | 0.0000 | 0.0000 | 0.0000 |
| 13 | Sarawak | 0.6499 | 0.6122 | 0.4245 | 0.6536 | 0.8118 | 0.4816 | 0.5087 | 0.4622 | 0.8131 | 0.4161 | 0.6070 | 0.6259 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 14 | SE Sabah | 0.5246 | 0.4977 | 0.2343 | 0.5559 | 0.7266 | 0.2056 | 0.0886 | 0.3672 | 0.6587 | 0.0984 | 0.0729 | 0.1051 | 0.5094 | * | 0.0000 | 0.0000 | 0.0000 |
| 15 | Sulu Sea | 0.6461 | 0.6212 | 0.4755 | 0.6557 | 0.7722 | 0.5043 | 0.5093 | 0.5039 | 0.7504 | 0.2967 | 0.5742 | 0.5979 | 0.6565 | 0.3412 | * | 0.0000 | 0.0000 |
| 16 | New Caledonia | 0.4872 | 0.2850 | 0.2846 | 0.1866 | 0.6326 | 0.2199 | 0.2423 | 0.2607 | 0.6905 | 0.1804 | 0.3829 | 0.4372 | 0.4736 | 0.2815 | 0.5124 | * | 0.0000 |
| 17 | PNG | 0.6885 | 0.6502 | 0.5019 | 0.6947 | 0.8403 | 0.2183 | 0.5678 | 0.1157 | 0.8666 | 0.4582 | 0.6686 | 0.7031 | 0.7218 | 0.5608 | 0.6916 | 0.5349 | * |

b) Rookery pairwise FSTs using haplotypic data (below diagonal) and their p values (above diagonal); insignificant comparisons are shaded.

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | North West Shelf | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0234 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 2 | Coral Sea Platform | 0.7381 | * | 0.0000 | 0.0000 | 0.0049 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0049 | 0.0010 |
| 3 | Gulf of Carpentaria | 0.1249 | 0.8219 | * | 0.0000 | 0.0000 | 0.0000 | 0.0479 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 4 | NGBR | 0.7429 | 0.5792 | 0.8273 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0518 | 0.0000 |
| 5 | SGBR | 0.8813 | 0.1124 | 0.9119 | 0.7972 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 6 | Ashmore Reef | 0.5132 | 0.2287 | 0.6590 | 0.5356 | 0.5457 | * | 0.0020 | 0.0000 | 0.0000 | 0.0010 | 0.0000 | 0.0010 | 0.0000 | 0.0000 | 0.0000 | 0.0186 | 0.0059 |
| 7 | Scott Reefs | 0.0833 | 0.6584 | 0.0512 | 0.7036 | 0.8601 | 0.3526 | * | 0.0000 | 0.0000 | 0.0186 | 0.0000 | 0.1797 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 8 | Micronesia | 0.9284 | 0.3920 | 0.9562 | 0.8263 | 0.5115 | 0.5394 | 0.9165 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0117 |
| 9 | Aru | 0.4762 | 0.6928 | 0.5417 | 0.7365 | 0.8700 | 0.4314 | 0.3073 | 0.9303 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 10 | Berau Islands | 0.2921 | 0.6841 | 0.2715 | 0.7228 | 0.8632 | 0.4009 | 0.0689 | 0.9158 | 0.2543 | * | 0.0459 | 0.1094 | 0.0000 | 0.0371 | 0.0000 | 0.0000 | 0.0000 |
| 11 | Java | 0.3577 | 0.7212 | 0.3008 | 0.7603 | 0.8883 | 0.4637 | 0.0962 | 0.9523 | 0.4968 | 0.0405 | * | 0.1279 | 0.0000 | 0.0059 | 0.0000 | 0.0000 | 0.0000 |
| 12 | Peninsular Malaysia | 0.2465 | 0.6560 | 0.2270 | 0.6912 | 0.8497 | 0.3525 | 0.0368 | 0.8969 | 0.2223 | 0.0399 | 0.0623 | * | 0.0400 | 0.0029 | 0.0000 | 0.0000 | 0.0000 |
| 13 | Sarawak | 0.3755 | 0.6719 | 0.3834 | 0.7119 | 0.8619 | 0.3906 | 0.1877 | 0.9116 | 0.3839 | 0.2075 | 0.2858 | 0.1163 | * | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 14 | SE Sabah | 0.3676 | 0.7411 | 0.2977 | 0.7751 | 0.8921 | 0.5035 | 0.1171 | 0.9516 | 0.4765 | 0.0372 | 0.1236 | 0.0885 | 0.3065 | * | 0.0000 | 0.0000 | 0.0000 |
| 15 | Sulu Sea | 0.5846 | 0.8215 | 0.5879 | 0.8412 | 0.9161 | 0.6697 | 0.4622 | 0.9662 | 0.6960 | 0.3087 | 0.6433 | 0.3839 | 0.5624 | 0.3748 | * | 0.0000 | 0.0000 |
| 16 | New Caledonia | 0.6860 | 0.3063 | 0.8258 | 0.0962 | 0.6969 | 0.2033 | 0.5601 | 0.7675 | 0.6516 | 0.6157 | 0.6985 | 0.5508 | 0.5796 | 0.7307 | 0.8501 | * | 0.0010 |
| 17 | PNG | 0.8676 | 0.2201 | 0.9268 | 0.7261 | 0.4233 | 0.2653 | 0.8106 | 0.1018 | 0.8515 | 0.8278 | 0.8864 | 0.7913 | 0.8092 | 0.8937 | 0.9380 | 0.5150 | * |

c) Rookery pairwise FSTs using Kimura2P molecular distances (below diagonal) and their p values (above diagonal); insignificant comparisons are shaded.