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Population genetic structure of Indo-West Pacific carcharhinid sharks: what do we know and where to from here?

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Supplementary Material – Detailed Review of Population Genetic Structure Studies on Carcharhinids Occurring in the Indo-West Pacific

This section sets out the specific details of published population genetic structure studies of carcharhinid species that occur in the Indo-West Pacific (IWP) region upon which the review proper is based. Species are grouped based on their lifestyle category. These lifestyle categories are based on those that Heist (2012) used to summarise the population genetic structure of elasmobranchs, except that we have divided coastal species into medium- and large-bodied. These groups show parallels with Chin *et al.*'s (2010) ecological categories of elasmobranch, although our habitat-associated group combines their estuarine and reef categories due to a low number of species.

Habitat-Associated Species

We define habitat-associated species as being those species whose range and distribution is restricted by the distribution of a specific habitat type. Consequently, species that are riverine or estuarine, found immediately adjacent to coral reefs, or the immediate fringes of oceanic islands are included in this lifestyle category.

Grey Reef Shark, *Carcharhinus amblyrhynchos*

The grey reef shark, *Carcharhinus amblyrhynchos*, is a pelagic, coral reef associated, apex predator that is common in waters of the IWP (Wetherbee *et al.* 1997; Compagno *et al.* 2005; Last and Stevens 2009). Pups are born at approximately 50 cm to 60 cm TL after a nine to twelve-month gestation. Maturity is attained at six to eight years and a size of 130 cm to 140 cm TL for males and 125 cm TL for females, and maximum size is around 180 cm to 190 cm TL (Wetherbee *et al.* 1997; Last and Stevens 2009) (Table 2). Because the distribution of *C. amblyrhynchos* is associated with coral reefs, it has been classified as habitat-associated (Wetherbee *et al.* 1997; Compagno *et al.* 2005; Last and Stevens 2009).

The population genetic structure of *C. amblyrhynchos* was first investigated by Horn *et al.* (2008). Fifteen nuclear microsatellite markers and sequence data for the entire mitochondrial control region were analysed for individuals from a number of locations across the IWP. The authors determined that the species comprises three distinct genetic lineages: eastern Indian Ocean, central Pacific, and southwest Pacific. They also concluded that there was no genetic subdivision within the southwest Pacific region (Horn *et al.* 2008).

In a study focused on the Coral Sea and Great Barrier Reef complex, Momigliano *et al.* (2015) employed 16 microsatellites and an 813 bp fragment of the mitochondrial DNA NADH dehydrogenase subunit 4 (NADH 4) gene to assess the genetic structure of 121 individuals. The study did not identify any population genetic structure along the entire 1200 km latitudinal gradient investigated.

Given that Horn *et al.* (2008) and Momigliano *et al.* (2015) both failed to detect genetic structure within regions (south-west Pacific and Great Barrier Reef respectively), this suggests that *C. amblyrhynchos* is capable of movement between at least nearby reefs. This is supported by Espinoza *et al.* (2014) who investigated movement patterns of *C. amblyrhynchos* using acoustic tagging telemetry in the Great Barrier Reef. That study revealed that juveniles were likely to move between neighbouring reefs, and at least some adults also migrated up to five reefs each individually separated by tens of kilometres of open water (Espinoza *et al.* 2014). This suggests that short stretches of open water are no barrier to gene flow for *C. amblyrhynchos*.

Subsequently, Momigliano *et al.* (2017) utilised 5517 single nucleotide polymorphisms (SNPs) from the nuclear genome and a segment of the mitochondrial NADH subunit 4 gene to investigate population structure between sites in Australia, Indonesia and the Indian Ocean. That study found evidence of genetic structure and determined that large distances of deep water present a barrier to gene flow. It also determined that genetic structure throughout contiguous habitat along continental shelves supports isolation by distance. This finding is important because it highlights the ability of more recently developed genomic techniques to discriminate subtle genetic differentiation that may not have been apparent using earlier techniques such as microsatellite analysis. The mitochondrial analysis in this study also showed greater differentiation in females, suggesting that this species also exhibits a sex-based pattern of dispersal.

Galapagos Shark, *Carcharhinus galapagensis*

The Galapagos shark, *Carcharhinus galapagensis*, is distributed globally in tropical and temperate locations around islands and atolls in oceanic and sometimes also shelf waters (Last and Stevens 2009). Four to 16 pups are born at 60 to 80 cm TL after a twelve-month gestation period (Last and Stevens 2009). The species matures at 205 to 230 cm TL for males and 235 to 240 cm TL for females and attains a maximum length of 300 cm TL (Last and Stevens 2009). Here we have classified the species as habitat-associated because it is found in waters immediately adjacent to islands, atolls or

reefs, even though those locations may be away from continental shelves, the species is not found in mid ocean away from islands or atolls (Last and Stevens 2009).

Corrigan *et al.* (2017) analysed data from 2152 nuclear SNPs and a 1044 bp segment of the mitochondrial NADH2 gene from 53 Galapagos sharks from 7 locations across their global range. They found clear separation between Atlantic and Indo-Pacific samples based on the nuclear data, but also that the two most frequent mitochondrial haplotypes were also shared with dusky sharks (*Carcharhinus obscurus*) (Corrigan *et al.* 2017). At maturity, the Galapagos shark is morphologically similar to the dusky shark (*Carcharhinus obscurus*) but is able to be distinguished internally by vertebral counts (Garrick, 1982). Consequently, Corrigan *et al.* (2017) have hypothesised that *C. galapagensis* arose as an oceanic form of *C. obscurus*.

Pazmino *et al.* (2018) analysed variation in 7200 SNPs and a 955 bp segment of the mitochondrial Control Region from 299 Galapagos sharks from ten sites including southern Africa, east Australia, Hawaii, south Pacific, eastern Pacific and the Galapagos Islands. Their results suggest that there are multiple populations of Galapagos shark (Galapagos Islands, Mexico, Hawaii and western Pacific) and that gene flow is restricted across the Pacific and between remote island groups (Pazmino *et al.* 2018).

Blacktip Reef Shark, *Carcharhinus melanopterus*

The blacktip reef shark, *Carcharhinus melanopterus*, is a predominantly reef associated benthic species (Mourier *et al.* 2013), although it also occurs in turbid tidal environments around mangroves (Chin *et al.* 2013a). It is distributed through the IWP and Pacific Ocean (Vignaud *et al.* 2014). The species reaches a maximum size of around 108 to 120 cm TL for males and 120 to 138 cm TL for females and has been observed to form aggregations of individuals of similar size and the same gender (Mourier *et al.* 2013). Males reach maturity at 111 cm TL in French Polynesia (Mourier *et al.* 2013) and 102 to 108 cm TL in Indonesia (White 2007) (Table 2). Because the distribution of *C. melanopterus* is dependent on coral reefs (Mourier *et al.* 2013), we have classified this species as habitat-associated.

Mourier and Planes (2013) investigated the population genetic structure of *C. melanopterus* by analysing 17 nuclear microsatellite loci in 264 individuals from 24 sites in French Polynesia. They determined that genetic structure exists between the sampling locations and that females are returning to specific locations during breeding seasons. Similarly, Vignaud *et al.* (2013) analysed 11 nuclear microsatellite loci from 165 individuals from 5 sites in French Polynesia and also found genetic structure. Vignaud *et al.* (2014) subsequently assessed the global population genetic structure of *C. melanopterus* by analysing 17 nuclear microsatellite markers in conjunction with a 600 to 800 bp segment of the mitochondrial control region and a 700 to 800 bp segment of the mitochondrial cytochrome-b gene. Their analysis sampled over 1000 individuals from 5 broad global regions (Red Sea, Western Australia, eastern Australia, New Caledonia and French Polynesia). They determined that the species is highly structured with little or no gene flow between regions. The microsatellite markers confirmed that genetic structure within the islands of French Polynesia was of similar magnitude to the structure shown between eastern and Western Australia. The mitochondrial markers also revealed unique haplotypes within each region, and of the 24 control region haplotypes and 22 cytochrome-b haplotypes, only 3 and 4 respectively were shared between regions, and only one haplotype was shared between eastern Australia and Western Australia (Vignaud *et al.* 2014). Their finding of population genetic structure within French Polynesia led them to conclude that short stretches of deep open ocean (a few hundred kilometres) are just as effective a barrier to gene flow as are long continental coastlines (Vignaud *et al.* 2014).

Speartooth Shark, *Glyphis glyphis*

Juvenile and subadult speartooth sharks, *Glyphis glyphis*, inhabit rivers and estuaries of northern Australia and southern New Guinea. Adults have not been recorded in Australia, consequently their habitat requirements and reproductive biology are poorly understood (Pillans *et al.* 2009). The species is critically endangered and within Australia is believed to persist in only three river drainages (two in the Northern Territory and one in Cape York) (Feutry *et al.* 2014). The species is born at 50 cm TL and may reach over 200 cm TL (Compagno *et al.* 2005). Size at maturity is unknown with the

largest specimens recorded in Australia (147 cm to 175 cm TL) being immature (Last and Stevens 2009) (Table 2). Because juvenile and subadult *G. glyphis* are found in rivers and estuaries (Last and Stevens 2009; Pillans *et al.* 2009), we have classified this as a habitat-associated species. However, we acknowledge that this classification is based on incomplete information regarding the full life history of the species, and that *Glyphis* species in general may have an oceanic adult dispersal phase (see Li *et al.* 2015).

Feutry *et al.* (2014) investigated the population genetic structure of *G. glyphis* by sequencing the entire mitochondrial genome and analysing single nucleotide polymorphisms (SNPs) in 93 individuals from three river drainages in northern Australia, one of which was separated by more than 1000 km from the other two. The mitogenomic results were also compared to more traditionally used mitochondrial markers including the control region, cytochrome-b, NADH 4, and 12S genes. Pairwise comparisons of the three river drainages based on the full mitogenome analysis revealed significant population genetic structure between all three river systems, indicating a lack of gene flow between systems. However, more traditionally employed mitochondrial markers did not always provide the same result. Specifically, the three most commonly used mtDNA markers in elasmobranch population genetic studies (control region, NADH 4 and cytochrome-b) all failed to detect any significant genetic differentiation (Feutry *et al.* 2014).

Whitetip Reef Shark, *Triaenodon obesus*

The whitetip reef shark, *Triaenodon obesus*, is a coral reef associated benthic species found in tropical coastal waters from the Red Sea, across the Indian Ocean, the tropical Indo-Pacific, and extending to islands in the eastern Pacific (Compagno 1984; Last and Stevens 2009). The species reaches maturity at 112 to 122 cm TL (Last and Stevens 2009) and at an age of seven to eight years. Pups are born at 52 to 60 cm TL in litters of one to four, and may reach a maximum size of 170 cm to 180 cm TL at an age of 19 years (Robbins 2006; Last and Stevens 2009) (Table 2). The species exhibits a sedentary behaviour unusual to Carcharhinidae where they rest in caves during the day and actively feed mainly at night (Randall 1977). They have small home ranges associated with individual reefs and a

maximum individual dispersal distances of less than 25 km (Nelson and Johnson 1980). Consequently, we have classified this as a habitat-associated species.

Population genetic structure for the whitetip reef shark was investigated by Whitney *et al.* (2012) who analysed a 1025 bp segment of the mitochondrial control region from 310 individuals from 25 sites across the Indo-Pacific. They found a complex pattern of genetic structure across the species' range. Significant population genetic structure was found between sites along the Great Barrier Reef, which was to be expected, given the sedentary behaviour of the species. However, genetic homogeneity was found in seven of the nine island samples from the Hawaiian archipelago; other island groups in the central Pacific also showed little evidence of population structure. Of the 15 distinct haplotypes recorded, only six were recorded in more than one individual, and only a single haplotype was identified in the eastern Pacific. Given that nine of the sampling locations had less than ten individuals sampled, it is reasonable to conclude that the full genetic diversity within each region was not representatively sampled, and the lack of apparent structure in some locations is probably an artefact of the inadequate sample sizes. Despite this, however, the pooled regional samples still suggest genetic structure exists over larger spatial scales for this species and that stretches of open ocean form contemporary barriers to gene flow. It is also apparent that the Indo-Pacific Barrier has historically contributed to isolation of populations of whitetip reef shark.

Medium-Bodied Coastal Species

We define medium-bodied coastal species as those species reaching a maximum size of no more than 265 cm TL and being distributed over continental shelf waters. They may be pelagic or benthopelagic and are not restricted to a specific habitat type.

Blacktip Sharks, *Carcharhinus limbatus* and *C. tilstoni*

The blacktip shark, *Carcharhinus limbatus*, has a global distribution in tropical, subtropical and warm temperate coastal waters (Compagno 1984), and occurs in a number of apparently geographically

separated populations (Castro 1996). Morphological characteristics such as size at birth, length at maturity and maximum length appear to vary over the global range of the species. Off the US Atlantic coast, the species is born at 55 cm to 60 cm TL and is mature at 145 cm for males and 156 cm for females (Castro 1996). In Indonesia, pups are born at 55 cm to 66 cm TL and males mature at 180 cm to 190 cm (White 2007). While in Australia, the species is born at 40 cm to 70 cm, matures at 180 cm TL and can reach a maximum size of 250 cm to 265 cm TL (Last and Stevens 2009; Harry *et al.* 2012) (Table 2).

The above-described geographic variation in morphological characteristics of *C. limbatus*, combined with discontinuities in the species' range, suggests that population structure may be high. This is confirmed by numerous genetic studies. Keeney *et al.* (2003) analysed a 1067 bp segment of the mitochondrial control region to investigate genetic differentiation in 169 juvenile *C. limbatus* from four nursery sites in the Gulf of Mexico and north west Atlantic. That study found significant haplotype differences between nursery sites and concluded that females are returning to the same region for breeding purposes. Keeney *et al.* (2005) subsequently expanded the previous study and analysed eight nuclear microsatellite markers as well as the entire mitochondrial control region of 323 individuals from the US Atlantic coast and Gulf of Mexico. This analysis revealed extensive population structure across nursery sites. This was especially apparent in the mtDNA which led them to conclude that females were exhibiting natal philopatry (Keeney *et al.* 2005). Keeney and Heist (2006) analysed a 1070 bp mitochondrial control region sequence of 364 individuals from seven geographical regions. That study also confirmed extensive genetic subdivision on a global scale and revealed distinct clades: the west Atlantic including the Gulf of Mexico and the Caribbean; the east Atlantic; and the Indo-Pacific (Keeney and Heist 2006; but see comments below about the taxonomic status of *C. limbatus*). However, it should be noted that no sample sites outside the west Atlantic had more than 14 individuals and the authors were therefore unable to determine if dispersal between the Atlantic and Pacific occurred before or after the opening of the Isthmus of Panama (Keeney and Heist 2006). These studies have subsequently been expanded by Sodre *et al.* (2012) and Gledhill *et al.*

(2015) who both sequenced the entire 1070 bp mitochondrial control region of additional samples from Brazil and Bimini respectively. Those studies again found genetic subdivision between sites within the west Atlantic (Sodre *et al.* 2012; Gledhill *et al.* 2015). In a study confined to the Red Sea and Arabian Sea, Spaet *et al.* (2015) found no genetic subdivision between locations when assessing variation observed from 12 nuclear microsatellite loci and a 1120 bp segment of the mitochondrial control region.

In a CSIRO report focusing on population structure of *C. limbatus* in Australia, Ovenden (2007) analysed five dinucleotide nuclear microsatellite markers and a 700 bp segment of the mitochondrial control region of 102 individuals from four sites (Indonesia, Northern Territory, Western Australia and Queensland). This study revealed significant population subdivision between all investigated sites based on the nuclear microsatellite markers. This led the authors to conclude that *C. limbatus* forms separate regional populations that should be managed independently (Ovenden 2007). It should be noted, however, that the mtDNA sequences were not significantly different between locations (Ovenden 2007). More recently, Almojil *et al.* (2018) found weak population structure in this species along the coasts of the Arabian Peninsular, Pakistan and South Africa when analysing 11 nuclear microsatellite markers.

The work of Naylor *et al.* (2012) suggests that *C. limbatus* may in fact be a complex of four separate species (*C. limbatus* in the Atlantic, *C. limbatus* in the Indo Pacific which they notionally call *C. cf limbatus*, *C. tilstoni* and also *C. amblyrhynchoides*). Whilst *C. tilstoni* is recognised as a separate species (see below), the taxonomy of this group is not fully resolved. The presence of multiple species would help to explain some of the regional morphological and genetic differences that have been reported for *C. limbatus*. This was foreshadowed by the earlier work of Keeney and Heist (2006) who placed *C. tilstoni* between the Atlantic and Indo-Pacific assemblages of *C. limbatus* based on neighbour-joining trees constructed from mitochondrial control region sequences.

The external morphology of the Australian blacktip shark, *Carcharhinus tilstoni*, is visually indistinguishable from *C. limbatus* and vertebral counts are required to separate them morphologically (Harry *et al.* 2012). *Carcharhinus tilstoni* is endemic to Australian waters, occurring from North-West Cape in Western Australia, northwards to Sydney in New South Wales (Boomer *et al.* 2010). *Carcharhinus tilstoni* pups are born at 62 cm TL, mature at 110 cm to 140 cm TL and reaches a maximum size of 160 cm to 200 cm TL (Last and Stevens 2009; Harry *et al.* 2012) (Table 2).

The population genetic structure of *C. tilstoni* was investigated by Ovenden (2007) who used five nuclear microsatellite markers and a 700 bp segment of the mitochondrial control region to assess 119 individuals from three sites (Western Australia, Northern Territory and Queensland). The study found no evidence of population genetic structure in either the nuclear or mitochondrial markers between any of the three study locations, and it was concluded that the species comprises a single stock.

Given the localised population genetic structuring of *Carcharhinus limbatus*, it has been hypothesised that *Carcharhinus tilstoni* arose from an isolated group of *C. limbatus* (Ovenden 2007; Naylor *et al.* 2012), and although the species are capable of hybridisation, the different life history traits (size at birth, size at maturity and maximum size) serve largely as reproductively isolating mechanisms (Harry *et al.* 2012)..

Sandbar Shark, *Carcharhinus plumbeus*

The sandbar shark, *Carcharhinus plumbeus*, is a benthopelagic coastal species with a global distribution, occurring in both tropical and temperate inshore waters (Compagno 1984), including northern and Western Australia, the north-west Pacific, east and south-west Africa, north and south Atlantic, and the Mediterranean (Compagno *et al.* 2005). The species is born at 52 to 75 cm TL, matures at 130 cm to 185 cm TL and reaches a maximum size of 240 cm TL (Last and Stevens 2009) (Table 2).

Portnoy *et al.* (2010) investigated genetic connectivity for *C. plumbeus* around the globe. They analysed fragment length polymorphism in eight nuclear microsatellite markers and the complete sequence of the mitochondrial control region in 335 individuals collected from distinct regions in the species' global range including Western Australia, Queensland, Taiwan, Hawaii, south-east Africa and the north-west Atlantic. Their analysis revealed extensive genetic structure on a global basis and found evidence of male-biased dispersal. Specifically, the allele frequencies for nuclear microsatellite markers did not vary significantly between Western Australia, Queensland, Taiwan or South Africa, but the mitochondrial sequence analysis was significantly different between each of those locations. Consequently, they concluded that gene flow between these regions is male mediated and females may exhibit philopatry (Portnoy *et al.* 2010). Their analysis is based on a broad scale sampling regime, and only included single sites in Western Australia, Queensland, Taiwan and Hawaii in the IWP. Consequently, questions about the population genetic structure of this species over medium and fine spatial scales remain unanswered.

Portnoy *et al.* (2010) also found the greatest population genetic structure, both from microsatellite loci and mitochondrial DNA, between Atlantic and non-Atlantic sites. Naylor *et al.* (2012) have suggested that the Atlantic and Indo-Pacific clades of *C. plumbeus* actually represent separate species.

Spottail Shark, *Carcharhinus sorrah*

The spottail shark, *Carcharhinus sorrah*, is a coastal pelagic species across the IWP (Last and Stevens 2009). The species is born at 45 cm to 60 cm TL (Compagno *et al.* 2005), matures at 90 cm to 95 cm TL in Australian waters (Last and Stevens 2009) and up to 118 cm TL elsewhere (Compagno *et al.* 2005), and attains a maximum size of 160 cm TL (Last and Stevens 2009) (Table 2).

Giles *et al.* (2014) investigated the population genetic structure of *C. sorrah* across most of its IWP range. They used sequence analysis of a 469 bp segment of the mitochondrial control region from 349 specimens from 21 sites. They found extensive population genetic subdivision throughout the sampled range, but because only mtDNA was analysed they were unable to conclude whether dispersal was philopatric or male biased. They did find significant genetic divergence over deep water

that divided continental shelves, particularly the Timor Passage and Coral Sea areas of the Indonesian Throughflow. Additionally, they found that the species can be divided into three geographic clades: Australia, New Caledonia, and south-east Asia-Indian Ocean. Each of these clades contained private haplotypes suggesting endemic lineages. They also found evidence of different size at maturity within Australia compared to elsewhere, giving support to Naylor *et al.*'s (2012) suggestion of a provisional new species for the Australian clade. Finally, Giles *et al.* (2014) determined that there was evidence of a historical barrier across the Torres Strait, a current open water barrier across the Timor Passage, but found no evidence of any barrier across the Sunda Shelf (Giles *et al.* 2014). The Timor Passage barrier was also confirmed by Ovenden *et al.* (2009), who used five nuclear microsatellite markers and a 1145 bp segment of mitochondrial control region to assess genetic divergence between Western Australia, the Gulf of Carpentaria, eastern Australia and Indonesia (north of the Timor Passage). This study showed evidence for distinct Indonesian and Australian clades. Each region had multiple unique haplotypes, with only one shared haplotype. Both the nuclear and mitochondrial markers demonstrated population genetic subdivision between all Australian sites and Indonesia. However, neither marker showed significant structure between the individual sites within Australia. Consequently, they concluded that Australia and Indonesia are genetically distinct stocks, but that there was no evidence of population genetic structure within Australian waters (Ovenden *et al.* 2009). Naylor *et al.* (2012) suggest that the barrier between Indonesia and Australia is not simply impeding gene flow but has led to speciation and that *C. sorrah* is actually a species complex. They have provisionally referred to the Australian cluster as *C. cf sorrah*. More recently, Almojil *et al.* (2018) found weak population structure along the coasts of the Arabian Peninsula, Pakistan and South Africa when analysing 15 nuclear microsatellite loci. However, Spaet *et al.* (2015) did not find structure between the Red Sea and Arabian Sea when assessing 9 nuclear microsatellite loci and 1120 bp of the mitochondrial control region.

Milk Shark, *Rhizoprionodon acutus*

The milk shark, *Rhizoprionodon acutus*, is a small benthic associated coastal species reaching a maximum size of 100 cm to 180 cm TL (Last and Stevens 2009). It is widely distributed along the African coasts and across the Indo-West Pacific. Pups are born in litters of up to eight, at 35 cm to 40 cm TL, reach maturity at two to three years and 75 cm TL, and have a maximum life span of eight years (Last and Stevens 2009) (Table 2). This comparatively short generation time is expected to make the milk shark more resilient to fishing pressure than other species of Carcharhinidae that have longer generation times (Ovenden *et al.* 2011).

Ovenden *et al.* (2011) studied the population genetic structure of the milk shark across its eastern Australian range, and Indonesia. Six nuclear microsatellite markers were analysed and compared to sequence divergence from an 873 bp segment of the mitochondrial NADH 4 gene. One hundred and ninety individuals from four sites along the Great Barrier Reef, and a further 17 individuals from a single Indonesian site (Bali), were analysed. The study found no evidence for population genetic structure along the east coast of Australia using either the nuclear or mitochondrial markers. However, both markers showed significant structure between eastern Australia and Indonesia. Ovenden *et al.* (2011) concluded that this was concordant with patterns seen for other benthic coastal species whose distributions cross known paleo-ecological barriers such as the Torres Strait. Naylor *et al.* (2002) suggest that *R. acutus* is actually a complex of four separate species (West coast of Africa; Gulf of Oman and India; Australia; and Borneo and the Philippines). Taking this into account, Ovenden *et al.* (2011) may have inadvertently included two species in their analysis and the deep-water barrier of the Torres Strait may have facilitated speciation rather than simply a reduction in gene flow. More recently, Spaet *et al.* (2015) found no genetic structure between the Red Sea and Arabian Sea when assessing 8 microsatellite loci and 1120 bp of mitochondrial control region.

Large-Bodied Coastal Species

We define large-bodied coastal species as those species reaching a maximum size of over 265 cm TL and being distributed over continental shelf waters. They may be pelagic or benthopelagic and are not restricted to a specific habitat type.

Silvertip Shark, *Carcharhinus albimarginatus*

The silvertip shark, *Carcharhinus albimarginatus*, is a large-bodied species distributed throughout the tropical Indo-Pacific region in association with continental shelf waters (Last and Stevens 2009). Six to eleven pups are born at 70 to 80 cm TL after a twelve-month gestation period, females mature at 170 cm TL and males at 195 cm TL, and the species attains a maximum length of 275 cm TL (Last and Stevens 2009) (Table 2).

In the only study of population genetic structure for silvertip sharks, Green *et al.* (2019) analysed data from 12 microsatellite loci in conjunction with a 994 bp section of the mitochondrial control region and 6461 nuclear SNPs. That study included samples from the Seychelles, Eastern Australia and Papua New Guinea. The authors concluded that there is gene flow for silvertip sharks between east Australia and Papua New Guinea, but not between that region and the Seychelles (Green *et al.* 2019).

Pig-eye Shark, *Carcharhinus amboinensis*

The pig-eye shark, *Carcharhinus amboinensis*, is a large pelagic shark common to coastal waters in tropical and subtropical IWP and eastern Atlantic (Last and Stevens 2009). The species grows to over 280 cm TL, matures at 210 cm to 215 cm TL and 13 years, and can live to over 30 years (Last and Stevens 2007; Tillett *et al.* 2011) (Table 2). Despite its large body size and potential for migration, no trans-oceanic movements have been recorded for the species (Tillett *et al.* 2012a).

Tillett *et al.* (2012a) investigated the genetic population structure of *Carcharhinus amboinensis* in waters of northern Australia by analysing five nuclear microsatellites, the nuclear RAG1 gene, and the mitochondrial control region and NADH 4 gene from 324 pig-eye sharks from five regions in northern Australia (Western Australian Kimberley coast, the Northern Territory, the Gulf of Carpentaria, north-east Queensland, and southern Queensland). Analysis of the nuclear markers

failed to reveal any population genetic structure, although the mitochondrial markers showed structure across the Torres Strait. Three main mitochondrial clades were revealed, but with differing frequencies east and west of Torres Strait. The authors concluded that this pattern of genetic diversity was due to repeated isolation events caused by glacial maxima closing Torres Strait, followed by subsequent pulses of gene flow when Torres Strait reopened (Tillett *et al.* 2012a). Naylor *et al.* (2012) found two distinct but geographically overlapping clusters of *C. amboinensis* (Western and northern Australia versus India, South Africa and northern Australia). Their analysis was based on only 10 samples in total, but the pairwise differences between clusters was sufficient for them to postulate the existence of two sympatric species of *C. amboinensis* in northern Australia.

Spinner Shark, *Carcharhinus brevipinna*

The spinner shark, *Carcharhinus brevipinna*, is found in tropical and warm temperate waters of the IWP, the Indian Ocean and the Atlantic (Last and Stevens 2009). It is a coastal demersal schooling species whose adults utilise nearshore habitats and juveniles use inshore areas as nursery habitats (White and Potter 2004). The species is born at 60 cm to 80 cm TL, mature at 190 cm to 200 cm TL and reaches a maximum size of 300 cm TL (Last and Stevens 2009) (Table 2).

The global population genetic structure of the species has never been studied in detail, however, Geraghty *et al.* (2013) studied connectivity in Australia and South Africa. An 857 bp segment of the mitochondrial NADH 4 gene was sequenced and compared for 430 individuals from four sites: the Northern Territory including the Gulf of Carpentaria, Queensland, New South Wales, and South Africa. No samples from Western Australia or elsewhere in the IWP were included. The results revealed a single dominant haplotype common to all sites, and significant genetic subdivision between South Africa and all Australian sites. They also showed evidence of weak genetic structure within Australia, with sharks from Queensland and the Northern Territory showing homogeneity, but both being divergent from those from New South Wales (Geraghty *et al.* 2013).

Bull Shark, *Carcharhinus leucas*

The bull shark, *Carcharhinus leucas*, is a large pelagic apex predator distributed throughout tropical and subtropical coastal waters of the world (Last and Steven 2009). The species is born at 55 cm to 80 cm TL (Last and Stevens 2009), matures at 9.5 years (Tillet *et al.* 2011) and 180 cm to 230 cm TL (Last and Stevens 2009), reaches a maximum size of between 312 cm TL (Tillett *et al.* 2011) and 320 cm TL (Last and Stevens 2009) and has a maximum longevity of over 27 years, and possibly as long as 50 years (Tillett *et al.* 2011) (Table 2). *Carcharhinus leucas* utilises estuaries and rivers as pupping sites and nursery areas and juveniles remain associated to nursery areas (Heupel and Simpfendorfer 2008). Adults are known to travel long distances (Martin 2005).

The longevity, size and potential for migration suggests that gene flow between regions for this species may be high (Tillett *et al.* 2011), however, the species has been shown to exhibit both population genetic structure and female philopatry. Karl *et al.* (2011) investigated population genetic structure of the species in the western Atlantic by analysing five nuclear microsatellite markers and two segments of the mitochondrial control region, totalling 800 bp, from 102 sharks from four sites (Brazil, east coast of Florida including Georgia and North Carolina, the west coast of Florida in the Gulf of Mexico, and the northern Gulf of Mexico). The microsatellites only revealed weak genetic structure between the Brazilian and Gulf of Mexico (Florida) sample sites, and not between any other sites. In contrast, the mitochondrial analysis showed significant genetic structure between all sites other than those located within the Gulf of Mexico. These contrasting results from the two genetic markers lead the authors to conclude that *C. leucas* was displaying female philopatry and has male-biased gene flow (Karl *et al.* 2011).

In a study focusing on *Carcharhinus leucas* in Australian waters, Tillett *et al.* (2012b) also found evidence of philopatry. They analysed three nuclear microsatellite markers, an 837 bp segment of the mitochondrial control region and a 4797 bp segment of the mitochondrial NADH 4 gene. These were analysed for 143 juvenile bull sharks sampled from rivers in seven regions in northern Australia. Their finding of no genetic structure in nuclear microsatellite markers combined with significant

structure in mitochondrial markers for these juvenile bull sharks from different regions lead them to conclude bull sharks show reproductive philopatry in northern Australia (Tillett *et al.* 2012b).

Naylor *et al.* (2012) found three separate clusters of *C. leucas* (Atlantic; South African; and Borneo). The pairwise differences between these clusters was sufficient for them to suggest that these clusters represented three different species of *C. leucas*. While individual genetic structure studies on this complex have only been conducted within regions, future studies would need to ensure that specimens are attributed to the correct species, particularly if they span multiple regions.

Dusky Shark, *Carcharhinus obscurus*

The dusky shark, *Carcharhinus obscurus*, is a large, slow growing coastal pelagic species that inhabits tropical, subtropical and temperate waters throughout the world (Compagno 1984; Last and Stevens 2009). They mature at approximately 280 cm TL and 20 years of age, producing litters of three to 14 pups every second or third year (Simpfendorfer 1999). Pups are born at 70 cm to 100 cm TL, and reach a maximum size of 365 cm TL (Last and Stevens 2009) (Table 2). Due to these extremely K-selected life history parameters, the species is particularly vulnerable to overfishing (Simpfendorfer *et al.* 2002).

Genetic connectivity for *C. obscurus* has been investigated by different researchers at global and regional levels. Ovenden *et al.* (2009) used four nuclear microsatellite loci and a 1145 bp segment of the mitochondrial control region to investigate genetic structure between Western Australia, Indonesia and eastern Australia. The nuclear microsatellite analysis in that study revealed no significant genetic structure between any of the three sites, however, the mitochondrial control region did show a significant divergence between Western Australia and Indonesia, suggesting that the Timor Trench may be acting as a barrier to gene flow. However, the sample sizes in this study were extremely small with only seven to 13 individuals sampled from each area (Ovenden *et al.* 2009). Consequently, the conclusion of genetic homogeneity between eastern and Western Australia but structure between Australia and Indonesia is only provisional.

Benavides *et al.* (2011) assessed the global population genetic structure of *C. obscurus* by analysing a 558 bp segment of the mitochondrial control region from 239 individuals from five global locations (eastern Australia, Western Australia, South Africa, Gulf of Mexico and the US Atlantic coast). Their study found genetic subdivision between sharks from three broad regions: Australia, Africa and the Atlantic US but no evidence of genetic subdivision between sharks from the US coast and the Gulf of Mexico, or between eastern and Western Australia (Benavides *et al.* 2011).

In contrast to the above studies, Geraghty *et al.* (2014) assessed an 857 bp segment of the mitochondrial NADH 4 gene from 423 individuals from four sites: New South Wales, Northern Territory, Western Australia, and Indonesia. That study revealed genetic differentiation between eastern and Western Australia, but not between the Northern Territory and either eastern or Western Australia. It also found evidence of structure between all Australian sites and Indonesia. A possible explanation for this is Isolation by Distance along the continental shelf waters of Australia. However, the authors also stipulate that the discovery of structure within Australia may be an artefact of the uneven sample sizes used in their study (New South Wales n = 301, Western Australia n = 57, Northern Territory n = 49, Indonesia n = 16), and they point out that sample sizes of 100 or more are required from each site in order to provide sufficient power to their analysis (Geraghty *et al.* 2014).

In a more recent study, Junge *et al.* (2019) analysed 8866 nuclear SNPs in *C. obscurus* samples from sites around Australia, Indonesia and South Africa. This study found no genetic differentiation between sites but was based on small sample sizes ranging from six to 28 samples per site.

The disparity between these findings may be explained by the fact that different genetic markers were employed in the three studies and that the number of samples per location in each study was often less than that required to adequately sample the full range of genetic diversity at each site (Geraghty *et al.* 2014). Regardless of this, however, the common finding across all these studies was that the species is not restricted to localised populations within Australia. This is confirmed by tagging studies that show the species is capable of broad scale movements within both the South African (Hussey *et*

al. 2009) and Australian regions (Rogers *et al.* 2013). Rogers *et al.* (2013) showed that dusky sharks in southern Australian waters routinely travel distances of over 2,000 km in a six-month period, suggesting an annual migration path along the Western Australian coast. This is supported by Hussey *et al.* (2009) who found a similar migration path along the eastern coast of South Africa. Based on the above studies, it is reasonable to conclude that *C. obscurus* forms single breeding stocks along contiguous stretches of continental shelf waters, but has little if any contemporary gene flow across open ocean basins.

Tiger Shark, *Galeocerdo cuvier*

The tiger shark, *Galeocerdo cuvier*, is a large apex predator distributed throughout the world's tropical and subtropical waters. It is primarily found in coastal areas, although often frequents waters offshore from continental shelves (Last and Stevens 2009). After a gestation of 12 to 16 months, litters of 30 or more pups are born at 50 to 80 cm TL. The species reaches sexual maturity at 300 cm TL and 7 to 8 years for males, and 330 cm TL and 7 to 12 years for females, and may reach a maximum size of up to 600 cm TL (last and Stevens 2009) (Table 2).

The species exhibits complex patterns of movement with individuals showing considerably differing behaviours. Individuals are known to have traversed ocean basins (Kohler *et al.* 1998) and recent satellite tracking has shown that males are capable of repeated long distance (> 7,500 km) annual migrations in the Atlantic (Lea *et al.* 2015). However other studies have shown that some individuals exhibit extended site fidelity while others do not (Heithaus *et al.* 2007). Such individual differences in movement combined with the observations that the species utilises both coastal and oceanic habitats make patterns of population genetic structure for this species difficult to predict.

In a study of the population genetic structure of tiger sharks, Bernard *et al.* (2016) analysed 10 nuclear microsatellite loci and a 1720 bp segment of mitochondrial DNA comprising the control region and the COI gene from 340 individuals from 10 locations across the species' global range. The authors concluded that there is genetic isolation between the western Atlantic and IWP but that isolation is

not of sufficient magnitude to warrant the two populations being regarded as separate species. They also concluded that within the Indo-Pacific region there is male-mediated gene flow as indicated by a lack of differentiation in nuclear DNA, and female philopatry indicated by differentiation in mitochondrial markers (Bernard *et al.* 2016).

More recently, Holmes *et al.* (2017) analysed nine nuclear microsatellite loci from samples throughout the Indo-Pacific and southern Atlantic. Using large sample sizes from many sites (Queensland n=69, New South Wales n=81, Western Australia n=56, Northern Territory n=62) they found a lack of differentiation between sites in the Indo-Pacific, but genetic structure between the Indo-Pacific and Atlantic populations, confirming that this species is wide ranging across ocean basins.

The findings of Bernard *et al.* (2016) and Holmes *et al.* (2017) both support the suggestion from Naylor *et al.* (2012) that the Atlantic and Indo-Pacific populations of *G. cuvier* are genetically distinct. However, Naylor *et al.* (2012) did not find the pairwise differences between those ocean basins great enough to warrant attributing them to separate species.

Sicklefin Lemon Shark, *Negaprion acutidens*

There are two species of lemon shark. The amphi-Atlantic lemon shark, *Negaprion brevirostris*, which occurs along tropical and subtropical coasts of the eastern Pacific and western Atlantic on either side of the Americas, and also on the coast of west Africa. The sicklefin lemon shark, *N. acutidens*, occupies a similar habitat along tropical and subtropical coasts of the IWP. The species are believed to have diverged some ten to 14 million years ago at the time of the Tethys Sea closure (Schultz *et al.* 2008). Both are large-bodied benthopelagic species. *Negaprion acutidens* is born at 50 cm to 70 cm TL, matures at 220 cm TL and can attain 300 cm TL (Last and Stevens 2009) (Table 2).

Schultz *et al.* (2008) provide data on nuclear microsatellite allele frequencies and sequence divergences in a 1090 bp segment of the mitochondrial control region from 58 individuals of the sicklefin lemon shark from five sites in the IWP. Samples from two of the locations (Taiwan and

New Caledonia) had five or less individuals and were omitted from the analysis of population genetic structure. The mitochondrial control region sequence analysis revealed no significant population genetic structure among the remaining sites (eastern Australia, Western Australia and French Polynesia). Similarly, the microsatellite loci showed no significant differentiation between eastern or Western Australia, but did show significant structure between those two sites and French Polynesia. Consequently, no evidence of female philopatry, or an Indo-Pacific barrier to gene flow, was found, and it was concluded that the species disperses widely along stretches of coastal habitat (Schultz *et al.* 2008).

Oceanic Species

We define oceanic species as those species that are predominantly found mid ocean, away from continental shelf waters and not in association with a specific habitat type.

Silky Shark, *Carcharhinus falciformis*

The silky shark, *Carcharhinus falciformis*, is a common epipelagic shark found in tropical and subtropical waters around the world (Last and Stevens 2009). The species is born at 70 cm to 85 cm TL, matures at 200cm to 210 cm TL and reaches a maximum size of 330 cm TL. Size at birth and maturity may, however, be smaller in Indonesian waters (55 cm TL and 180 cm TL respectively) (Last and Stevens 2009) (Table 2).

Galvan-Tirado *et al.* (2013) assessed the global population genetic structure of this species by assessing a 732 bp segment of the mitochondrial control region of 353 individuals from 22 sites. Those sites were grouped into three broad regions: western Pacific (Indonesia and New Caledonia); eastern Pacific (sites along the west coast of central and south America); and oceanic (sites from the eastern equatorial Pacific Ocean). They found weak but significant structure between the east and west Pacific, but no evidence of structure within the western Pacific sites between Indonesia and New Caledonia, even though those sites are on opposite sides of both the Indonesian Throughflow (Timor

Passage) and the Torres Strait (Galvan-Tirado *et al.* 2013). The lack of differentiation found in the western Pacific may be due to the low sample sizes in that region (Indonesia n = 37; New Caledonia n = 8). In addition, no significant population genetic structure was found between sites in the eastern Pacific. This pattern of divergence lead to the conclusion that there has been a population expansion of silky shark from the western Pacific to the eastern Pacific (Galvan-Tirado *et al.* 2013).

Clarke *et al.* (2015) analysed the entire 1063 to 1069 bp mitochondrial control region of 276 silky sharks from six widely separated regional areas covering the majority of the species' range. Two distinct clades were identified (western Atlantic and IWP). The western Atlantic samples (Brazil, Gulf of Mexico and northern Atlantic) showed no significant population genetic structure. However, all Indo-Pacific samples were significantly differentiated (Clarke *et al.* 2015). The contrasting results in the IWP between these two studies is likely to be a function of smaller sample sizes employed by Galvan-Tirado *et al.* (2013), and the larger mtDNA fragment size analysed by Clarke *et al.* (2015).

More recently, Domingues *et al.* (2018b) assessed variation in a 707 bp segment of the mitochondrial control region of 211 silky sharks from five locations across the north-west and south-west Atlantic. That study found significant population structure between the five locations and also determined that the Indo-Pacific assemblages of silky shark diverged from the western Atlantic assemblages during the Pleistocene.

Oceanic Whitetip Shark, *Carcharhinus longimanus*

The oceanic whitetip, *Carcharhinus longimanus*, is a large-bodied predator distributed across the world's tropical and subtropical oceans, most commonly found in water above 20° C. It is an oceanic, epipelagic species whose abundance increases away from continental shelves and inshore waters (Bonfil *et al.* 2008). Pups are born at 55 cm to 75 cm TL after a nine to twelve-month gestation in litters averaging 6.2 pups (Seki *et al.* 1998). Maturity is reached between 170 cm and 195 cm TL at four to seven years, and a maximum size of 245 cm to 325 cm TL is attained at around 17 years of age (Bonfil *et al.* 2008; Last and Stevens 2009) (Table 2).

Camargo *et al.* (2016) investigated the population genetic structure of *C. longimanus* using a 724 bp segment of the mitochondrial control region from 215 individuals from eight locations across the western Atlantic, eastern Atlantic and Indian oceans. A total of 12 mitochondrial haplotypes were identified, two of which were present in all regions, however, evidence of restricted gene flow between the east and west Atlantic was found. Sample sizes from the Indian Ocean were too small to be meaningfully interpreted, and no samples were analysed from the Pacific (Camargo *et al.* 2016).

Blue Shark, *Prionace glauca*

The blue shark, *Prionace glauca*, is an oceanic epipelagic shark with a global distribution in warm tropical, subtropical and temperate waters (Compagno *et al.* 2005; Last and Stevens 2009). Pups are born at 35 cm to 50 cm TL, mature at 220 cm TL and are capable of reaching a maximum size of over 380 cm TL and age of 20 to 26 years (Skomal and Natanson 2003; Last and Stevens 2009) (Table 2).

Given its wide distribution, the species is expected to exhibit broad genetic homogeneity within regions (Skomal and Natanson 2003). This was confirmed in an investigation into the genetic population structure of *P. glauca* in the IWP region by Ovenden *et al.* (2009), where no evidence of genetic subdivision was identified. The results were based on the analysis of five nuclear microsatellite markers and the mitochondrial control region (1145 bp) from 60 individuals from 4 locations (Western Australia, eastern Australia, Indonesia and the mid-north Pacific). This finding of genetic homogeneity is consistent with tagging studies showing that the species is capable of travelling vast distances including traversing ocean basins (Kohler *et al.* 2002). It has been confirmed by more recent studies. King *et al.* (2015) found no evidence of genetic structure between individuals from ten north Pacific sites when comparing allele ratios from 14 nuclear microsatellite loci. Taguchi *et al.* (2015) found no evidence of variation in haplotype frequencies in mitochondrial cytochrome-b sequences in individuals from 10 IWP sites. Bailleul *et al.* (2017) concluded genetic homogeneity between Mediterranean, North Atlantic and Pacific samples based on an analysis of nine nuclear microsatellite markers and mitochondrial cytochrome-b sequences, and Verissimo *et al.* (2017) also

found genetic homogeneity between juveniles from the North and South Atlantic when analysing 12 nuclear microsatellites and mitochondrial control regions fragments.

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