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research paper

Extensive genetic population structure in the Indo–West Pacific spot-tail shark, *Carcharhinus sorrah*

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ABSTRACT.—*Carcharhinus sorrah* (Mülle and Henle, 1839) is a coastal pelagic shark of the tropical and subtropical Indo–West Pacific, reaching 1.6 m total length. The species is widely harvested in line, net, and trawl fisheries over tropical continental shelves. We investigated mtDNA genetic differentiation in *C. sorrah* across the majority of the species' range, and examined the importance of six major historical and contemporary biogeographic features in shaping population genetic structure in this species. The present study includes dense sampling for a shark species across the Indo–West Pacific, with 349 specimens sampled from 21 collection locations from the northwestern Indian Ocean, Southeast Asia, New Caledonia, and to southerly distribution limits in Australia. Based on 469 base pairs of the control region, we found extensive genetic population structure, with allopatric lineages confined to Australia, New Caledonia, and the remaining surveyed area. Significant genetic subdivisions were observed over stretches of deep water dividing shelf habitat, particularly the Indonesian Throughflow–Timor Passage and Coral Sea, consistent with strong shelf habitat associated dispersal. Male length at maturity was consistent with a larger size throughout Southeast Asia and the Arabian Sea than known from Australia. *Carcharhinus sorrah* currently is assessed range-wide on the IUCN Red List (Near Threatened) based largely on Australian demographic data, which may under-represent overharvest risk in other parts of the species' range. The present study highlights the need for independent risk assessment and management for *C. sorrah* in Australia, Southeast Asia and the northwestern Indian Ocean, and New Caledonia.

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Unlike most marine invertebrates and teleost fishes, chondrichthyan fishes (sharks, rays, and chimaeras) lack a planktonic larval stage, so that realized dispersal is driven primarily by adult vagility and habitat use. Documented patterns of mtDNA population genetic structure in sharks have ranged from almost global panmixia in oceanic species (e.g., Hoelzel et al. 2006, Castro et al. 2007) to large-scale structuring within regions separated by continents and oceanic expanses for predominantly coastal pelagic/benthopelagic species (e.g., Duncan et al. 2006, Schultz et al. 2008, Portnoy et al. 2010, Benavides et al. 2011, Daly-Engel et al. 2012), and to more localized population structure in less vagile demersal species and small benthopelagic species (e.g., Stow et al. 2006, Ahonen et al. 2009, Chabot and Allen 2009, Naylor et al. 2012). In addition to these general expectations of population structure based on vagility (generally associated with size, Musick 2004) and broad habitat preference, total habitat use including reproductive behavior and episodic migration is an important determinant of realized dispersal in sharks. For example, repeated use of specific nursery areas for parturition (reproductive philopatry) has been observed in a number of vagile live-bearing shark species, leading to spatial population structure, in many cases sex-biased (e.g., Keeney and Heist 2006, Portnoy et al. 2010, Karl et al. 2011, Blower et al. 2012, Tillett et al. 2012b). Substantial genetic population structure has also been observed over narrow deep channels in large-bodied demersal species (e.g., Gaida 1997, Dudgeon et al. 2009), and low differentiation has been observed over long distances in a small-bodied demersal reef shark (Whitney et al. 2012).

The relative influence of seascape features on dispersal can be investigated by comparing genetic connectivity over a range of biogeographic sites that may be, or have been, a barrier to gene flow. Land barriers such as the Isthmus of Panama and the Old World Barrier (i.e., separation between the eastern Atlantic and the Indo–West Pacific) are total barriers to gene exchange among ocean basins for tropical chondrichthyans, whereas the effects of selective or partial barriers to dispersal such as the East Pacific Barrier and the Southeast Asian archipelagos are less resolved (Briggs 1999, Rocha et al. 2007, reviewed in Dudgeon et al. 2012). Southeast Asia's complex network of islands forms an array of partial and historically intermittent biogeographic barriers dividing the tropical Indian and West Pacific oceans (Fig. 1), and is a global center of species richness in marine taxa, including chondrichthyans (Fowler et al. 2005). The wide variety of intraspecific phylogeographic patterns that have been described for marine species across this area indicate that a range of processes are involved (e.g., reviewed in Gaither and Rocha 2013, Carpenter et al. 2011). Chondrichthyan studies to date have included few sampling points within these megadiverse archipelagos (a notable exception being Naylor et al. 2012), limiting evaluation of the relative impact of specific historical and contemporary barriers to dispersal. Seascape features of particular interest that may impede, or have impeded, dispersal include; the deep trenches associated with the Indonesian Throughflow current, the Coral Sea (the oceanic expanse separating the Australian east coast from the western Pacific islands), the northwestern Indian Ocean (the oceanic expanse separating Southeast Asia and the Middle East, with contiguous continental shelf), and the major Pleistocene land bridges (Sunda Shelf and Torres Strait) (Fig. 1).

The Indonesian Throughflow is a major feature of the tropical central Indo-Pacific seascape, transporting water from the Pacific Ocean to the Indian Ocean through a network of islands as part of the global thermohaline circulation pathway (Gordon 1986). This current exits via the Indonesian Archipelago through major adjacent

outlets at the Timor Passage (separating Timor/Rote and the Australian shelf) and the Ombai Strait (separating Alor and Timor), and a minor outlet at the Lombok Strait (separating Bali and Lombok), and is associated with deep trenches dividing shelf habitat (Fig. 1). A shared genetic discontinuity has been observed over the Indonesian Throughflow (Timor Passage) in *Carcharhinus sorrah* (Mülle and Henle, 1839), described in Ovenden et al. (2009), smaller more demersally oriented *Rhizoprionodon acutus* (Rüppell, 1837), described in Ovenden et al. (2011), and demersal *Stegostoma fasciatum* (Hermann, 1793) (Makassar Strait), described in Dudgeon et al. (2009). No discontinuity was evident in the larger more mobile coastal pelagic species *Sphyrna lewini* (Griffith and Smith, 1834) and *Carcharhinus obscurus* (Lesueur, 1818) or oceanic *Prionace glauca* (Linnaeus, 1758) (Ovenden et al. 2009). This seascape feature coincides broadly with a site of division between Australian and Southeast Asian bioregions, each with distinct chondrichthyan faunas with high species endemism (Briggs 1999, Last and Stevens 2009, Last and White 2011), and over which multiple cases of cryptic lineage diversification have been observed (e.g., Naylor et al. 2012).

As well as a diverse fauna, Southeast Asia has high chondrichthyan harvest in artisanal and industrial fisheries as both target and bycatch, particularly in inshore habitats (Bonfil 2002, Fowler et al. 2002, 2005). Most of this harvest is currently not well described and subject to minimal enforceable species-specific management, and likely exceeds sustainable levels for many species in these waters (White and Kyne 2010, Lam and Sadovy 2011). Understanding range-wide connectivity of stocks is essential to devising management strategies for species distributed over multiple international borders in this region (Ovenden 2013).

The present study investigates population structure in *C. sorrah*, a coastal pelagic shark of the tropical and subtropical Indo–West Pacific region (Last and Stevens 2009), reaching approximately 1.6 m total length (closer to 1.3 m in Australia, Harry et al. 2013). The species occurs predominantly in midwater or near the surface on continental and insular shelves over coral reefs and muddy bottoms to at least 140 m depth (Compagno 1984), to 80 m in Australia (Last and Stevens 2009), and has also been observed to intermittently occupy shallow inshore habitat (Simpfendorfer and Milward 1993, Knip et al. 2012).

The species is a common catch component of line, net, and trawl (particularly longline and gillnet) fisheries in tropical parts of its range, and is utilized for fins, flesh, cartilage, and other minor products. *Carcharhinus sorrah* specimens are often confused in the field with other sympatric congeners with conspicuous black fin tips, particularly *Carcharhinus brevipinna* (Mülle and Henle, 1839), *Carcharhinus limbatus* (Mülle and Henle, 1839), *Carcharhinus tilstoni* (Whitley, 1950), *Carcharhinus amblyrhynchoides* (Whitley, 1934), *Carcharhinus melanopterus* (Quoy and Gaimard, 1824), and potentially *Carcharhinus leiodon* (Garrick, 1985) (recently resurrected in Moore et al. 2011), and the rare *Carcharhinus hemiodon* (Mülle and Henle, 1839). Superficial similarity among *Carcharhinus* species is a continued obstacle to assessing the scale and characteristics of harvest for this species and the entire genus (e.g., Boomer et al. 2010, Tillett et al. 2012a).

Extensive capture surveys and commercial fishery data from northern Australia indicate that *C. sorrah* occupy inshore and offshore habitat across the continental shelf, with a much higher catch per unit effort (CPUE) in inshore shelf habitat compared to further offshore (Lyle 1987, Salini et al. 2006). While caught over the inner and outer shelf at a range of sizes, a catch-and-release study in these waters found

that the median size of tagged *C. sorrah* was significantly larger offshore (>35 km) (Stevens et al. 2000). Stevens et al. (2000) also found that although the species is capable of moving long distances, with individuals recaptured up to 1116 km away, almost half of the study specimens were recaptured within 50 km of their tagging site. Most recaptures were made within 3 yrs, with a maximum of 9.9 yrs; however, there was no correlation between time at liberty and distance traveled.

A number of previous studies have provided evidence that indicate likely demographic discontinuity between northern Australian and central/eastern Indonesian *C. sorrah*, despite their geographic proximity. A genetic study found evidence for genetic discontinuity based on the mtDNA control region and five microsatellite loci (Ovenden et al. 2009). A second study based on mtDNA ND2 sequences (Naylor et al. 2012) found substantial genetic divergence between Timor Sea/Gulf of Carpentaria specimens (n = 4) and those from Borneo, the South China Sea, Thailand, and India (n = 45). This mtDNA divergence was supported by phenotypic differentiation, and, as the type locality of *C. sorrah* is Java, Indonesia (Eschmeyer, Catalog of Fishes), a provisional new species *C.* cf *sorrah* was proposed for the northern Australian specimens (Naylor et al. 2012). Further evidence of differentiation was provided by two studies of fisheries landing compositions in Indonesia (Java, Bali, Lombok, Sumatra), which found male size at maturity to be larger than that previously recorded in Australia (White 2007, Fahmi and Sumadhiharga 2007). Across northern Australia, genetic studies of *C. sorrah* have suggested a single fishery stock (Lavery and Shaklee 1989, Ovenden et al. 2009). Studies to date have given an insight into differentiation in the species across a number of locations; however, no single study has yet investigated the extent of genetic variation across the species' range.

Carcharhinus sorrah is one of the most common species in coastal shark fisheries in tropical northern Australia (e.g., Stevens and Wiley 1986), and is commonly captured in western Southeast Asia and the northwestern Indian Ocean (e.g., Stevens and Wiley 1986, Vidthayanon 2002, Fahmi and Sumadhiharga 2007, White 2007, Akhilesh et al. 2011, Moore et al. 2012a). In northern Australian waters, the incidence of this species in target and bycatch fisheries is well described and *C. sorrah* is of low overharvest concern (Salini et al. 2006). Range wide, *C. sorrah* is classified as "Near Threatened" on the IUCN Red List (close to meeting the criteria for Vulnerable A2bd+A3bd; Pillans 2009), based overwhelmingly on Australian biological data. Recent findings suggesting that Australian *C. sorrah* may be demographically unique highlight the need for range-wide data on stock structure and genetic diversity.

The present study represents the most extensive survey of population genetic diversity in *C. sorrah* to date, including 349 specimens sampled from 21 collection locations from New Caledonia to Africa, sequenced for 469 base pairs of the mtDNA control region. In addition, morphological measures that indicate male reproductive maturity were collected from Southeast Asia and the Arabian Sea to compare with published data for Indonesia and Australia. The present study: (1) describes range-wide patterns of diversification in *C. sorrah* and explores the geographic extent of previously observed patterns in genetic structure, (2) assesses the relative importance of six Indo–West Pacific marine biogeographic features in influencing population structure in this species, (3) identifies key demographic units relevant to management, and (4) provides a baseline for the identification of *C. sorrah* fins, fillets, and other harvested and traded products that originate from geographically distinct lineages.

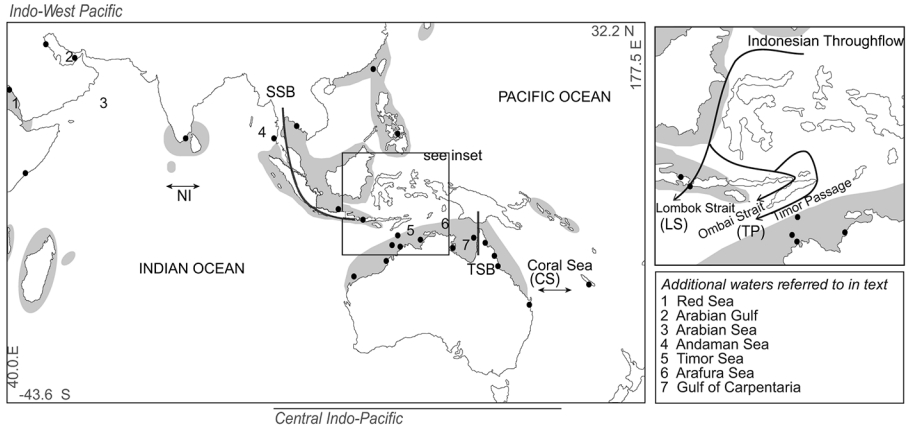

Figure 1. Indo–West Pacific collection sites of *Carcharhinus sorrah* specimens, with recorded species distribution (shaded) after Last and Stevens (2009, western range extends further west on African coast than depicted). A-priori biogeographic barriers considered in this study: historical Sunda Shelf Barrier and Torres Strait Barrier (SSB, TSB); the contemporary Indonesian throughflow (ITF) (inset), including the major outlet at the Timor Passage/Ombai Strait (TP) and minor outlet at the Lombok Strait (LS); the Coral Sea (CS); and the contiguous continental shelf across the Northern Indian Ocean (NI), between sites in the Andaman Sea, Thailand and Arabian Gulf.

Methods

Study Area, Site Selection, and Tissue Sample Collection.—Muscle or skin tissue samples were taken from fisheries specimens throughout the distribution of *C. sorrah* in the tropical and subtropical Indo–West Pacific, from the Red Sea to Taiwan, the west coast of Australia approximately to Carnarvon, and east coast of Australia to Moreton Bay, and New Caledonia (Fig. 1, Table 1).

Sites were selected to span the biogeographic features of interest. The historical Sunda Shelf Barrier (SSB) lies along the contemporary Isthmus of Kra, Thailand, separating the Gulf of Thailand and the East Andaman Sea. The historical Torres Strait Barrier (TSB) extends north of the current tip of Cape York Peninsula, Australia, separating the Arafura and Timor Seas from the northern Coral Sea (Fig. 1). The Sunda Shelf Barrier was estimated to have persisted as a land bridge for 54% of the past 250,000 yrs in six events at ≤40 m below present level (BPL), and the Torres Strait Barrier for 91% of past 250,000 yrs in three events at ≤10 m BPL (reviewed in Voris 2000). The contemporary Indonesian Throughflow (ITF) separates sites either side of the major outlet zone encompassing the Timor Passage and adjacent Ombai Strait (TP: estimated at 83% of combined outlet flow, approximately 160 and 35 km wide respectively, and each over 2000 m deep in parts), and either side of the minor outlet, the Lombok Strait (LS: estimated at 17% of outlet flow, at approximately 350 m deep and approximately 38 km wide; Gordon et al. 2010, Rosenfield et al. 2010).

Samples from Kuwait, Thailand, Taiwan, Philippines, and Indonesia were collected from whole sharks landed by artisanal or commercial fishing fleets using net or line gear (Table 1). Specimens were identified as *C. sorrah* by their morphology and photographed for verification. Sex was recorded and total length (L_T) taken with the caudal fin in a natural position. Specimens were sourced primarily from local inshore operations at landing sites where fleets operate within a somewhat restricted

Table 1. Sample collection locations and associated sample sizes, collection particulars and metrics of genetic diversity for 349 individuals. Geographic coordinates represent midpoints among sampling sites for landing sites (LS), and midpoints among individual captures for vessel captures (VC). Average per site pairwise nucleotide diversity/ population mutation rate $\theta(\pi)$ and standard deviations given, and Tajima's D (none significant at $P < 0.002$ after Bonferroni adjustment). EA = Eastern Australia, NA = Northern Australia, WA = Western Australia.

Collection location	Sample site type	Lat	Long	No. specimens	No. haplotypes	$\theta(\pi)$ (SD)	Tajima's D
South Queensland (EA)	VC	−26.97	153.25	10	6	0.26 (0.20)	0.55
Central Queensland (EA)	VC	−18.97	146.60	11	4	0.30 (0.23)	0.14
North Queensland (EA)	VC	−16.64	145.86	30	8	0.28 (0.20)	−0.35
Far North Queensland (EA)	VC	−14.16	143.87	22	6	0.31 (0.22)	−1.13
East Gulf of Carpentaria (NA)	VC	−12.60	141.74	26	7	0.26 (0.19)	−1.54
West Gulf of Carpentaria (NA)	VC	−14.46	136.48	20	5	0.19 (0.15)	−1.82
West, Inner Sahul Shelf (NA)	VC	−13.45	129.88	21	7	0.24 (0.18)	−1.04
West, Outer Sahul Shelf (NA)	VC	−11.90	124.56	9	3	0.10 (0.11)	−1.36
North, Inner Rowly Shelf (WA)	VC	−15.27	124.07	14	7	0.60 (0.29)	−1.29
North, Outer Rowley Shelf (WA)	VC	−14.76	123.20	5	3	0.38 (0.31)	1.57
Central (WA)	VC	−17.95	121.87	22	7	0.33 (0.23)	−1.00
South (WA)	VC	−21.57	114.35	14	6	0.35 (0.25)	−1.60
New Caledonia	LS	−22.29	166.42	10	3	0.12 (0.12)	−0.69
Visayas, Philippines	LS	10.28	123.89	5	3	0.26 (0.23)	−1.05
PengHu Islands, Taiwan	LS	23.56	119.57	7	1	—	—
Lombok, Indonesia	LS	−8.79	116.53	40	7	0.22 (0.17)	−0.32
Java and Bali, Indonesia	LS	−6.39	111.01	20	7	0.18 (0.15)	−1.20
Gulf of Thailand	LS	12.92	100.85	10	4	0.12 (0.12)	−0.69
East Andaman Sea, Thailand	LS	9.02	98.24	21	7	0.27 (0.20)	−0.76
Kerala, India	LS	9.93	76.20	1	1	—	—
Arabian Gulf	LS	26.65	50.86	21	5	0.17 (0.14)	−1.30
Red Sea	LS	21.48	39.13	9	2	0.10 (0.11)	−1.36
Kenya	LS	−3.33	40.36	1	1	—	—

distance (approximately <300 km). To ensure that the origins of specimens were represented by their landing sites, approximate fishing grounds were assessed for each vessel contributing specimens by interview, trip length, observation of fishing gear used and catch composition. Further, specimens within each collection location were collected from multiple fishing events, typically at multiple nearby landing sites. Coordinates given for each collection location represent geographic midpoints between these landing sites. Care was taken in the field to avoid inclusion of specimens suspected to have been caught at a distant location or possibly from the other side of a focal biogeographical feature. These efforts were taken to recognize and overcome the potential limitations of using landing site specimens from mobile fleets to test geographically explicit theories about vagile sharks in a complex seascape.

Samples from Kenya, Qatar, United Arab Emirates, Saudi Arabia, New Caledonia, and India originated from market and landing site surveys and research captures (Table 1). Samples from Australia originated from fishery observer programs and research captures: coordinates for collection locations represent geographic midpoints among capture sites (Table 1).

DNA Sequencing and Alignment.—DNA was extracted using a Chelex protocol (Walsh et al. 1991) with 200 µl Chelex 100 (20%) and 5 µl Proteinase K (20mg/

ml). DNA was amplified from the 5′ end of the mitochondrial control region using the forward primer GwF 5′-CTGCCCTTGGCTCCCAAAGC-3′ (Pardini et al. 2001) and 470R2 5′-GCCATTAAAGGGAACTAGRGGA-3′ designed in Primer3 (Rozen and Skaletsky 2000, Salini et al. 2007). Amplifications were conducted in 25 µl volumes containing; 10× Taq buffer, 1mM dNTPs, 5 pmol of each primer, 0.25 units of Taq (Clontech), 40–120 ng of template DNA. Thermocycler conditions consisted of an initial denaturation of 95 °C for 1 min, 35 cycles of denaturation at 95 °C for 30 s, followed by a combined annealing and extension at 63 °C for 1 min, and a final extension at 68 °C for 3 min. Amplicons were purified with Exonuclease I and Antarctic Phosphatase (New England Biolabs) at 1 unit μl^{-1} of template. Purified amplicons were either prepared in-house and sequenced on an ABI 3130 Genetic Analyzer, or outsourced to Macrogen, Korea. Sequence data were aligned and ambiguities inspected by eye in CodonCodeAligner 3.7.11. Unique haplotypes were identified in Arlequin 3.5.

Haplotype Network.—To display relationships among haplotypes, statistical parsimony networks were estimated for this locus using TCS 1.21 (Clement et al. 2000) with a 95% connection limit. Gaps were treated as missing rather than a 5th state and a single nucleotide deletion recoded as an Adenine-Thymine base pair to reduce overweighting. Reticulations were retained in the network to avoid interpretive bias caused by their exclusion (Posada and Crandall 2001).

Genetic Diversity.—Genetic variation was described for each collection location by the number of haplotypes (h), average per site pairwise nucleotide diversity estimated as $\theta(\pi)$ (Tajima 1983). Tajima's D (Tajima 1989) was estimated to test whether variation in each sampled population was consistent with expectations under a neutral mutation hypothesis. Significance was tested using one-tailed P-values with Bonferroni correction, with critical value $P < 0.002$ (Rice 1989). All tests were performed in Arlequin 3.5 (Excoffier et al. 2005) for sampling sites with at least five specimens.

General Spatial Patterns of Differentiation.—Genetic differentiation was assessed based on mtDNA sequence data using analysis of molecular variance (AMOVA) under the Tamura and Nei (1993) substitution model, implemented in Arlequin 3.5 (Excoffier et al. 2005). This analysis partitions the total genetic variation into that which is found among designated regions (Φ_{CT}), among designated populations (Φ_{ST}), and among populations within regions (Φ_{SC}). Φ-statistics take evolutionary distance among haplotypes into consideration (Excoffier et al. 1992), but are otherwise analogous to conventional allele frequency-based F-statistics (Wright 1951). An initial matrix of pairwise Φ-statistics was calculated among all sites with at least five specimens. Kenya and India were each represented by a single specimen, and as such were included in the haplotype network, but excluded for population analyses. To test for sex-biased differences, a subset of males and females were run separately for seven populations in the data set.

We tested for isolation by distance relationship using Rousset's (1997) transformation of Φ_{ST} and the log of overwater distances among sites (calculated in ArcGIS 9), and assessed the significance of the linear relationship by permutation (Mantel test). In addition, we used multiple regression on distance matrices (Legendre et al. 1994) to determine whether any of the hypothesized geographic barriers provided

additional population structure independent from geographic distance. Forward model selection was used to evaluate each of the a priori barriers described previously, using the model selection criteria in Legendre et al. (1994) which are appropriate for regressions based on distance matrices. The significance of linear relationships was evaluated by permutation using the lmPerm package (Wheeler 2010) of R (R Core Development Team 2008) in RStudio version 0.96.331. Given the sharp genetic discontinuity over the short distance between western Australia and Indonesia, isolation by distance was tested among Australian specimens by Mantel test with 10,000 permutations in Arlequin 3.11.

Hypothesis Testing of A Priori Barriers.—We examined six a priori hypothesized biogeographic barriers across the collection area; the historical Sunda Shelf Barrier (SSB), historical Torres Strait (TSB), the Indonesian Throughflow at its major outlet site at the Timor Passage/Ombai Strait (TP) and minor outlet site at the Lombok Strait (LS), the oceanic expanse of the Coral Sea (CS), and the oceanic expanse of the northwestern Indian Ocean with continental shelf continuity (NI). Each barrier was hypothesized as representing either a total or partial barrier to dispersal that occurred historically or is ongoing (Fig. 1). To infer genetic differentiation over the six barriers, pairwise Φ_{ST} values were first compared between the two nearest populations spanning each barrier (where $n \geq 10$).

These six barriers were further arranged into five temporal scenarios hypothesized to co-occur at current or previous sea levels (Table 2). Each scenario includes the different dispersal barriers that would have existed at three different sea levels, <10 m BPL, <40 m BPL, and present day, as detailed in Table 2. The relative impact of each scenario on the observed genetic structure was tested using AMOVAs that divided populations into regions defined by the relevant barriers (10,100 permutations). To assess which division of populations best explained the observed data, a spatial analysis of molecular variance was implemented in SAMOVA 1.0 (Dupanloup et al. 2002). SAMOVA uses a simulated annealing procedure, which selects arrangements that maximize the proportion of genetic variation among groups of populations (Φ_{CT} values) for a user-specified number (K), thereby identifying sites of genetic "barriers" (Dupanloup et al. 2002). SAMOVA analyses were performed for 2–7 groups, for 100 simulated annealing processes with 1000 permutations of populations among groups (Table 2).

Coalescent Estimation of Migration.—To investigate directions and relative magnitude and timing of gene flow over each biogeographic feature, sequence data were applied to the coalescent Isolation with Migration model, implemented in IMa2 2.0 (Hey 2010) following the methodology in Hey and Nielsen (2007). Mutation scaled migration rate (model parameter *m*) and divergence times (model parameter *t*) were estimated for each nearest population pair spanning the a priori barriers of interest. In each case, a null model of no gene flow was tested against an alternate model of gene flow. Although coalescent estimators are ideally suited to datasets consisting of multiple loci, use of single-locus data can be informative if the limitations are recognized (Hey and Nielsen 2004, Kronforst et al. 2006, Manolopoulou and Emerson 2012). The Hasegawa, Kishino and Yano (HKY) mutation model (Hasegawa et al. 1985) was used as the best fit to our data. Reasonable priors for model population parameters *m*, *t*, and θ were empirically obtained based on preliminary runs, maximum prior values were $m = 10$, $t = 10$, and $\theta = 40$. To assess whether the observed sample

Table 2. (A) AMOVA results for 6 a-priori biogeographical scenarios for combinations of a-priori barriers which divided populations into 4–7 groups; NI (northwestern Indian Ocean), SSB (Sunda Shelf Barrier), LS (Lombok Strait), TP (Timor Passage/Ombai Strait), TS (Torres Strait), and CS (Coral Sea). All values were significant for 10,100 permutations at a significance level of $P = 0.05$. (B) Resulting scenarios for 2–7 groupings of sampling subpopulations selected by SAMOVA, each for 100 simulated annealing processes with 1000 permutations of populations among groups. The scenarios with the best fit to the data by each method are (A) Scenario D (AMOVA) and (B) K = 4 (SAMOVA), which both correspond to the same set of barriers.

(A) AMOVA	NI	SSB	LS	TP	TS	CS	Proposed biogeographic scenario	Groups	Φ_{ST}	P	Φ_{SC}	P	Φ_{CT}	P
Scenario A	Y	Y	.	Y	Y	Y	Sea level ≤ 40 m BPL	6	0.775	<0.0001	0.021	0.06941	0.770	<0.0001
Scenario B	Y	.	.	Y	Y	Y	Sea level ≤ 10 m BPL	5	0.781	<0.0001	0.019	0.07861	0.777	<0.0001
Scenario C	Y	.	Y	Y	.	Y	Contemporary sea level including Lombok Strait	5	0.772	<0.0001	−0.005	0.66851	0.773	<0.0001
Scenario D	Y	.	.	Y	.	Y	Contemporary sea level excluding Lombok Strait	4	0.820	<0.0001	0.057	0.0001	0.809	<0.0001
Scenario E	Y	Y	Y	Y	Y	Y	All barriers	7	0.768	<0.0001	−0.010	0.73208	0.770	<0.0001
(B) SAMOVA	NI	SSB	LS	TP	TS	CS	Additional observed discontinuities	Groups	Φ_{ST}	P	Φ_{SC}	P	Φ_{CT}	P
K = 2	.	.	.	Y	.	.		2	0.827	<0.0001	0.360	<0.001	0.730	<0.0001
K = 3	.	.	.	Y	.	Y		3	0.827	<0.0001	0.179	<0.001	0.790	<0.0001
K = 4	Y	.	.	Y	.	Y	Matches Scenario D	4	0.818	<0.0001	0.057	<0.001	0.807	<0.0001
K = 5	Y			Y	.	Y	Arabian Gulf and Red Sea	5	0.817	<0.0001	0.062	<0.001	0.804	<0.0001
K = 6	Y	.	.	Y	.	Y	Arabian Gulf and Red Sea, Philippines and SEA	6	0.814	<0.0001	0.063	<0.001	0.802	<0.0001
K = 7	Y	.	.	Y	.	Y	Arabian Gulf and Red Sea, Philippines and SEA, Rowley Shelf and Australia	7	0.810	<0.0001	0.056	<0.001	0.799	<0.0001

distributions could be expected to be a reasonable estimate of the true posterior probability, initial simulations were undertaken to ensure that effective sample size (ESS) values and within-run variability were indicative of sufficient chain mixing (as per program documentation), and among-run variability was compared. Analyses entailed four metropolis-coupled chains, for 100 million total steps (100,000 data collection steps), after a burn-in of 1 million steps. Posterior probabilities were reported for population migration (i.e., Nm) rates for each population pair of interest, indicating the rate at which the genes of a given population 0 are supplanted by incoming migrating genes from population 1 (i.e., N_0M_{0-1}). To determine significance of observed posterior probability curves for model parameters, log-likelihood tests were performed to test whether the peak was significantly greater than probability at zero. Model parameters were not converted to actual divergence times and migration rates per generation, as our dataset consisted of a short mtDNA gene region, and a large degree of error can arise in inference from inaccurate estimates (Burridge et al. 2008, Henn et al. 2009).

Simulations of gene flow between New Caledonia and eastern Australia were not included because haplotypes for this single locus dataset indicated fixed differences supporting reciprocal monophyly. Such data are not suitable for the Isolation with Migration model as there is insufficient information to resolve a number of model parameters (Hey and Nielsen 2004).

Biological Parameters.—To investigate concordance of male size at reproductive maturity with those reported from Indonesia and Australia, total length (L_T), outer clasper length (L_C), and clasper calcification were recorded in males (as a proxy for male reproductive maturity after Bass 1973) in Southeast Asian specimens. Male size at maturity was represented by the length at which 50% of males had calcified claspers (L_{T50}) in each of the compared studies (Stevens and Wiley 1986, White 2007, Harry et al. 2013). For the Arabian Gulf, all specimens taken for the genetic study were immature. Therefore to also compare this region, additional data were later sourced from Bahrain, Yemen, the United Arab Emirates, and Oman.

Results

Haplotype network.—Sequence data were obtained for 469 base pairs of the control region for 349 *C. sorrah* specimens. Thirty-nine haplotypes were identified across the study region (GenBank Accession Numbers KF819736–KF819774). Observed haplotypes were almost exclusively associated with three distinct geographic regions: Australia, New Caledonia and Southeast Asia/northwestern Indian Ocean (Fig. 2A). All specimens in New Caledonia had private haplotypes not recorded elsewhere in the study. Almost all specimens from Australia similarly had haplotypes restricted to that region, with the exception of six specimens from northern and western Australia, which had either of two haplotypes otherwise geographically restricted in this study to the Middle East and Southeast Asia.

Genetic Diversity.—One to eight haplotypes were recorded at each sampling location (median = 6), and Taiwan specimens all shared a single haplotype (n = 7), (Table 1). There were 26 (5.5%) variable positions, of which 15 (3.2%) were parsimony informative. Percentage nucleotide diversity was low and did not differ markedly across the study area [0.10% (SD 0.11) to 0.60% (SD 0.29); Table 1], with a maximum

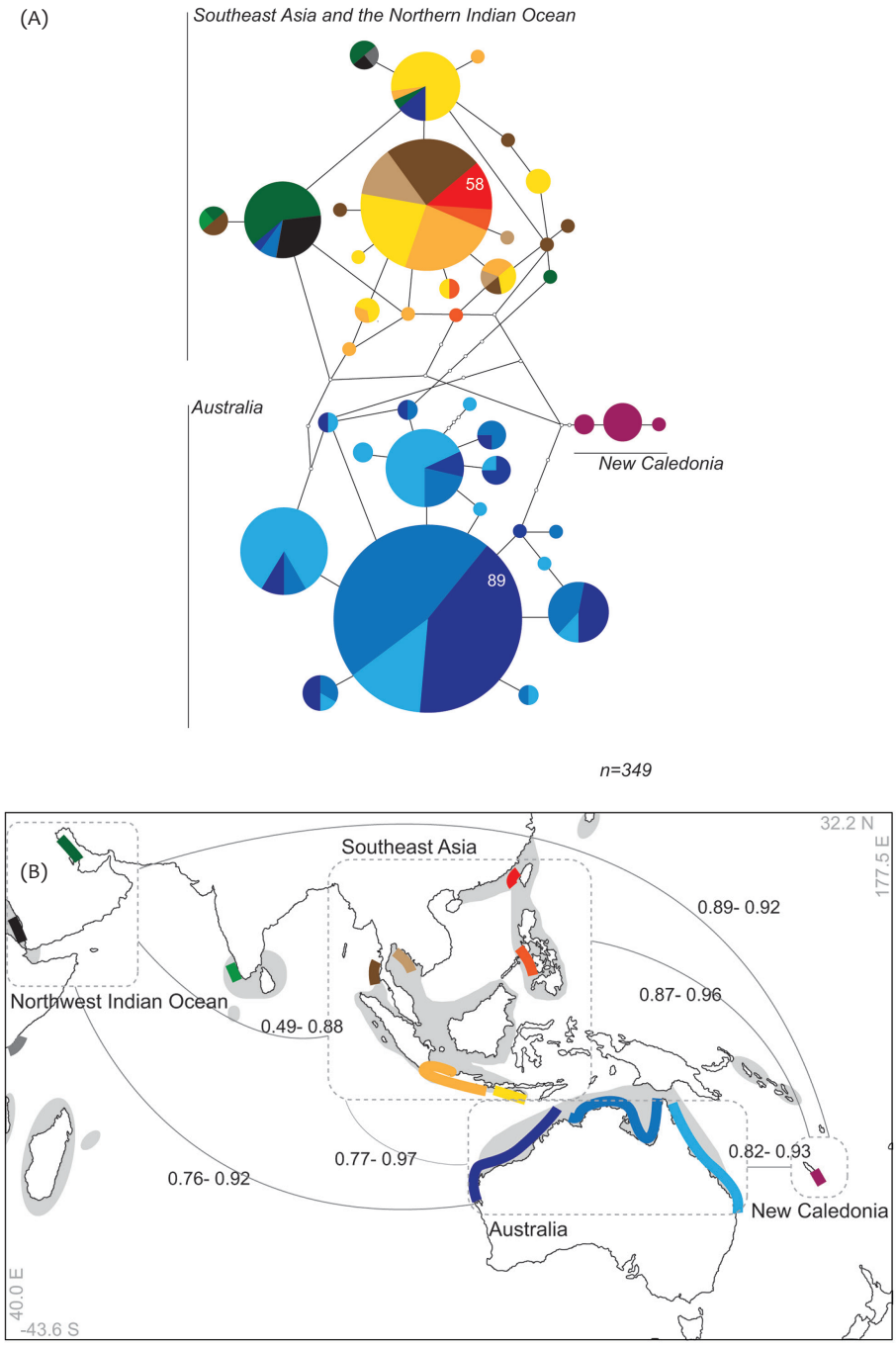

Figure 2. (A) Haplotype parsimony network for *Carcharhinus sorrah* (*n* = 349), color coded by geographical locations (given in 2B). Representative sample sizes given in white for the two most common haplotypes (89, 58). (B) Collection regions (including multiple adjacent sites) colored to show spatial distribution of haplotypes (in the haplotype network in A). *Carcharhinus sorrah* distribution shaded gray following Last and Stevens (2009). Value ranges given between geographic regions are minimum and maximum pairwise Φ_{ST} among all population pairs in each of those regions (AMOVA, Tamura and Nei 1993; Appendix 1).

sequence divergence of 2.8%. Tajima's *D* values did not signify significant deviation from expectations under neutral equilibrium conditions.

General Spatial Patterns of Differentiation.—Extensive genetic structure was evident among populations spanning the study region (global Φ_{ST} = 0.73, P < 0.0001). Across all sites, 119 out of 210 population pairs (56.7%) showed statistically significant genetic differentiation after strict Bonferroni adjustment (significance level of P = 0.0002; mean Φ_{ST} = 0.70, median = 0.82; Appendix 1). Significant pairwise Φ_{ST} values are summarized for the four regions found to explain the most variation in this study by SAMOVA and AMOVA (Fig. 2B).

Populations within Australia exhibited low, but significant, genetic structure (Φ_{ST} = 0.05, P = 0.002). New Caledonian specimens comprised three haplotypes, each connected by a single mutation (Fig. 2A). Southeast Asian specimens were largely represented by a single common haplotype, sampled in all sites of that region. Northwestern Indian Ocean haplotypes were closely related to those of Southeast Asia, with some shared haplotypes, and some interspersion of unique haplotypes in the network (Φ_{ST} = 0.38, P < 0.0001).

Overwater distance was a significant predictor of pairwise Φ_{ST} values (R^2 = 0.262, P < 0.0001). The Timor Passage/Ombai Strait and Coral Sea were the only tested features that were significant independent factors beyond overwater distance as evaluated by multiple regression on distance matrices (Legendre et al. 1994); the final best-fitting linear model included overwater distance, the Timor Passage/Ombai Strait and the Coral Sea, and explained 74% of the variance in Φ_{ST} values (R^2 = 0.741, P < 0.0001; Fig. 3). Among Australian populations, there was support for an isolation by distance model based on overwater distances (r = 0.27, P = 0.044). Tested male and female subsets of populations yielded Φ_{ST} values with the exact same pattern of significance.

Hypothesis Testing of A Priori Barriers.—For population pairs spanning the six a priori barriers, there was very strong genetic partitioning across the Coral Sea (Φ_{ST} = 0.89, P < 0.0001) and Timor Passage/Ombai Strait (Φ_{ST} = 0.80, P < 0.0001), strong partitioning between the Arabian Gulf and East Andaman Sea (Φ_{ST} = 0.51, P = 0.0001), and comparatively weaker partitioning across the Lombok Strait (Φ_{ST} = 0.13, P = 0.002), and Torres Strait (Φ_{ST} = 0.10, P = 0.004) (the latter two not significant after Bonferroni correction). No significant partitioning was evident across the historical Sunda Shelf Barrier (Φ_{ST} = 0.02639, P = 0.24334; Table 3, Appendix 1).

For all a priori biogeographic scenarios, a large degree of variation in the data set was explained by each region-level subdivision (Table 2). The SAMOVA scenario that explained the most among-region differentiation (Φ_{CT} = 0.80) with least within-group differentiation (Φ_{SC} = 0.06) in the dataset matched a priori biogeographic Scenario D (Φ_{CT} = 0.81, P < 0.0001). That is, SAMOVA analyses defined the best fit to this dataset (for any of the two to seven groupings) as that scenario in which populations were divided into four groups: the northwestern Indian Ocean, Southeast Asia, Australia, and New Caledonia (Table 2). This matched hypothesized biogeographic Scenario D, which explained the most variation of all the scenarios tested by AMOVA. However, in both AMOVA and SAMOVA analyses, the best-fit scenario was only a slightly better fit to the data than a number of comparable alternative scenarios.

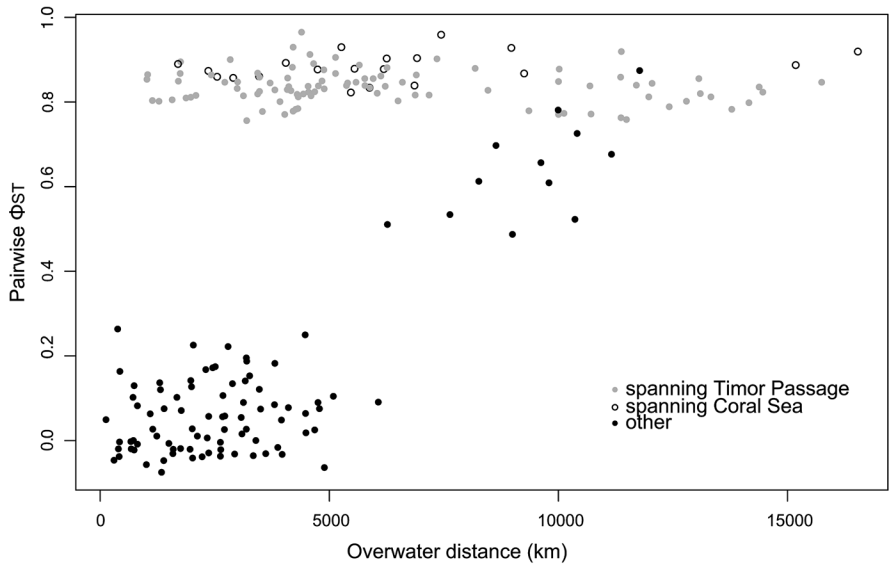

Figure 3. Plot of the relationship between pairwise Φ_{ST} values among sampling locations and overwater distance, with those spanning the Timor Passage/Ombai Strait (gray circles) and Coral Sea (open circles) highlighted. These three variables explained 74% of the variance among values ($R^2 = 0.741$, $P < 0.0001$).

Coalescent Estimation of Migration.—IMa2 analyses estimated that the greatest probabilities of non-zero gene flow among tested pairs were westward across the historical Sunda Shelf Barrier, and approximately symmetrical (although zero migration could not be statistically rejected) across the Torres Strait and Lombok Strait (Fig. 4, Table 3). All other estimates of migration rate tested had confidence intervals that included 0, and log-likelihood tests did not reject a null model of zero gene flow (Table 3, Fig. 4). Significance tests supported a hypothesis of historical isolation of *C. sorrah* over the Timor Passage, northwestern Indian Ocean and Torres Strait (Fig. 4, Table 3). Conversely, no significant historical divergence was indicated over the Sunda Shelf Barrier or Lombok Strait (Fig. 4, Table 3).

Biological Parameters.—Total length and clasper lengths from male *C. sorrah* specimens from Australia and Indonesia for which length and clasper data were available were consistent with findings from previous studies (Stevens and Wiley 1986, White 2007, Harry et al. 2013). In male specimens from other Southeast Asian sites, clasper length (L_C) to total length (L_T) relationships were consistent with a size at maturity as observed in Indonesia $L_{T50} = 1117$ (White 2007), rather than the considerably smaller size at maturity recorded for specimens in adjacent northern Australian waters $L_{T50} = 900$ (Stevens and Wiley 1986) or $L_{T50} = 929$ (Harry et al. 2013) (Fig. 5). The largest male and female specimens were 1382 and 1622 mm, respectively, both from the Indian Ocean, compared to 1310 and 1138 mm in Harry et al. (2013) from Australia, and 1235 and 1572 mm in White (2007) in Indonesia. All male Arabian Gulf and New Caledonian specimens with both genetic samples and morphological data were immature. Additional Arabian Sea maturity data for this species were more consistent with lengths at maturity in Southeast Asia than Australia (Fig. 5).

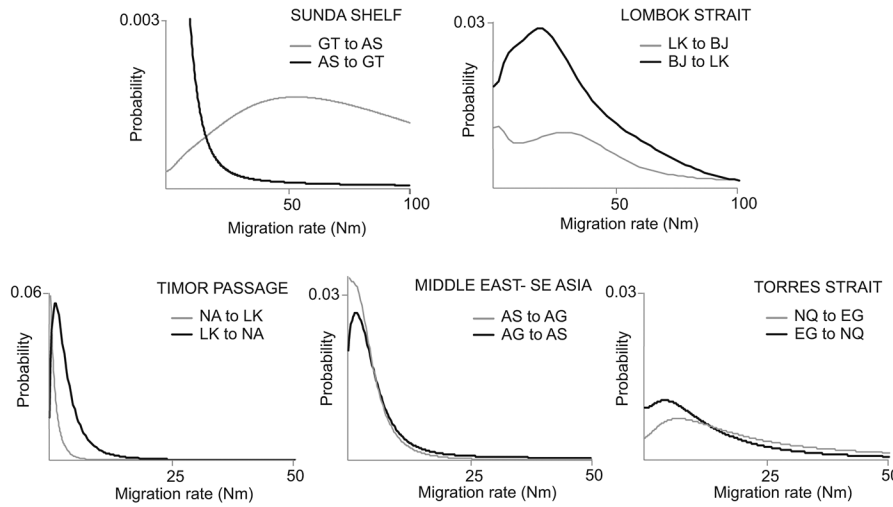

Figure 4. IMa2 posterior probability curves of population migration rates for the nearest population pairs spanning six a priori biogeographic barriers (black: eastward, gray: westward). Note x and y axes vary. GT = Gulf of Thailand, AS = Andaman Sea, Thailand, LK = Lombok, BJ = Bali/Java, NA = Northern Australia–Inner Rowley Shelf, AG = Arabian Gulf, NQ = Eastern Australia–North Queensland, EG = Northern Australia–East Gulf of Carpentaria.

The smallest male with fully calcified clasper encountered in Yemen, Oman, UAE, and Bahrain was 1090 mm (n = 65). Moore et al. (2012a) similarly recorded 1080 mm in Kuwait, Qatar, and Bahrain (n =7).

Discussion

In the present study, we described mtDNA genetic differentiation across the majority of *C. sorrah*'s range based on mtDNA sequence data, and tested the importance of several biogeographic features on the formation and maintenance of population genetic structure in this species. We found extensive population genetic structure, including divergent private haplotypes in Australia and New Caledonia suggestive of allopatric endemic lineages. Although *C. sorrah* is known to be a relatively vagile species using the upper water column across the continental shelf, we found that deep waters dividing contiguous continental shelf habitat were strong predictors for mtDNA genetic population structure. Isolation by distance patterns were observed along expanses of continental shelf. Morphological data for male Southeast Asian and Arabian Sea specimens were consistent with a larger size at male maturity than in Australia, providing supporting evidence for demographic differentiation between these lineages. Finally, specimens recorded in this study extend the recognized distribution of this species (according to Carpenter and Niem 1998, Compagno 1984, Last and Stevens 2009) to the southeast (New Caledonia), the northwest (Arabian Gulf, concurring with Moore et al. 2012a), and to Coolangatta in Southeast Queensland (concurring with S Taylor unpubl data). In the following sections, we discuss our detailed findings of genetic structure over the biogeographic features of interest, consider observed genetic differentiation in the context of habitat use in this species, and consider the range-wide management implications of our findings.

Table 3. Genetic differentiation (Φ_{ST}), and Isolation with Migration (IMa2) simulation maximum likelihood (ML) estimates of directional migration rates and divergence time between the most proximal pairs of sampling populations ($n \geq 10$) spanning each of the six a priori barriers. Φ_{ST} values significant at $P < 0.05$, with non-significant values marked as NS. IMa2 maximum likelihood estimates are given in relative per-locus units from model output, not converted to demographic migration rates or temporal units. Confidence intervals are given as 95% Highest Posterior Densities (HPD). Directions in notation for population migration rates (e.g., Nm 1 > 2) are given forward in time: i.e., here, the rate at which population 2 receives migrants from population 1. Compass directions are given backward in time, ie indicating whether gene flow has been eastward or westward over time. For coalescent model parameters, significant P values from log-likelihood tests indicated by * for $P > 0.0001$ and ** for $P < 0.0001$. NA = Northern Australia, EA = Eastern Australia.

								Coalescent ML estimates (HPD)		
A-priori barrier spanned	Population 1 (West)	Population 2 (East)	n1	n2	Overwater distance (km)	Φ_{ST}	P	East–West (Nm 1 > 2)	West–East (Nm 2 > 1)	Divergence time
Sunda Shelf	East Andaman Sea, Thailand	Gulf of Thailand	21	10	2,713.5	0.026	0.0260^{NS}	53.27 (4.5–157.8)*	0.10 (0.0–23.5)	4.61 [0.4–9.9]
Lombok Strait	Java and Bali, Indonesia	Lombok, Indonesia	20	40	744.4	0.130	0.0020	3.00 (0.0–1,122.0)	18.99 (0.0–716.6)	0.30 [0.0–9.9]
Timor Passage	Lombok, Indonesia	Inner Rowly Shelf (NA)	40	14	1,142.4	0.804	<0.0001	0.04 (0.0–2.9)	1.10 (0.0–9.9)	3.79 [1.3–9.9]**
Torres Strait	East Gulf of Carpentaria (NA)	North Queensland (EA)	26	22	715.3	0.101	0.0040	4.30 (0.0–108.0)	7.10 (0.0–111.6)	0.62 [0.2–9.9]*
Northwestern Indian Ocean	Arabian Gulf	East Andaman Sea, Thailand	21	21	6,272.4	0.511	<0.0001	0.10 (0.0–13.5)	1.70 (0.0–24.7)	0.94 [0.5–9.9]*
Coral Sea	South Queensland (EA)	New Caledonia	10	10	1,696.1	0.890	<0.0001	—	—	—

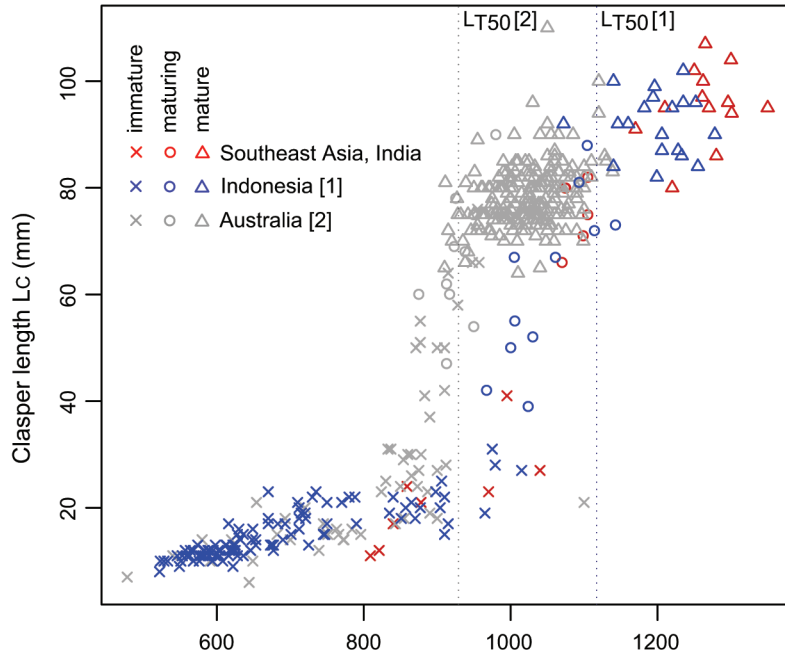

Figure 5. Clasper length (L_C) and total length (L_T) relationships in male *Carcharhinus sorrah*, categorised by non-calcified claspers (immature), partially calcified claspers (maturing) and fully calcified claspers (mature) for specimens from Southeast Asia (this study, shown in red), Indonesia ([1] White 2007, shown in blue), and Australia ([2] Harry et al. 2013, shown in gray). Published size at maturity (L_{T50}) reported for Australia (Harry et al. 2013) and Indonesia (White 2007) are indicated with vertical lines. Male specimens from Southeast Asian sites were consistent with the larger size at maturity (L_{T50}) observed in Indonesia.

Biogeographic Features and Patterns of Gene Flow.—The overall pattern of differentiation was best explained by isolation by distance in combination with major discontinuities associated with the Indonesian Throughflow (TP: Timor Passage/ Ombai Strait), and the Coral Sea (CS: nearest population pairs $\Phi_{ST} = 0.89$, $P < 0.0001$). These variables explained 74% of the variance in pairwise Φ_{ST} values by multiple regression on distance matrices, which allows independent estimation of genetic disjunctions from the effect of geographic distance (Fig. 5).

Hierarchical methods of genetic partitioning (AMOVA and SAMOVA) identified disjunctions that were basically congruent with the multiple regression based on distance matrices, in that the best fitting biogeographical scenario in both cases described these two seascape features (TP and CS) and the northern Indian Ocean continental shelf (NI) (i.e., TP + CS + NI , $\Phi_{CT} = 0.81$; Table 2, Fig. 2B). However, this best fitting biogeographic scenario yielded a Φ_{CT} value only marginally higher than other tested biogeographic scenarios (Table 2), demonstrating the high degree of structure in the dataset (Fig. 2B). There was no significant gene flow detected across either the Timor Passage or northwestern Indian Ocean by IMa2 analyses, and historical isolation was evident (Table 3, Fig. 3). The major biogeographic features of interest are discussed here in detail with reference to other studies.

Indonesian Throughflow.—In the present study, we examined differentiation across the two trenches at the main outlets of the Indonesian Throughflow current, the major outlet zone at the Timor Passage/Ombai Strait (TP: approximately 160 and 35 km wide respectively, and each over 2000 m in parts), and the minor outlet at the Lombok Strait (LS: approximately 38 km wide and 350 m deep). Estimating the effects of these putative barriers by using sampling sites positioned west of the Lombok Strait (Bali/Java), between the two trenches (Lombok), and southeast of the Timor Passage (outer edge of the Australian shelf; Fig. 1), we found strong genetic divergence over the Timor Passage zone as discussed above ($\Phi_{ST} = 0.80$, $P < 0.0001$), and only minor divergence spanning the Lombok Strait ($\Phi_{ST} = 0.13$, $P = 0.002$) (Table 3, Fig. 3). For the Lombok Strait, IMa2 posterior probabilities suggested low-level bidirectional contemporary gene flow, but a null model of no gene flow could not be rejected. The Lombok Strait was the only site with significantly differentiated Φ_{ST} from other populations within Southeast Asia, suggesting limited migration across the Strait.

These results suggest that the Timor Passage/Ombai Strait trenches and adjacent deep waters are a sufficiently large and deep seascape feature to act as an ongoing, but permeable, barrier to adult dispersal in *C. sorrah*. These results are consistent with those findings of Ovenden et al. (2009), which describe a genetic break between northern Australia and Lombok/Java in *C. sorrah,* and those of Naylor et al. (2012), which describe a break between northern Australia and Indonesia (Kalimantan). Despite this strong observed mtDNA divergence, six specimens from northern Australia did not group with the other 198 Australian specimens.

These six specimens, caught in the Timor and Arafura Seas and the Gulf of Carpentaria, displayed two haplotypes otherwise observed only in Southeast Asia and the northwestern Indian Ocean (Fig. 2A). A similar result was observed in Ovenden et al. (2009), and may suggest low abundance dispersal across the Timor Passage, with these specimens noted in Australian waters either themselves migrants or descendants of migrants. Limited evidence for gene flow suggests that if individuals are dispersing across this zone, they may not be interbreeding. In Indonesia, *C. sorrah* is thought to extend as far east as Sumbawa, Sumba and western Flores, where shelf habitat becomes very limited (White et al. 2006). These islands are divided from the Australian shelf by the band of deep water extending north along the Timor Passage. However, if *C. sorrah* is present further east in Indonesian waters, the route between the Tanimbar Islands and Arafura Sea may constitute less of a barrier to movement in this species. Further research would be needed to test these hypotheses.

Northwestern Indian Ocean.—Populations spanning contiguous northern Indian Ocean shelf habitat between Thailand and the Arabian Gulf showed substantial differentiation ($\Phi_{ST} = 0.51$, $P = 0.0001$). Haplotypes in this region were closely related but largely unique among locations, although one haplotype was shared widely (Thailand, Arabian Gulf, India; Fig. 2A). Some specimens from the Middle East had unique haplotypes that were more closely related to haplotypes sampled only in Southeast Asia (Fig. 2A). Although *C. sorrah*'s presence is patchy west of Southeast Asia in published species distributions, fishery landings data suggest that this species' distribution is relatively continuous right along the northern Indian Ocean coastline to the African Coast. Moving west from Thailand toward the Arabian Gulf, the species is recorded in fishery landings data from Myanmar (Anon 2011), the Andaman

and Nicobar Islands (Rajan et al. 2012) and Bangladesh (Hoq et al. 2011). Landings data from India suggest that this species is less commonly captured in Orissa and West Bengal (close to the Ganges river delta), but commonly captured from Andhra Pradesh in the east to Gujarat in the west (P Devadoss, Central Marine Fisheries Institute Kerala, unpubl data, Akhilesh et al. 2011). Captures have been recorded in Pakistan (Pillans 2009), Oman at the mouth of the Arabian Gulf (Henderson et al. 2007, Moore et al. 2012b), and beyond as discussed in the present study.

Although significant contemporary gene flow was detected from Southeast Asia west into the Indian Ocean, no significant gene flow was estimated in this study between Thailand's Andaman Coast and the Arabian Gulf (Fig. 3), although this could be expected over this long distance. Separation of haplotypes by only one or two mutations between Southeast Asia and the northwestern Indian Ocean despite some geographical restriction (Fig. 2A) may underestimate demographic separation of these regions given low-level migration along contiguous habitat.

Pleistocene Land Barriers.—Here we investigated two land barriers across this region during periods of decreased sea level in the Pleistocene epoch, the Sunda Shelf and Torres Strait. The Sunda Shelf Barrier has often been invoked to explain diversification between Indian and Pacific Ocean marine biotas (e.g., Rocha et al. 2007), although detailed sampling coverage throughout the Southeast Asian region has been insufficient to test alternative sites of diversification (Carpenter et al. 2011, Keyse et al. 2014). We detected no differentiation over the Sunda Shelf (Φ_{ST} = 0.03, P = 0.03), measured here between the Thai Andaman Sea and the Gulf of Thailand on opposing coasts of the now fragmented land barrier. Contemporary gene flow was indicated westward across the historical Sunda Shelf Barrier (Table 3, Fig. 3), indicating no lingering signature of historical vicariance. A significant but weak signal was detected across the Torres Strait, a secondary location of sea level change vicariance (Φ_{ST} = 0.101, P = 0.004), with IMa2 posterior probability peaks indicating low-level symmetrical gene flow that could not discount zero gene flow (Fig. 3). Divergence time, however, was significantly greater than zero (Table 3), possibly indicating a remnant pattern from Pleistocene vicariance over the Strait as seen in other marine species (Chenoweth et al. 1998, Mirams et al. 2011). Therefore, no obvious effect of the Sunda Shelf is evident in the contemporary *C. sorrah* mtDNA genealogy, but patterns are consistent with a historical division across the Torres Strait.

General Patterns of Differentiation and Correlation to Habitat Use.—Overall patterns of differentiation observed in our study are consistent with localized dispersal in *C. sorrah* along contiguous shelf habitat, with very limited evidence of dispersal over stretches of deep open water dividing shelf habitat. These findings corroborate catch and movement data from northern Australia indicating that although *C. sorrah* is common in midwater and near the surface across inshore and offshore continental shelf (Lyle 1987, Salini et al. 2006) and is capable of moving long distances, the species mainly moves alongshore in localized areas (Stevens et al. 2000). Very shallow inshore waters have been observed to be important for primary and secondary nursery habitat for both sexes (Simpfendorfer and Milward 1993, Knip et al. 2012). The degree of genetic subdivision observed is nevertheless surprising given the species' vagility and relatively short overwater distances between divergent lineages.

Although more research is required to determine whether this species exhibits sex-biased reproductive philopatry, there is not yet evidence that they do. A passive acoustic tracking study observed both male and female adults (950–1270 mm L_T) repeatedly visited a shallow Queensland bay over a three year period, spending between 8 and 408 (median = 183) total days in <5 m of water (Knip et al. 2012). Ovenden et al. (2009) observed the same patterns of genetic differentiation between Australia and Indonesia in both mtDNA and five microsatellite loci. Male maturity data here mirror the large-scale pattern of differentiation between Australia and Southeast Asia/the northwest Indian Ocean indicated by matrilineal mtDNA.

While these catch and movement studies give insight into the habitat use of *C. sorrah*, these observations are limited to specimens detected within pre-defined geographic possibilities (spatial extent of each fishery and internal distribution of fishing effort/position of acoustic receivers). Future studies could also investigate whether shallow offshore features such as the Sahul Banks on the outer Sahul Shelf may be important habitat for this species, and whether habitat use and behavior may differ in other parts of the distribution.

The genetic patterns observed in the present study share similarities with other studies of live-bearing coastally oriented pelagic sharks exhibiting dispersal along contiguous shelf habitat. Although there is a general relationship between size and vagility among coastally-oriented shark species and realized dispersal, existing examples also highlight the difficulty of generalization based on a few representatives of such a behaviorally and taxonomically diverse group of fishes. For example despite high shelf habitat preference in benthopelagic *Negaprion acutidens* (Rüppell, 1937), which reaches 3 m total length and is known to spend the majority of its time near the bottom, little genetic differentiation has been observed over deep zones of up to 800 km wide, indicating that stretches of deep water allow sufficient episodic dispersal to prevent genetic isolation of populations (Schultz et al. 2008).

Management Implications.—Our findings raise two important policy issues for managers across this species' range: (1) the possibility of cryptic speciation, or demographically distinct species, and (2) the presence of many separate stocks. Here, we have described a unique genetic lineage widespread in Australian waters to subtropical limits (n = 204), with negligible evidence of gene flow among neighboring lineages. Our phenotypic data from Southeast Asia and the northwestern Indian Ocean suggest that populations in these regions are consistent with male size at maturity previously observed in Indonesia (L_{T50} = 1117; White 2007), which is larger than those observed for Australian specimens (L_{T50} = 900; Davenport and Stevens 1988, Stevens and Mcloughlin 1991), and (L_{T50} = 929; Harry et al. 2013) (Fig. 5). The present study's genetic and phenotypic findings are concordant with the provisional designation of a new species *C.* cf *sorrah* in Australian waters as suggested by Naylor et al. (2012), but this requires detailed morphological confirmation. In White (2007), litter size and birthing season were also found to differ from those found in previous Australian studies.

Under the current species description of *C. sorrah*, our study implies that the surveyed range of the species is composed of separate stocks in Australia, the Southeast Asia/northern Indian Ocean region, and New Caledonia, between which migrants are very unlikely to make a substantive contribution to fisheries population sizes. We suggest that each of these regions should be subject to separate risk assessment

and management, with particular emphasis on the need to assess stocks outside Australia. Australian demographic data are likely to under-represent current overharvest risk for *C. sorrah* in Southeast Asia and the northern Indian Ocean given that a larger size at maturity increases intrinsic susceptibility to overexploitation (e.g., Garcia et al. 2008). The species is subject to very high levels of exploitation in this region, with negligible migration from populations in comparatively heavily-managed waters of northern Australia. Observations of very shallow inshore habitat use in this species at multiple life stages underscores the susceptibility of *C. sorrah* to overexploitation in densely populated coastal regions with active artisanal fishing sectors.

Further study is required to establish the spatial extent and morphological characteristics of *C. sorrah* at the eastern and western extremes of the species' range in the Western Pacific and off Africa. New Caledonia has a unique chondrichthyan fauna (Last and Seret 1999), and further study could resolve whether this lineage is unique or shared with other western Pacific islands where *C. sorrah* may occur. Previous data also suggest there may be morphological differentiation off Africa (Bass 1973).

This study further contributes baseline data for determining the likely geographic origins of *C. sorrah* fins in the international shark fin trade. In particular, *C. sorrah* fins and fillets originating from Australian stocks could in most cases be identified using this marker with a narrow margin of uncertainty. Assigning the geographic origin of fins in trade using mtDNA baselines is useful for testing research hypotheses about patterns of shark harvest and trade and in certain types of forensic casework (e.g., Chapman et al. 2009). Applying genetic identification techniques to routinely monitor the species composition of shark fins in international trade is a promising source of data for estimating corresponding levels of harvest in the absence of species-specific data from fisheries (Clarke et al. 2006a,b). Incorporating intraspecific data would allow such datasets to be made relevant to specific management jurisdictions.

In conclusion, the present study describes genetic variation in *C. sorrah* across the majority of the species' Indo–West Pacific range. Surveys included in the present study support a number of range extensions to the previously recorded distribution. We describe extensive population structure consistent with high shelf proclivity and dispersal along contiguous continental shelf, but not over stretches of deep water dividing shelf habitat. Given that movement studies to date do not suggest sex-biased reproductive philopatry, and that even limited episodic migration is sufficient to equalise signatures of mtDNA structuring, these findings are somewhat surprising given that *C. sorrah* contributes large numbers to pelagic fisheries over outer continental shelf habitat. Our data suggest that *C. sorrah* should be assessed independently for fisheries management and harvest risk assessment in Australia, Southeast Asia and the northwestern Indian Ocean, and New Caledonia. Genetic and phenotypic data presented here provide evidence for genetic and demographic separation over the Timor Passage, and support the provisional description of *C.* cf *sorrah* in Australian waters proposed by Naylor et al. (2012). Further investigation into the genetic composition, morphological characteristics, and distributional limits of stocks in the western and eastern extremes of *C. sorrah*'s range would increase resolution of management priorities and taxonomic status of this widely exploited shark species.

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Appendix 1. Analysis of molecular variance pairwise Φ_{ST} values among the 21 sites with 10+ individuals with no structure imposed, and *P*-values (significance level 0.0002 with Bonferroni adjustment). Significance indicated for 10,100 permutations, * is $P > 0.0001$, ** is $P < 0.0001$, NS is not significant at $P = 0.0002$. NA = Northern Australia, EA = Eastern Australia, WA = Western Australia.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Arabian Gulf	1		**	**	**	**	**	**	**	**	**	**	**	**	NS	**	**	**	**	**	**	**
East Andaman Sea, Thailand	2	0.51		NS	NS	NS	**	**	NS	**	**	**	**	**	**	NS	**	**	**	**	**	**
Gulf of Thailand	3	0.70	0.03		NS	NS	**	**	NS	*	**	**	**	**	**	NS	**	**	**	**	*	**
Java and Bali, Indonesia	4	0.61	0.01	0.00		NS	**	**	NS	**	**	**	**	**	**	NS	**	**	**	**	**	**
Lombok, Indonesia	5	0.49	0.06	0.19	0.13		**	**	NS	**	**	**	**	**	**	NS	**	**	**	**	**	**
West, Inner Sahul Shelf (NA)	6	0.84	0.84	0.88	0.86	0.85		NS	**	NS	NS	NS	NS	NS	**	**	**	NS	NS	NS	NS	NS
West Gulf of Carpentaria (NA)	7	0.84	0.84	0.89	0.87	0.85	0.01		**	NS	NS	NS	NS	NS	**	**	**	NS	NS	NS	NS	NS
Visayas, Philippines	8	0.61	−0.02	−0.03	−0.04	0.17	0.85	0.86		*	**	**	**	NS	NS	NS	*	**	*	NS	NS	NS
Central Queensland (EA)	9	0.82	0.82	0.86	0.85	0.84	0.06	0.14	0.82		NS	NS	NS	NS	**	*	**	NS	NS	NS	NS	NS
East Gulf of Carpentaria (NA)	10	0.81	0.82	0.86	0.84	0.83	−0.01	−0.02	0.83	0.08		NS	NS	NS	**	**	**	NS	NS	NS	NS	NS
Far North Queensland (EA)	11	0.79	0.80	0.84	0.83	0.82	0.13	0.14	0.80	0.00	0.10		NS	NS	**	**	**	NS	NS	NS	NS	NS
North Queensland (EA)	12	0.80	0.82	0.85	0.84	0.83	0.06	0.10	0.82	−0.05	0.06	0.00		NS	**	**	**	NS	NS	NS	NS	NS
South Queensland (EA)	13	0.84	0.83	0.88	0.86	0.85	0.05	0.15	0.83	−0.08	0.11	0.03	−0.03		*	*	*	NS	NS	NS	NS	NS
Red Sea	14	−0.06	0.53	0.78	0.66	0.52	0.84	0.86	0.68	0.82	0.81	0.78	0.80	0.85		**	**	**	**	**	*	**
PengHu Islands, Taiwan	15	0.73	0.02	0.03	−0.03	0.18	0.89	0.91	0.07	0.88	0.87	0.85	0.86	0.90	0.88		**	**	**	**	*	**
New Caledonia	16	0.89	0.87	0.93	0.90	0.88	0.88	0.89	0.90	0.87	0.86	0.86	0.86	0.89	0.92	0.96		**	**	**	*	**
Central (WA)	17	0.77	0.78	0.82	0.81	0.80	0.03	−0.03	0.78	0.09	−0.02	0.09	0.07	0.11	0.76	0.83	0.83		NS	NS	NS	NS
North, Inner Rowly Shelf (WA)	18	0.77	0.78	0.81	0.81	0.80	−0.02	−0.02	0.76	0.00	−0.04	0.06	0.02	0.03	0.76	0.82	0.82	−0.04		NS	NS	NS
South (WA)	19	0.78	0.78	0.82	0.82	0.81	0.01	−0.04	0.77	0.08	−0.03	0.08	0.06	0.09	0.77	0.84	0.84	−0.06	−0.04		NS	NS
North, Outer Rowley Shelf (WA)	20	0.85	0.83	0.88	0.87	0.85	0.08	0.23	0.82	0.12	0.17	0.22	0.14	0.09	0.86	0.91	0.88	0.16	0.05	0.12		NS
West, Outer Sahul Shelf (NA)	21	0.88	0.86	0.93	0.90	0.87	0.00	−0.02	0.90	0.20	−0.04	0.18	0.13	0.25	0.92	0.97	0.93	−0.01	0.01	−0.02	0.26	