1-1-2021

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Recommended Citation

Gray, Howard W.I.; Chen, Ing; Moura, André E.; Natoli, Ada; Nishida, Shin; Tanabe, Shinsuke; Minton, Gianna; Ponnampalam, Louisa S.; Kiani, Muhammad S.; Culloch, Ross; Gore, Mauvis; Särnblad, Anna; Amir, Omar; Berggren, Per; Collins, Tim; Willson, Andrew J.; Baldwin, Robert; and Hoelzel, A. Rus, "Comparative biogeography and the evolution of population structure for bottlenose and common dolphins in the Indian Ocean" (2021). *All Works*. 4200.
https://zuscholars.zu.ac.ae/works/4200

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Received: 18 March 2020 | Accepted: 23 January 2021
DOI: 10.1111/jbi.14102

Journal of Biogeography WILEY

RESEARCH ARTICLE

Comparative biogeography and the evolution of population structure for bottlenose and common dolphins in the Indian Ocean

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Funding information
All sources of funding are acknowledged in the acknowledgements section.

Handling Editor: Sergio Floeter

Abstract

Aim: In the marine environment, where there are few physical boundaries to gene flow, there is often nevertheless intraspecific diversity with consequences for effective conservation and management. Here, we compare two closely related dolphin species with a shared distribution in the Indian Ocean (IO) to better understand the biogeographic drivers of their population structure.

Location: Global oceans and seas with a focus on the Indian Ocean

Taxon: *Tursiops* sp. and *Delphinus* sp.

Methods: Bayesian, ordination, assignment, statistical and phylogenetic analyses to assess phylogeography, connectivity and population structure using microsatellite and mitochondrial DNA genetic markers.

Results: Both *Tursiops* sp. and *Delphinus* sp. showed population structure across the western IO and, in each case, populations in the Arabian Sea (off India, Pakistan and Oman) were most differentiated. Comparisons with other populations worldwide revealed independent lineages in this geographic region for both genera. For *T. aduncus*, (for which multiple sites within the IO could be compared), Bayesian modelling best supported a scenario of expansion southwards following a bottleneck event resulting in differentiation between the northern and western IO. For *Delphinus*, the same pattern is even more pronounced. Populations in the Arabian Sea region of the northwestern IO show genetic isolation for each of the two genera, consistent with other studies of cetacean species in this region.

Main conclusions: We propose that changes in the intensity of the southwest monsoon during the climate cycles of the Pleistocene could have affected regional patterns of productivity and represent an important biogeographic driver promoting the observed patterns of differentiation and population dynamics seen in our focal species. Patterns of population genetic structure are consistent with phenotypic differences, suggesting an influence from distinct habitats and resources, and emphasising the need for effective conservation measures in this geographic region.

KEYWORDS
biodiversity, conservation, Delphinus, phenotype, phylogeography, Tursiops

1 | INTRODUCTION

In the marine environment, where barriers to dispersal can be difficult to identify, panmixia across large spatial scales may be expected and is sometimes observed (Palumbi, 1992). However, geography, oceanography, climate and historical vicariance, among other factors, have been shown to shape biogeographic provinces that correspond to phylogeographic patterns common to a range of marine taxa (see Bowen et al., 2016). One example is the division between the Indo-Polynesian and western Indian Ocean provinces, with further subdivision within each region (Bowen et al., 2016). In addition to patterns of species diversity, genetic breaks among populations within a species also occur within regions, sometimes showing structure shared among different species. For example, in the Indian Ocean (IO), population genetic differentiation between the Red Sea and the western IO is common (e.g. for the grouper fish, *Cephalopholis hemistiktos*, Priest et al., 2015; and the anglerfish, *Pomacanthus maculosus*, Torquato et al., 2019). Another break point exists dividing the western IO region at points near Tanzania where there is a major current division north and south (e.g. for the seagrass *Thalassia hemprichii*, Jahnke et al., 2019; and the spiny lobster *Panulirus Homarus*, Singh et al., 2018). Isolation of populations in the Arabian Sea off Oman from those to the east and the west has also been reported (e.g. for the sea-star *Acanthaster planci*, Vogler et al., 2012; and the spiny lobster, Singh et al., 2018). Understanding the processes that generate these patterns of population structure is important towards a better understanding of the evolution of biodiversity, and for the more effective conservation of diversity for species impacted by anthropogenic factors such as climate change.

In this study we focus on marine mammal species in the IO region. Marine mammals are highly mobile, but often exhibit population genetic differentiation within their range of potential dispersion (e.g. Hoelzel, 2009). In particular, we focus on dolphins in the genera *Tursiops* and *Delphinus*. The Delphinidae radiated recently (McGowen et al., 2009; Moura et al., 2020), and some genera are still paraphyletic in some analyses (e.g. Amaral, Jackson, et al., 2012; Kingston et al., 2009; McGowen et al., 2009). This is especially the case for comparisons among *Delphinus* spp. and *Tursiops* spp. (e.g. Moura, Nielsen, et al., 2013; Moura et al., 2020). We investigate the biogeography of these genera in the western IO to better understand the drivers that generate differential patterns of genetic structure in the context of their biology and life history, and in the context of broader regional patterns for marine species.

Two species of bottlenose dolphin are formally recognised: the common bottlenose dolphin, *T. truncatus*, and the Indo-Pacific bottlenose dolphin, *T. aduncus* (SMM, 2019). Within *T. aduncus*, we consider three putative lineages, all occurring within the IO. These are as follows: (1) the holotype lineage, which dominates the west

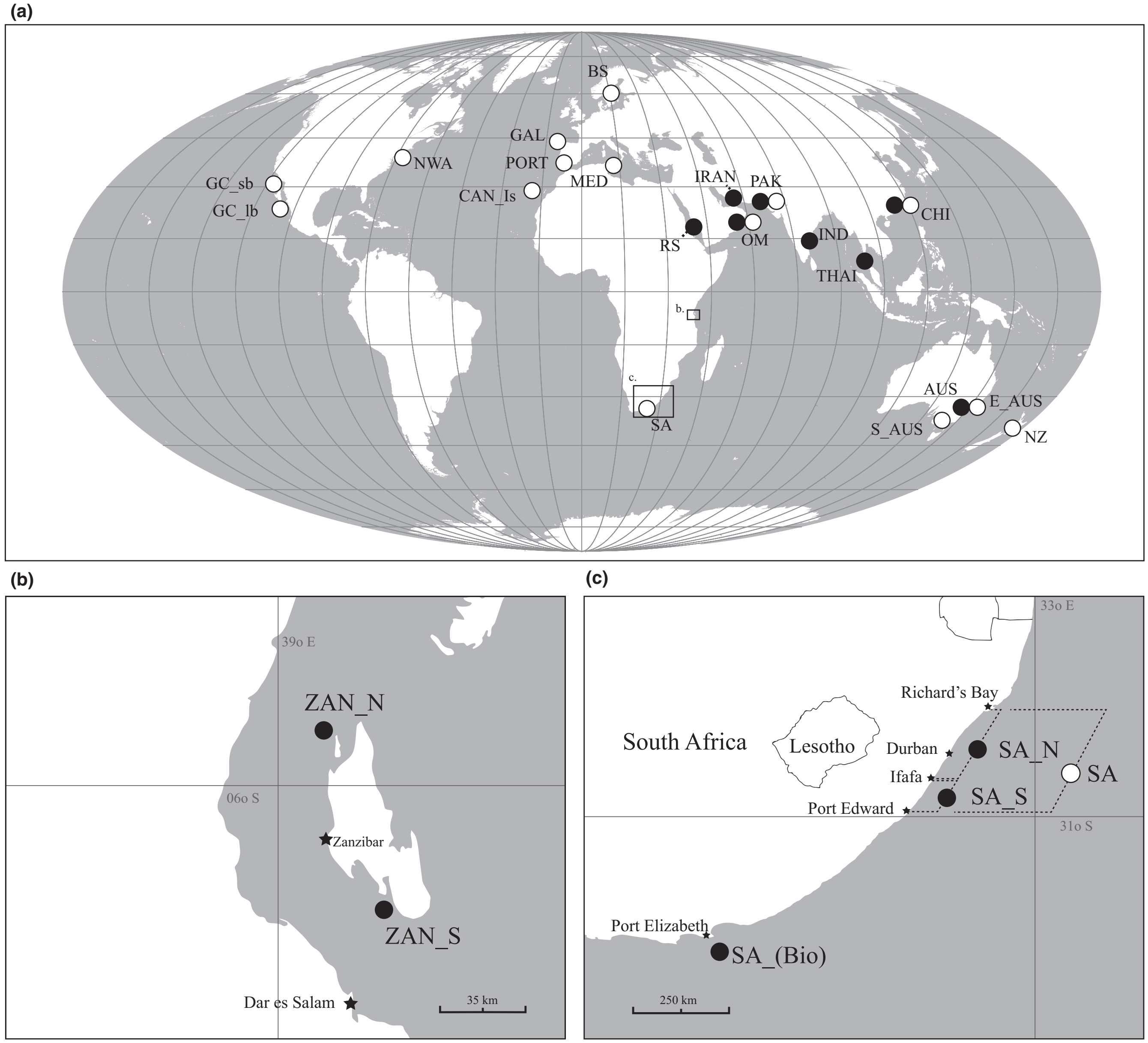


FIGURE 1 Map showing sampling locations of populations of *Tursiops* and *Delphinus* considered. Box (a) A Mollweide (equal area) global projection illustrating sample locations from populations of *Tursiops* and *Delphinus*. Black circles = *Tursiops*, White circles = *Delphinus*, OM = Oman, IND = India, PAK = Pakistan, IRAN = Iran, RS = Red Sea (*T.aduncus* holotype specimen), THAI = Thailand, CHI = China, AUS = Southeast Australia, PORT = Portugal, BS = Black Sea, CAN_Is = Canary Islands (Spain), E_AUS = Eastern Australia, S_AUS = Southern Australia, GAL = Galicia (Spain), GC_lb = long-beaked *D. delphis* Gulf of California (previously known as *D. capensis*), GC_sb = short-beaked *D. delphis* Gulf of California, MED = Mediterranean, NWA = Northwest Atlantic, NZ = New Zealand. Box b) Sample locations from Zanzibar. ZAN_N = North Zanzibar, ZAN_S = South Zanzibar. Box c) Sample locations from South Africa. SA_(Bio) = South Africa (Migratory), SA_N = South Africa (North KwaZulu-Natal Coast), SA_S = South Africa (South KwaZulu-Natal Coast), SA = South Africa *Delphinus*

and northwest IO, originally described off South Africa (Natoli et al., 2004) and later matched to the *T. aduncus* holotype in the Red Sea (Perrin et al., 2007); (2) the Australasian lineage (Wang et al., 1999) and (3) a new putative Arabian Sea lineage of *T. aduncus* from the northwest IO (Gray et al., 2018). Gray et al., proposed that *T. aduncus* lineages diverged in Australasia during the Pleistocene and that repeated exposure of the Sunda and Sahul shelves during this time may have facilitated several allopatric divergence events, as has been proposed for other marine species in the region (Gaither & Rocha, 2013). However, other isolating mechanisms in the IO would have been required to prevent homogenisation between adjacent lineages during interglacials. Possible isolating mechanisms include a geographic barrier (e.g. formation of a land bridge; Dowling & Brown, 1993), oceanographic boundary (e.g. sea-surface temperatures and primary productivity; Fontaine et al., 2007; Mendez et al., 2011), an ecological break (e.g. gaps in prey distribution; Bilgmann et al., 2007) or local adaptation in sympatry to different prey compositions (Adams & Rosel, 2006; Hoelzel, 1994; Hoelzel & Dover, 1991; Moura et al., 2015). Climate fluctuations over the Pleistocene, for instance, monsoonal shifts during glacial/inter-glacial periods, and their effects on primary production in the northern IO (Almogi-Labin et al., 2000; Fontugne & Duplessy, 1986), may have changed the presence or permeability of a barrier.

In *Delphinus*, there is a phenotypically distinct population in the Arabian Sea region of the IO. Long- and short-beaked morphotypes have been described around the world, although clines and intermediate forms are also found (Jefferson & Van Waerebeek, 2002; Murphy, Herman, Pierce, Rogan, & Kitchener, 2006; Pinela, Aguilar, & Borrell, 2008). Genetic analyses consistently showed long- and short-beaked dolphins to be polyphyletic (Amaral, Beheregaray, et al., 2012; Natoli et al., 2006), which suggests that regional lineage sorting is incomplete and multiple coastal populations might have converged independently on a long-beaked morphotype (Amaral, Beheregaray, et al., 2012; Natoli et al., 2006). Two long-beaked populations stand out phylogenetically from the rest. One is found in the eastern tropical Pacific (Rosel et al., 1994; Segura-Garcia et al., 2016), previously identified as *D. capensis* (Heyning & Perrin, 1994), but now provisionally referred to as *D. delphis bairdii* (after Hershkovitz, 1966). The other is the Arabian Sea population within the IO, which is currently classified as the subspecies, *D. delphis tropcialis* (SMM, 2019), based on morphological analyses (Jefferson & Van Waerebeek, 2002). Global phylogeography showed *D. d. tropicalis* in the IO forms a distinct lineage, diverging basally with populations outside the northeast Pacific (Amaral, Beheregaray, et al., 2012). Furthermore, a genetically differentiated long-beaked *D. delphis* morphotype is found off South Africa (Natoli et al., 2006).

Here, we use comparative data from *Tursiops spp*. and *Delphinus spp*. to test hypotheses about the biogeographic drivers of genetic differentiation, especially within the IO, and the implications for effective conservation. We consider the relative roles of environmental change, ecology and life history during the evolution of biogeographic structures for these highly mobile taxa.

2 | MATERIALS AND METHODS

2.1 | Samples and DNA extractions

Sample numbers and geographical origins are shown in Table S1 and Figure 1 and include genotypes or haplotypes generated in this study for 285 *T. aduncus* (from 5 regions), 37 *T. truncatus* (from two regions) and 114 *Delphinus* sp. samples (from two regions; see Table S1). Additional mtDNA sequences were obtained from other studies, accessed from Genbank (details in Table S1 on locations, source and numbers for each marker type). Samples were obtained from biopsy, bycatch, stranded animals and from skeletal material (Table S1). The *Delphinus* samples from Portugal (location denoted as 'PORT' in Figure 1) were included as an outgroup, representative of the short-beaked form. Sample sets from the IO were as extensive as logistically possible for each species, but it was not possible to match regions precisely. Standard phenol–chloroform DNA extraction protocols were carried out on tissue samples (Hoelzel, 1998). For bone samples, QIAquick PCR purification columns (Qiagen, BmbH, Germany) were used to perform DNA extractions, according to manufacturer's protocols.

2.2 | Microsatellite analysis

Most samples were screened for 18 published microsatellite loci (Table S2, after Moura et al., 2013). Due to restrictions imposed by poor sample quality, a sub-set of seven loci (Dde84, Dde66, Dde69, Dde59, Dde70, Dde72 and KWM12a) were amplified and screened for the India and Pakistan *T. aduncus* samples, included only in a subset of analyses (see Results). Samples were obtained from colleagues as biopsies, bycatch or strandings. Given that repeat biopsies can be mistakenly collected from a large group, and repeat labelling is possible in public collections from bycatch and strandings, to be cautious we check for duplicates. Samples that were identical at all loci were considered to be duplicates, although it is possible that they have matching genotypes by chance. However, given the low chance of separate individuals sharing genotypes at all loci, we removed one individual from duplicate pairs from further analyses (3 among *Tursiops* samples and 2 for *Delphinus*). Null alleles, large allele dropout and scoring errors were checked using MicroChecker (Van Oosterhout et al., 2004). When null alleles were detected, their influence on F_{ST} values was investigated using FreeNA (Chapuis & Estoup, 2007). Deviations from Hardy–Weinberg equilibrium (HWE) were assessed in Arlequin v. 3.5 (Excoffier & Lischer, 2010). Pairwise linkage disequilibrium between loci was assessed for each population through a likelihood ratio test utilising the Expectation-Maximisation (EM) algorithm (1,000 permutations, Bonferroni correction applied; Slatkin & Excoffier, 1996). Loci putatively under selection were identified in Lositan (Antao et al., 2008) using the Infinite Alleles mutation model for 5×10^4 simulations, applying the 'neutral mean F_{ST}' and the 'force mean F_{ST}' options. A 95% confidence limit and false discovery rate of 0.05 were applied.

F-statistics were estimated in Arlequin and significance determined through 100 permutations with Bonferroni correction applied. Microsatellite allelic richness was calculated using Fstat v. 2.9.3.2 (Goudet, 2001) and Welch's *t*-test was used to investigate differences in richness between putative populations. A Factorial Correspondence Analysis (FCA) was performed on the microsatellite genotypes in Genetix (Belkhir, Borsa, Chikhi, Raufaste, & Bonhomme, 2004). The number of populations (*K*) was assessed using Structure v. 2.3 (Pritchard et al., 2000), applying the admixture ancestry and correlated allele frequency models. The burn-in length was set to 10^5 followed by 10^6 iterations. The parameter ALPHAPROPSD was set to 0.5 to improve mixing. Ten independent runs were assessed for each value of *K* ranging from 1 to 8. The most likely value for *K* was determined using the web server Clumpak (Kopelman et al., 2015; http://clumpak.tau.ac.il/index.html).

BayesAss v. 1.3 (Wilson & Rannala, 2003) was used to investigate recent gene-flow patterns. The burn-in length was set to 10^6

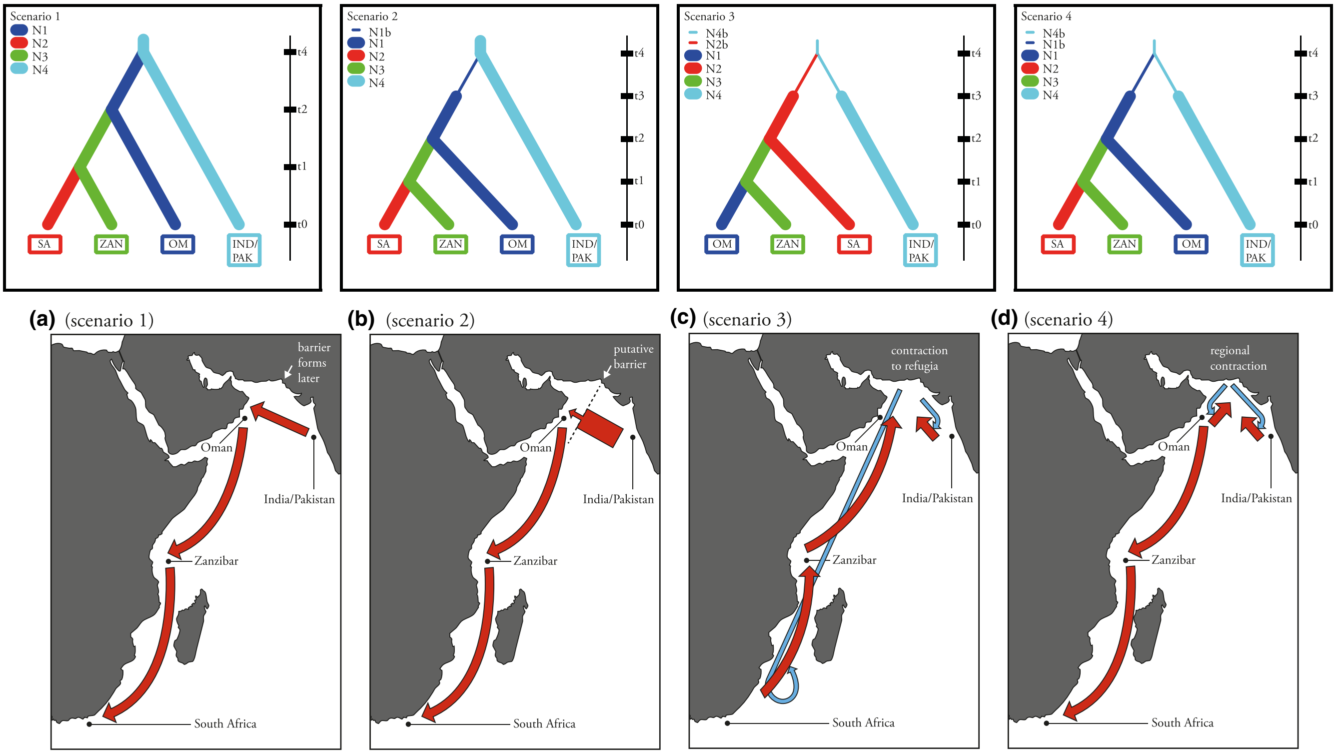


FIGURE 2 Demographic scenarios tested in DIYabc for *Tursiops aduncus*. OM = Oman, ZAN = Zanzibar, SA = South Africa, IND/PAK = India/Pakistan, *t* = time, *N* = effective population size (*Ne*). Times are not shown to scale. Scenario 1: OM and IND/PAK diverge (*t*4) in the northern IO, without a founding event, and other populations are established from one of the lineages in a southward direction without an initial founding event. Scenario 2: OM and IND/PAK diverge (*t*4) and OM experiences a reduced *Ne* as founders immigrate across a barrier into the western Indian Ocean. Populations founded in Oman recover (*t*3) and a southward expansion follows, establishing populations off ZAN and SA. Scenario 3: IND/PAK and SA ancestors diverge and experience a historic reduction in *Ne* (*t*4) due to a contraction to northern and southern glacial refugia. Populations recover (*t*3) and populations expand out of South African refugia in a northwards direction, establishing populations off ZAN and OM. Scenario 4 (best supported): IND/PAK and OM ancestors diverge and experience a historic reduction in *Ne* (*t*4) due to a contraction to northern refugia. Populations recover (*t*3) and populations expand out of Oman in a southwards direction, establishing ZAN and SA populations

followed by 10^7 Markov chain Monte Carlo (MCMC) iterations with a sampling interval of 1,000 iterations. All mixing parameters, Δ*A*, Δ*F* and Δ*M*, were set to 1 to improve chain mixing. Trace files were viewed in TRACER v. 1.6 (Rambaut et al. 2014) and the log probability was examined for convergence and good chain mixing. Analyses were run multiple times to check runs had converged on similar posterior mean parameter estimates. A Circos plot of migration dynamics was generated in R v. 3.0 (R Core Team, 2013) from the BAYESASS output using the package 'circlize' (Gu et al. 2014), following Sander et al. (2014).

2.3 | Mitochondrial DNA analysis

A 479 bp fragment of the mtDNA control region hypervariable region 1 (HVR1) was sequenced for *Tursiops* and *Delphinus* samples. For analyses, fragment lengths were matched to published sequences meaning that 267 and 308 bp were used for *Tursiops* and *Delphinus* respectively. PCR reactions were performed in 20 µl final reaction volumes containing approximately 1.0 µl of template DNA, 1.25 U of GoTaq Flexi DNA polymerase, 10x buffer (Promega), 0.2 mM dNTP, 3 mM $MgCl_2$ and 0.2 µM of each primer: TRO (L15812) 5' CCT CCC TAA GAC TCA AGG AAG 3' (developed at the Southwest Fisheries Science Centre, Zerbini et al., 2007) and D (H16498) 5' CCT GAA GTA AGA ACC AGA TG 3' (Rosel et al., 1994). The PCR profile included initial heating at 95°C for 2 min, followed by 40 cycles of 95°C for 40 s, annealing temperature of 60°C for 40 s and 72°C for 1 min, and a final 72°C extension for 10 min. PCR products were purified with QIAgen PCR purification columns (Qiagen, GmbH, Germany) and sequenced using an ABI automated sequencer. Further sequences were obtained from GenBank. In total, 299 sequences of *T. aduncus*, 53 sequences of *T. truncatus* and 660 sequences of *Delphinus* sp. were utilised in this study (see Table S1).

Alignment of sequences was performed using the 'Muscle' algorithm (Edgar, 2004) as implemented in GENEIOUS v. 7.1.2 (http://www.geneious.com, Kearse et al., 2012). ARLEQUIN was used to calculate pairwise F_{ST} and Φ_{ST} between putative populations. To calculate Φ_{ST}, a Tamura-Nei genetic distance model was applied with a gamma-correction shape parameter value of α = 0.191 identified as the best model using BIC in JMODELTEST v. 2.1.6 (Darriba et al. 2012). Haplotype (*h*) and nucleotide (π) diversities were estimated and pairwise comparisons were made between populations using

TABLE 1 Pairwise F_{ST} values for all *Tursiops aduncus* populations considering 14 microsatellite loci (below diagonal) and 7 microsatellite loci (above diagonal)

	OM	SA_(Bio)	SA_N	SA_S	ZAN_N	ZAN_S	IND_ PAK
OM	–	0.048*	0.043*	0.044*	0.028*	0.014	0.117*
SA_(Bio)	0.049*	–	0.008	0.002	0.084*	0.058*	0.160*
SA_N	0.040*	0.001	–	0.012	0.087*	0.050*	0.164*
SA_S	0.054*	−0.001	0.006	–	0.096*	0.065*	0.170*
ZAN_N	0.046*	0.081*	0.069*	0.089*	–	0.017	0.139*
ZAN_S	0.047*	0.081*	0.065*	0.088*	0.015*	–	0.140*

*, significant ($p < 0.001$). OM = Oman, SA_(Bio) = South Africa (Migratory), SA_N, South Africa (North KwaZulu-Natal Coast), SA_S, South Africa (South KwaZulu-Natal Coast), ZAN_N, North Zanzibar, ZAN_S, South Zanzibar and IND_PAK, combined data from India and Pakistan.

Welch's *t*-test. Tajima's *D* and Fu's F_S neutrality test statistics were estimated (Fu, 1997; Tajima, 1989). These may indicate population expansion when significantly negative or contraction when positive. For all tests requiring correction for multiple analyses, p-values are reported after Bonferonni correction.

A median-joining haplotype network (Bandelt et al., 1999) was generated for the *Tursiops* and *Delphinus* datasets using PopART (ε = 0; http://popart.otago.ac.nz, Leigh & Bryant, 2015). For the *Delphinus* dataset, a large number of ambiguous loops were exhibited in this network, making interpretation and visualisation difficult (see Results). Therefore, a minimum-spanning tree was also computed in Arlequin based on pairwise distances between haplotypes and was visualised using HapStar v. 0.7 (Teacher & Griffiths, 2011). The caveat to using the simplified minimum-spanning tree is that it is arbitrarily selected from several, equally optimal trees.

2.4 | Inference of *T. aduncus* demographic history in the Western Indian Ocean

To test hypotheses for the demographic history of *T. aduncus* populations in the western IO (and associated barrier mechanisms), four scenarios (Figure 2) were tested using Approximate Bayesian Computation (ABC) as implemented in DIYabc v. 2.0.4 (Cornuet et al., 2014). These scenarios were thought to be credible given the geographic distributions of putative populations, available data on the diversity of this species in the IO and historical patterns of environmental change (Gray et al., 2018). In particular, scenario 1 assumes linear progression and connectivity from India to Oman to Zanzibar to South Africa. The other three scenarios assume one or two founder events and the same linear progression (scenarios 2 and 4, respectively), or a convergence of expansions from South Africa and from India (scenario 3). Note that there are too many possible permutations to test them all with sufficient power, and support for any of these scenarios only suggests that it is the best fit among those tested. An untested scenario may fit the data better. A dataset representing four *T. aduncus* populations (Oman, Zanzibar, South Africa and India–Pakistan) was used, consisting of seven microsatellite loci, and 267 bp of mtDNA control-region sequences. Randomly selected samples of 20 for South Africa and Zanzibar were used in order to avoid oversampling alleles compared to the less well-sampled populations (Leberg, 2002). For the mtDNA locus, an HKY substitution model (Hasegawa et al., 1985) was applied with a gamma-correction shape parameter value of $\alpha = 0.67$ with 55% invariant sites, as identified using Bayesian Information Criteria (BIC) in jModeltest. No samples were available for a similar analysis for *Delphinus* within the IO.

A Generalised Stepwise Mutation model was applied to the microsatellite loci (Estoup et al., 2002). Four million datasets were simulated across the four scenarios. A Principal Component Analysis (PCA) was carried out to see how well the simulated data fit the observed data. Posterior probabilities of parameters were estimated based on the closest 1% of simulated data to the observed data. Assessment of which scenario was performing the best was carried out using the logistic regression method (Beaumont, 2008; Fagundes et al., 2007). Conversion to divergence time estimates was based on a generation time of 21 years (after Taylor et al., 2007).

3 | RESULTS

3.1 | *Tursiops* spp.

Microsatellite TexVet9 was monomorphic and D08, KWM2a and KWM1b had evidence for null alleles, deviation from HWE (Table S3) or showed evidence for directional selection. These were removed, leaving 14 loci for further analyses. The average missing data across these loci was 0.4%. Allelic richness was similar among populations (Table S4), and pairwise comparisons between populations were not significantly different ($p > 0.05$).

Of the seven loci used for the India and Pakistan samples, only one locus (Dde70) deviated significantly HWE ($p < 0.05$). Linkage disequilibrium was not detected between any loci. Null alleles were detected in Dde66 and Dde70 in the SA_S and IND_PAK populations, respectively, but removal of these loci or null allele adjustment did not alter the pattern of genetic differentiation. Therefore, all seven loci were retained for further analyses, without adjustment. Pairwise comparisons of allelic richness for seven loci between populations were not significantly different ($p > 0.05$, Welch's *t*-test).

Pairwise F_{ST} was significant for most comparisons between locations (Table 1). The FCA using the 14 microsatellite loci

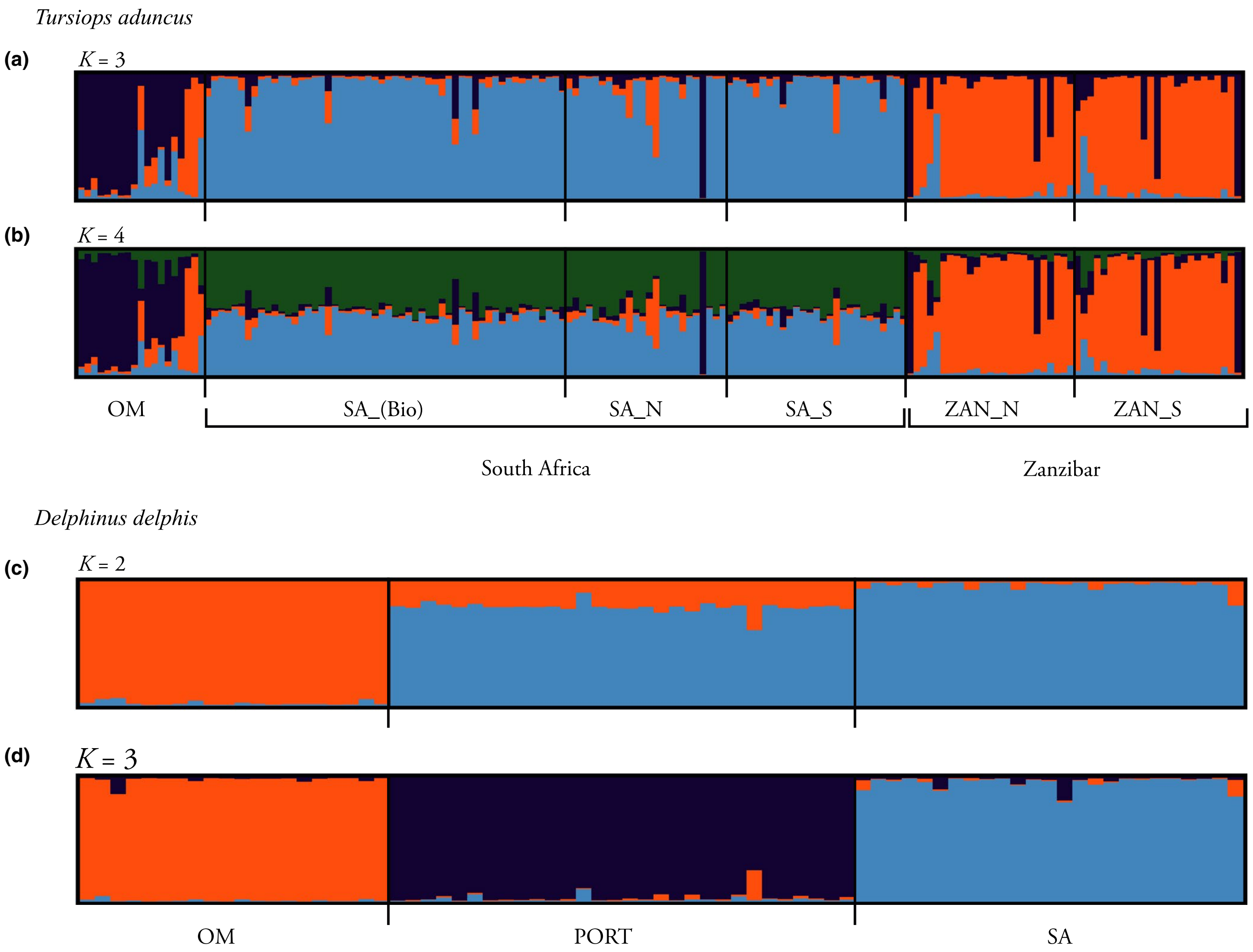
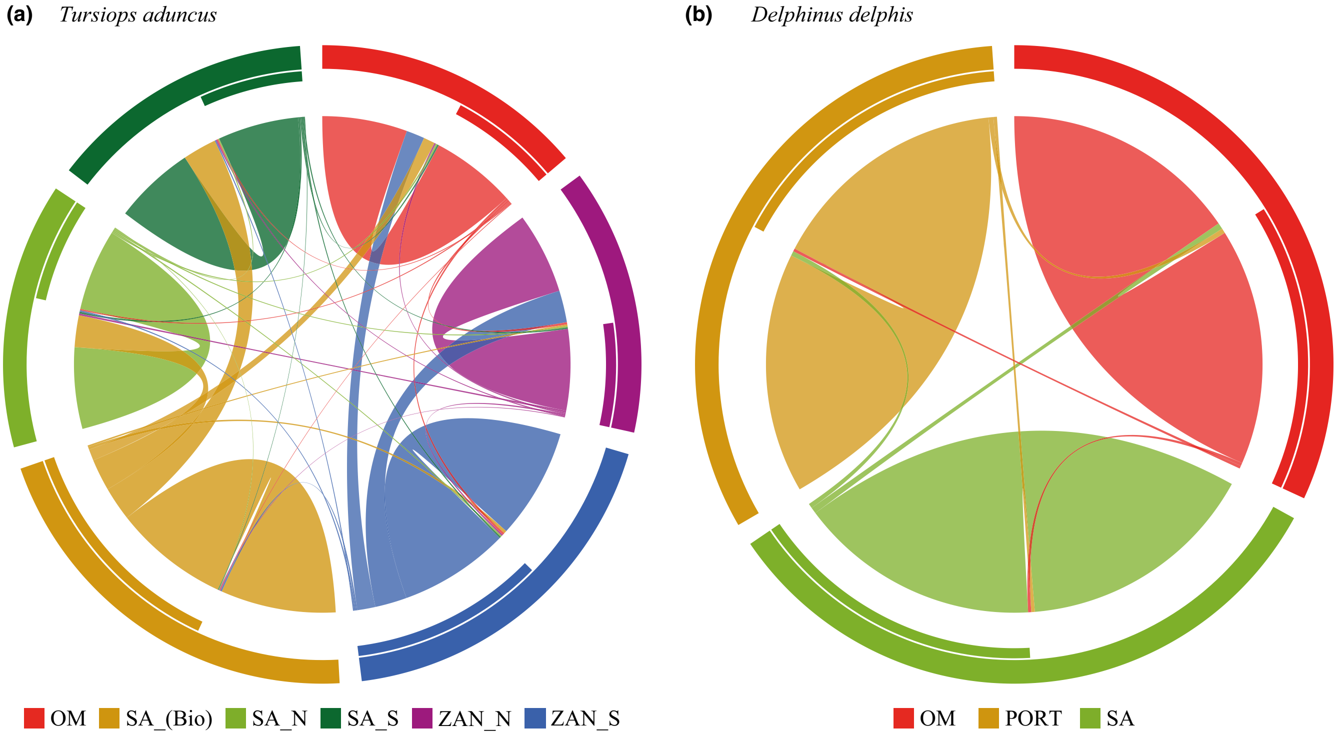


FIGURE 3 Probability assignment of individuals based on microsatellite loci. Assignments carried out in Structure and generated using CLUMPAK. Plots (a) $K = 3$ and (b) $K = 4$ were generated for *T.aduncus* data without locprior information. Plots (c) $K = 2$ and (d) $K = 3$ were generated in the same way for *D. delphis* data. Vertical coloured bars represent individuals and black lines delineate the respective putative populations sampled. OM = Oman (*Tursiops n* = 19, *Delphinus n* = 20), SA_(Bio) = South Africa (Migratory) (*n* = 56), SA_N = South Africa (North KwaZulu-Natal Coast) (*n* = 24), SA_S = South Africa (South KwaZulu-Natal Coast) (*n* = 27), ZAN_N = North Zanzibar (*n* = 26), ZAN_S = South Zanzibar (*n* = 25), PORT = *Delphinus* Portugal (*n* = 30) and SA = *Delphinus* South Africa (*n* = 25)

T. aduncus dataset clusters Oman, South Africa and Zanzibar separately (Fig. S1). Factors 1, 2 and 3 accounted for 84.44% of the total variance, contributing 47.3%, 25.48% and 11.66%, respectively. The seven-locus FCA for *Tursiops* clearly differentiates the India–Pakistan (IND_PAK) sample set from other putative populations (Fig. S2a). Clustering analysis in STRUCTURE (14 loci) gave $\Delta K = 3$ (representing Oman, South Africa and Zanzibar), and although the highest [Ln *P*(*D*)] was for $K = 4$, this provided no further geographic resolution (Figure 3). Analyses using seven loci revealed a similar pattern with the addition of India–Pakistan as a fourth population (strongly differentiated as indicated earlier in Gray et al., 2018; Fig. S3). Estimates of contemporary, directional gene flow (using BayesAss and 14 loci; Figure 4a, Table S5) showed asymmetrical migration northwards from the South Africa migrating population (SA_Bio) to the other South Africa populations (SA_S = 26.6%, SA_N =28.3% from SA_Bio) and Oman (OM =9.5% from SA_Bio). However, migration from South Africa to Zanzibar appears to be minimal (1.4–2.3%). Southern Zanzibar (ZAN_S) is also an important source for dispersal to northern Zanzibar (ZAN_N =26.6% from ZAN_S) and Oman (OM=15.5% from ZAN_S). Southbound migration appears to be minimal.

Based on the microsatellite DNA data, logistic regression of the posterior probabilities of each evolutionary scenario in the ABC analysis revealed refugial re-expansion out of the northern IO (scenario 4) to be the best supported (Figure 2, Figure S5). The next best supported scenario (scenario 3) was associated with a refugial re-expansion out of South Africa. Confidence intervals for scenario 4 did not overlap with the other scenarios for 1% of the simulated datasets while confidence intervals for the other scenarios overlapped substantially, suggesting that scenario 4 outperformed the others. Posterior estimates of parameters were inferred using the closest 1% of the simulated datasets to the observed data (Table 2).



(a) *Tursiops aduncus*

(b) *Delphinus delphis*

FIGURE 4 Patterns of migration between (a) *T.aduncus* and (b) *D. delphis* populations. Circos plot generated from BayesAss output for 14 microsatellites in R, using the package 'circlize'. The outflow of a population (emigration) is illustrated by a double bar in the respective segment. A single bar is indicative of movement into the population (immigration). Non-migrants are included in both the inflow and outflow of a population. Migration curve widths are proportional to the number of migrants. OM = Oman, SA_(Bio) = South Africa (Migratory), SA_N = South Africa (North KwaZulu-Natal Coast), SA_S = South Africa (South KwaZulu-Natal Coast), ZAN_N = North Zanzibar, ZAN_S = South Zanzibar, PORT = Portugal and SA = South Africa

For *Tursiops*, there were 82 mtDNA haplotypes and 24 polymorphic sites with few haplotypes being shared among putative populations (Table S6). Pairwise F_{ST} and Φ_{ST} values were highly significant ($p < 0.001$ after Bonferroni correction) for the majority of comparisons (Table S7). Relatively low values of π and h were observed in the South African, Zanzibar and Australia populations, whereas order of magnitude higher values were seen in the CHI_THAI, IND_PAK, NWIO_Tt and CHI_Tt populations (see Table S4 for details and definitions). Pairwise comparisons between populations for π and h using Welch's t-test (Table S8) generally show that the ARABIA, CHI_THAI, IND_PAK, NWIO_Tt and CHI_Tt populations have significantly higher π and h than other populations. Values for Tajima's D and Fu's F_S were not statistically significant ($p > 0.05$ after Bonferroni correction; Table S9). From the *Tursiops* median-joining network, there is clear separation between *T. truncatus* and *T. aduncus* lineages (Figure 5). The three lineages of *T. aduncus* are also clearly separated.

3.2 | *Delphinus* spp.

Null alleles were detected in six loci, Dde65 (SA), Dde69 (OM), EV37Mn (PORT and SA), KWM2a (PORT), TexVet5 (PORT) and KWM1b (OM). Significant HWE deviation was detected in five loci, but in each case in just one putative population (Table S10). No linkage disequilibrium was detected between any loci for any population ($p < 0.05$). Positive selection was detected in Dde66, AAT44 and D08. In light of these tests, the four loci with strongest evidence for deviation from expectations, D08, Dde66, AAT44 and EV37, were removed. Adjustment for null alleles revealed similar F_{ST} values between adjusted and unadjusted loci and removal of loci with null alleles did not alter the differentiation pattern. Therefore, 14 loci were retained. The average missing data across all remaining loci was 0.02%. Pairwise comparisons of allelic richness between populations were not significantly different ($p > 0.05$, Welch's t-test).

Pairwise F-statistics between putative populations were all highly significant (OM vs SA, $F_{ST} = 0.096$; OM vs. PORT, $F_{ST} = 0.073$; SA vs. PORT, $F_{ST} = 0.065$; all $p < 0.001$ after Bonferroni correction). From the FCA, Factors 1 and 2 accounted for 100% of the total variance, contributing 55.8% and 44.2% respectively (Fig. S1). All three populations were clearly differentiated from each other. In the clustering analysis, the highest hierarchical level for K (Evanno et al., 2005), and the highest posterior probability [Ln $P(D)$], were $K = 3$ (Oman, South Africa and Portugal; Figure 3d). Estimates of gene flow for *Delphinus* (Figure 4b and Table S11) suggest that contemporary migration among Portugal, South Africa and Oman is limited, with <2.5% of each population consisting of migrants (per generation).

For *Delphinus*, 294 mtDNA haplotypes and 96 polymorphic sites were identified (Table S12). Of the 45 shared haplotypes, the majority were shared exclusively between populations in the

TABLE 2 Parameter estimates for highest performing scenario (4) in DIYabc analysis for *Tursiops aduncus*

Parameter	Mean	Median	Mode	95% HPD	Years BP (Median)	95% HPD
N1	11,100	10,800	10,200	4,210–19,100		
N2	3,680	3,170	2,130	658–9,040		
N3	11,200	11,100	11,900	4,200–18,900		
N4	20,800	21,200	22,800	9,680–29,400		
t1	288	210	104	36–1,060	4,410	760–22,260
t2	895	718	430	193–2,880	15,078	4,053–60,480
t3	3,880	3,440	2,300	232–9,320	72,240	4,872–195,720
N1b	4,580	4,320	2,780	442–9,570		
N4b	6,640	5,620	2,220	536–17,600		
t4	6,830	6,290	4,730	1,880–14,000		
µmic_1	1.6E-04	1.5E-04	1.0E-04	1.0E-04–3.2E-04		
pmic_1	5.1E-01	4.9E-01	4.0E-01	1.8E-01–9.4E-01		
snimic_1	1.5E-07	3.6E-08	1.0E-08	1.0E-08–1.0E-06		
useq_2	1.5E-06	1.4E-06	1.4E-06	8.2E-07–2.3E-06		
k1seq_2	477,000	468,000	314,000	22,900–966,000		

N1 = Oman effective population size (Ne); N2 = South Africa Ne; N3 = Zanzibar Ne; N4 = India/Pakistan Ne; t1= divergence time (generations) of Zanzibar and South Africa; t2 = time (generations) Oman diverged from ancestral South Africa/Zanzibar; t3 = recovery time after founding/bottleneck event; N1b = ancestral Oman population Ne (unsampled); N4b = ancestral India/Pakistan population Ne (unsampled); t4 = time India/Pakistan diverged from other lineages; µmic = mean mutation rate for microsatellite loci; pmic = mean P coefficient for microsatellite loci; snimic = mean SNI rate for microsatellite loci; µseq = mutation rate for mitochondrial sequences; kseq = mean coefficient kC/T; YrsBP are the converted years BP for times using the median value of the posterior distribution and a generation time of 21 years.

Atlantic, Mediterranean and Black Sea ($n = 21$). The long-beaked population in the Gulf of California (Segura-Garcia et al. 2016) shared one haplotype with the population off Pakistan and another with New Zealand. No haplotypes were shared with the populations off Oman or China. Pairwise F_{ST} and Φ_{ST} values were mostly highly significant ($p < 0.001$; Table S13). Measures of π and h are given in Table S14. Pairwise Welch's *t*-tests (Table S8) suggest the Oman and Gulf of California populations have significantly reduced π ($p < 0.05$). Values for Tajima's D were not statistically significant, however, Fu's F_S were large and negative ($p < 0.02$; indicative of expansions; Table S9). The *Delphinus* median-joining network (Figure 6) and minimum-spanning tree (Figure S4) showed haplotypes forming three clusters corresponding to a highly diverse *D. delphis* group (distributed worldwide), long-beaked *D. delphis* (Gulf of California) and *D. d. tropicalis* in the northwest IO (Oman and Pakistan).

4 | DISCUSSION

4.1 | Population structure

At least four break points have been identified within the IO for a range of species: between the IO and the Indo-Pacific (e.g. Bowen et al., 2016), between the IO and the Red Sea (e.g. Torquato et al. 2019), between the Arabian Sea and the western IO (e.g. Singh et al., 2018), and along the western coast of the IO north and south of points near Madagascar and Tanzania (e.g. Jahnke et al., 2019; see review in the Introduction). *T. aduncus* and *Delphinus spp*. showed genetic structure within the IO between South Africa and Oman reflecting a division along the western IO coast, although this comparison is on a large geographic scale. For *T. aduncus*, finer-scale analysis was possible, revealing differentiation between Oman, Zanzibar and South Africa and between northern and southern Zanzibar (the latter as reported previously; Särnblad et al. 2011). Jahnke et al., (2019) found differentiation among seagrass populations sampled at locations around Zanzibar, as well as over a broader geographic range along the coast, which they propose was associated with the major current systems in that region (the East African Coastal Current, the North East Madagascar Current and the South Equatorial Current). Mendez et al. (2011) found population structure in humpback dolphins, *Sousa plumbea*, in the western IO and correlated this with various environmental factors including currents and sea surface temperature. We have no data to indicate what the barrier to gene flow may be for *T. aduncus* in this region, although it seems plausible that the current systems affect the distribution of prey which in turn affect site fidelity in the dolphin populations.

The clearest break point in our dataset is the isolation of populations for each species in the Arabian Sea. The degree of differentiation was strong for *Delphinus*, and from the analyses incorporating populations from around the world, the population in the northwest IO (*D. d. tropicalis*) stands out as especially differentiated from other regions of the species distribution (Amaral, Beheregaray, et al.,

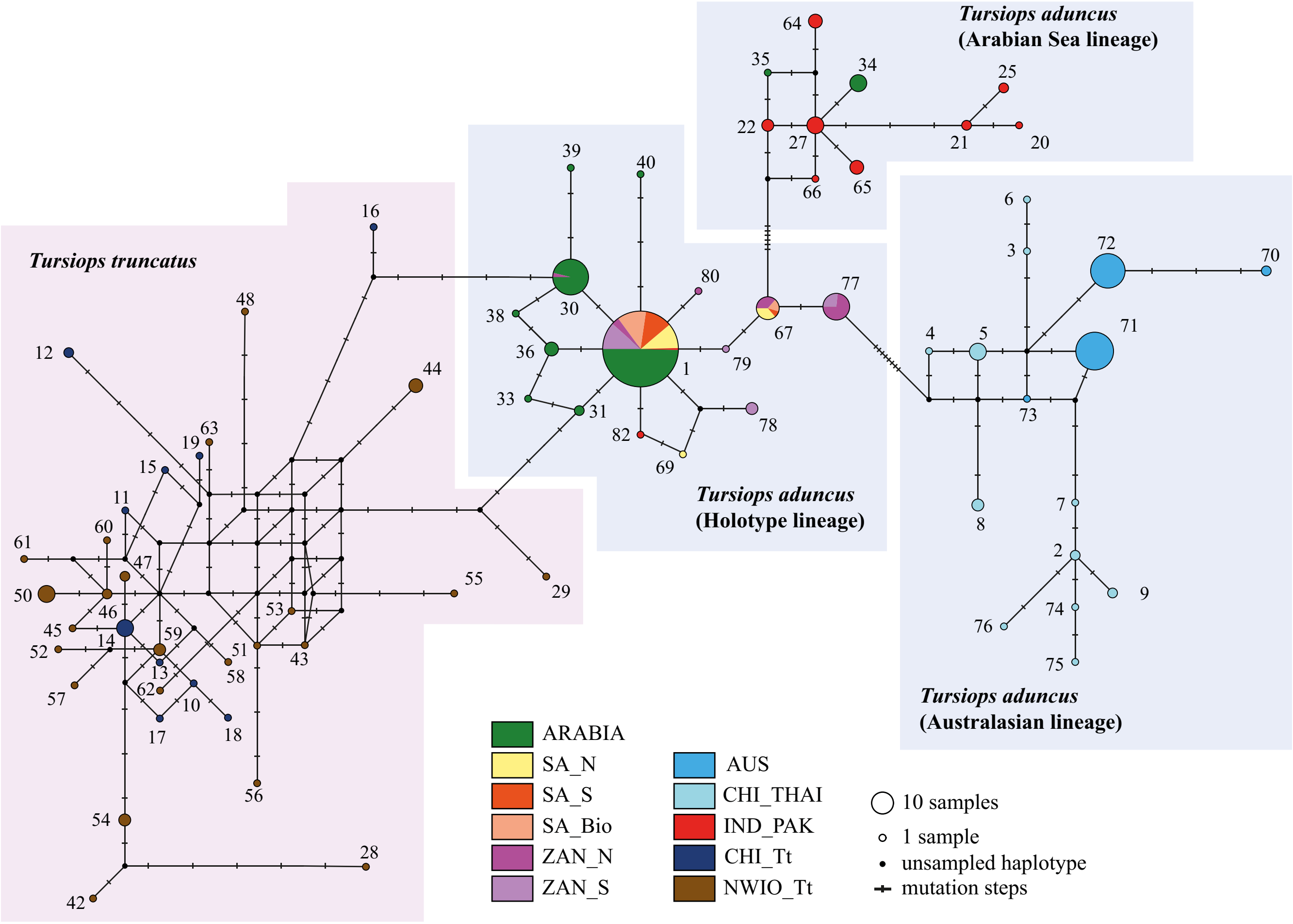


FIGURE 5 Median-joining haplotype network for *Tursiops*. Generated in PopART from mtDNA control region sequences. ARABIA = sequences from Oman, Iran and the Red Sea, SA_N = South Africa (North KwaZulu-Natal Coast), SA_S = South Africa (South KwaZulu-Natal Coast), SA_(Bio) = South Africa (Migratory), ZAN_N = North Zanzibar, ZAN_S = South Zanzibar, AUS = Southeast Australia, CHI_THAI = includes sequences from China and Thailand, IND_PAK = includes samples from India and Pakistan, CHI_Tt = *T.truncatus* from China and NWIO_Tt = *T. truncatus* from the northwest Indian Ocean

2012, Figure 6, Figure S4). This is consistent with earlier studies investigating *D. d. tropicalis* morphology (Jefferson & Van Waerebeek, 2002). Our *T. aduncus* samples from Oman were also significantly differentiated from all other putative populations in our study (see Table 1). Other taxa show population differentiation around the Arabian Peninsula, including various species of sharks (see Naylor et al., 2012). For the hammerhead shark, *Sphyrna lewini*, isolation was suggested to be associated with contiguous shelf habitat around the peninsula distinct from the surrounding deep ocean habitat (Spaet et al., 2015). Highly significant differentiation for all comparisons with the India–Pakistan *T. aduncus* population has been revealed, consistent with the phylogenetic placement of this population as a separate lineage (Gray et al., 2018).

4.2 | Contemporary gene flow

Estimates of contemporary migration patterns between *T. aduncus* populations in the western IO indicate asymmetric gene flow northwards. This suggests that individuals moving out of South Africa and Zanzibar are migrating to populations further north. This bias has also been reported in *S. plumbea*, where no southbound migration was detected between populations off Oman, Tanzania or Mozambique (based on mtDNA data in Mendez et al., 2011). For *Delphinus*, inference of contemporary migration rates between the eastern Atlantic, South Africa and Oman revealed limited genetic exchange between these locations. The population off Oman exhibited the most immigration but contributed the fewest immigrants to other populations.

Dolphin distributions are often associated with the distribution of foraging habitat and prey (Hastie et al., 2004; Torres et al., 2008). For example, along the coast on Kwa Zulu Natal (South Africa) *T. aduncus* follows the seasonal migration of sardines (Peddemors, 1999). *T. aduncus* and *D. d. tropicalis* in the northwest IO may express a higher degree of site fidelity due to habitat-specific foraging specialisations, as seen for both genera elsewhere (e.g. Ball et al., 2017; Natoli et al., 2005; Moura, Sillero, Rodrigues, & 2012). The exceptionally long rostrum, characteristic of *D. d. tropicalis* (Jefferson

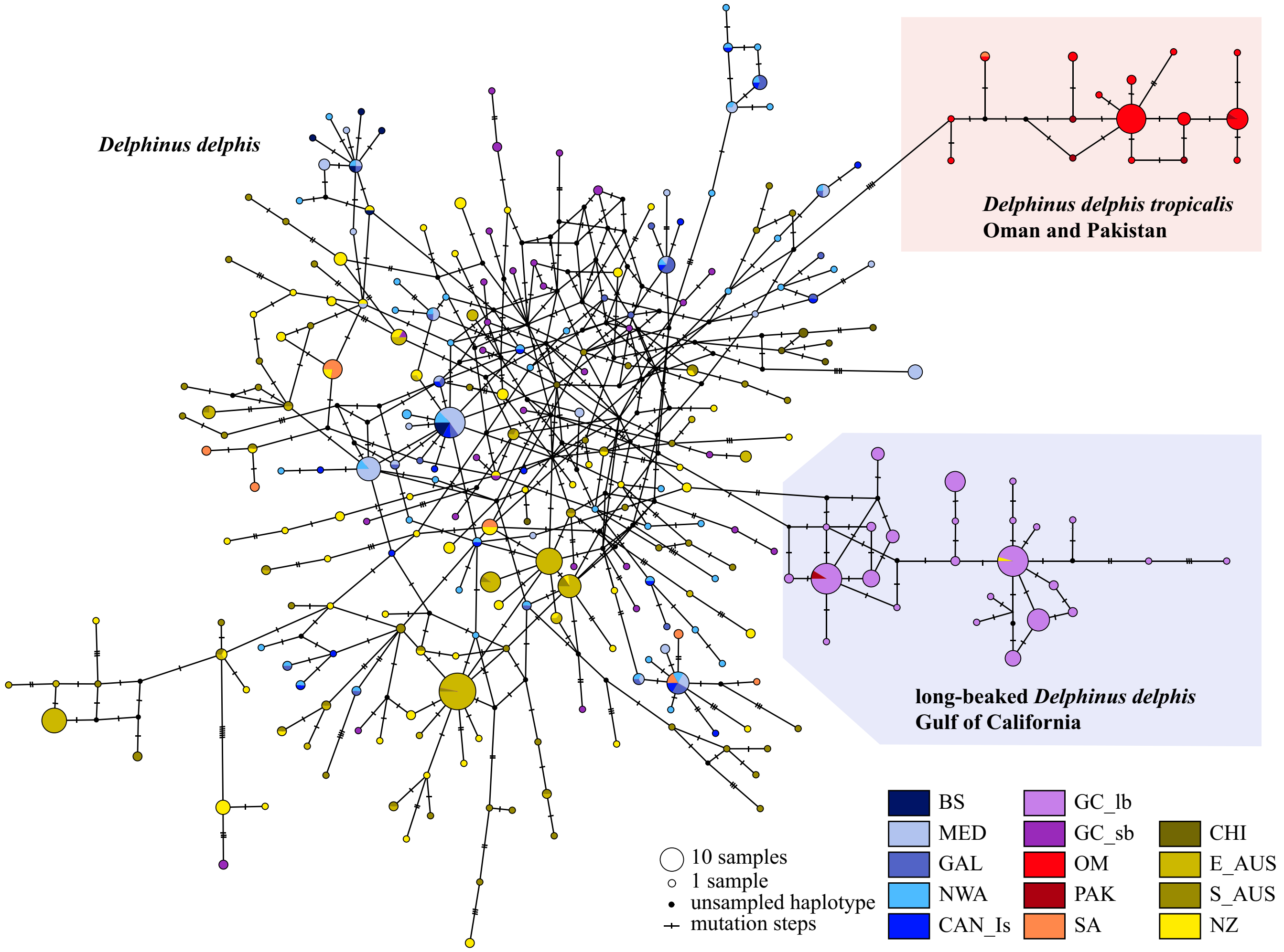


FIGURE 6 Median-joining haplotype network for *Delphinus*. Generated in PopART from mtDNA control region sequences. BS = Black Sea, MED = Mediterranean, GAL = Galicia (Spain), NWA = Northwest Atlantic, CAN_Is = Canary Islands (Spain), GC_lb = long-beaked *D. delphis* Gulf of California (previously known as *D. capensis*), GC_sb = short-beaked *D. delphis* Gulf of California, OM = Oman, PAK = Pakistan, SA = South Africa, CHI = China, E_AUS = Eastern Australia, S_AUS = Southern Australia and NZ = New Zealand.

& Van Waerebeek, 2002) might suggest adaptation to local prey, environmental conditions or habitat-specific foraging strategies. However, the available documentation of *D. d. tropicalis* stomach contents from India and Pakistan (James et al., 1986; Krishnan et al., 2008; Pilleri & Gihr, 1972) suggests their prey species are not particularly distinct from prey composition data for *D. delphis* elsewhere (e.g. Meynier et al., 2008; Pusineri et al., 2007).

There is clinal variation in *Delphinus* rostral length as one moves along the IO coastline, reaching an extreme off India (Jefferson & Van Waerebeek, 2002), consequent with waters that are characterised by high turbidity, due to river influx (Longhurst, 2010) and coastal mudbanks (Vivekanandan et al., 2003). It is possible that the longer rostra exhibited in *D. d. tropicalis* and *T. aduncus* are either adapted to targeting prey in low-visibility environments or are advantageous in foraging over habitats that are specific to coastal waters (as also proposed for crocodiles; McCurry et al., 2017). A longer rostrum is a characteristic shared with spinner dolphins, *Stenella longirostris* (Van Waerebeek et al., 1999) and humpback dolphins, *S. plumbea* (Jefferson & Van Waerebeek, 2004) in the coastal waters of this region, suggesting convergence on a long-beaked phenotype (or phenotypic plasticity) in response to shared environmental gradients (e.g. turbidity, common in the Arabian Sea due to the northeast and southwest monsoon systems). A similar example of convergent skull shape and beak length evolution among river dolphin species has been proposed, possibly associated with foraging behaviour (Page & Cooper, 2017). Adaptive and/or plastic responses to environmental gradients have been documented in other taxa, such as adaptation to altitude in common frogs, *Rana temporaria* (Bonin et al., 2006) and clinal variation in coat pigmentation of oldfield mice, *Peromyscus polionotus*, in response to soil type (Mullen & Hoekstra, 2008). These adaptive transitions in phenotype can lead to assortative mating and population differentiation, and are therefore important to identify and understand in the context of effective biodiversity conservation. In our study they could help to explain patterns of differentiation in the absence of physical barriers to gene flow.

4.3 | Consideration for an isolating mechanism in the Northwest Indian Ocean

The *T. aduncus* holotype lineage likely expanded into the western IO from the north. The ABC analyses corroborate this and suggest a reduced population size in the ancestral lineages of the holotype and Arabian Sea lineages, indicative of a genetic bottleneck in the northern IO (although note that the ABC analysis cannot assess models not included, and makes simplifying assumptions). The distributions of samples that match the Arabian Sea *T. aduncus* lineage appear to overlap with those of the holotype lineage, suggestive of secondary contact between them. Even though there is an overlap in range, the transition between the lineages occurs over a relatively short distance, suggesting the presence of an isolating mechanism east of the Strait of Hormuz (Gray et al., 2018).

During glacial periods, the intensity of the southwest monsoon would have reduced, causing a decrease in upwelling and productivity in the northern IO (Fontugne & Duplessy, 1986). At the same time, productivity would have increased in the Bay of Bengal and Andaman Sea due to intensification of the northeast monsoon (Almogi-Labin et al., 2000; Fontugne & Duplessy, 1986). Such a disruption may have facilitated the early bottleneck and divergence between the holotype and Arabian Sea lineages, supported in the ABC analyses. Our mean estimate for the timing of this event would be consistent with this hypothesis, although the confidence limits are broad (see Table 2). Later divisions occur during the late Pleistocene or Holocene, according to our estimates (Table 2), possibly during the period of rapid warming following the last glacial period.

An ecological isolating mechanism may also be present, whereby dolphins in the western and northern IO have adapted to a particular locality. The relatively pronounced differentiation of *D. d. tropicalis* in this region together with differentiation of the local population of *T. aduncus* from neighbouring regions would be consistent with this hypothesis. Other cetaceans in the region show similar patterns in their population structure and biogeography. For example, Arabian Sea humpback whales, *Megaptera novaeangliae*, are a genetically isolated, non-migratory population restricted to the region since ~70 Ka (Minton et al., 2011; Pomilla et al., 2014). It is worth noting that the differentiation pattern seen in both genera in the IO is distinct from the North Atlantic, where bottlenose dolphins (*T. truncatus*) show strong differentiation across a geographic range where common dolphins (*D. delphis*) do not (Moura, Natoli, et al., 2013; Natoli et al., 2005).

5 | CONCLUSIONS

Our data highlight the unique biogeography of the northern IO for both focal genera, consistent with studies of other regional marine taxa. We suggest that morphological and genetic differentiation in this region are both consistent with a pattern of environmental change over the Quaternary that altered local patterns of productivity and habitat characteristics affecting prey resource and foraging strategy. Strong differentiation in the region identifies local populations of various species, including *T. aduncus* and *Delphinus* spp. as priority conservation units. Our study further identifies substructure at a fine geographic scale across the western IO range for *T. aduncus*, suggesting the need for multiple management units (including several off South Africa; c.f. Natoli et al., 2008, and two off Zanzibar; c.f. Särnblad et al., 2011). Over the longer term it seems that geological and oceanographic processes established an environment in the northern IO conducive to differentiation and speciation in these marine genera.

ACKNOWLEDGEMENTS

This study was partly supported by the Environment Society of Oman (ESO), The Rufford Small Grants for Nature Conservation, Darwin Initiative, WWF (Pakistan) and the Ministry of Education, Culture, Sports, Science and Technology, Japan (MEXT) to a project on Joint Usage/Research Center – Leading Academia in Marine and Environmental Research (LaMer), Ehime University (Japan). Thanks are due to Tomohiko Isobe for his assistance at es-BANK with samples from India. For providing samples we would like to acknowledge, Vic Peddemors and The Natal Shark Board (South Africa), the Oman Natural History Museum and the Museum am Löwentor, Staatliches Museum für Naturkunde, in Stuttgart, Germany. Thanks are due to Oman's Environment Authority (former Ministry of Environment and Climate Affairs) for providing permits to collect samples. Thanks are also due to Five Oceans Environmental Services LLC. and ESO for their assistance and support to collect, store and ship samples. Koen Van Waerebeek, Ken Findlay, Rupert Ormond, Babar Hussain and Umer Waqas are duly acknowledged for their fieldwork assistance. Samples from Portugal were collected during the PhD grant SFRH/BD/28012/2006 awarded to AEM by the Portuguese Fundação para a Ciência e Tecnologia, with logistic support by the companies Marina de Portimão, Nautiradar and AngelPilot. Biopsy sampling was carried out under permit from the Portuguese Institute for the Conservation of Nature and Biodiversity (ICNB). Sample collection in Zanzibar was funded by grants from the Western Indian Ocean Marine Science Association MASMA Programme and WWF Sweden. Biopsies were collected in Zanzibar under research permits issued by the Zanzibar Research Committee. We are grateful to Narriman Jiddawi, Juma Kifana and colleagues at the Institute of Marine Sciences, University of Dar es Salaam (Zanzibar, Tanzania) for their support. All ethical standards have been followed.

DATA AVAILABILITY STATEMENT

mtDNA control region haplotype data are available on Genbank at accession numbers: MW423866-MW423934 and MW430052-MW430054. Microsatellite DNA datafiles are available on the Dryad database at: https://doi.org/10.5061/dryad.3r2280gfb

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BIOSKETCH

Howard Gray (lead author) and **Rus Hoelzel** (corresponding author) are molecular ecologists who have worked extensively on understanding evolutionary process and the implications for conservation policy for marine mammal species. Co-authors include molecular ecologists and marine mammal biologists with experience in marine systems in general, and in the Indian Ocean environment in particular.

Authors' contributions: HG & ARH designed the study and wrote the paper. HG performed lab work, analyses and collected samples; IC, SN and ST performed lab work and contributed Indian samples, curated in Japan; AM, AS, MK, RC, AN, LP, GM, PB, MG, TC, AW & RB collected samples, provided fieldwork expertise and contributed regional knowledge. All authors read and commented on the manuscript draft.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Gray HW, Chen I, Moura AE, et al. Comparative biogeography and the evolution of population structure for bottlenose and common dolphins in the Indian Ocean. *J Biogeogr*. 2021;00:1–15. https://doi.org/10.1111/jbi.14102