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Multiple management units of short-beaked common dolphins subject to fisheries bycatch off southern and southeastern Australia

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ABSTRACT: Worldwide, fisheries bycatch remains one of the greatest immediate threats to cetacean populations. In Australia, short-beaked common dolphins are subject to bycatch mortality in 2 fisheries: the purse-seine fishery for sardines off central South Australia and the gillnet fishery for gummy sharks off southern Australia. The cumulative impact of bycatch from both fisheries on the dolphin population(s) in these regions are unknown. We used information from microsatellite markers and mitochondrial DNA to investigate population genetic structure and estimate contemporary migration rates in 332 biopsied and 15 stranded samples of common dolphins. Samples were collected from 11 locations along ~3500 km of coastline in southern and southeastern Australia. Bayesian and traditional analyses of population genetic structure revealed the presence of at least 6 management units of common dolphins, of which a minimum of 3 are potentially impacted by the 2 fisheries. These management units need to be managed separately for conservation purposes and for monitoring and mitigation of common dolphin fishery interactions off southern and southeastern Australia. We suggest that substructuring and migratory movements of common dolphins across these regions may be driven by spatial variations in oceanography, upwelling events and/or fish distribution. This study exemplifies how information on genetic substructuring in a neritic top predator can be valuable for fisheries bycatch management.

KEY WORDS: Fine-scale structure · Genetic structure · Gillnet · Purse seine · Oceanography · *Delphinus delphis*

INTRODUCTION

Globally, fisheries bycatch remains one of the greatest immediate threats to cetacean populations (Reeves et al. 2005, 2013). Over the last few decades, cetaceans in the order of hundreds of thousands have died yearly in fisheries around the world (e.g. Perrin 1968, 1969, Northridge & Hoffmann 1999, Read et al. 2003). Although fishery operational interactions with cetaceans have been documented for many fisheries worldwide, quantification of the bycatch and reduction of mortality has only been achieved for very few fisheries (Reeves et al. 2005). For example, in the tuna purse-seine fishery in the Eastern Tropical Pacific, >4 million short-beaked common dolphins *Delphinus delphis*, pantropical spotted dolphins *Stenella attenuata* and spinner dolphins *Stenella longirostris* were killed as bycatch between 1960 and 1972 (Wade 1995). This bycatch has been substantially reduced over the last 2 decades after extensive scientific research was undertaken to assess the impact of this fishery on the dolphin populations (e.g.

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Gerrodette & Forcada 2005), and strict bycatch mitigation methods and changes to fishing practices were implemented. However, research shows that none of these 3 species have shown signs of population recovery after depletion (Wade et al. 2007).

Research that focuses on identifying population genetic structuring of species that are impacted by fishery operational interactions can help to guide fisheries managers in bycatch management decisions. Genetic data have been widely used to identify units for conservation management (i.e. management units, MUs) (Frankham et al. 2010, Allendorf et al. 2013). Significant divergence of allele frequencies at nuclear or mitochondrial loci between populations is a key criterion in recognising MUs — these are usually thought to be demographically distinct populations that should be managed to ensure the viability of the larger metapopulation or species (Moritz 1995, Waples & Gaggiotti 2006). The identification of MUs is central to the management of natural populations and crucial for monitoring effects of human activity on species abundance (Palsbøll et al. 2007). MUs often respond independently to harvesting and management (e.g. Dizon et al. 1992), and this needs to be considered when mitigating fishery operational interactions with dolphins.

In Australian waters, the only common dolphin species present is the short-beaked common dolphin *Delphinus delphis* (hereafter referred to as common dolphin) (White 1999, Bell et al. 2002, Bilgmann et al. 2008, Möller et al. 2011). In southern and southeastern Australia, common dolphins are subject to bycatch mortality in Australian State and Commonwealth fisheries (e.g. Hamer et al. 2007, AFMA 2013). Operational interactions of common dolphins occur (1) with purse-seine vessels of the South Australian Sardine Fishery (SASF) in central South Australia (South Australian State water fishery) (Hamer et al. 2007) and (2) with the gillnet fishery for gummy sharks of the Southern and Eastern Scalefish and Shark Fishery (SESSF) off southern and southeastern Australia (Australian Commonwealth fishery) (AFMA 2013).

The SASF was established in 1991 and concentrates its purse-seine fishing activities in southern Spencer Gulf and Investigator Strait, South Australia (Rogers & Ward 2006, Hamer et al. 2007). Around 34 000 tonnes of sardines are caught each year and the majority of this catch is used to feed wild-caught southern bluefin tuna *Thunnus maccoyii* farmed near Port Lincoln, South Australia (Ward et al. 2012). Operational interactions of the SASF with common dolphins occur when dolphins are foraging on sardines *Sardinops sagax* targeted by the fishery (Hamer et al. 2008), which is one of the dolphin's main prey items in the area (Kemper & Gibbs 2001, Gibbs 2011). In 2004 to 2005, high bycatch rates of common dolphins in the SASF were discovered during an initial 7 mo observer programme. An estimated 1728 common dolphins were encircled and 377 dolphins died over this period (Hamer et al. 2008). Following this discovery, the SASF was temporarily closed, a 'threatened and endangered species' (TEPS) working group was established and a Code of Practice (CoP) developed to mitigate operational interactions with TEPS, particularly with common dolphins (Hamer et al. 2008, Ward et al. 2010). An observer programme was implemented in 2006 as part of the CoP. It required independent observers to be on board the fishing vessels for 10 to 30% of the fleet's fishing time (Hamer & Ward 2007, Hamer et al. 2008). Based on the observer data, estimated encirclement and mortality rates of common dolphins varied between 2005 and 2013, with an overall trend of reduction (Ward et al. 2013). The CoP has the potential of greatly reducing common dolphin bycatch rates, but observer coverage is low (6.6% in 2011 to 2012; and 9.8% in 2012 to 2013) and underreporting in fisheries logbooks when no observer is on board remains a problem to be resolved (Ward et al. 2012, 2013). A recent improvement to the CoP requires observer coverage from 2013 onwards to be calculated per net set rather than fleet's fishing time, because the latter overestimated the % observer coverage in years prior to 2013, i.e. the % coverage listed above (Ward et al. 2013).

Operational interactions with dolphins also occur in Australia's southern and southeastern continental shelf areas in the gillnet, hook and trap (GHAT) sector of the SESSF (AFMA 2013). The gillnet fishery started in the early 1970s and targets gummy sharks *Mustelus antarcticus* for human consumption (Walker et al. 2005). Although the gillnet fishery has been operating since the 1970s, high bycatch rates of dolphins only became known in 2010 when an observer programme was initiated to monitor interactions with endangered Australian sea lions (AFMA 2011, Hamer et al. 2011). Based on interaction reports by the gillnet fishery from 2011, the Australian Fisheries Management Authority (AFMA) estimated that at least 60 dolphin interactions occurred in that year, but this was likely to be an underestimate (AFMA 2011). In 2012–2013, 19 further dolphin interactions were reported, of which all but one were fatal (AFMA 2013). Operational interactions with this fishery are usually fatal for the dolphins involved, with a mortality rate of ~95% (AFMA 2011). The analysis of 40 dolphin mortalities recorded by electronic cam-

eras revealed that 38 were common dolphins *Delphinus delphis* and 2 bottlenose dolphins *Tursiops* spp. (AFMA 2013). Common dolphins are therefore likely to be the most frequently bycaught cetacean species in this fishery, although other cetacean and pinniped species potentially also become entangled. To mitigate operational interactions of the GHAT sector with dolphins, AFMA implemented a temporary gillnet closure in 2011 in waters of high dolphin interactions off eastern South Australia. Adjacent to the closure zone, a 'Dolphin Observation Zone' was created with mandatory 100% observer coverage either by independent observers or on board electronic monitoring systems (AFMA 2011). AFMA's *Regulation Impact Statement 2013* highlighted the lack of information about dolphin distribution and movements and recognised the need to clarify whether subpopulations of genetically distinct animals may be involved in gillnet fishery interactions (AFMA 2013).

This study aimed to identify MUs in common dolphins along the southern and southeastern Australian continental shelf to assist conservation and management of populations impacted by fisheries activities. Our previous studies on the population structure of common dolphins in southern Australia revealed genetic differentiation between South Australian and southeastern Tasmanian dolphins (Bilgmann et al. 2008). However, a gap in sampling between South Australia and Tasmania did not allow for clarification of whether this structure was due to a pattern of isolation by distance or a population boundary. Genetic differentiation was also found between Pacific Ocean and Indian Ocean common dolphins from Australia (Amaral et al. 2012), but there was also a major gap in sampling in southern Australia. In the present study, we used a larger number of samples (n = 308) collected along 3500 km of coastline and 2 gulfs, and a larger number of microsatellite loci (n = 14). This filled the sampling gaps of previous studies and enabled investigation of fine-scale genetic structure with enhanced statistical power (Table S1 in the Supplement at www.int-res.com/articles/suppl/m500p265_supp.pdf). Furthermore, we estimated contemporary migration rates among populations and interpreted the genetic data in relation to local geography, oceanography and prey distribution to propose potential drivers of genetic structuring. Our results revealed the presence of fine-scale genetic structure and a minimum of 6 common dolphin MUs in these regions. Based on our findings we provide recommendations for the management of fishery operational interactions with common dolphins in southern Australia.

MATERIALS AND METHODS

Study area and samples

Biopsy samples of free-ranging common dolphins were collected from 11 sampling locations in southern and southeastern waters off the Australian continent between 2004 and 2012: Western Australia — Albany, Esperance (n = 67); South Australia — Great Australian Bight, Spencer Gulf, Investigator Straight and Gulf St. Vincent, Robe (n = 182); Victoria — Portland, Melbourne, East of Wilsons Promontory (n = 63), Tasmania — southeastern Tasmania (n = 15); and New South Wales — Eden (n = 20). Samples from southeastern Tasmania originated from multiple stranding events (Fig. 1). The westernmost samples

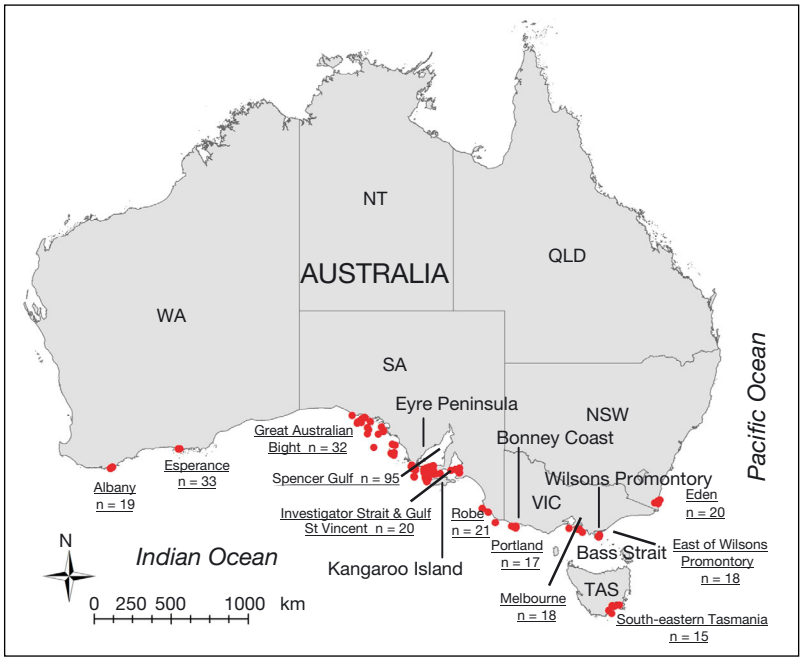

Fig. 1. Sampling regions of common dolphins in southern and southeastern Australia: (1) Albany, (2) Esperance, Western Australia (WA); (3) Great Australian Bight, (4) Spencer Gulf and south of the gulf, (5) Investigator Strait and Gulf St. Vincent, (6) Robe, South Australia (SA); (7) Portland, (8) Melbourne, (9) East of Wilsons Promontory, Victoria (VIC); (10) Eden, New South Wales (NSW); and (11) southeastern Tasmania, Tasmania (TAS). Dots represent exact locations of collected samples in the sampling regions. Sampling regions are underlined. Numbers represent sample sizes after removal of duplicate samples

were obtained from King George Sound, Albany, in Western Australia (35° 4′ S, 117° 59′ E) and the easternmost from Eden, in New South Wales (36° 54′ S, 150° 3′ E). Sampling locations between these 2 regions were located in coastal and continental shelf waters and were approximately equally spaced. Biopsy samples were collected from multiple dolphin schools (Table 1) using a hand-held biopsy pole system for bow-riding dolphins (Bilgmann et al. 2007) or a remote biopsy gun system (PAXARMS) (Krützen et al. 2002). Dolphins that were sighted in close spatial proximity (i.e. with distances of <50 m between individuals), while displaying similar behaviour or bow-riding, were considered as one school. Biopsy samples were preserved in either 90% ethanol or salt saturated DMSO and stored at −20°C.

Genetic methods

Genomic DNA was extracted following a salting-out protocol modified from Sunnucks & Hales (1996). The sex of each dolphin was genetically determined by PCR following Möller et al. (2001). Each dolphin was genotyped for 14 polymorphic microsatellite markers: 8 tetranucleotides, Tur4_80, Tur4_87, Tur4_105, Tur4_141, Tur4_142, Tur_F10, Tur_E12 (Nater et al. 2009), Dde59 (Coughlan et al. 2006); and 6 dinucleotides, Dde66 (Coughlan et al. 2006), KW12 (Hoelzel et al. 1998), EV1, EV37 (Valsecchi & Amos 1996), MK6 and MK8 (Krützen et al. 2001). Microsatellite amplification was carried out following Amaral et al. (2012). For each dolphin sample, a 438 bp fragment of the mtDNA control region was amplified following PCR conditions described in Möller & Beheregaray (2001) and sequenced in an ABI 3130 (Applied Biosystems).

Data analysis methods

Microsatellites

We used MICROCHECKER v.2.2.3 to identify genotyping errors (Van Oosterhout et al. 2004) and CERVUS 3.0 (Marshall et al. 1998) to identify potential duplicate samples. For the latter, all sample pairs that showed up to 2 differing alleles were re-checked for potential scoring errors. After re-checking, samples were considered duplicates if (1) all genotypes were identical, (2) mtDNA control region sequences matched and (3) the animals were of the same sex. A total of 20% of samples were also re-genotyped to assess reliability. We tested for departures from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium between pairs of loci using GENEPOP v.4.0.1 (Rousset 2008). The Bayesian clustering method implemented in the program STRUCTURE v.2.3.3 (Pritchard et al. 2000, Hubisz et al. 2009) was used to assess population structure and to identify the most likely number of populations (K). We ran 5 independent STRUCTURE runs for each value of K between 1 and 13 using the following parameters: 100 000 burn-in, 1 million iterations, correlated allele frequency model, admixture model of ancestry, and with and without location information (LOCPRIOR). The most likely number of K was determined with STRUCTURE HARVESTER v.0.9.62 (Earl & vonHolt 2012), using the Evanno method (Evanno et al. 2005). Furthermore, we used GENELAND v.3.0.0 (Guillot et al. 2009), a geo-referenced Bayesian clustering approach, to compare the sample clustering with that determined by STRUCTURE. Identified populations were then re-tested for departures from HWE using GENEPOP. Genetic diversity measures, including number of alleles per locus (NA), expected (H_E) and observed

Table 1. Samples of common dolphins from southern and southeastern Australia grouped into the 6 identified management units (MUs). Sample size, number of sampled males (M) and females (F), and number of schools sampled are displayed for each MU and overall. IO: Indian Ocean; PO: Pacific Ocean. Information is also provided about environment type: gulf, coastal or shelf waters

Population	Ocean basin	Sample size	M	F	Sampled schools
MU 1 (Albany, Western Australia)	IO (coastal)	19	6	13	5
MU 2 (Esperance, Western Australia)	IO (coastal)	33	22	11	7
MU 3 (Great Australian Bight, South Australia)	IO (coastal, shelf)	32	18	14	9
MU 4 (Eyre Peninsula, South Australia to Wilsons Promontory, Victoria)	IO (coastal, gulf, shelf)	143	73	70	63
MU 5 (East of Wilsons Promontory, Victoria)	IO (coastal)	18	8	10	4
MU 6 (southeastern Australia, New South Wales and Tasmania)	PO (coastal, shelf)	63	35	28	16
Total		**308**	**162**	**146**	**104**

(H_O) heterozygosities were determined in Arlequin v.3.5.1.2 (Excoffier & Lischer 2010). Allelic richness (*AR*), which adjusts for differences in sample sizes, was calculated in FSTAT v.2.9.3.2 (Goudet 1995).

To test for a relationship between genetic and geographic distance, we used a mantel permutation procedure implemented in GENEPOP and performed a spatial autocorrelation analysis in GENALEX 6.5 (Peakall & Smouse 2012). We chose variable distance size classes for the spatial autocorrelation analysis between 0 and 3000 km, with steps of 20 km up to 100 km, steps of 100 km between 100 and 600 km, and 400 km between 600 and 3000 km.

For a further assessment of genetic differentiation between populations, we used ARLEQUIN for Wright's fixation index (F_{ST}) pairwise comparisons. In addition, we calculated Slatkin's fixation index (R_{ST}) and Jost's D_{est} pairwise comparisons in GENALEX. Contemporary migration rates (over the last few generations) among the identified common dolphin populations were estimated using BAYESASS v.3.0.1 (Wilson & Rannala 2003). Five independent runs were performed using 1 million burn-in and 11 million Markov Chain Monte Carlo (MCMC) repetitions, and a sampling interval of 100. The mixing parameters were adjusted according to Rannala (2007). The reliability of migration rate estimates was assessed by checking for consistency in the estimates between runs. The MCMC Trace Analysis Package TRACER v.1.5 (Rambaout & Drummond 2009) was used to combine the results from the 5 independent runs, and trace files were examined for sufficient burn-in length and to confirm evidence of convergence and mixing.

Mitochondrial DNA

Mitochondrial DNA control region sequences were aligned and edited in SEQUENCER v.4.1.2 (Gene Codes Corporation). ARLEQUIN v.3.5.1.2 was used to estimate haplotypic (*h*) and nucleotide (π) diversities for populations determined in STRUCTURE and GENELAND based on microsatellite data. Genetic differentiation for mtDNA was estimated based on these same groupings. We used Φ_{ST} which takes haplotype frequency and nuclear distance into account, applying the Tamura-Nei model of sequence evolution (gamma correction, $\alpha = 0.5$) previously determined by MODELTEST v.3.06 (Posada & Crandall 1998) to be the most suitable for these common dolphins (Bilgmann et al. 2008). Finally, we constructed a haplotype network with NETWORK v.4.6.1.0 (Bandelt et al. 1999) to assess genealogical relationships.

RESULTS

Samples

A total of 332 biopsy samples of free-ranging common dolphins were collected across southern and southeastern Australia and 15 samples from strandings in southeastern Tasmania (Fig. 1). Duplicate samples (n = 39) were identified and removed, with only 3 showing up to 2 mismatched alleles due to scoring errors. All remaining samples (n = 308) were used for the data analysis of microsatellites and mtDNA control region sequences. The 20% of samples that were re-genotyped and re-scored yielded the same genotypes for all individuals (i.e. an error rate of 0%). One of the 14 microsatellite loci, Dde59, showed a null allele frequency of 12% and was therefore removed from the data set. For the other loci, either no evidence for null alleles was found or the estimated frequency was relatively small (<5%). All further microsatellite data analyses were therefore conducted using the 13 remaining loci.

Microsatellites — genetic differentiation

Results from the Bayesian clustering method implemented in the program STRUCTURE showed clustering of common dolphins from southern and southeastern Australian waters into 6 genetically differentiated populations. Although these results were obtained for both the admixture and no admixture model, we present results for the admixture model only, as this is more appropriate for data sets representing closely related populations (Pritchard et al. 2010). These 6 genetically distinct populations were obtained in 2 steps. First, STRUCTURE confirmed the previously identified genetic separation of Australian Indian Ocean versus Pacific Ocean common dolphins ($K = 2$, using the method of Evanno et al. 2005) (Bilgmann et al. 2008, Möller et al. 2011, Amaral et al. 2012). Common dolphins sampled off southern Australia (Indian Ocean) had a high membership probability to population 1 (with the exception of 3 dolphin schools that had the majority of animals clustered with population 2), while all individuals sampled off southeastern Australia (Pacific Ocean) had a high membership probability to population 2 (Fig. 2a). The schools that had individuals from the Indian Ocean sample that clustered with the Pacific Ocean population 2 were schools 63 (n = 17), 81 (n = 8) and 84 (n = 3). These schools also had a minority of individuals that assigned with high probability to the Indian

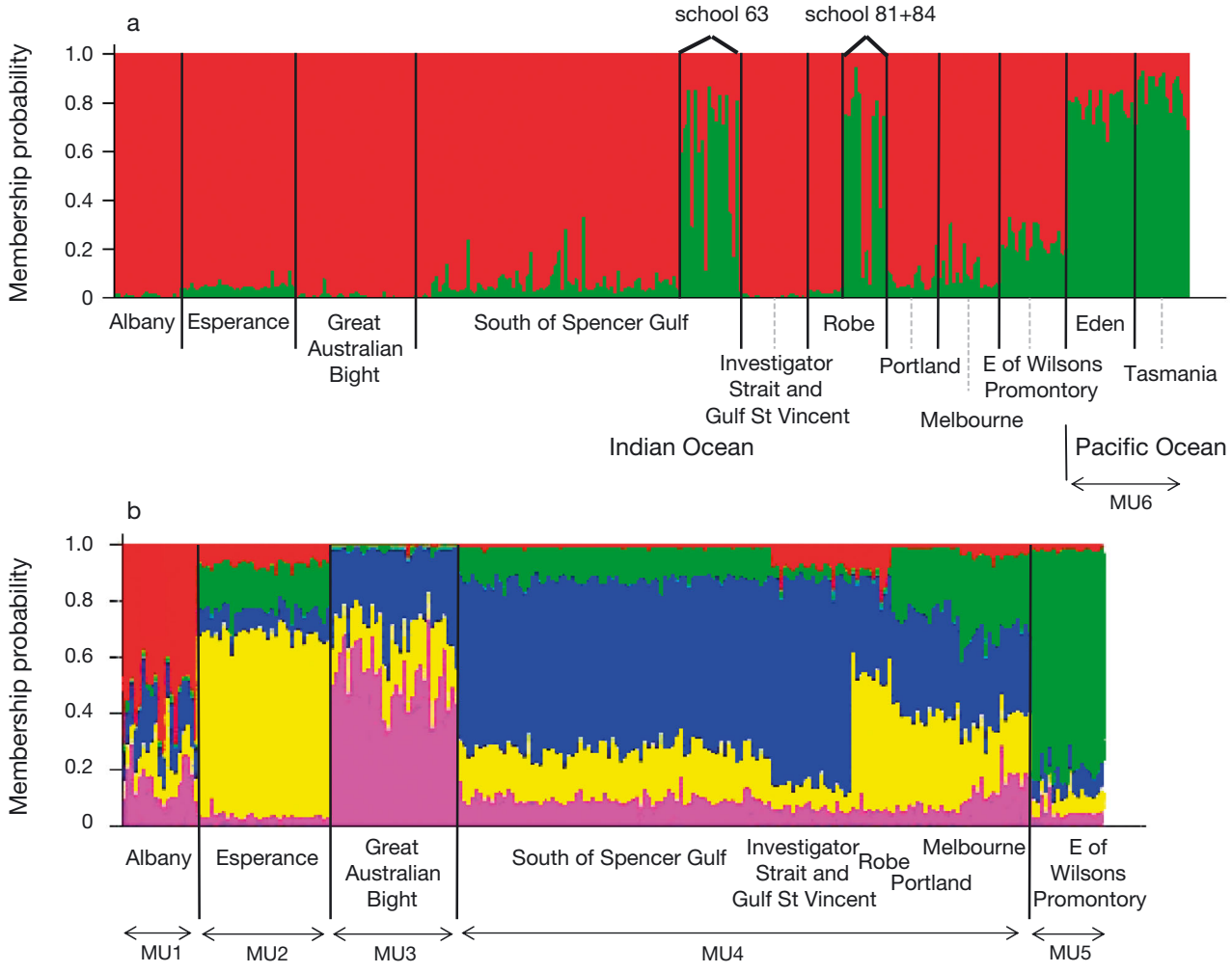

Fig. 2. Results from the analysis in STRUCTURE showing colour-coded membership probabilities of dolphins to the respective populations. Each dolphin is represented by one vertical line. Sampling locations are presented along the *x* axis. (a) Graph of the first analysis step showing the clustering of common dolphins from southern and southeastern Australia into 2 populations located in the Indian and Pacific oceans (n = 308). Displayed in green is management unit MU 6, which includes dolphin schools 63, 81 and 84. Displayed in red are all other samples from southern Australia for which further clustering was elucidated in a second analysis in STRUCTURE. (b) Graph of the second analysis step showing the clustering of common dolphins from southern Australia (Indian Ocean) into 5 further populations (n = 241; animals of the Pacific Ocean MU 6 and the 3 schools with potential migratory dolphins were excluded from the analysis to increase the statistical power of the program). Each dolphin is represented by one vertical line and the colours show the membership probabilities for the 5 populations. Dolphins were grouped into MUs (MU 1 to MU 5) based on colour patterns and the strongest differences between these colour patterns determined the grouping into 5 populations ($K = 5$ determined with the Evanno method)

Ocean sample, showing evidence for mixed schools of Indian and Pacific ocean dolphins. For the data analyses that required *a priori* grouping of individuals, we grouped all sampled dolphins from the 3 schools that contained Pacific Ocean dolphins with the Pacific Ocean population (population 2). This was done because we could not differentiate whether mixed schools occurred due to random aggregation, social mixing or potential interbreeding. Thus, the strategy of moving all individuals from the 3 schools to the Pacific cluster was used to ensure genetic differentiation among the populations was not overestimated. However, it may potentially bias the results towards slightly lower genetic differentiation between Pacific Ocean and Indian Ocean populations.

In a second step in STRUCURE, we removed from the data set the Pacific Ocean population 2 (individuals from Eden and southeastern Tasmania, and all individuals of the 3 potential migratory groups for a conservative approach) to provide higher statistical power in subsequent analyses of population 1. We then performed the analyses (n = 241) with and

without sampling location information (LOCPRIOR model; Hubisz et al. 2009) (Fig. 2b, with LOCPRIOR; Fig. S1 in the Supplement, without LOCPIOR). The advantages of the LOCPRIOR models in STRUCTURE are that they are able to use sampling location information when the ancestry of individuals is correlated with the locations, but do not falsely infer structure when it is not present (Pritchard et al. 2010). In this second analysis, STRUCTURE identified an additional 5 genetically differentiated clusters ($K = 5$, using the method of Evanno et al. 2005) when location information was given (Fig. 2b), but showed no subdivision when location information was not used as a prior (highest posterior probability at $K = 1$; Fig. S1 in the Supplement). A similar analysis was undertaken by excluding population 1 (Indian Ocean) and running the same models in STRUCTURE including only the individuals of population 2 (Pacific Ocean). No further subdivision in the Pacific Ocean sample was suggested by STRUCTURE ($K = 1$), with and without sampling location information (results not shown). Further STRUCTURE analysis did not suggest additional subdivision of Indian Ocean population 4, and this was despite the subtle level of substructure suggested in the graphical output for the Robe, Portland and Melbourne samples. Altogether, STRUCTURE identified 6 populations in southern Australia: 5 in the Indian Ocean that showed moderate levels of genetic differentiation among each other, and 1 in the Pacific Ocean (south-eastern Australia) with marked genetic differentiation from all others in the Indian Ocean (Fig. 2b).

The spatial model in GENELAND (Guillot et al. 2009) identified the same 6 populations as in STRUCTURE (Fig. 3). The only difference was a slight shift of one population boundary west into the Great

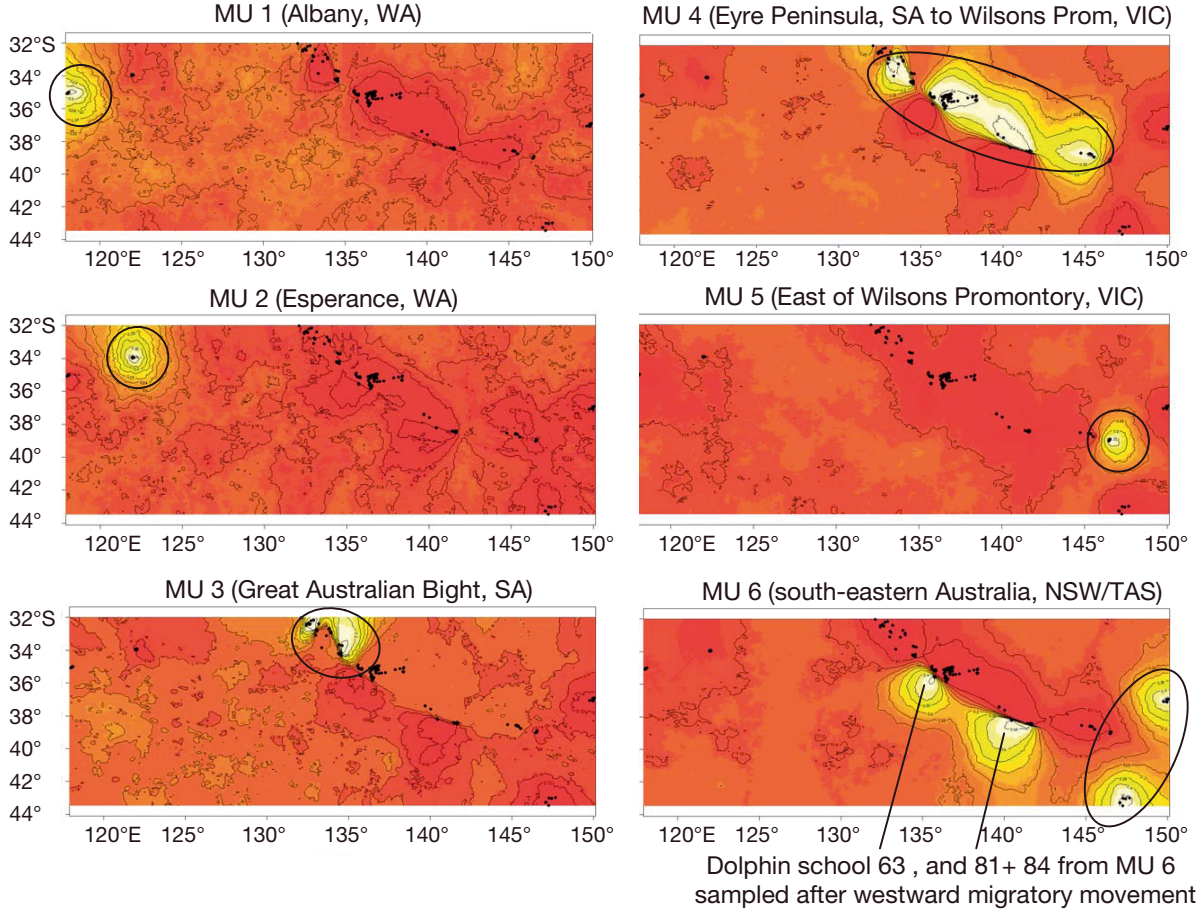

Fig. 3. Posterior probabilities and population membership from the spatial model in GENELAND for short-beaked common dolphins sampled in 11 sampling regions of southern and southeastern Australia. Black lines represent spatial positions of genetic discontinuities. The colour scaling specifies the range between a high (white) and low (red) membership probability to a population or management unit (MU). Approximate geographic location and boundaries of the 6 MUs are indicated with black circles or ovals. Coastline is not depicted

Table 2. Summary of genetic variability for 6 management units (MUs) of common dolphins from southern (Indian Ocean) and southeastern Australia (Pacific Ocean), based on mtDNA control region sequences and 13 microsatellite loci. *NH*: number of haplotypes; *h*: haplotypic diversity; π: nucleotide diversity; *NA*: mean number of alleles per locus; *AR*: allelic richness; H_E: mean expected heterozygosity; H_O: mean observed heterozygosity. Values in parentheses are standard errors. IO: Indian Ocean; PO: Pacific Ocean

Population	mtDNA			Microsatellites			
	NH	*h*	π	*NA*	*AR*	H_E	H_O
MU 1 IO (Albany, Western Australia)	6	0.84 (0.05)	0.0156 (0.0086)	5.3	5.1	0.63 (0.17)	0.64 (0.20)
MU 2 IO (Esperance, Western Australia)	8	0.80 (0.05)	0.0161 (0.0086)	6.6	5.6	0.63 (0.15)	0.64 (0.16)
MU 3 IO (Great Australian Bight, South Australia)	13	0.89 (0.04)	0.0200 (0.0105)	6.5	5.4	0.60 (0.19)	0.59 (0.18)
MU 4 IO (Eyre Peninsula, South Australia to Wilsons Promontory, Victoria)	44	0.95 (0.01)	0.0215 (0.0110)	10.0	5.9	0.61 (0.14)	0.64 (0.14)
MU 5 IO (East of Wilsons Promontory, Victoria)	4	0.47 (0.13)	0.0072 (0.0044)	5.9	5.7	0.65 (0.15)	0.65 (0.17)
MU 6 PO (southeastern Australia, New South Wales and Tasmania)	38	0.98 (0.01)	0.0180 (0.0094)	10.5	7.2	0.77 (0.10)	0.75 (0.10)

Australian Bight. GENELAND also corroborated the identification of the potential migratory schools of common dolphins from southeastern Australia (Fig. 3). For all further analyses, we used the population boundaries identified in STRUCTURE, since genetic clustering matched geographic locations of samples best. Sample sizes for the 6 identified common dolphin populations ranged between 18 and 143 with similar sex ratios for each population and altogether (Table 1). The populations showed no deviations from HWE (Tables 2 & S2 in the Supplement) after sequential Bonferroni correction.

Pairwise F_{ST} comparisons revealed significant to highly significant genetic differentiation between all populations. R_{ST} pairwise comparisons were slightly lower than F_{ST}, and Jost's D_{est} values were higher. All 3 measures showed either significant ($p \leq 0.05$) or highly significant ($p \leq 0.001$) results for the pairwise comparisons. We therefore only report F_{ST} values here, which ranged between 0.007 ($p \leq 0.05$) and 0.055 ($p \leq 0.001$) for the 5 populations off southern Australia (Indian Ocean), and between 0.045 ($p \leq 0.001$) and 0.082 ($p \leq 0.001$) between the Indian and Pacific oceans (Table 3).

To exclude the possibility that kinship structure may have influenced the results, analyses (F_{ST} and Bayesian modelling) were repeated by excluding 1 of each pair of individuals with a relatedness value higher than 0.5 (theoretical value for first-order relationships) in a given locality. Mean pairwise relatedness (r) values were estimated in COANCESTRY v.1.0.1.2 (Wang 2011), using the index of Queller & Goodnight (1989). Only 33 pairs of all pairwise sample combinations had r values higher than 0.5 within localities, and results of genetic structure analyses remained very similar when excluding 1 of each pair (data not shown). Therefore, the whole data set was kept for analyses.

Mantel tests revealed no significant correlation between genetic and geographic distance regardless of whether we tested all MUs or the Indian Ocean MUs only ($p = 0.26$ and $p = 0.20$, respectively). A spatial autocorrelation analysis (excluding the 3 migratory dolphin schools to not bias the correlation of genetic and geographic distance) revealed that dolphin samples separated by <60 km showed a significant positive autocorrelation, whereas those separated by ~1800 km and >2500 km were significantly less related to each other (Fig. S2 in the Supplement). In an isolation by distance scenario,

Table 3. Pairwise fixation indices between 6 common dolphin management units (MUs) from southern and southeastern Australia based on mtDNA control region sequences and 13 microsatellite loci. Mitochondrial Φ_{ST} values are above the diagonal; microsatellite Wright's fixation index (F_{ST}) values are below. For location descriptions of MU 1 to 6 see Fig. 5. *$p \leq 0.05$, **$p \leq 0.001$

	MU 1	MU 2	MU 3	MU 4	MU 5	MU 6
MU 1		−0.008	0.111**	0.065**	0.339**	0.082**
MU 2	0.033**		0.131**	0.092**	0.345**	0.103**
MU 3	0.038**	0.018**		0.063**	0.297**	0.064**
MU 4	0.024**	0.007*	0.009**		0.232**	0.033**
MU 5	0.055**	0.018*	0.047**	0.025**		0.234**
MU 6	0.082**	0.058**	0.079**	0.062**	0.045**	

we would expect that genetic relatedness would consistently decrease over increasing geographic distance, with relatedness values falling outside the 95% confidence interval. Thus, in agreement with the Mantel test, we did not find significant isolation by distance for common dolphins in southern and southeastern Australia.

Migration rates

Estimated contemporary migration rates between most of the 6 identified populations were very low (m = 0.00 to 0.01) (Table 4). Moderate migration rates (m = 0.24 to 0.29) were estimated only for individuals migrating from the 4 populations of Albany (MU 1), Esperance (MU 2), Great Australian Bight (MU 3) and East of Wilsons Promontory (MU 5) into the population of Eyre Peninsula to Wilsons Promontory (MU 4). This latter population, which shows an influx of individuals from neighbouring common dolphin populations, is located in the geographic region where fishery operational interactions occur with both the purse-seine and gillnet fisheries. Genetic migration into this population was estimated to be unidirectional, i.e. dolphins are rarely spreading alleles out of this population into others (Table 4). The estimated influx of individuals into MU 4 from nearby populations (MU 1, 2, 3 and 5) could also be an effect of unequal samples sizes. In analyses using BAYESASS, smaller populations often show higher proportions of individuals in the population migrating compared with larger populations (Wilson & Rannala 2003), and accuracy of estimates generally improves with increased sample sizes (Wilson & Rannala 2003, Faubet et al. 2007). Extremely low genetic migration rates (m = 0.00 to 0.07, bidirectional) were estimated between the Australian Pacific Ocean population and any of the remaining 5 Indian Ocean populations, confirming the marked genetic differentiation between dolphins from the 2 ocean basins.

Table 4. Contemporary migration rates estimated in BAYESASS among 6 short-beaked common dolphin management units (MUs) from southern and southeastern Australia. Values in **bold** represent rates of residency for dolphins in each MU. Estimated migration rates >0.10 are displayed in *italics*

Migration into:	Origin: MU 1	MU 2	MU 3	MU 4	MU 5	MU 6
MU 1	**0.68**	0.01	0.01	0.00	0.01	0.00
MU 2	0.01	**0.68**	0.01	0.00	0.01	0.00
MU 3	0.01	0.01	**0.68**	0.00	0.01	0.00
MU 4	*0.27*	*0.28*	*0.30*	**0.98**	*0.24*	0.07
MU 5	0.01	0.01	0.01	0.00	**0.68**	0.01
MU 6	0.01	0.01	0.01	0.01	0.04	**0.91**

Mitochodrial DNA control region — genetic differentiation and genealogical relationships

Mitochondrial DNA Φ_{ST} values also showed highly significant levels of genetic differentiation for most pairwise comparisons, with the exception of Albany and Esperance (Φ_{ST} = 0.00, $p > 0.05$) (Table 3). In contrast to the microsatellite F_{ST} values, a higher level of genetic differentiation between the Pacific Ocean population (southeastern Australia) and those from the Indian Ocean (southern Australia) could not be detected for mtDNA. The constructed network showed a star-like phylogeny with high haplotypic diversity (Fig. 4). Although haplotype frequencies differed between populations, no clear separation in geographic regions was detected in the network. The Pacific Ocean population shared 8 of its 41 sampled

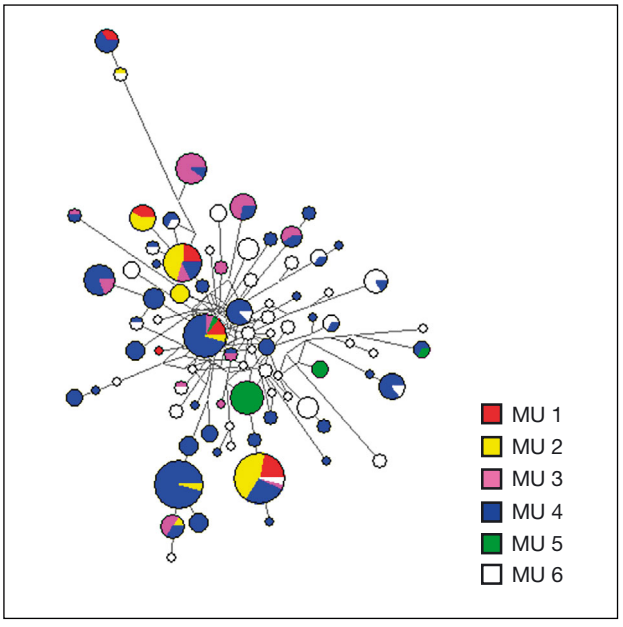

Fig. 4. Median-joining network of mtDNA control region sequences for the 6 identified management units (MU 1 to MU 6) of short-beaked common dolphins in southern and southeastern Australia. Sizes of circles are proportional to the number of individuals that exhibit a particular haplotype. The 6 MUs are colour coded and each pie chart (haplotype) shows the proportion of individuals from a particular MU. The length of lines in the network is proportional to the number of mutational steps between haplotypes. For details of geographic location and boundaries of each MU see Fig. 5

haplotypes with populations from the Indian Ocean. A total of 83 haplotypes were sampled from both ocean basins together. GenBank Accession Numbers of sequences in the haplotype network are KJ493702–KJ493765, FJ175421, FJ175422, FJ175434, FJ175437, FJ175439–FJ175442, FJ175444, FJ175446, FJ175447, FJ175449, HQ223452, HQ223454, HQ223455, HQ223459, HQ223461, HQ223471, and HQ223472.

Genetic diversity

Levels of genetic diversity were moderate for all southern Australian populations and relatively high for the southeastern Australian population (Tables 2 & S2, the latter in the Supplement). Mitochondrial DNA diversities were relatively high for all populations with the exception of the East of Wilsons Promontory population. Most of the dolphins sampled in this location had the same haplotype for the mtDNA control region (Table 2, Fig. 4).

DISCUSSION

Common dolphin MUs in southern and southeastern Australia and their relation to ocean basins and oceanographic features

Our population genetic analysis of common dolphins from shelf, coastal, gulf and embayment waters of southern and southeastern Australia revealed marked levels of genetic structure that are best explained by the existence of 6 distinct populations (Fig. 5). Population differentiation was detected along a west–east distribution rather than among gulf, coastal and shelf waters. However, no significant isolation by distance was detected over this spatial scale (Fig. S2 in the Supplement). The levels of genetic differentiation and inferred low contemporary migration rates detected among the 6 populations suggest that these populations should be considered as 6 MUs for conservation and management purposes. These represent the minimum number of MUs for this species in southern and southeastern Australia. Additional MUs could potentially be present in regions where little or no genetic sampling effort has yet taken place (e.g. Bremer Bay in Western Australia, Port Phillip Bay in Victoria, and waters off northern and western Tasmania). Five of these MUs are located in the Indian Ocean (off southern Australia), and the sixth one in the Pacific Ocean (off southeasthern Australia). The latter showed a higher level of genetic differentiation from all others, as previously reported (Bilgmann et al. 2008, Möller et al. 2011, Amaral et al. 2012). This is in contrast to short-beaked common dolphins in the North Atlantic where panmixia was reported over similar spatial scales (Moura et al. 2013). Our analyses presented here fill the sampling gap of previous studies along the southern Australian coast and indicate that isolation by distance does not explain the marked genetic differentiation found within the Indian Ocean, and between Indian Ocean and Pacific Ocean common dolphins in Australia. Oceanographic currents in coastal and pelagic waters off Australia differ markedly between the Pacific and Indian oceans (Cirano & Middleton 2004). Southeastern Australia

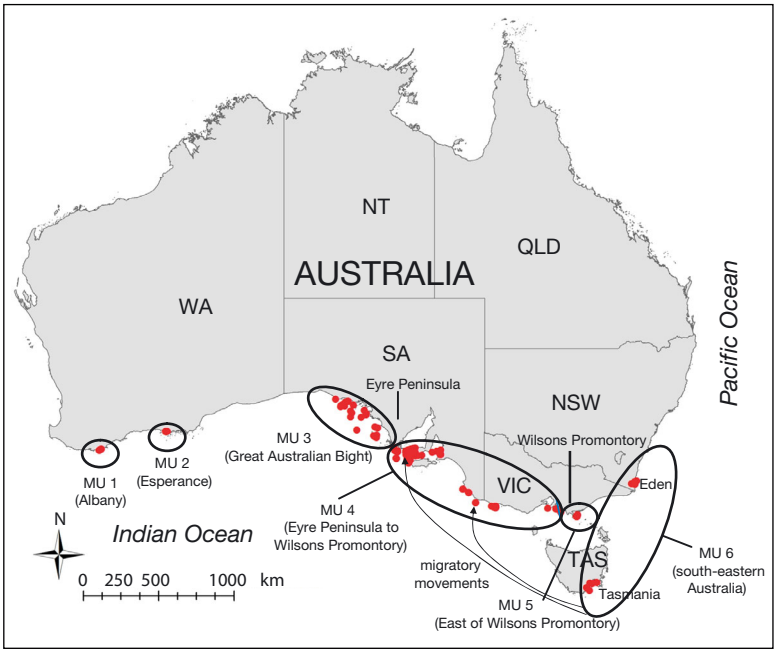

Fig. 5. Location and approximate boundaries of the 6 identified management units (MU 1 to MU 6) of short-beaked common dolphins in southern and southeastern Australia. MU 1: Albany, Western Australia (embayment of King George Sound); MU 2: Esperance, Western Australia (region of the Recherche Archipelago); MU 3: Great Australian Bight, South Australia (shelf and coastal waters); MU 4: Eyre Peninsula in South Australia to Wilsons Promontory in Victoria (including both South Australian gulfs, Investigator Strait, and coastal and shelf waters and western Bass Strait); MU 5: East of Wilsons Promontory, Victoria (coastal waters of northern Bass Strait); and MU 6: Southeastern Australia (coastal and shelf waters off Eden, New South Wales, and southeastern Tasmania)

(Pacific Ocean) is influenced by oceanographic conditions associated with the East Australian Current, whereas southern Australia (Indian Ocean) forms one of the longest stretches of southward-facing coastline in the world and exhibits a very complex oceanography (Cirano & Middleton 2004). Over the southern Australian continental shelf where common dolphins were biopsy sampled as part of this study, in particular in the Great Australian Bight, the predominant currents show an eastward flow in winter and a westward flow in summer (Middleton & Bye 2007). In general, the complex oceanography in southern Australia drives upwellings in relatively stable locations each year: the Bonney coast, the region west of Kangaroo Island and off western Eyre Peninsula (Middleton & Bye 2007). These upwellings cause significant spatial variation in primary productivity (Van Ruth et al. 2010), leading to variation and patchiness in schools of small pelagic fish (Ward et al. 2009), which are targeted by common dolphins as one of their primary prey (Gibbs 2011). Although the oceanography of the region is not very well understood, it is possible that the substructuring observed in common dolphins is driven by spatial variation in oceanography and/or fish distribution. Associations of common dolphins to specific water masses with varying fish assemblages were previously suggested for Eastern Australia (Möller et al. 2011).

Common dolphin migratory movements into upwelling areas across an ocean basin boundary

The contemporary migration rates inferred in this study between Australia's Pacific Ocean common dolphins (MU 6) and those from the Indian Ocean (MU 1 to MU 5) were very low. Interestingly, dolphin schools composed primarily of individuals genetically identified as belonging to Pacific Ocean MU 6 were biopsy sampled on 3 occasions in the Indian Ocean off southern Australia (MU 4). This suggests that Pacific Ocean dolphins show migratory movements into southern Australia, crossing an ocean basin boundary. The migratory movements, which occurred in April 2007, February 2011 and January 2012, correspond with the location and timing of upwelling events in the region. Unique shelf water upwelling occurs each year west of Kangaroo Island, South Australia, and along the Bonney coast, eastern South Australia and eastern Victoria, in summer and autumn (November to April) (Middleton & Bye 2007, Van Ruth et al. 2010). Where upwelling occurs, high primary productivity caused by nutrient-rich water near the surface supports high densities of small pelagic schooling fish (Ward et al. 2009). The upwellings that occur off Kangaroo Island and the Bonney coast are believed to be important drivers of the ecology of this region (Middleton & Bye 2007) and common dolphins from southeastern Australia may migrate across an ocean basin boundary to feed. Our results indicate that mixed dolphin schools of local MU 4 and migratory MU 6 dolphins occur in these areas and may feed on the same food resources. However, our estimates of migration rates indicate negligible contemporary gene flow between migrant and local dolphins, suggesting that they rarely interbreed, even when occurring in the same geographic region. Migratory movements of Indian Ocean common dolphins in the opposite direction were not detected.

A better understanding of migratory movements of common dolphins is particularly important when schools move through areas in which commercial fisheries operate, making them subject to operational interactions (i.e. in purse-seine and/or gillnet fisheries off southern Australia). For example, purse-seine fishing vessels of the SASF operate in the upwelling area west of Kangaroo Island, and the Commonwealth gillnet fishery utilises the Bonney upwelling region. Consequently, not only the local common dolphin MU 4 is at risk of depletion, but potentially also the Pacific Ocean MU 6 when individuals of this unit migrate into fishing areas. Assignment tests of genetic samples of dolphin bycatch from fisheries to their MU of origin could clarify which dolphin MUs are subject to fishery operational interactions.

Implications for fisheries management

The presence of 6 MUs of short-beaked common dolphins in southern and southeastern Australia, and the observed migratory movements of common dolphins across an ocean basin boundary, emphasises the urgent need for an immediate reassessment of management practices of operational interactions between common dolphins and the SASF (purse-seine fishery) and the SESSF (gillnet fishery). This includes consideration of location, geographic boundaries, and genetic and demographic properties of each MU, and an assessment of which MUs are impacted and to what extent. Considering population genetic structuring in species that are impacted by fishery operational interactions is key to successful management and mitigation of these fishery interac-

tions. For example, recent changes to management practices in the gillnet fishery off South Australia were adopted after it was discovered that female Australian sea lion genetic structure was driven by fine-scale foraging site fidelity (Lowther et al. 2012). As a result, AFMA implemented spatial closures around sea lion colonies in the area to protect this species from gillnet fishery interactions at the colony (subpopulation) level. To enhance the current *Australian Sea Lion Management Strategy*, extreme bycatch trigger limits (1 to 2 animals per 12 mo period in 6 zones, and 5 animals in a 7th zone) have been adopted for determining spatial closure in cases where trigger limits are reached (AFMA 2012b).

For common dolphins off South Australia, our results showed that the core SASF purse-seine fishing areas of Spencer Gulf and Investigator Strait, north of Kangaroo Island (Hamer et al. 2008), fall into the geographic region of common dolphin MU 4 (Eyre Peninsula, South Australia to Wilsons Promontory, Victoria) and therefore this MU is likely to be the most impacted by the SASF. At least 2 further MUs are potentially impacted by this fishery: MU 3 (Great Australian Bight, South Australia) because of its proximity to the core purse-seine fishing areas; and MU 6 (southeastern Australia) due to migratory movements of common dolphins from this MU into central South Australia where the SASF operates. If common dolphins from the MU 6 are also bycaught, it would imply that operational interactions have a much larger impact on common dolphins in Australia than previously thought.

Similar to the purse-seine fishery, the gillnet fishery of the SESSF is likely to impact on the local Indian Ocean MU 4 and the Pacific Ocean MU 6 from southeastern Australia due to migratory movements of dolphins into or through core fishing areas. MU 3 and MU 5 are potentially also impacted considering the locations of recent fatal dolphin interactions in this fishery (AFMA 2013). Future research is needed to (1) identify which MUs are subject to operational interactions in the purse-seine and gillnet fisheries off southern Australia, and to what level these are impacted, (2) obtain information on the life history of southern and southeastern Australian common dolphins, (3) conduct abundance estimates for common dolphins in areas of MU 4 that have previously not been surveyed, and for the southeastern Australian MU 6, and (4) apply ecological modelling approaches, such as population viability analysis (PVA), to assess long-term sustainability of these MUs. Aerial surveys across South Australian waters and the collection of specimens and genetic samples of bycaught common dolphins in the SASF and SESSF will provide important information (abundance, life history, MU of origin) to carry out PVA and assess population-level impacts of bycatch.

Specifically, for management and mitigation of operational interactions in both fisheries (purse-seine and gillnet), we highlight the importance of implementing 100% observer coverage on all fishing vessels during all months the fisheries operate. Previous research has confirmed that the CoP, developed to mitigate operational interactions with dolphins in the SASF, could lead to a false sense that the problem has been solved (Wiley at al 2008). Bycatch mitigation programmes are most effective when 100% observer coverage is in place (see Bilgmann et al. 2008). Only with an understanding of the abundance of common dolphins across southern Australian waters and robust estimates of bycatch rates in the SASF and SESSF fisheries will a population-level assessment and long-term management for sustainability of these MUs be possible.

CONCLUSIONS

Fishery operational interactions with cetaceans, and in particular with dolphins, are a problem yet to be solved. This study exemplifies how information on genetic structure and the identification of MUs in a coastal and neritic top predator can provide valuable information for fisheries bycatch management. Our results revealed genetic structure for common dolphins over a small spatial scale, in a region that is heavily utilised by fisheries. The genetic structure of common dolphins in southern Australia appears to be related to geographic (ocean basins) and oceanographic (currents and upwellings) features, potentially driven by spatial variations in fish distribution. We also detected migratory movements of schools of common dolphins from the Pacific Ocean into upwelling areas of the Indian Ocean off southern Australia. These upwelling areas with high fish abundance are also frequently utilised by purse-seine and gillnet fisheries, thus putting both local and migratory common dolphins at risk of operational fishery interactions. As a result of the fine-scale genetic structure found for common dolphins in the area and the proposal of 6 MUs, there is a need to manage fishery operational interactions at the MU level. This includes identifying which MUs are impacted by which fishery, assessing the magnitude of impact, and evaluating the sustainability of the impacted MUs under different bycatch scenarios.

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