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Common dolphins subject to fisheries impacts in Southern Australia are genetically differentiated: implications for conservation

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Abstract

Interactions between short-beaked common dolphins *Delphinus delphis* and the fishing industry of South Australia (SA) have lead to serious concerns over the long-term viability of the local dolphin population. Common dolphins are gregarious animals with high vagility and are expected to display limited genetic differentiation over large spatial scales. Here, we investigate population genetic structure of southern Australian common dolphins using mitochondrial DNA control region sequences and seven microsatellite markers. We found unexpected levels of genetic differentiation for short-beaked common dolphins over a distance of ~1500 km. Although no genetic structure was observed in common dolphins along the coast of SA, we detected marked differentiation between dolphins from SA and south-eastern Tasmania, suggesting a minimum of two genetic populations in southern Australia. We hypothesize that the ephemeral distribution of small pelagic fish enhances movement and dispersal between dolphin groups at a local level. However, clear differences in water temperature, habitat features and fish abundance between SA and Tasmania may contribute to the contemporary isolation observed between dolphin populations. Our findings have important consequences for developing conservation management strategies, because SA has the largest purse-seine fishery by weight in Australia, and substantial numbers of fatal common dolphin interactions have occurred. In 2004/2005 alone, an estimated 1728 common dolphins were encircled and 377 died over a 7-month period. If these impacts lead to a reduction in population size, it is unlikely that dolphins from the adjacent south-eastern Tasmanian population will replace the lost individuals. Recommendations for assessing the impacts of the fishery are presented. The information herein may also have implications for fisheries–marine mammal interactions in coastal and neritic habitats in other areas of the world. Moreover, we demonstrate that a species commonly thought to be wide ranging can show an unexpected degree of genetic differentiation.

Introduction

Interactions between dolphins and purse-seine fisheries are known to occur in many parts of the world and have previously been reported in several states of Australia, including Western Australia, Queensland and South Australia (SA) (see Shaughnessy *et al*., 2003). The South Australian purse-seine fishery for sardines is the largest fishery by weight in Australia (Rogers & Ward, 2005). Interactions of this fishery occur mainly with short-beaked common dolphins *Delphinus delphis* in the area of Spencer Gulf and the eastern Great Australian Bight. Because of a growing demand for small pelagic fish such as sardines to support the thriving local finfish aquaculture industry, the activity of the sardine fishery has rapidly increased since it started in 1991 (Ward, McLeay & Rogers, 2005). As a result of this high demand for sardines, it is unlikely that exploitation of this fishery will decrease in the near future.

Between 1985 and 2000, the South Australian Museum collected 361 cetacean carcasses from strandings and by-catch events in SA. Necropsies of these animals, composed mainly of dolphins, revealed that 50% of all causes of deaths that could be determined were human related, that is fatal entanglements and intentional killings (Kemper *et al*., 2005). Moreover, as part of a purse-seine fishery observer programme in 2004/2005 Hamer, Ward & McGravey (2008) reported that over a 7-month period, an estimated 1728 common dolphins were encircled and 377 died in

southern Spencer Gulf and the eastern Great Australian Bight.

Impacts from the sardine fishery may also be indirect due to prey depletion through overfishing (Bearzi *et al*., 2006; Trites, Christensen & Pauly, 2006). In the Mediterranean Sea, prey depletion due to overexploitation of anchovies and sardines has been suggested as the primary cause for the disappearance of common dolphins from many areas in which they used to be the most abundant dolphin species (Bearzi *et al*., 2006). Because direct and potentially indirect impacts of the fishing industry may cause a threat to common dolphins in SA, detailed biological information is needed for the implementation of long-term conservation management strategies. This includes identifying populations and their boundaries, determining levels of genetic variability and assessing dispersal between populations.

Two species of common dolphins *D. delphis* (short-beaked form) and *Delphinus capensis* (long-beaked form), are recognized worldwide (Jefferson & Van Waerebeek, 2002), but only *D. delphis* is found in SA (e.g. White, 1999; Bell, Kemper & Conran, 2002). In southern Australia, short-beaked common dolphins are frequently found over the continental shelf, including Spencer Gulf in SA and areas around Tasmania – both are areas that are heavily targeted by local fishing industries (Ward & Staunton-Smith, 2002; Shaughnessy *et al*., 2003; Ward *et al*., 2006). From a geographic perspective, the continental shelf in SA lacks obvious barriers for common dolphin dispersal and therefore genetic differentiation in a highly mobile and gregarious species such as the common dolphin is expected to be low.

Knowledge of genetic structure and dispersal is central to the identification of management units (MUs) for dolphins in the area. When combining this with other biological information such as demography, mitigation strategies can be developed to ensure long-term population viability. Here, we aim to elucidate population genetic structure and levels of gene flow between common dolphins from SA and south-eastern Tasmania in southern Australia. We discuss how local oceanography in combination with prey distribution and habitat type may influence the patterns of genetic structure over different geographic scales. We also compare our results with those from a genetic study of coastal bottlenose dolphins (*Tursiops* sp.) from SA (Bilgmann *et al*., 2007*b*). The results of our analysis of genetic structure and dispersal of common dolphins are used to propose MUs with the aim of protecting the genetic diversity and integrity of local populations.

Materials and methods

Sampling regions

We used samples obtained from five regions in southern Australia. In 2004 and 2005, biopsy samples were collected from free-ranging short-beaked common dolphins (hereafter referred to as common dolphins) during boat surveys conducted in Spencer Gulf and the Great Australian Bight (SA) between 32°01′S, 132°10′E and 35°18′S, 136°85′E. Bow-riding dolphins were sampled with an extendable hand-held biopsy pole (Bilgmann *et al*., 2007*a*). A total of 56 common dolphin samples were obtained. Biopsies from each region in SA were obtained from multiple dolphin groups. No sampling attempts were made on dependent calves. All biopsy samples were preserved in 100% ethanol.

Tissue samples from common dolphin carcasses that stranded in south-eastern Tasmania were provided by the South Australian Museum and by the Department of Primary Industries, Water and Environment in Tasmania. The carcasses were collected during seven stranding events between 1995 and 2005. Dolphins from SA and south-eastern Tasmania were grouped into five sampling regions by pooling individuals together which were in geographic proximity, resulting in the following regions: eastern Great Australian Bight 1–3 (EGAB-1, EGAB-2, EGAB-3), Spencer Gulf (SG) and south-eastern Tasmania (SETAS) (Fig. 1). Individuals that were sampled in areas between different sampling regions were assigned to the region of closest geographic proximity. Sample numbers differed between sampling regions, ranging from seven to 20 (Table 1).

Genetic methods

Extraction of DNA and genetic sexing

Dolphin skin tissue was used to extract total DNA using a salting-out protocol modified from Sunnucks & Hales (1996). The sex of each individual was determined by polymerase chain reaction (PCR) to amplify fragments of the ZFX and SRY genes as reported in Gilson *et al*. (1998). PCR conditions were as reported in Möller *et al*. (2001).

Mitochondrial DNA (mtDNA) screening and sequencing

Amplification of a fragment of the mtDNA control region was undertaken by PCR using primers: Dlp-1.5 (5′-TCA CCC AAA GCT GRA RTT CTA-3′) and Dlp-5 (5′-CCA TCG WGA TGT CTT ATT TAA GRG GAA-3′) (Baker *et al*., 1993). PCR conditions and reaction mix were as reported in Möller & Beheregaray (2001). The single-stranded conformation polymorphism analysis was used to screen the amplified mtDNA control region fragments for sequence variation following Sunnucks (2000). PCR products of selected individuals were purified with an Ultra-Clean 15 DNA Purification Kit (Mo Bio, Carlsbad, CA, USA) and sequenced in an ABI 377 automated DNA sequencer according to the manufacturer's instructions. Using a phylogenetic approach, mtDNA control region sequences of short-beaked and long-beaked common dolphins obtained from GenBank were used to confirm that all samples from the two regions were of the short-beaked form (tree not shown).

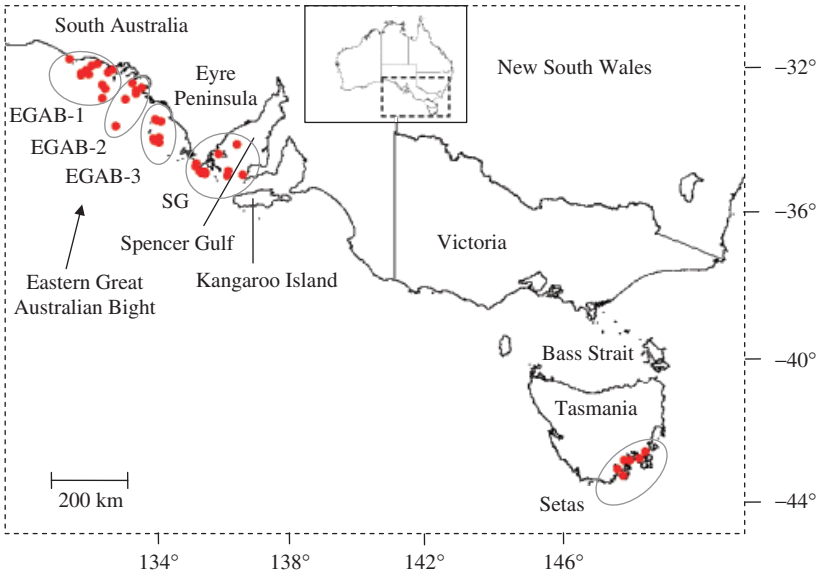

Figure 1 Map showing sampling regions of common dolphins in South Australia and Tasmania. Dots represent localities within each region [EGAB-1–3, eastern Great Australian Bight 1 ($n=19$), 2 ($n=7$) and 3 ($n=10$); SG, region of Spencer Gulf ($n=16$); SETAS, south-eastern Tasmania ($n=20$)].

Table 1 Common dolphin sampling regions in South Australia and south-eastern Tasmania with abbreviations, total number of samples and sex of sampled individuals

Region	Abbreviation	Sample size	F	M	Unknown sex
Eastern Great Australian Bight 1	EGAB-1	19	10	8	1
Eastern Great Australian Bight 2	EGAB-2	7	3	4	0
Eastern Great Australian Bight 3	EGAB-3	10	3	7	0
Spencer Gulf	SG	16	9	7	0
South-eastern Tasmania	SETAS	20	12	8	0

Microsatellite genotyping

Individuals were genotyped at seven polymorphic cetacean microsatellite loci: KW2, KW12 (Hoelzel, 1998), EV1, EV37 (Valsecchi & Amos, 1996), MK5, MK6 and MK8 (Krützen *et al.*, 2001) using the protocol reported in Möller *et al.* (2001). Individuals with known genotypes at each locus were used as reference samples to enable a uniform scoring between gels. To ensure the reliability of the PCR, selected individuals for each locus were re-amplified and re-electrophoresed. The program Micro-Checker v. 2.2.3 (Van Oosterhout et al., 2004) was used to screen the microsatellite data for genotyping errors. In addition, the microsatellite dataset was screened for individuals with identical genotypes using the software MStools v. 3.1 (Park, 2001) to potentially identify dolphins that were biopsy sampled more than once in the field. We also calculated the probability of identity [P(ID)] for full-sibs in our dataset using GenAlEx v. 6 (Peakall & Smouse, 2006). P(ID) is the probability that two individuals sampled from a population will have identical multilocus genotypes (Waits, Luikart & Taberlet, 2001).

Data analysis

mtDNA data analysis

mtDNA control region sequences were aligned with the program Sequencher 4.2 (Gene Code Corp., Ann Arbor, MI, USA). For each sampling region, we estimated genetic variability at the haplotype (h) and nucleotide (π) levels in Arlequin v. 2.001 (Schneider, Roessli & Excoffier, 2000). Arlequin was also used to estimate the genetic differentiation between sampling regions using F_{ST} and Φ_{ST} and to determine the statistical significance of these values. The Φ_{ST} values were estimated using the Tamura–Nei model of sequence evolution as suggested by Modeltest v. 3.06 (Posada & Crandall, 1998). We constructed a network with the statistical parsimony method of Templeton, Crandall & Sing (1992) in order to examine the genealogical relationships among haplotypes. The analysis was performed in TCS v. 1.21 (Clement, Posada & Crandall, 2000).

Microsatellite data analysis

The dataset was assessed for deviations from Hardy–Weinberg equilibrium using an exact test in Genepop v. 3.4 (Raymond & Rousset, 1995) based on a Markov chain method and 1000 iterations. In addition, Genepop was used to test for linkage disequilibrium, and to estimate the mean number of alleles per locus (NA), allele frequencies, and expected (H_E) and observed (H_O) heterozygosities. Allelic richness (AR), which takes sample size into account, was calculated in FSTAT v. 2.9.3 (Goudet, 2001). Estimates of genetic differentiation at microsatellite loci based on F_{ST} pairwise sampling region comparisons (Weir & Cockerham, 1984) were carried out in Arlequin. F_{ST} is based on the infinite alleles model of mutation for microsatellites and performs better than R_{ST} (Slatkin, 1995), considering the

relatively low sample size and number of loci of this study (Gaggiotti *et al.*, 1999).

The Bayesian clustering method implemented in the program Structure v. 2.0 (Pritchard, Stephens & Donnelly, 2000) was used (initial burn-in period 10^5 iterations, run of 10^6, for values of K between 1 and 5) to test for the presence of population structure and to estimate the number of populations (K) that best explain levels of observed genetic differentiation. The most likely number of populations in the dataset was determined by assessing log probabilities of individual runs. No prior information on sampling location was given, and the admixture model and both correlated and uncorrelated allele frequency models were used. Consistency of posterior probability $P(X/K)$ estimates was assessed by carrying out five independent runs for each value of K using the same values for burn-in and MCMC repetitions. In addition, we performed an analysis in Structure excluding the individuals from south-eastern Tasmania in order to further examine levels of differentiation in SA.

We then tested for a relationship between genetic distances based on F_{ST} and geographical distances in kilometres by carrying out a Mantel permutation procedure implemented in Genepop. Significance was assessed using 10 000 iterations. This analysis was performed excluding individuals from the geographically distant region of south-eastern Tasmania. To further investigate potential correlations between genetic and geographic distances at different spatial scales, we performed a spatial autocorrelation analysis in GenAlEx v. 6 (Peakall & Smouse, 2006). Here, we used variable distance class sizes ranging from 0 to 2000 km, with steps of 20 km for distances below 100 km, 100 km between 100 and 500 km, and 500 km between 500 and 2000 km. In addition, we tested for sex bias in dispersal by comparing three different measures: (1) sex-specific F_{ST}; (2) mean corrected assignment indices (AIc); (3) mean relatedness between same-sex pairs, using the software FSTAT. Corrected assignment indices measure the probability of individuals being born locally. Statistical significance was assessed by applying 10 000 randomizations for each test (Goudet, 2001).

Finally, we estimated recent migration rates (over the last few generations) between dolphins from SA and south-eastern Tasmania using the Bayesian multilocus genotyping approach implemented in the program BayesAss v. 1.3. (Wilson & Rannala, 2003). This approach allows inferences about asymmetric migration rates between regions, and populations are not required to be in migration-drift or Hardy–Weinberg equilibrium. The MCMC was run for 6.0×10^6 iterations, with a burn-in of 10^6 iterations. Posterior probability distributions were inferred by sampling every 2000 iterations.

Results

Samples

The screening for potential individuals that were biopsy sampled more than once in the field identified four pairs of samples with identical genotypes at all microsatellite loci. Given that the P(ID) for full-sibs in our dataset is reasonably low [P(ID) = 0.001] and that pairs of samples showed identical mtDNA control region haplotypes and were of the same sex, these samples were considered duplicates and only one of each pair was included for further analyses. After excluding these samples, our dataset contained 72 individuals (52 biopsy sampled in four regions in SA and 20 collected from dolphin carcasses in south-eastern Tasmania) (Fig. 1, Table 1).

Genetic variability

Mitochondrial control region sequences of 446 bp were aligned for the 72 samples and compared for sequence variation. In total, we detected 35 haplotypes defined by 45 polymorphic sites. Haplotypic and nucleotide diversities for the five sampling regions were high, ranging between 0.87 ($\pm$0.06) and 0.97 ($\pm$0.03), and 0.017 ($\pm$0.009) and 0.022 ($\pm$0.013), respectively (Table 2). Distribution and frequency of mtDNA control region haplotypes differed considerably between sampling regions (Table 3). In total, 22 unique haplotypes were detected for SA (GenBank accession numbers FJ175416–FJ175437), and 13 for south-eastern Tasmania (GenBank accession numbers FJ175438–FJ175450). Within SA, we found between five and 12 haplotypes in each sampling region, of which between one and nine were unique for a region. A relatively large number

Table 2 Summary of genetic variability in common dolphins from South Australia and south-eastern Tasmania based on mitochondrial DNA (mtDNA) control region sequences and seven microsatellite markers

		mtDNA			Microsatellites			
	Sample size	NH	*h*	π	NA	AR	H_E	H_O
EGAB-1	19	9	0.87 (0.06)	0.017 (0.009)	6.9	4.2	0.64 (0.09)	0.63 (0.09)
EGAB-2	7	6	0.95 (0.10)	0.021 (0.013)	5.1	4.7	0.74 (0.04)	0.69 (0.08)
EGAB-3	10	5	0.84 (0.08)	0.022 (0.013)	6.1	4.6	0.66 (0.08)	0.67 (0.07)
SG	16	12	0.97 (0.03)	0.019 (0.011)	7.7	4.6	0.68 (0.05)	0.66 (0.07)
SETAS	20	13	0.95 (0.03)	0.017 (0.009)	11.4	8.3	0.89 (0.01)	0.78 (0.04)

Values in parentheses are standard errors.

NH, number of haplotypes; NA, mean number of alleles per locus; *h*, haplotypic diversity; π, nucleotide diversity; AR, allelic richness; H_E, mean expected heterozygosity; H_O, mean observed heterozygosity.

Table 3 Distribution of mtDNA control region haplotypes for four common dolphin sampling regions in South Australia (EGAB-1, EGAB-2, EGAB-3 and SG) and south-eastern Tasmania (SETAS)

Locality	h1	h2	h3	h4	h5	H6	h7	h8	h9	h10	h11	h12	h13	h14	h15	h16	h17	h18	h19	h20	h21	h22	h23	h24	h25	h26
SA																										
EGAB-1	6	4			2		**2**	1			1	1	1			1										
EGAB-2	2	1						1			1	1						**1**								
EGAB-3	3		2	**3**							1											**1**				
SG			2		1	**2**			**2**	**2**			1	**1**	**1**		**1**		**1**	**1**	**1**					
TAS																										
SETAS																							**3**	**3**	**2**	**2**
Total	11	5	4	3	3	2	2	2	2	2	3	2	2	1	1	1	1	1	1	1	1	1	3	3	2	2

Locality	h27	h28	H29	H30	h31	h32	h33	h34	h35	Total
SA										
EGAB-1										19
EGAB-2										7
EGAB-3										10
SG										16
TAS										
SETAS	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	20
Total	2	1	1	1	1	1	1	1	1	72

The number of sampled haplotypes (h1–h35) is reported for each locality. Numbers in bold denote haplotypes which are unique to a sampling region.

mtDNA, mitochondrial DNA; EGAB-1, Eastern Great Australian Bight 1; EGAB-2, Eastern Great Australian Bight 2; EGAB-3, Eastern Great Australian Bight 3; SG, Spencer Gulf; SA, South Australia, TAS, Tasmania.

of haplotypes ($n = 17$) were represented only once in the dataset (Table 3).

For microsatellites, we observed no significant departures from Hardy–Weinberg equilibrium across sampling regions or loci. We found no evidence for linkage disequilibrium between all loci pairs. The total number of alleles per locus ranged from 8 to 14. Values for AR were similar among sampling regions in SA (AR = 4.2–4.7), but almost twice as high for south-eastern Tasmania (AR = 8.3) (Table 2). Values for expected (H_E) and observed (H_O) heterozygosities differed little between sampling regions in SA and were higher in south-eastern Tasmania, although H_o was not significantly so (Table 2).

Genetic differentiation

For mtDNA, estimates of F_{ST} and Φ_{ST} revealed that dolphins from sampling regions in SA are significantly differentiated from dolphins in south-eastern Tasmania (pairwise Φ_{ST} ranged between 0.09 and 0.19; Table 4). Within SA, we detected no significant pattern of population differentiation between regions. Results for mtDNA were similar for both F_{ST} and Φ_{ST} (only Φ_{ST} values are reported; Table 4). Exceptions from the non-significant pattern involved comparisons between EGAB-1 and EGAB-3 and EGAB-1 and SG. Based on the results from other analyses and DNA markers, we suggest that the weak but significant mtDNA differentiation detected in these comparisons relates to the relatively small sample sizes for these regions.

For microsatellites, significant population differentiation was also detected between all SA regions and south-eastern Tasmania using F_{ST} (pairwise F_{ST} ranged between 0.05 and 0.11; Table 4). Within SA, we found no genetic differentiation for any sampling region comparison, suggesting a lack of population genetic structure for common dolphins from the eastern Great Australian Bight and the region of Spencer Gulf. In agreement with these results, a Mantel test for association between genetic distance and geographic distance among sampling regions in SA revealed no significant correlation ($P = 0.081$).

Table 4 Pairwise fixation indices between four common dolphin sampling regions in South Australia and one in south-eastern Tasmania, based on mtDNA control region sequences and seven microsatellite markers

	EGAB-1	EGAB-2	EGAB-3	SG	SETAS
Eastern Great Australian Bight (EGAB-1)		−0.02	0.10*	0.12**	0.18**
Eastern Great Australian Bight (EGAB-2)	0.00		0.03	0.05	0.17**
Eastern Great Australian Bight (EGAB-3)	−0.01	−0.02		0.01	0.19**
Spencer Gulf (SG)	0.02	−0.01	0.00		0.09**
South-eastern Tasmania (SETAS)	0.11**	0.05**	0.08**	0.09**	

Mitochondrial Φ_{ST} values are above the diagonal, and microsatellite F_{ST} values are below.

*$P<0.05$. **$P<0.01$.

mtDNA, mitochondrial DNA.

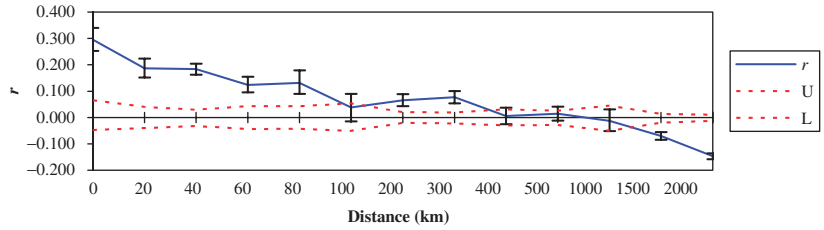

Figure 2 Correlogram showing spatial genetic autocorrelation (*r*) of common dolphins from South Australia and south-eastern Tasmania, as a function of distance in kilometres. The dotted lines represent the upper and lower 95% confidence intervals (CIs) of exhibiting no genetic structure. Error bars represent the 95% CIs determined by bootstrapping.

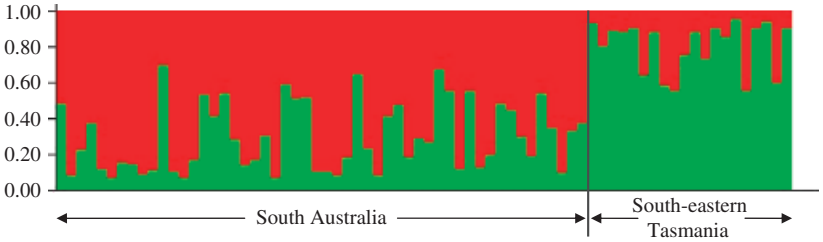

Figure 3 Structure results for common dolphin from South Australia and south-eastern Tasmania. Each vertical column represents one individual dolphin, and the separation of the column into two colours represents the estimated probability of either belonging to one or the other population.

The spatial autocorrelation analysis across sampling regions in SA and south-eastern Tasmania revealed a significant positive autocorrelation (i.e. a greater than random genetic similarity) among dolphin samples separated by <80 km. By contrast, dolphins separated by more than 1500 km (this involves all comparisons between SA and Tasmania) were significantly less related to each other (Fig. 2). Exclusion of south-eastern Tasmanian individuals from the spatial autocorrelation analysis did not change the general pattern observed for individuals from SA, and in agreement with the Mantel test, we did not find significant isolation by distance for individuals from SA.

The results from the Bayesian clustering method implemented in Structure also indicated that dolphins from these two regions belong to two separate populations (Fig. 3). A large proportion of dolphins from SA showed a high probability of membership in one population, whereas all dolphins from south-eastern Tasmania were assigned to another population (Fig. 3). In five independent runs, the posterior probabilities for each value of K were highest at $K = 2$. The clustering of dolphins into two populations was independent of the allele frequency model used. When excluding individuals from south-eastern Tasmania, Structure still suggested that individuals from the four sampling regions in SA belong to only one population. In this case, the posterior probabilities for each value of K were highest at $K = 1$. This pattern was also independent of the allele frequency model chosen.

The estimated rates of migration of dolphins between the two regions, determined with BayesAss, were very low and asymmetric. The migration rate from south-eastern Tasmania to SA was much lower [$m = 0.01$; confidence interval (CI) = 0.0002–0.0294] than the migration rate in the opposite direction ($m = 0.12$; CI = 0.0286–0.2164). Multiple runs showed consistent results, and the 95% CIs suggested that the data contained sufficient information for reliable migration rate estimates.

Genealogical relationships

The mtDNA control region network shows incomplete maternal lineage sorting between SA and south-eastern Tasmania (Fig. 4). In spite of the suggestion of a common origin for these two populations, not a single haplotype (out of 35 haplotypes) was shared between these two regions (Fig. 4). In contrast, among the South Australian dolphins, eight of the 22 haplotypes were shared between sampling regions. This analysis strongly corroborates the pattern of population subdivision, but also indicates that the restriction to dolphin dispersal between SA and south-eastern Tasmania is likely to be relatively recent.

Lack of sex-bias in dispersal

The sex of one individual could not be determined due to a minute sample and was therefore excluded from these analyses. Testing for sex-bias in dispersal of common dolphins from SA revealed no significant differences in either F_{ST} or the mean AIc of males and females (Table 5). The mean relatedness values of same-sex pairs were also not significantly different between males and females (Table 5). Although sample sizes for each sex were small for some sampling regions and the number of loci was at the lower range for detecting mild sex-biases in dispersal, the observed levels of microsatellite variability should allow reasonable discrimination (Goudet, Perrin & Waser, 2002). Overall, these results suggest that male and female common dolphins from SA exhibit similar dispersal patterns.

Discussion

Our analysis based on multiple DNA markers indicates that southern Australia is home to a minimum of two distinct populations of short-beaked common dolphins. Common dolphins from the regions of eastern Great Australian Bight and Spencer Gulf (SA) belong to a genetic population

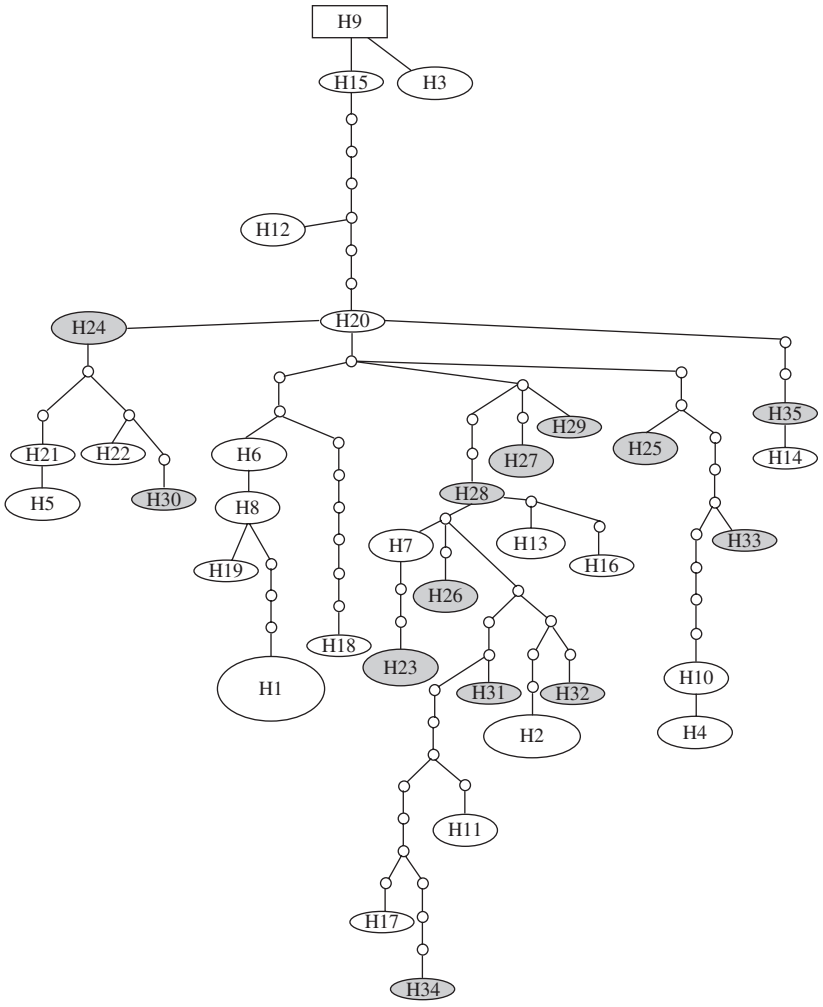

Figure 4 Haplotype network for mitochondrial DNA control region sequences of common dolphins from South Australia (white) and south-eastern Tasmania (grey). The size of the ovals is proportional to the number of individuals showing the particular haplotype in the area. Haplotype H9 was considered to be ancestor based on coalescence theory. Each line indicates one mutation between haplotypes, and the small circles between the connecting lines represent missing haplotypes.

Table 5 Sex-specific F_{ST}, mean relatedness between same-sex pairs and mean corrected assignment index (AIc) for common dolphins in South Australia

	Females	Males	*P*-value
F_{ST}	−0.0097	0.0070	0.84
Relatedness of same-sex pairs	−0.0195	0.0136	0.84
Mean AIc	0.4838	−0.3974	0.11

different from that of those from south-eastern Tasmania. The level of genetic differentiation detected implies that there is little if any contemporary dispersal of dolphins between SA and south-eastern Tasmania. The genetic differentiation reported here over a relatively small geographic distance is unprecedented based on what is known elsewhere for this highly vagile species (see e.g. Natoli *et al.*, 2006; Amaral *et al.*, 2007). As discussed below, this finding has important consequences for the development of conservation management strategies given the impacts of the SA fishing industry on the dolphin population (see Hamer *et al.*, in press). If these impacts lead to a reduction in population size, it is unlikely that dolphins from the adjacent south-eastern Tasmanian population will effectively replace the lost individuals.

Lack of genetic differentiation in SA

We did not detect any significant pattern of population genetic structure in common dolphins along the four South Australian regions included in this study. The lack of genetic differentiation across the regions of Spencer Gulf and the Great Australian Bight was supported by multiple analyses based on both mtDNA and nuclear microsatellite markers. This included analyses suggesting no sex-bias in dispersal between the two sexes. We propose that the high dispersal of common dolphins along the South Australian coast is mediated by the distribution of sardines (*Sardinops sagax*). Sardines are one of the most important components of the diet of common dolphins in SA (Kemper & Gibbs, 2002), and the area of Spencer Gulf and the Great Australian Bight support large populations of this species (Ward & Staunton-Smith, 2002; Dimmlich *et al.*, 2004; Rogers & Ward, 2005). In other regions of the world, such as the Mediterranean Sea and South Africa, common dolphins are also associated

with areas of high sardine densities (Cockcroft, 1990; Peddemors, 1999; Cañadas, Sagarminaga & Garcia-Tiscar, 2002). We hypothesize that these temporary fish aggregations, which form in areas of local upwellings (Ward *et al.*, 2006), enhance dolphin movement and dispersal across the region as dolphin groups will concentrate around aggregations and disperse as prey patches are depleted.

The apparent lack of population structure detected for common dolphins in SA is in contrast with the pattern observed for coastal bottlenose dolphins (*Tursiops* sp.), which show significant microsatellite F_{ST} values between the five sampling regions in the same area ($F_{ST} = 0.063$–0.098) (Bilgmann *et al.*, 2007*b*). Coastal bottlenose dolphins show fine-scale genetic structure with one population identified for Spencer Gulf and another for coastal waters west of the gulf in the Great Australian Bight (Bilgmann *et al.*, 2007*b*). The preference of short-beaked common dolphins for locally abundant pelagic schooling fish is in contrast to that of coastal bottlenose dolphins (*Tursiops* sp.) in SA, which tend to concentrate on local benthic prey often associated with seagrass beds (Kemper & Gibbs, 2002). The prey preferences of common dolphins, their tendency to aggregate in large schools (Evans, 1994; Acevedo-Gutiérrez, 2002), in addition to their high mobility and fluid fission–fusion social system (Bruno, Politi & Bearzi, 2004) are likely to have a large effect on increasing population connectivity of this species at a regional scale.

Genetic differentiation between common dolphins from SA and south-eastern Tasmania

We detected marked genetic differentiation between common dolphins from SA (Great Australian Bight and Spencer Gulf) and south-eastern Tasmania. The level of genetic differentiation at nuclear loci which was detected over a relatively small geographic distance (~1500 km) is in stark contrast to that found for common dolphins in the eastern Atlantic and the eastern North Atlantic over much larger scales (Natoli *et al.*, 2006). For instance, in the Atlantic, gene flow was high even between the eastern and western margins of the ocean across distances >5000 km (Natoli *et al.*, 2006).

Our analyses suggest that a simple model of isolation by distance does not account for the genetic differentiation observed between SA and south-eastern Tasmania, although we cannot completely exclude it because of incomplete sampling of individuals from a region in between these two areas. Common dolphins are also known to occur in eastern SA, Victoria, and areas around Tasmania, thus additional sampling from these areas would provide sufficient resolution to answer this question. However, given the level of differentiation detected between SA and south-eastern Tasmania and the lack of significant isolation by distance within the South Australian region, the overall structure appears to be better explained by the separation of dolphins into two genetic populations. We hypothesize that differences in oceanographic features (e.g. sea temperature) and habitat features between SA and south-eastern Tasmania have influenced the distribution of targeted prey species and, as a result, have contributed to the contemporary isolation observed between dolphins from the two areas. Sea water temperatures differ between the warm-temperate shelf waters of SA (16–21 °C) and the colder waters of south-eastern Tasmania (11–15 °C) (CSIRO, 2007). Furthermore, SA and south-eastern Tasmania fall into separate marine biogeographical provinces, which show clear and distinct differences in habitat features and invertebrate fauna (Bennett & Pope, 1953; O'Hara & Poore, 2000; O'Hara, 2001; Waters & Roy, 2003). Distribution of fish also differs between these provinces (Hedley, 1926; Whitley, 1932; Paxton, Allen & Douglass, 2006). For example, in southern Australia, the diet of Australian little penguins *Eudyptula minor* differs between the area of Bass Strait and south-eastern Tasmania (Gales & Pemberton, 1990), making apparent the differences in fish abundance and distribution at each locality. Therefore, we may also expect to find differences in the diet of common dolphins from SA and south-eastern Tasmania. The partial isolation between the dolphins from SA and south-eastern Tasmania may be due to their strong spatial association with the most abundant schooling fish they prey on (Cañadas *et al.*, 2002) This differs between the two regions – sardines (*S. sagax*) and anchovies (*Engraulis australi*) in SA (Kemper & Gibbs, 2002; Ward *et al.*, 2006); jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) in south-eastern Tasmania (Furlani, Gales & Pemberton, 2007; R. Gales, pers. comm.). Nonetheless, this hypothesis does not exclude the possibility of an initial scenario of allopatric differentiation for these two populations influenced by Pleistocene sea-level changes and associated episodes of emergence of the Bassian land-bridge. Several examples now exist in the literature about the influence of these historical events in shaping population divergence and, in some cases, speciation in coastal marine organisms from southern Australia (e.g. surf barnacle and starfish; Waters *et al.*, 2005; York, Blacket & Appleton, 2008; Waters, in press). The proposal of a recent allopatric scenario is consistent with our mtDNA analysis. Although not a single haplotype (out of 35 maternal lineages) was shared between the two regions, no phylogeographical pattern was apparent, which suggests recent isolation and a lack of current gene flow among populations (Fig. 4). Future research using a larger number of samples from additional localities is needed to clarify the patterns of population history and genetic structure of common dolphins in southern Australia.

Management implications

Mortalities of common dolphins in interactions with the South Australian fishing industry (Kemper *et al.*, 2005) represent a concern for the long-term viability of this dolphin population. An assessment of the impact of this industry on local dolphins is currently impossible, because no information is available on the size of the dolphin population and its boundaries east and west over the shelf.

Abundance estimates of common dolphins in the area are therefore urgently needed.

Considering the marked genetic differentiation between common dolphins from SA and south-eastern Tasmania, the agreement of this pattern with local oceanographic boundaries and habitat differences, and estimated low migration rates, we recommend that dolphins from these two regions should be considered separate MUs. Accordingly, dolphin by-catch mitigation strategies within SA should be devised on the assumption that interactions impact a finite population in the area of Spencer Gulf and the eastern Great Australian Bight. Given that dolphin–fisheries interactions are concentrated in this region in SA and in order to assess the effect of these impacts, we recommend to (1) continue monitoring and estimating the magnitude of fishery interactions; (2) develop methods to estimate common dolphin abundance across this area; (3) given that distribution may be closely linked with prey distribution, quantify dolphin diet, prey abundance and distribution in this area; (4) further investigate population genetic structure of common dolphins in adjacent areas.

Pelagic dolphin species are frequently assumed to comprise large panmictic populations (Hoelzel, Goldsworthy & Fleischer, 2002). Many of these populations have been dramatically reduced in recent decades due to fisheries interactions (Northridge, 1984, 1991). This study highlights the importance of identifying population boundaries even in marine species with widespread, seemingly uniform distributions.

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