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ORIGINAL PAPER

Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current

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Abstract Oceanographic processes play a significant role in shaping the genetic structure of marine populations, but it is less clear whether they affect genetic differentiation of highly mobile vertebrates. We used microsatellite markers and mtDNA control region sequences to investigate the spatial genetic structure of short-beaked common dolphins (*Delphinus delphis*) in southeastern Australia, a region characterised by complex oceanographic conditions associated with the East Australian Current (EAC). A total of 115 biopsy samples of dolphins were collected from six localities spanning approximately 1,000 km of the New South Wales (NSW) coastline. We found evidence for contrasting genetic diversity and fine-scale genetic structure, characterised by three genetically differentiated populations with varying levels of admixture. Spatial genetic structure was not explained by a model of isolation by distance, instead it coincides with main patterns of oceanographic variation along the EAC. We propose that common dolphins along the EAC may be adapted to three water masses recently characterised in this region.

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Introduction

Understanding spatial genetic connectivity of marine populations is essential for conservation management and for identifying factors that promote genetic differentiation in the marine environment. Life-history traits, such as dispersal capability and local recruitment, as well as effective population size, ocean conditions and historical factors are recognised as playing an important role in shaping genetic structure of marine organisms (e.g. Galarza et al. 2009; Gonzalez and Zardoya 2007; Palumbi 2004).

In cetacean populations, habitat association, foraging specialisations and kin interactions, in combination with past bottlenecks and periods of expansion and contraction, can lead to discontinuous relationships between genetic and geographic distance (reviewed in Hoelzel 2009). Accordingly, habitat discontinuities and changes in oceanographic features, prey distribution and philopatric behaviour have been identified as influencing the spatial genetic structure of several delphinid species (e.g. Bilgmann et al. 2007a; Fullard et al. 2000; Hoelzel et al. 1998a; Mendez et al. 2010; Möller et al. 2007; Natoli et al. 2005; Rosel et al. 2009).

Common dolphins are globally distributed in temperate regions (Perrin 2009) and some tropical zones with unusually cold, productive waters (Jefferson et al. 2009). Two species (*Delphinus delphis* and *D. capensis*) and two

subspecies (*D. capensis tropicalis* and *D. delphis ponticus*) are currently recognised (Perrin 2009), but the taxonomy is controversial and a revision of the genus is required (Amaral et al. 2009). Common dolphins are highly gregarious animals with groups generally composed of dozens to hundreds of individuals (Bearzi et al. 2003; Jefferson et al. 2007). They have a fluid social structure, with some evidence for segregation in age and sex classes (Neumann et al. 2002; Perrin 2009), but kinship relationships are unlikely to be of importance (Viricel et al. 2008). Although their movements or migratory patterns are not well understood, they are highly mobile and capable of long-range dispersal (hundreds of kilometres), which can be associated with the movement of their prey (e.g. in association with the sardine migration in southern Africa, Cockcroft and Peddemors 1990). Common dolphins are believed to be generalist predators feeding mainly on small schooling fish and squid (Jefferson et al. 2007), and their diet is thought to vary both seasonally and regionally according to the distribution and abundance of prey items (e.g. Meyner et al. 2008; Young and Cockcroft 1994). However, in many areas, sardines and anchovies predominate in their diet (e.g. Kemper and Gibbs 2002; Meyner et al. 2008; Young and Cockcroft 1994) and, in fact, most of their global distribution (Jefferson et al. 2007, 2009) appears to coincide with the distribution of these fishes (Grant and Bowen 1998). In Australia, common dolphins appear to be restricted to subtropical and temperate waters from southern Queensland around the south of the continent to Western Australia (Jefferson and van Waerebeek 2002). In southeastern and southern Australia, they appear to occur mainly in medium water depths over the continental shelf (Möller, pers. obs.). In this region, only the short-beaked form (currently recognised as *D. delphis*) has been reported (Bell et al. 2002; Bilgmann et al. 2008). In general, common dolphins have not been well surveyed in Australia, and specific ranges, movements and population sizes are currently unknown (DEWHA 2010).

The few studies of the population genetic structure of common dolphins around the world have been predominantly reliant upon samples from stranded animals (e.g. Amaral et al. 2007; Mirimin et al. 2009; Natoli et al. 2006; Rosel et al. 1994; but see Bilgmann et al. 2008). High genetic differentiation has been reported between short-beaked and long-beaked forms (Natoli et al. 2006; Rosel et al. 1994). In California, for example, genetic differentiation combined with morphological divergence led to the proposal of the two species (Heyning and Perrin 1994; Rosel et al. 1994). In short-beaked common dolphins, low to moderate genetic differentiation has been reported only at geographical scales $\geq$1,500 km (e.g. Bilgmann et al. 2008; Mirimin et al. 2009). Low genetic differentiation was uncovered between western and eastern basins of the North Atlantic, but populations within basins were homogenous—although samples originated only from high latitudes (Mirimin et al. 2009). In Australia, significant genetic differentiation has been reported between short-beaked common dolphins from South Australia and southeastern Tasmania (~1,500 km apart), but not within approximately 600 km of the central South Australian coastline (Bilgmann et al. 2008).

This study investigates the spatial genetic structure of common dolphins in southeastern Australia along the New South Wales (NSW) coast, a region where the East Australian Current (EAC) dominates oceanographic conditions (Fig. 1). The EAC is a warm western boundary current that flows southward and is characterised by four broad stages: the formation, which occurs along the mid-Queensland (QLD) coast from about 15°S to 24°S; the intensification, mainly between 22°S (QLD) to 35°S (NSW); the separation, where the current decelerates and detaches from the coast at around 31°S (NSW), then turns sharply eastward between 32°S and 35°S to flow as the Tasman Front; and the decline, where the southward flow gradually weakens and becomes highly variable in strength and direction (Ridgway and Dunn 2003; Mata et al. 2006). South of the EAC separation, the region is characterised by periodic eddy formation (Godfrey et al. 1980; Ridgway and Dunn 2003; Mata et al. 2006). However, the processes controlling the timing and the spatial scales of current separation and eddy shedding remain unclear; the separation point varies seasonally and there are times when the current separates from the continental slope north of 30°S (Mata et al. 2006).

The EAC zone of separation, which extends for approximately 150 km (Ridgway and Dunn 2003), has been proposed to disrupt intra-specific genetic homogeneity in a direct developer snail (Hoskin 2000). A different perspective about biotic connectivity in this region has recently emerged in studies of planktonic dispersers. These studies provided evidence for fine-scale genetic structure south of the EAC separation point in species with high dispersal potential (e.g. for the sea urchin, *Centrostephanus rodgersii*, Banks et al. 2007; for the abalone, *Haliotis coccoradiata*, Piggott et al. 2008).

Here, we use data from highly resolving microsatellite DNA markers and mtDNA control region sequences to test the hypothesis that the oceanographic variation found along the EAC has impacted on the contemporary genetic structure of a highly mobile marine vertebrate—the short-beaked common dolphin (*D. delphis*). Our prediction was that genetic subdivision would be expected across the separation point of the EAC from the coast, which would act as an environmental barrier separating a northern from a southern group of regional subpopulations. Our results support this prediction but also revealed the presence of additional genetic structure, a surprising finding that may relate

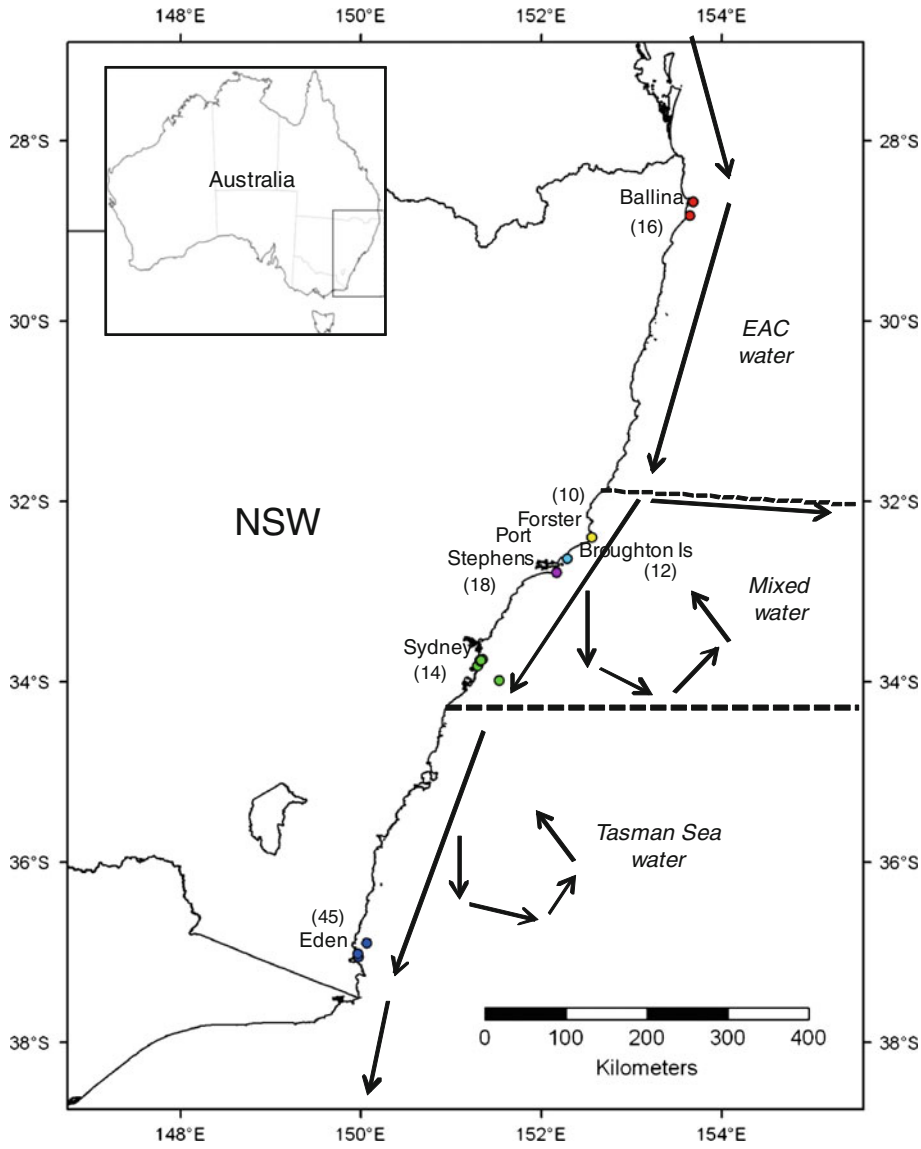

Fig. 1 Position of short-beaked common dolphin schools biopsy sampled in six localities along the New South Wales coast in southeastern Australia (sample size at each locality is given in brackets). Schematic representation of the East Australian Current (EAC) is represented by *black arrows* (*loop arrows* represent eddies). The three water masses (EAC, Mixed and Tasman Sea) characterised for the region are also shown, with their boundaries (as observed in spring 2002) represented by the *dotted lines* (adapted from Keane and Neira 2008)

to adaptation of these dolphins to distinct water masses recently characterised for the region.

Materials and methods

Study area and biopsy sampling

Biopsy samples were collected from 14 schools of common dolphin in six localities in NSW between 2003 and 2006, covering approximately 1,000 km of the coastline (Fig. 1, Table 1). Schools ranged in size from three individuals to over 100 dolphins (Fig. 1, Table 1). Samples were obtained using an extendable hand held biopsy pole for bow riding dolphins (Bilgmann et al. 2007b) or a Paxarms (Timaru, New Zealand) biopsy rifle modified to deliver darts (Krützen et al. 2002). Calves were not sampled.

Genetic analyses

DNA extractions were carried out using a salting-out protocol (Sunnucks and Hales 1996). Amplification of 450-bp of the mtDNA control region was conducted according to conditions detailed in Möller and Beheregaray (2001). Amplified fragments were screened for sequence variation by the single-stranded conformation polymorphism (SSCP) analysis (Sunnucks et al. 2000), with several representatives of identified SSCP phenotypes sequenced in an ABI 377 DNA sequencing system according to the manufacturer's instructions. Seven nuclear microsatellite markers (loci KWM2, KWM12, Hoelzel et al. 1998b; MK5, MK6, MK8, Krützen et al. 2001; EV1, EV37, Valsecchi and Amos 1996) were PCR-amplified for all samples as described in Möller and Beheregaray (2004). The sex of individuals sampled was determined by amplifying fragments of the ZFX and SRY

Table 1 Number of biopsy samples of short-beaked common dolphins collected at each of six localities in southeastern Australia, including sex, number of schools, range of school size observed, and years of sampling

Locality	N (dupl)	M:F	N schools	School size*	Years
Ballina	16	7:9	2	3–40	2005
Forster	10 (2)	4:4	1	30	2004
Broughton Is	12	7:4	1	50	2003
Port Stephens	18 (1)	11:6	1	100	2003
Sydney	14	3:7	6	4–20	2005–2006
Eden	45 (1)	22:22	3	30–50	2004–2005
Total	115 (4)	54:52	14	3–100	2003–2006

Dupl number of duplicate samples, *M:F* number of genetically assigned males and females

* School sizes of 20–100 animals were estimated in bins of 10

genes by the polymerase chain reaction (PCR) (Gilson et al. 1998). PCR conditions are reported in Möller et al. (2001).

Data analyses

Mitochondrial DNA control region sequences were edited and aligned in SEQUENCHER v.4.1.2 (Gene Codes Corporation, MI). Genetic diversity at the haplotype (h) and nucleotide (π) levels was estimated for samples at each locality using ARLEQUIN v.3.1 (Excoffier et al. 2005). Values of haplotype diversity that take into account differences in sample size between localities were obtained through a rarefaction analysis using CONTRIB (Petit et al. 1998). Genetic differentiation using F_{ST}, which takes into account haplotype frequencies, and Φ_{ST}, which takes into account genetic distance, were estimated using ARLEQUIN. Φ_{ST} values were estimated using the Tamura-Nei model (gamma correction, $\alpha = 0.5$) as suggested by MODELTEST v.3.06 (Posada and Crandall 1998), using the Akaike's information criterion, as the most appropriate model of sequence evolution for the dataset. Genealogical relationships of the haplotypes were investigated by constructing a median-joining network in NETWORK v.4.510 (Bandelt et al. 1999) with default settings.

For microsatellites, the dataset of each putative population was initially checked for genotyping or scoring errors, caused by null alleles, stuttering and short allele dominance, using MICRO-CHECKER 2.2.3 (van Oosterhout et al. 2004). Genetic variability was then estimated by calculating number of alleles and expected (H_E) and observed (H_O) heterozygosities using GENEPOP v.3.4 (Raymond and Rousset 1995). Allelic richness (AR), which takes sample size into account, was estimated using FSTAT v.2.9.3 (Goudet 2001). Tests for deviations from Hardy–Weinberg equilibrium (HWE), applying an exact test and 10,000 iterations, and tests for linkage disequilibrium were also conducted in GENEPOP. Significance levels for the multiple tests were B–Y corrected to balance the risks of Type 1 and Type 2 errors (Narum 2006), including for the F_{ST} analysis (below).

To evaluate the power of the dataset to differentiate individuals, so that potential duplicate samples could be removed, we calculated the probability of identity for full siblings (PID_{sib}) in GenAlEx v.6 (Peakall and Smouse 2006). Initially, we estimated PID_{sib} including all samples as a single population but the analysis was later repeated for each population when genetic subdivision was disclosed.

Genetic differentiation between pairs of putative populations was investigated by computing F_{ST} (significance assessed by 10,000 permutations) using ARLEQUIN v.3.1 (Excoffier et al. 2005). Analysis of F_{ST} was preferred over R_{ST} (Slatkin 1995) as F_{ST} is more conservative for estimation when sample sizes and number of loci are relatively small (Gaggiotti et al. 1999). In addition, a Bayesian clustering approach based on a spatial model (coloured Poisson-Voronoi tessellation) in GENELAND v.3.1.4 was used to infer the number of populations and their spatial boundaries. This model makes use of genotypes and spatial coordinates of sampled individuals to cluster them into populations that are approximately at Hardy–Weinberg equilibrium, considering linkage equilibrium between loci (Guillot et al. 2009). For this analysis, an allele frequency correlated model was used, with 100,000 MCMC iterations and thinning of 100, with 10 independent runs, and minimum number of populations set to one and maximum set to seven (number of samples plus one to test for the possibility of further subdivision in the dataset). For comparison, we also used the Bayesian clustering method implemented in STRUCTURE 2.3.1 (Hubisz et al. 2009), which does not take into account spatial information, to test the assignment of individual samples to genetic clusters. The number of clusters (K) was inferred from the posterior probability distribution Pr (K/X) calculated from the posterior probability of the data Log Pr (X/K). For this analysis, we used a burn in period of 100,000 iterations, runs of 10^6, values of K between one and seven (number of samples plus one), series of five independent runs for each value of K, with the admixture model using sampling locations as prior, and the correlated allele frequency model.

Isolation by distance (IBD) was tested using a Mantel test in IBDWS v.3.16 (Jensen et al. 2005), with statistical significance assessed using 10,000 randomisations. Geographical distances between the central positions of the six sampling locations were calculated using the shortest distance via the coastal environment approximately at the 50 m isobath.

Sex bias in dispersal was tested by comparing two statistical descriptors between males and females (F_{ST} and mean corrected assignment indices, *mAIc*) using FSTAT v.2.9.3, with significance assessed by 10,000 randomisations (Goudet 2001). F_{ST} and *mAIc* are expected to be higher for the more philopatric sex than for the more dispersing sex (Goudet et al. 2002).

A coalescence-based analysis with a Maximum Likelihood strategy was employed to assess the possibility of asymmetric migration and estimate migration rates in MIGRATE v.2.1.2 (Beerli 2008) using the microsatellite dataset. The dataset was partitioned into three populations for analysis; northern NSW (Ballina), central NSW (Forster, Broughton Island, Port Stephens and Sydney) and southern NSW (Eden). This partitioning was based on the results obtained with the spatial model in GENELAND, which identified these three as the most likely number and boundaries of genetic clusters in the dataset, in corroboration with the results from STRUCTURE and the F_{ST} based on the mtDNA control region data. For the MIGRATE analysis, the Brownian motion model was used, and the migration rate ($M = m^*\mu$) and theta ($\Theta = 4N_e\mu$) (Beerli 2008) were initially estimated with F_{ST} (Markov chain settings were 10 short chains, 100,000 trees sampled; 3 long chains, 1,000,000 trees sampled, 10,000 trees discarded). A second simulation was carried out with *M* values from the initial run and same Markov chain settings. A third simulation was then conducted to ensure convergence of results (30 short chains, 100,000 trees sampled; 5 long chains, 1,000,000 trees sampled, 10,000 trees discarded).

Results

Samples, Hardy–Weinberg equilibrium and linkage disequilibrium

In total, 115 samples were obtained, ranging from 12 to 46 at each locality (Table 1). From these samples, four were considered duplicate samples based on a very low probability of identity for full siblings (range of $PID_{sib} = 0.001-0.003$), identical mtDNA control region haplotypes, microsatellite genotypes and same sex, with one of each pair subsequently removed from the data analyses. Of the remaining 111 samples, 54 were sexed as males and 52 as females, with five samples not successfully sexed (Table 1). There was no evidence for null alleles, stutter bands or short allele dominance in the microsatellite dataset. There was also no evidence for Hardy–Weinberg disequilibrium at any locus or putative population, nor was there linkage disequilibrium between any locus pair comparison after B–Y correction.

Diversity and differentiation at mtDNA and genealogical relationships of haplotypes

SSCP analysis and sequencing of 450 bp of the mtDNA control region revealed 29 haplotypes, with between three and 22 haplotypes identified per locality (Appendix 1, Table 2). Haplotypic diversity varied considerably between localities, with lower diversity found in Ballina, northern NSW, and higher diversity in Eden, southern NSW (Table 2). Nucleotide diversity was moderate to high, and again, higher at Eden compared to the other localities (Table 2). There was low to high genetic differentiation between pairs of localities with F_{ST} values ranging from −0.08 to 0.59 (Table 3), and an overall F_{ST} of 0.26 ($P < 0.0001$). The same trend, albeit with generally larger values, was found for the Φ_{ST} pairwise comparisons (data not shown). Localities in central NSW (Forster, Broughton Island, Port Stephens, Sydney, Fig. 1) were, with one exception, not significantly different from each other, whereas Ballina in northern NSW and Eden in southern NSW (Fig. 1) were significantly different from all other localities (Table 3). The median-joining network depicted a complex branching pattern. A group of closely related, highly divergent lineages, including one high frequency haplotype, was mostly represented by individuals from northern NSW. Another two closely related and high frequency haplotypes were generally represented by samples from central NSW. By contrast, several highly divergent and low frequency haplotypes were represented by individuals from southern NSW (Fig. 2).

Table 2 Summary of genetic variability at 450 bp of the mtDNA control region and seven microsatellite markers in short-beaked common dolphins from six localities in southeastern Australia

Locality	mtDNA					Microsatellites			
	N	Hap N	Hap r	*h*	π	Na	AR	He	Ho
Ballina	16	3	1.3	0.34	0.008	5.4	4.72	0.70	0.66
Forster	8	4	3	0.64	0.006	5.7	5.71	0.76	0.71
Broughton Is	12	5	2.9	0.67	0.008	6.9	5.79	0.75	0.71
Port Stephens	17	4	1.9	0.63	0.004	6.4	5.4	0.76	0.71
Sydney	14	4	1.7	0.4	0.002	7	5.79	0.74	0.66
Eden	44	22	5.8	0.95	0.016	11	6.87	0.82	0.74

Hap N number of haplotypes, *Hap r* number of haplotypes after rarefaction, *h* haplotypic diversity, π nucleotide diversity, *Na* average number of alleles, *AR* allelic richness (average number of alleles adjusted for sample size), *He* expected heterozygosity, *Ho* observed heterozygosity

Table 3 Fixation indices (F_{st}) for short-beaked common dolphins between six sampled localities in southeastern Australia based on seven microsatellite markers and 450 bp of the mtDNA control region

	Ballina	Forster	Broughton Is	Port Stephens	Sydney	Eden
Microsatellite						
Ballina		0.010*	0.006*	0.0001*	0.0001*	0.0001*
Forster	0.037		0.233	0.152	0.0001*	0.001*
Broughton Is	0.041	0.012		0.002*	0.002*	0.0001*
Port Stephens	0.049	0.018	0.047		0.0001*	0.0001*
Sydney	0.058	0.071	0.054	0.053		0.0001*
Eden	0.042	0.039	0.031	0.035	0.047	
MtDNA						
Ballina		0.003*	0.0001*	0.0001*	0.0001*	0.0001*
Forster	0.436		0.999	0.099	0.645	0.0001*
Broughton Is	0.428	−0.084		0.092	0.475	0.0001*
Port Stephens	0.491	0.113	0.086			0.008*
Sydney	0.594	−0.026	−0.011	0.249		
Eden	0.301	0.168	0.165	0.177	0.273	

F_{st} estimates are given below diagonals and P values above diagonal

* Significant after B–Y correction (critical P value = 0.01507)

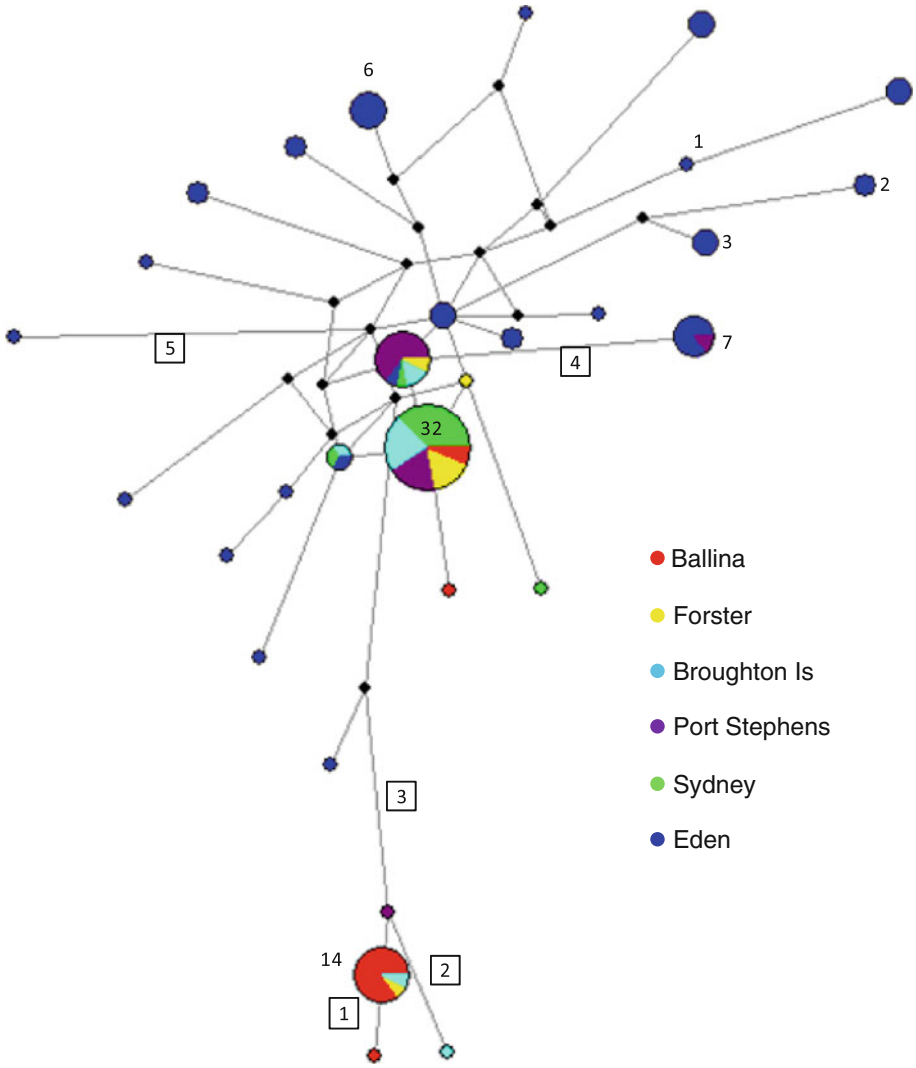

Fig. 2 Median-joining network of mtDNA control region haplotypes of short-beaked common dolphins sampled in six localities of southeastern Australia. Size of circles is proportional to the number of individuals bearing a haplotype (examples are given besides circles). *Colours* represent the proportional of individuals from each locality bearing a haplotype. Length of lines is proportional to the number of mutational steps separating haplotypes (examples are given within squares besides lines). *Small black circles* represent missing, intermediate haplotypes

Variability, differentiation and spatial structure at microsatellites

Genetic variability at microsatellite loci was moderate to high (Appendix 2). Similar to the mtDNA haplotypic diversity, allelic richness was highest at Eden in southern NSW (Table 2). Low to moderate genetic differentiation was found between pairs of localities, with F_{ST} values ranging between 0.01 and 0.07 (Table 3), and an overall F_{ST} of 0.05 ($P = 0.011$). Analogous to the mtDNA results, Ballina in northern NSW and Eden in southern NSW were significantly different from all other localities. However, some pairwise comparisons in central NSW were also significantly different (comparisons including Sydney and some including Broughton Island; Table 3). The Bayesian clustering approach based on the spatial model in GENELAND suggested three as the most likely number of populations in the region. These are represented by (1) samples collected off Ballina in northern NSW; (2) samples collected off Eden in southern NSW; and (3) samples collected off Forster, Broughton Island, Port Stephens and Sydney (Fig. 3). These results were corroborated by those from the Bayesian model implemented in Structure (Fig. 4), with highest probability obtained when $K = 3$ groups [$P(K/X) = 1$ for $K = 3$ groups and $P(K/X) = \sim 0$ for $K = 1$–2, and 4–7 groups]. Varying levels of admixture were observed for the samples into the three populations. The membership proportion of Ballina samples to population (1) was high, with $Q = 0.73$, and the membership proportion of Eden samples to population (3) was very high, with $Q = 0.94$. By contrast, most of the samples from the central localities were more admixed, but they still had their highest membership proportion to population (2), with $Q = 0.52$ for Forster, $Q = 0.48$ for Broughton Island, $Q = 0.84$ for Port Stephens, and $Q = 0.48$ for Sydney.

To exclude the possibility that kinship structure was influencing the results, analyses (F_{ST} and Bayesian modelling) were repeated by excluding one 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 GenAlEx v. 6, using Queller and Goodnight (1989) index. Only 11 pairs had r values higher than 0.5 within localities, and results of spatial structure analyses remained very similar when excluding one of each pair (data not shown). Therefore, the whole dataset was kept for analyses.

The analysis of IBD across the entire sampling area based on microsatellites ($Z = 314.2164$, $r = 0.1773$, $P = 0.3451$) and mtDNA ($Z = 1819.5400$, $r = 0.5697$, $P = 0.14$) revealed no overall association between F_{ST} and marine geographic distance.

Sex-biased dispersal and migration rates

Analyses of dispersal tendencies between males and females using F_{ST} (♂ = 0.05, ♀ = 0.05, $P = 0.41$) and mean

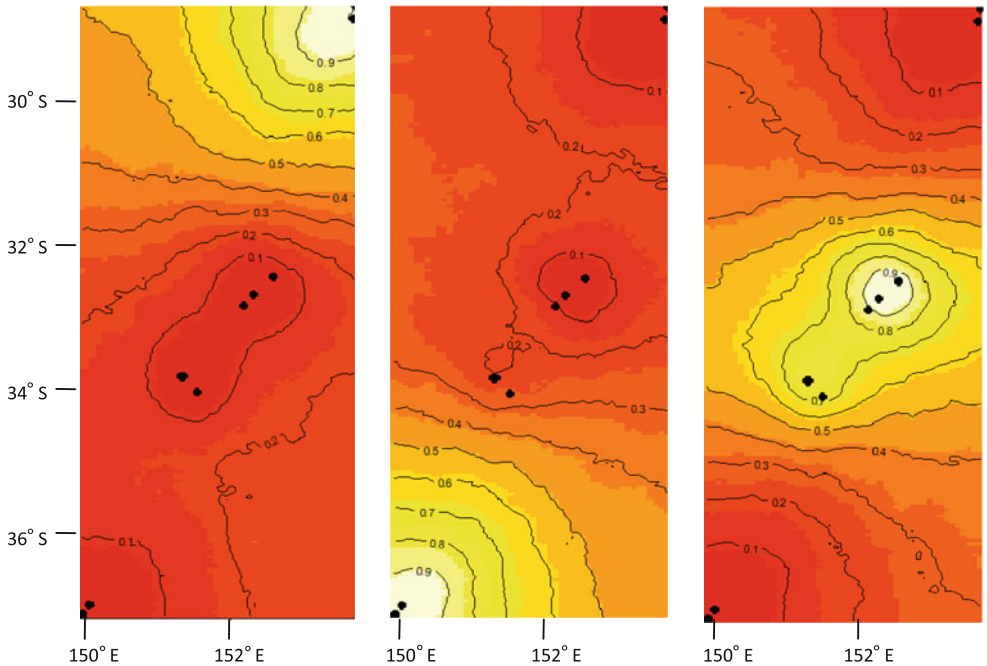

Fig. 3 Posterior probabilities of population membership and genetic discontinuities from the spatial model in GENELAND for short-beaked common dolphins sampled in six localities of southeastern Australia. Contour lines indicate the spatial position of genetic discontinuities and *lighter colours* suggest higher probabilities of population membership. Three genetic clusters were identified, each depicted in one of the maps: *left map* population in northern NSW, *central map* population in southern NSW, *right map* population in central NSW. Please note that coastline is not depicted

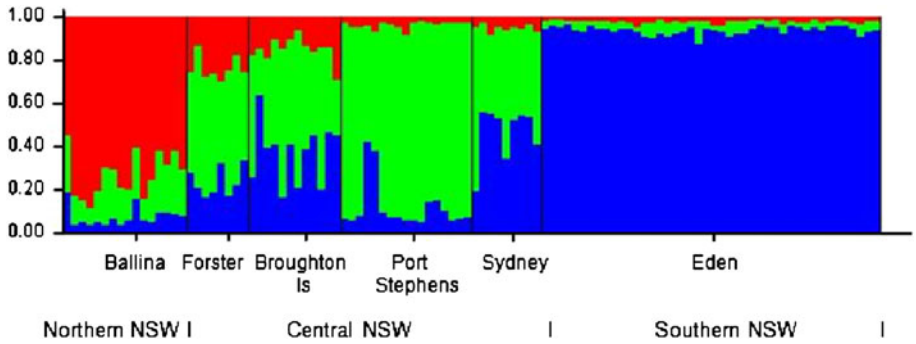

Fig. 4 Bayesian clustering from STRUCTURE for short-beaked common dolphins sampled in six localities of southeastern Australia. The most likely number of genetic clusters in the data set was identified as three. Each individual is represented by a vertical column partitioned into three coloured segments, with the length proportional to the individual's estimated membership coefficient into the three groups: Northern NSW, Central NSW and Southern NSW

Table 4 Maximum likelihood estimation of asymmetric migration rates (M) in MIGRATE based on seven microsatellite markers between three populations of short-beaked common dolphins in southeastern Australia

		To		
	θ	Northern NSW	Central NSW	Southern NSW
From				
Northern	5.741		4.225	2.597
NSW	(5.318–6.176)		(3.761–4.723)	(2.362–2.844)
Central	6.33	0.013		0.298
NSW	(5.658–7.104)	(0.004–0.03)		(0.223–0.388)
Southern	23.577	0.013	3.96	
NSW	(20.540–26.964)	(0.004–0.03)	(3.501–4.467)	

The three populations were previously identified by genetic models in GENELAND and STRUCTURE. 95% confidence intervals of estimates are provided in brackets

($M = m^*\mu$), $\Theta = 4N_e\mu$

assignment indices (♂ = 0.05, ♀ = − 0.06, $P = 0.58$) suggested that there is no significant sex bias in dispersal. Estimation of migration rates using the maximum likelihood approach suggests asymmetric migration between the three genetic populations identified by the Bayesian models. Comparatively, very low migration was found from central and southern NSW to northern NSW; low migration was detected from central NSW to southern NSW; and moderate migration was estimated from northern and southern NSW to central NSW (Table 4).

Discussion

Fine-scale genetic structure in short-beaked common dolphins along the EAC

Common dolphins in NSW coastal waters show fine-scale genetic structure, at the scale of few hundred kilometres, with at least three genetically differentiated populations with varying levels of admixture located in southern, central and northern NSW. These results were supported by analyses conducted with the microsatellite and mitochondrial DNA control region data sets (Table 3, Figs. 3, 4). The spatial scale of genetic structure presented here was unexpected, given the capacity for long-range dispersal by these animals. For example, low to moderate genetic differentiation in this species has been previously reported only at geographical scales ≥1,500 km (e.g. Bilgmann et al. 2008; Mirimin et al. 2009). The pattern of fine-scale genetic structure observed in our study is not explained by a simple model of isolation by distance, instead it appears to coincide with variation in oceanographic conditions along the EAC (e.g. Godfrey et al. 1980; Ridgway and Dunn 2003). The northern dolphin population is located in the area of EAC intensification, the central population is located in the EAC zone of separation, an area characterised

by periodic eddy formation, and the southern population is located in the EAC's area of decline, where the influence of the EAC weakens. These areas were recently characterised by three different water masses with different temperature profiles (but negligible variability in salinity), including the warmer EAC waters, the mixed (EAC and Tasman Sea) waters, and the colder Tasman Sea waters (Keane and Neira 2008). Furthermore, these water masses were shown to present different fish larval assemblages (Keane and Neira 2008). Other studies have also found evidence for genetic discontinuity associated with the EAC zone of separation (e.g. for the sea urchin, *Centrostephanus rodgersii*, Banks et al. 2007; for the gastropod, *Bedeva hanleyi*, Hoskin 2000; for the snapper, *Pagrus auratus*, Sumpton et al. 2008). Variation in ocean current circulation, through its influence on larval transport and recruitment appear to be responsible for the patterns observed in such studies (e.g. Banks et al. 2007). However, for the active disperser common dolphin, a more plausible explanation is that the genetic differentiation observed reflects the adaptation of these animals to the three different water masses of the EAC. Differences in water temperature and dissimilar distribution and abundance of schooling fish species have also been suggested to explain the genetic differentiation found between common dolphins occurring in South Australia and Tasmania (Bilgmann et al. 2008). In South Australia, sardines (*Sardinops sagax*) and anchovies (*Engraulis australis*) are known to comprise the majority of common dolphin diet (Kemper and Gibbs 2002), while in Tasmania their diet is more likely to include jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidius*) (Furlani et al. 2007). In another delphinid, the common bottlenose dolphin (*Tursiops truncatus*), population genetic structure along a contiguous distributional range from the Black Sea to the eastern North Atlantic was found to coincide with transitions between habitat regions characterised by oceanographic features such as surface salinity, productivity and temperature (Natoli et al. 2005). On smaller geographic scales, salinity gradients, habitat type and foraging specialisations have also been proposed to contribute to genetic differentiation between other bottlenose dolphin populations (e.g. Bilgmann et al. 2007a; Möller et al. 2007; Sellas et al. 2005; Wiszniewski et al. 2009).

Asymmetric migration between the common dolphin populations

The NSW common dolphins appear to show a striking asymmetric migration pattern. A coalescence-based analysis of nuclear microsatellite DNA suggested that migration has occurred mostly from southern and northern NSW to central NSW (Table 4). This is also apparent in the results of the Bayesian analysis of STRUCTURE, which shows higher levels of admixture for the individuals belonging to the central population (Fig. 4). Analyses of sex-biased dispersal refuted the hypothesis of male-biased dispersal, as is generally observed in terrestrial mammals, and suggests that both males and females migrate. Interestingly, a similar pattern of asymmetric migration and no sex bias in dispersal has been recently reported for coastal Indo-Pacific bottlenose dolphins inhabiting the same region (Wiszniewski et al. 2009). While migration from northern to central NSW for these animals may be due to the southward flow of the EAC, migration from southern to central NSW is more difficult to explain. This could be related to the process of eddy formation after the EAC's separation point from the coast, which causes retroflection of the EAC northward (Godfrey et al. 1980; Ridgway and Dunn 2003). For instance, just south of Sugarloaf Point (which is located at 32.5°S and generally considered the point of separation), the northward currents are common and eddies are considered circular (Tilburg et al. 2001). Concomitantly, migration could be mediated by northward movement of dolphins following migration of their prey. Sardines, which are known to be important in the diet of common dolphins in South Australia (Kemper and Gibbs 2002), migrate north along the NSW coast to secondary spawning areas in southern QLD (Ward et al. 2003), a pattern also observed for other marine fish species on the east coast of Australia (e.g. for the snapper *Pagrus auratus*; Sumpton et al. 2008). Along the east coast of South Africa, for example, common dolphins are known to move northward during the annual sardine migration to take advantage of this plentiful food resource (Cockcroft and Peddemors 1990; Young and Cockcroft 1994). Our estimates of migration rates, however, have to be taken with caution, given the assumptions of equilibrium and population size parity inherent to these analyses (Beerli 2008), as well as the small sample sizes and number of microsatellite markers used.

Differences in genetic variability between common dolphin populations

The three identified populations along the NSW coast show considerable differences in genetic variation, particularly at the mtDNA level. Haplotypic diversity (adjusted for sample size) was much higher in southern NSW compared to northern NSW and intermediate in central NSW. The median-joining network shows that many of the low frequency haplotypes found in southern NSW are also

highly divergent from each other. The high diversity found in southern NSW is comparable to that reported for other populations of short-beaked common dolphins (Amaral et al. 2009; Mirimin et al. 2009; Natoli et al. 2006), including those in other parts of Australia. In a study of common dolphins in South Australia and Tasmania, Bilgmann et al. (2008) reported similar levels of genetic diversity at the same segment of the mtDNA control region. The generally high genetic diversity characteristic of short-beaked common dolphins on a global scale has been suggest to represent a signature of large, long-term effective population size (Amaral et al. 2009). Lower diversity in central and northern NSW, generally represented by closely related and few abundant haplotypes in each of the two regions, may be due to range expansion by a small number of maternal lineages from southern to northern NSW, and could be characteristic for these animals at their distributional range margin at lower latitudes, where waters are less productive. However, information at small geographical scales from other regions around the world would be required to test this hypothesis.

Implications for conservation and management and for the design of Marine Protected Areas (MPAs) in NSW

Common dolphin populations, particularly those inhabiting near-shore coastal environments, are subject to a range of anthropogenic impacts throughout their global distribution. Australia's east coast is no exception and, in a global study of cumulative human impacts on marine ecosystems, the NSW coast was classified as a region with medium to high impacts (Halpern et al. 2008). In this area, common dolphins are exposed to interactions with nature-based tourism (Gill and Burke 1999) and numerous commercial fisheries (Scandol et al. 2008) and are subject to entanglement in anti-shark netting programs (Krogh and Reid 1996). Results from this study, particularly the delineation of three common dolphin populations which show low to moderate levels of genetic connectivity, should be taken into account by the relevant wildlife management agencies (NSW Department of Environment and Climate Change, Department of Primary Industries and Marine Parks Authority NSW). These results should also be considered when identifying additional areas for marine protection in NSW (NSW Marine Parks Authority 2006). At present, six multiple use marine parks and 12 small aquatic reserves have been declared in NSW. These MPAs currently lie within four coastal bioregions (Tweed-Moreton, Manning Shelf, Hawkesbury Shelf and Batemans Shelf) and one marine province (Lord Howe). Two of the common dolphin populations identified in this study were sampled within two of these marine parks: the northern population within Cape Byron Marine Park in the Tweed-Moreton bioregion; and the central population within the Port Stephens-Great Lakes Marine Park in the Manning Shelf bioregion. Nonetheless, protected status has yet to be afforded any site in one of NSW's coastal bioregions, the Twofold Shelf. This bioregion coincides with the area where the southern common dolphin population was identified. This population shows the highest genetic diversity compared to the other two populations, and appears to be the main source of migrants to the central population. While attaining protection for animals with large home ranges such as dolphins within marine parks may be a challenge, it seems important that a MPA in the Twofold Shelf bioregion be established. A large-scale assessment of genetic diversity and connectivity of other marine organisms in NSW, including additional marine vertebrates with long-dispersal capabilities, would contribute towards a better understanding on the role of the EAC in shaping genetic structure in this region and the implications of this for the design of MPAs in NSW and adjacent states.

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Appendix 1

See Table 5.

Table 5 List of mtDNA control region haplotypes of short-beaked common dolphins sampled in six localities in southeastern Australia (GenBank accession numbers HQ223451–HQ223479)

Haplotype	Ballina	Forster	Broughton Island	Port Stephens	Sydney	Eden	Total
1	2	5	7	6	11		31
2		1	2	9	1	1	14
3						2	2
4						3	3
5						3	3
6						6	6
7			1		1	1	3
8						3	3
9						2	2
10		1					1
11				1		6	7
12						1	1
13					1		1
14						1	1
15						1	1
16						1	1
17						1	1
18						1	1
19						1	1
20	1						1
21						3	3
22						2	2
23				1			1
24			1				1
25						2	2
26						1	1
27						1	1
28	13	1	1				15
29						1	1
Total	16	8	12	17	14	44	111

Appendix 2

See Table 6.

Table 6 Number of alleles, observed (Ho) and expected (He) heterozygosities, and Hardy–Weinberg equilibrium *P* values at microsatellite loci

Loci	Ballina	Forster	Broughton Island	Port Stephens	Sydney	Eden	Total
EV1							
No. Alleles	5	6	7	8	6	18	19
Ho	0.625	0.75	0.727	0.688	0.643	0.86	
He	0.669	0.821	0.695	0.838	0.69	0.921	
P	0.307	0.041	0.398	0.053	0.412	0.303	
EV37							
No. Alleles	7	7	7	7	7	12	15
Ho	0.875	0.875	0.667	0.882	0.385	0.773	
He	0.779	0.884	0.765	0.847	0.663	0.819	
P	0.042	0.263	0.022	0.436	0.365	0.036	

Table 6 continued

Loci	Ballina	Forster	Broughton Island	Port Stephens	Sydney	Eden	Total
KW2							
No. Alleles	4	6	8	6	6	8	9
Ho	0.562	0.5	0.667	0.688	0.786	0.75	
He	0.671	0.866	0.807	0.779	0.819	0.857	
P	1.000	0.181	1.000	0.117	0.037	0.091	
KW12							
No. Alleles	6	5	6	7	9	10	11
Ho	0.688	0.875	0.5	0.706	0.857	0.636	
He	0.802	0.83	0.735	0.827	0.857	0.83	
P	0.266	0.519	0.867	0.612	0.032	0 175	
MK5							
No. Alleles	5	4	5	3	6	8	10
Ho	0.5	0.375	0.667	0.353	0.615	0.791	
He	0.519	0.348	0.576	0.401	0.558	0.73	
P	0.330	1.000	0.682	0.234	0.818	0 613	
MK6							
No. Alleles	5	7	8	7	8	12	13
Ho	0.625	1	0.917	0.882	0.75	0.721	
He	0.685	0.857	0.841	0.759	0.871	0.858	
P	0.042	0.959	0.705	0.833	0.034	0.040	
MK8							
No. Alleles	6	5	7	7	7	9	11
Ho	0.75	0.625	0.833	0.765	0.571	0.659	
He	0.796	0.732	0.818	0.846	0.698	0.755	
P	0.022	0.426	0.510	0.566	0.093	0.318	

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