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Influences of past climatic changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*)

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Abstract

Climatic oscillations during the Pleistocene have greatly influenced the distribution and connectivity of many organisms, leading to extinctions but also generating biodiversity. While the effects of such changes have been extensively studied in the terrestrial environment, studies focusing on the marine realm are still scarce. Here we used sequence data from one mitochondrial and five nuclear loci to assess the potential influence of Pleistocene climatic changes on the phylogeography and demographic history of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). Population samples representing the three major morphotypes of *Delphinus* were obtained from 10 oceanic regions. Our results suggest that short-beaked common dolphins are likely to have originated in the eastern Indo-Pacific Ocean during the Pleistocene and expanded into the Atlantic Ocean through the Indian Ocean. On the other hand, long-beaked common dolphins appear to have evolved more recently and independently in several oceans. Our results also suggest that short-beaked common dolphins had recurrent demographic expansions concomitant with changes in sea surface temperature during the Pleistocene and its associated increases in resource availability, which differed between the North Atlantic and Pacific Ocean basins. By proposing how past environmental changes had an effect on the demography and speciation of a widely distributed marine mammal, we highlight the impacts that climate change may have on the distribution and abundance of marine predators and its ecological consequences for marine ecosystems.

Keywords: adaptive evolution, speciation, cetaceans, phylogeography, taxonomy

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Introduction

Global fluctuations in climate during the Pleistocene and its associated sea level changes have altered sea surface temperatures and the flow of ocean currents (Hewitt 1996, 2000; Clark *et al.* 1999). Such historical events have influenced the distribution and connectivity of marine organisms, leading species to extinction as well as acting as drivers of biodiversity (Hewitt 1996). The majority of studies assessing the influence of climatic oscillations on the phylogeography of marine

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organisms have so far been conducted either at regional spatial scales (e.g. Banguera-Hinestroza *et al.* 2010; Taguchi *et al.* 2010) or in species with larval dispersal (e.g. Larmuseau *et al.* 2009; Lopez *et al.* 2010). In contrast, such studies are rare in actively dispersing marine predators, particularly those distributed over a global scale (but see Pastene *et al.* 2007).

Cetaceans are a group of marine mammals that radiated from their terrestrial ancestors around 53 Ma (Arnason *et al.* 2004). Patterns of ocean restructuring during climatic oscillations in the Oligocene and Miocene have been suggested to account for the radiation of extant cetacean species (Steeman *et al.* 2009). Throughout their evolutionary history, dietary specializations are thought to have lead to ecomorphological diversity (Slater *et al.* 2010) as well as to convergent evolution (Natoli *et al.* 2004, 2006), particularly in the Delphinidae, which is the most speciose family of marine mammals (LeDuc 2009). Within the Delphinidae, the subfamily Delphininae includes the recently evolved and closely related polytypic genera *Tursiops*, *Stenella* and *Delphinus*, whose taxonomy, phylogenetic relationships, phylogeography and evolutionary history are still under debate (e.g. LeDuc *et al.* 1999; Natoli *et al.* 2004, 2006; Caballero *et al.* 2008; Möller *et al.* 2008).

Common dolphins (genus *Delphinus*) are widely distributed and abundant small cetaceans that present great morphological variability throughout their distribution. These dolphins occupy a near top position in the marine food chain and their distribution is thought to be associated with that of their prey and with specific water masses characterized by different temperature regimes (Ballance *et al.* 2006; Möller *et al.* 2011; Amaral *et al.* 2012), including 'upwelling-modified' waters in both tropical (Ballance *et al.* 2006) and temperate regions (Bilgmann *et al.* 2008). These 'upwelling-modified' waters are regions of highly variable oceanographic features, characterized by year round or seasonal rising of cool nutrient-rich waters from the bottom of the ocean towards the surface (Au & Perryman 1985).

Common dolphins are currently listed as a species of least concern in the IUCN Red List of Threatened Species, partly owing to the deficit of data, but are included in Appendix II of CITES, which regulates the trade of wildlife products. The rising number of bycatches in various pelagic fisheries has, however, raised concerns regarding the status of some populations (e.g. Bilgmann *et al.* 2008; Mangel *et al.* 2010).

Two species and four subspecies are currently recognized within the genus: the short-beaked common dolphin, *Delphinus delphis* Linnaeus, 1758, distributed in tropical and temperate continental shelf and pelagic waters of the Atlantic, Pacific and Southeast Indian Oceans (hereinafter referred to as the short-beaked morphotype); the long-beaked common dolphin, *Delphinus capensis* Gray, 1828, distributed in nearshore tropical and temperate waters of the Pacific and Southern Atlantic Oceans (hereinafter referred to as the long-beaked morphotype); the Arabian common dolphin, *D. c. tropicalis* van Bree 1971, restricted to the Indian Ocean (hereinafter referred to as the *tropicalis* form); and the Black Sea common dolphin, *D. d. ponticus* Barabash, 1935, restricted to the Black Sea (Perrin 2009).

Previous molecular studies based on mitochondrial DNA (mtDNA) data corroborated the separation of the short- and long-beaked morphotypes occurring in California as two species (Rosel *et al.* 1994). However, when populations from other regions were analysed, a disagreement between morphological and genetic characters was found (LeDuc *et al.* 1999; Kingston & Rosel 2004; Natoli *et al.* 2006; Amaral *et al.* 2007). A highly divergent mtDNA clade including short-beaked individuals from the Northeast Atlantic and *tropicalis* individuals from the Indian Ocean was reported (Amaral *et al.* 2007) and long-beaked populations from the Northeast Pacific and off South Africa showed high levels of differentiation, suggested as an independent evolutionary event and convergence on the same morphotype (Natoli *et al.* 2006). As for short-beaked populations, patterns of genetic partitioning varied from low levels of differentiation found in the North Atlantic (Natoli *et al.* 2006; Amaral *et al.* 2007; Mirimin *et al.* 2009; Querouil *et al.* 2010) to fine-scale population structure reported along the eastern (Möller *et al.* 2011) and southern Australian coasts (Bilgmann *et al.* 2008; Amaral *et al.* 2012). However, to the best of our knowledge, no studies to date have investigated the phylogeography of common dolphins in the light of past climatic changes, and biogeographic hypotheses about the origin of *Delphinus* have not been proposed.

Studies on some cetacean species other than *Delphinus* have suggested an impact of palaeoceanographic changes on the population history of these animals. For example, an extended period of global warming during the Pliocene has been suggested as a factor triggering speciation of minke whales (Pastene *et al.* 2007). Likewise, changes in primary productivity during the Pleistocene glaciations, and related abundance of prey, are thought to have shaped the phylogeography of the dusky dolphin (Harlin-Cognato *et al.* 2007). The Northern Hemisphere glaciations are also thought to have influenced the demography and phylogeography of the harbour porpoise (Taguchi *et al.* 2010) and the white-beaked dolphin (Banguera-Hinestroza *et al.* 2010).

Our study aims to assess the influence of climate oscillations during the Pleistocene on the population demography, historical population structure and

Table 1 Biogeographic scenarios and predictions hypothesized for the origin and dispersal of the genus *Delphinus*

Biogeographic scenario	Predictions	Examples
Eastern Indo-Pacific origin with subsequent dispersal into Atlantic Ocean via southern Africa	Atlantic Ocean lineages are less variable and nested within Indo-Pacific Ocean lineages; Atlantic Ocean populations show lower effective population size, and more recent signals of demographic changes	Fishes (Bremer *et al.* 1998; Grant & Bowen 2006; Martinez *et al.* 2006), prawns (Teske *et al.* 2009), sea turtles (Bowen *et al.* 1997), sea birds (Avise *et al.* 2000), sharks (Duncan *et al.* 2006) and dolphins of the genus *Stenella* (Perrin *et al.* 1978; Perrin 2007)
South Atlantic or South Indian Ocean origin with eastward dispersal towards the Pacific Ocean facilitated by the circumpolar temperate current	Pacific Ocean lineages are less variable and nested within Atlantic and Indian Ocean lineages; Pacific Ocean populations show lower genetic effective population sizes and more recent signals of demographic changes	Many marine organisms in the Southern Hemisphere (see Waters 2008), and dolphins of the genus *Cephalorhynchus* (Pichler *et al.* 2001)

geographic distribution of common dolphins, a highly mobile marine predator. We test two possible biogeographic scenarios, and associated predictions, for the origin and dispersal of *Delphinus*, which have been previously proposed for several marine organisms (Table 1).

Our first scenario is an origin in the eastern Indo-Pacific Ocean, with subsequent dispersal into the Atlantic Ocean basin via southern Africa (Table 1, Fig. 5). The dispersal between Indian and Atlantic Ocean basins would be facilitated by the Agulhas current system, which occasionally projects warm water masses westward around South Africa (Peeters *et al.* 2004). This passage was, however, intermittent, with long-term periods of isolation between the Atlantic and Indian Ocean basins (Peeters *et al.* 2004), leaving a signal in the mtDNA phylogenies of many marine organisms (examples, Table 1). Our second scenario relates to an origin in the South Atlantic or South Indian Ocean, with eastward dispersal towards the Pacific Ocean, facilitated by the circumpolar temperate west-wind drift ocean current present during the Plio-Pleistocene (Table 1, Fig. 5). This current was established around Antarctica with the opening of the Drake Passage between South America and Antarctica, leading to prevailing eastward currents and winds.

Common dolphins are marine predators with a distribution that is putatively linked with major water masses and pelagic resources (Ballance *et al.* 2006; Möller *et al.* 2011; Amaral *et al.* 2012). Therefore, we hypothesize that the genetic architecture of common dolphin populations may contain signals related to major past changes in oceanographic conditions. The latter might include demographic expansions chronologically associated with Pleistocene changes in sea surface temperature and its related increases in resource

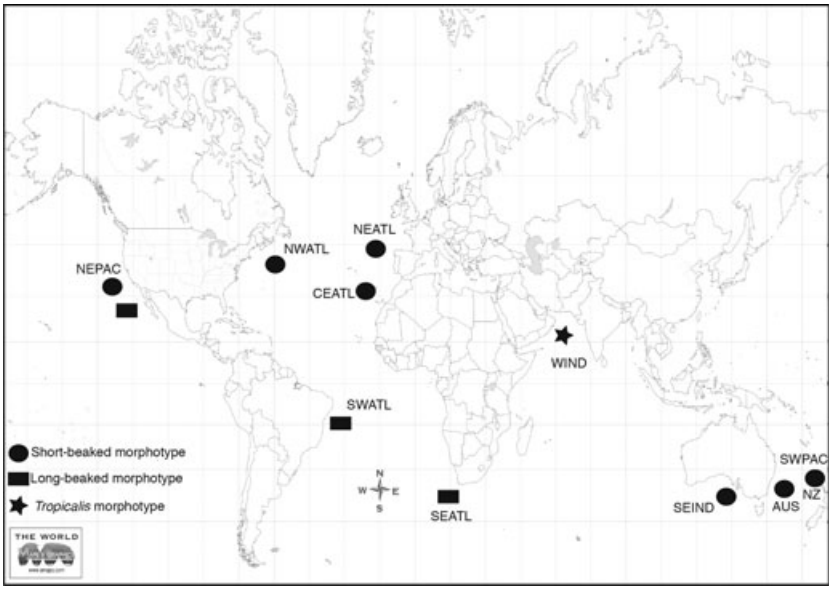

Fig. 1 Map showing sampling locations for the common dolphin populations analysed in this study. (NEPAC, Northeast Pacific; NWATL, Northwest Atlantic; CEATL, Central Eastern Atlantic; SWATL, Southwest Atlantic; SEATL, Southeast Atlantic; WIND, Western Indian Ocean; SEIND, Southeast Indian Ocean; SWPAC_AUS, Southwest Pacific Australia; SWPAC_NZ, Southwest Pacific New Zealand).

availability (Lawrence *et al.* 2006). An understanding of the phylogeography and historical patterns of common dolphin dispersal will contribute to our knowledge of how glaciations have impacted upon marine populations at a global scale.

Material and methods

Sampling and DNA extraction

In total, we analysed 343 common dolphin samples representing 10 oceanic regions and all main morphotypes of *Delphinus* (Fig. 1, Table 2). For the short-beaked morphotype, the sampled regions were the Northeast Atlantic (NEATL), $n = 63$; the Central Eastern Atlantic (CEATL), $n = 21$; the Northwest Atlantic (NWATL), $n = 27$; the Northeast Pacific (NEPAC), $n = 26$; the Southwest Pacific, $n = 41$ (encompassing eastern Australian waters, SWPAC_AUS) and $n = 40$ (encompassing New Zealand waters, SWPAC_NZ) and the Southeast Indian Ocean (southern Australian waters, SEIND), $n = 27$ (Fig. 1). For the long-beaked morphotype, the sampled regions were the Northeast Pacific, $n = 40$; the Southeast Atlantic (SEATL), off South Africa, $n = 26$ (these samples are here classified as long-beaked following Samaai *et al.* (2005) and P. Best (pers. comm.)); and the Southwest Atlantic (SWATL), off Brazil, $n = 7$. Finally, for the *tropicalis* form, $n = 25$, samples were obtained from the Arabian Sea in the Western Indian Ocean (WIND). Tissue samples were obtained either from stranded animals or from dart biopsying live animals and preserved in 99% ethanol. About 144 samples from NWATL, NEPAC, SEATL and WIND were received from the Southwest Fisheries Science Center, Marine Mammal and Turtle Research Sample Collection (SWFSC-NOAA, La Jolla, CA, USA) as extracted DNA. DNA from remaining samples was extracted from muscle or skin tissue using either a standard proteinase K and two phenol-chloroform-isoamyl extractions (Rosel & Block 1996), or a salting-out method (Sunnucks & Hales 1996).

DNA sequencing

mtDNA. The cytochrome *b* gene was amplified and sequenced (1121 bp) using primers on the transfer RNA (tRNA) genes for the 343 samples (GenBank Accession Numbers JX264568–JX264703; Data deposited in the Dryad repository: doi:10.5061/dryad.3pf37). The L-strand primer was on tRNA glutamine (L14724, 5′-TGACTTGAARAACCAYCGTTG 3′) and the H-strand primer on tRNA threonine (5′CCTTTTCCGGTTTACAAGAC 3′) (LeDuc *et al.* 1999). The thermocycle profile and PCR conditions used are described in Amaral *et al.* 2007. The PCR products were cleaned by adding 0.5 U of shrimp alkaline phosphatase and 5 U of exonuclease I and incubating at 37 °C for 30 min and 80 °C for 15 min. Both strands were directly sequenced (BigDye Terminator CycleSequencing; Applied Biosystems) on an ABI 3730 automated sequencer. All sequences obtained were aligned using the software Sequencher, version 4.2 (Gene Codes Corporation).

Nuclear loci. Three anonymous nuclear loci developed from *Delphinus delphis* [Del_12, Del_15 and Del_18 (Amaral *et al.* 2010)] and two introns [CHRNA1 (Roca *et al.* 2001) and PLP (Lyons *et al.* 1999)] were PCR amplified and sequenced for a subset of the samples, which comprised 90 common dolphin specimens (short-beaked morphotype: NE Atlantic, $n = 9$; CE Atlantic, $n = 10$; NW Atlantic, $n = 9$; SW Pacific Australia, $n = 6$, SW Pacific New Zealand, $n = 10$; NE Pacific, $n = 11$, SE Indian, $n = 5$; long-beaked morphotype: SE Atlantic, $n = 7$; SW Atlantic, $n = 7$; NE Pacific, $n = 11$; *tropicalis* form: W Indian, $n = 5$) (GenBank Accession Numbers JX205962–JX206411; Data deposited in the Dryad repository: doi:10.5061/dryad.3pf37) (Table 2). The PCRs were performed in 25 μL mixture containing 10–100 ng DNA, 0.2 mM each dNTP, 0.3 μM each primer, 1 U Taq Polymerase and 1× Taq buffer. PCR products were cleaned, sequenced and aligned as above. To obtain all alleles for each nuclear locus, we used the Bayesian approach implemented in Phase 2.1.1 (Stephens *et al.* 2001; Stephens & Donnelly 2003). The default settings

Table 2 Molecular markers sequenced for this study with information on the number of base pairs sequenced, variable sites and total haplotypes and nucleotide substitution models obtained using jModeltest

Marker	Length (bp)	Variable sites	Total haplotypes	Model
Cytochrome *b*	1121	192	175	TRN + G (0.418)
CHRNA1	379	12	26	SYM + I (0.9580)
Del_12	801	21	33	K80 + I (0.8878)
Del_15	746	20	33	TIM + I (0.9638)
Del_17	733	13	21	TIM + I (0.9605)
PLP	775	13	16	HKY + I (0.9695)
Total	4555	271	304	

were used, except that we only accepted haplotype reconstructions with Bayesian posterior probabilities of $\geq$ 95%. Tests for recombination were performed for each locus using the maximum chi-square test of Smith (1992). For some of the statistical analyses, we used a concatenated nuclear data set generated with the program MESQUITE v. 2.75 (Maddison & Maddison 2007).

Statistical analyses

Genetic diversity and historical population dynamics. In all analyses, each morphotype occurring in each oceanic region was considered as a putative population. Sequence diversity measures for mtDNA and each nuclear locus (nucleotide and haplotype diversities) were separately estimated in DNAsp v. 5.10.01 (Librado & Rozas 2009).

Mismatch distributions (MMD; Rogers & Harpending 1992) and the demographic parameters τ, θ_0 and θ_1 were estimated for the mtDNA data set in Arlequin v. 3.5 (Excoffier & Lischer 2010). Goodness of fit was assessed by the sum of square deviations (SSD) and the Harpending's raggedness index (Harpending 1994) between the observed and the expected mismatch with their significance determined by a parametric bootstrap. The Harpending's raggedness index quantifies the smoothness of the observed pairwise difference distribution and a nonsignificant result indicates an expanding population (Harpending 1994). The relationship Tau $\tau = 2\mu kt$ was used to estimate the time of expansion (t), where k is number of nucleotides sequenced and μ is the mutation rate per nucleotide. We used the average mutation rate estimated for the delphinid mitochondrial genome, 9.86×10^{-9} substitutions per nucleotide per year (Vilstrup *et al.* 2011). In addition to the mismatch analysis, we used a coalescent-based multilocus method, the Extended Bayesian Skyline Plot, which takes genealogy into account and is expected to provide a better estimate of demographic history than other methods (Drummond *et al.* 2005). Moreover, by allowing the analysis of multiple loci, this nonparametric Bayesian MCMC method provides a powerful framework to estimate changes in population size through time (Drummond *et al.* 2005). Analyses were performed for each putative population using sequence data for the cytochrome *b* gene and for the five nuclear loci using mutation rates as described above for the cytochrome *b* gene and a rate of 4.79×10^{-10} substitutions per nucleotide site per year for the nuclear loci (averaged substitution rates of seven autosomal nuclear introns, Alter *et al.* 2007). 10^7 MCMC generations were run in the program BEAST v. 1.6.1 (Drummond & Rambaut 2007), where this method is implemented. As not all models of nucleotide evolution are available to choose in BEAST, the HKY model was chosen because it was the most approximate model to those we obtained in jModeltest (Posada 2008) for each locus (Table 2); all other parameters were set as suggested by the authors (Heled & Drummond 2008). Convergence of the MCMC chains was inspected using Tracer v. 1.5 (Rambaut & Drummond 2007) by visually checking the effective sample size (ESS) values.

Population differentiation and phylogeography. Population differentiation was tested by calculating pairwise F_{ST} using Tamura–Nei distances for both mtDNA and the concatenated nuclear DNA data sets in Arlequin v. 3.5 (Excoffier & Lischer 2010). Significance was tested through 10 000 permutations and multiple tests were adjusted using sequential Bonferroni (Rice 1989). An analysis of molecular variance (AMOVA) was also computed using the following hierarchical levels: (i) all putative populations of short-beaked and long-beaked morphotypes; (ii) short-beaked populations from different ocean basins (i.e. the Atlantic, the Pacific and SE Indian Ocean); and (iii) long-beaked from different ocean basins (i.e. the Atlantic, the Pacific and Western Indian Ocean). Significance was also tested through 10 000 permutations in Arlequin.

Genealogical relationships at the haplotype level were inferred using the median-joining network as implemented in Network v. 4.6.0.0 (Bandelt *et al.* 1999). Haplotypes were colour-coded according to different morphotypes occurring in each ocean basin, and not according to putative populations, for example, short-beaked populations from the Atlantic Ocean were all coded with the same colour, as were the short-beaked populations from the Pacific Ocean.

In addition, phylogenetic relationships among the different morphotypes from each oceanic region were estimated using the species tree method implemented in *BEAST (Heled & Drummond 2010), which runs in BEAST v.1.6.2 (Drummond & Rambaut 2007). This method estimates species tree under the multispecies coalescent model, which assumes gene trees to be embedded inside a species tree by following the stochastic coalescent process back in time (Heled & Drummond 2010). Individuals were again combined by each oceanic region for each morphotype. *Stenella coeruleoalba* (one of the putative sister taxa of *Delphinus* and *Sousa chinensis* (the basal taxa of the Delphininae phylogeny)) were used as outgroups (LeDuc *et al.* 1999). A strict molecular clock model was used for mitochondrial and all nuclear loci following preliminary runs in BEAST, which established no significant deviations from a strict clock (95% high posterior density interval of the posterior distribution included zero). A substitution rate of 0.00986 substitutions per site per lineage per million years was

used for the mtDNA and the nuclear rate was set as relative to the mtDNA rate. The prior was set to the default option of the program, the Yule process. Three runs of 500 million MCMC generations sampling every 10 000 generations were run and combined using LogCombiner v. 1.61 after a conservative burnin of 10%. The program TRACER v.1.5 was run to ensure mixing and convergence of the posterior distribution and parameters by examining ESS. TreeAnnotator v.1.6.1 (Rambaut & Drummond 2010) was subsequently used to summarize the obtained trees in a single, consensus tree that represents the posterior distribution.

Population divergence times and migration rates based on mtDNA. The MCMC approach implemented in the program MDIV (Nielsen & Wakeley 2001) was used to obtain estimates of divergence times and migration rates. To minimize the number of pairwise comparisons, we pooled sampled regions for short-beaked and for long-beaked populations that showed no significant genetic subdivision (i.e. those populations with a statistically nonsignificant pairwise φ_{ST}) into groups (see Results). We pooled the short-beaked populations from NEATL and CEATL into one group, and the long-beaked populations from SWATL and SEATL into another group. These were used as representatives of each morphotype in the Atlantic Ocean. Within the Pacific Ocean, we only considered the short-beaked population from NEPAC for the comparisons, as this population is significantly differentiated from the SWPAC_AUS and SWPAC_NZ populations. All other geographic regions and morphotypes were considered individually. The estimated parameters were θ ($\theta = 2N_{ef}\mu$) where N_{ef} is the effective population size and μ is the mutation rate, M ($M = 2N_{ef}m$) where m is the migration rate and T ($T = t/N_{ef}$) where t is the divergence time. These parameters were obtained using a finite sites model (HKY) to allow for the possibility of multiple mutations per site (Palsboll *et al.* 2004). We ran 3×10^6 cycles with a burn-in of 5×10^5. Maximum values for T and M were set at 10 and 40, respectively. Five runs with different random seeds were run for each comparison, giving similar results for all parameters, which suggested that the number of chains used was adequate. Divergence time (t) was calculated as in Brown *et al.* 2007; using the formula $t = T*\theta/(2u)*g$. T and θ are generated by the program, u is the mutation rate and g is the generation time. u was calculated as $2*\mu*k$, where μ is the mutation rate per nucleotide and k is the length of the sequence. As above, 9.86×10^{-9} substitutions per nucleotide site per year were the mutation rate used for the cytochrome *b* gene (Vilstrup *et al.* 2011). An approximate generation time of 7 years was considered since it is within the range of the age of sexual maturity described for female common dolphins for the Pacific and Atlantic oceans (Murphy *et al.* 2009; Perrin 2009).

Results

Genetic diversity

Haplotype and nucleotide diversities for the mtDNA were high for most populations, with short-beaked populations from the Pacific Ocean showing higher diversity than those from the Atlantic Ocean (Table 3). In comparison, long-beaked common dolphins showed low diversity for all populations, except SWATL for which we had a small sample size. For the nuclear loci, after phasing of heterozygous sites, the final data set comprised 900 alleles. The five nuclear loci were polymorphic across the entire data set but not for every surveyed putative population sampled (Table 3). Overall, levels of haplotypic and nucleotide diversity at nuclear loci were lower than for the cytochrome *b* (Table 3). Although sample size was smaller for the nuclear data set, it is unlikely that this affected levels of diversity observed. The short-beaked populations from the Pacific Ocean showed the highest nucleotide diversity in CHRNA1 and PLP (0.00721 for SWPAC_NZ and 0.00166 for NEPAC, respectively) (Table 3).

Population differentiation, genealogical and phylogenetic relationships

Pairwise F_{ST} values based on cytochrome *b* and on the concatenated nuclear loci were concordant, showing significant differentiation between most putative populations (Table S1, Supporting information). Overall, high differentiation was found between long-beaked and short-beaked populations. High differentiation was observed between all pairwise long-beaked population comparisons. On the other hand, significant pairwise divergence was found between short-beaked populations across different oceans, but low or no differentiation was detected between populations from the same oceanic region or in close geographic proximity (e.g. between CEATL and NEATL ($\varphi_{ST} = 0.0167$, $P > 0.05$ for mtDNA and 0.039, $P > 0.05$ for nuDNA) and between SWPAC_AUS and SWPAC_NZ ($\varphi_{ST} = 0.0048$, $P > 0.05$ for mtDNA and 0.0155, $P > 0.05$ for nuDNA)).

The AMOVA analyses showed significant genetic structure among all populations for all molecular markers (Table 4). For the cytochrome *b* gene, no significant differences between oceans were detected for short-beaked and long-beaked populations ($\varphi_{CT} = 0.0299$, $P = 0.1682$; $\varphi_{CT} = 0.5642$, $P = 0.1634$, respectively). By contrast, for the nuclear loci data set, significant differences were found between oceans for the short-beaked populations

Table 3 Indices of genetic diversity and neutrality tests for common dolphin populations: *N*, number of individuals sequenced; N*h*, number of haplotypes; Hd, haplotype diversity; π, nucleotide diversity

		Short-beaked								Long-beaked		*tropicalis* form
Marker	Statistics	NEATL	CEATL	NWATL	NEPAC	SWPAC_AUS	SWPAC_NZ	SEIND	NEPAC	SEATL	SWATL	WIND
mtDNA	*N*	63	21	27	26	41	40	27	40	26	7	25
	Nh	26	10	18	23	27	31	18	10	9	2	7
	Hd	0.911 ± 0.023	0.833 ± 0.005	0.960 ± 0.021	0.991 ± 0.013	0.948 ± 0.0007	0.988 ± 0.008	0.969 ± 0.017	0.755 ± 0.057	0.809 ± 0.058	0.286 ± 0.196	0.587 ± 0.110
	π	0.005 ± 0.0007	0.003 ± 0.0004	0.005 ± 0.0003	0.009 ± 0.0008	0.007 ± 0.0005	0.009 ± 0.0006	0.005 ± 0.0007	0.004 ± 0.0007	0.006 ± 0.0010	0.003 ± 0.0018	0.005 ± 0.0016
CHRNA1	*N*	9	10	9	11	6	10	5	11	7	7	5
	Nh	7	8	8	10	1	10	3	5	4	1	4
	Hd	0.837 ± 0.057	0.821 ± 0.072	0.745 ± 0.102	0.848 ± 0.062	0	0.889 ± 0.051	0.711 ± 0.086	0.623 ± 0.010	0.626 ± 0.110	0	0.867 ± 0.107
	π	0.004 ± 0.0006	0.004 ± 0.0005	0.004 ± 0.0010	0.005 ± 0.0008	0	0.007 ± 0.0007	0.006 ± 0.0007	0.004 ± 0.0009	0.002 ± 0.0005	0	0.006 ± 0.0010
PLP	*N*	9	10	9	11	6	10	5	11	7	7	5
	Nh	2	1	2	6	5	4	2	4	4	1	1
	Hd	0.366 ± 0.112	0	0.209 ± 0.116	0.801 ± 0.053	0.742 ± 0.116	0.537 ± 0.104	0.356 ± 0.159	0.593 ± 0.008	0.495 ± 0.151	0	0
	π	0.0005 ± 0.0001	0	0.0003 ± 0.0001	0.002 ± 0.0003	0.001 ± 0.0003	0.0008 ± 0.0002	0.0005 ± 0.0002	0.0009 ± 0.0002	0.001 ± 0.0004	0	0
Del_12	*N*	9	10	9	11	6	10	5	11	7	7	5
	Nh	7	7	6	5	6	4	4	1	7	7	3
	Hd	0.810 ± 0.070	0.842 ± 0.057	0.719 ± 0.078	0.472 ± 0.125	0.879 ± 0.060	0.642 ± 0.087	0.711 ± 0.117	0	0.846 ± 0.074	0.824 ± 0.078	0.689 ± 0.104
	π	0.003 ± 0.0003	0.003 ± 0.0005	0.003 ± 0.0004	0.001 ± 0.0004	0.002 ± 0.0004	0.001 ± 0.0002	0.002 ± 0.0006	0	0.002 ± 0.0004	0.003 ± 0.0004	0.002 ± 0.0004
Del_15	*N*	9	10	9	11	6	10	5	11	7	7	5
	Nh	8	1	1	1	1	1	1	7	6	1	1
	Hd	0.889 ± 0.047	0	0	0	0	0	0	0.727 ± 0.0077	0.758 ± 0.1160	0	0
	π	0.003 ± 0.0006	0	0	0	0	0	0	0.003 ± 0.0007	0.003 ± 0.0006	0	0
Del_17	*N*	9	10	9	11	6	10	5	11	7	7	5
	Nh	5	1	1	1	1	1	1	1	1	1	2
	Hd	0.693 ± 0.0860	0	0	0	0	0	0	0	0	0	0.200 ± 0.1540
	π	0.0017 ± 0.0004	0	0	0	0	0	0	0	0	0	0.0006 ± 0.0000

Table 4 Results from analysis of molecular variance (AMOVA) of population structure in common dolphins obtained for the cytochrome *b* gene (mtDNA) and for the concatenated nuclear loci (nuDNA). Statistically significant values are highlighted in bold. ϕ_{ST}, among populations within groups; ϕ_{CT}, populations among groups; ϕ_{SC}, among populations within groups

	Comparison levels	Source of variation	% variation	ϕ-statistics	*P*
mtDNA	All populations	Among populations	30.48		
		within populations	69.52	ϕ_{ST} = 0.305	**<0.001**
	Short-beaked ocean basins	Among oceans (ATL, PAC, SEIND)	2.99	ϕ_{CT} = 0.030	0.168
		Among populations within oceans	7.92	ϕ_{SC} = 0.082	**<0.001**
		Within populations	89.08	ϕ_{ST} = 0.109	**<0.001**
	Long-beaked ocean basins	Among oceans (ATL, PAC, WIND)	56.48	ϕ_{CT} = 0.565	0.163
		Among populations within oceans	1.90	ϕ_{SC} = 0.044	0.129
		Within populations	41.62	ϕ_{ST} = 0.584	**<0.001**
nuDNA	All populations	Among populations	20.4		
		within populations	79.6	ϕ_{ST} = 0.204	**<0.001**
	Short-beaked ocean basins	Among oceans (ATL, PAC, SEIND)	7.98	ϕ_{CT} = 0.080	**0.014**
		Among populations within oceans	2.84	ϕ_{SC} = 0.031	**0.027**
		Within populations	89.18	ϕ_{ST} = 0.108	**<0.001**
	Long-beaked ocean basins	Among oceans (ATL, PAC, WIND)	−23.21	ϕ_{CT} = −0.232	0.838
		Among populations within oceans	60.6	ϕ_{SC} = 0.492	**<0.001**
		Within populations	62.62	ϕ_{ST} = 0.374	**<0.001**

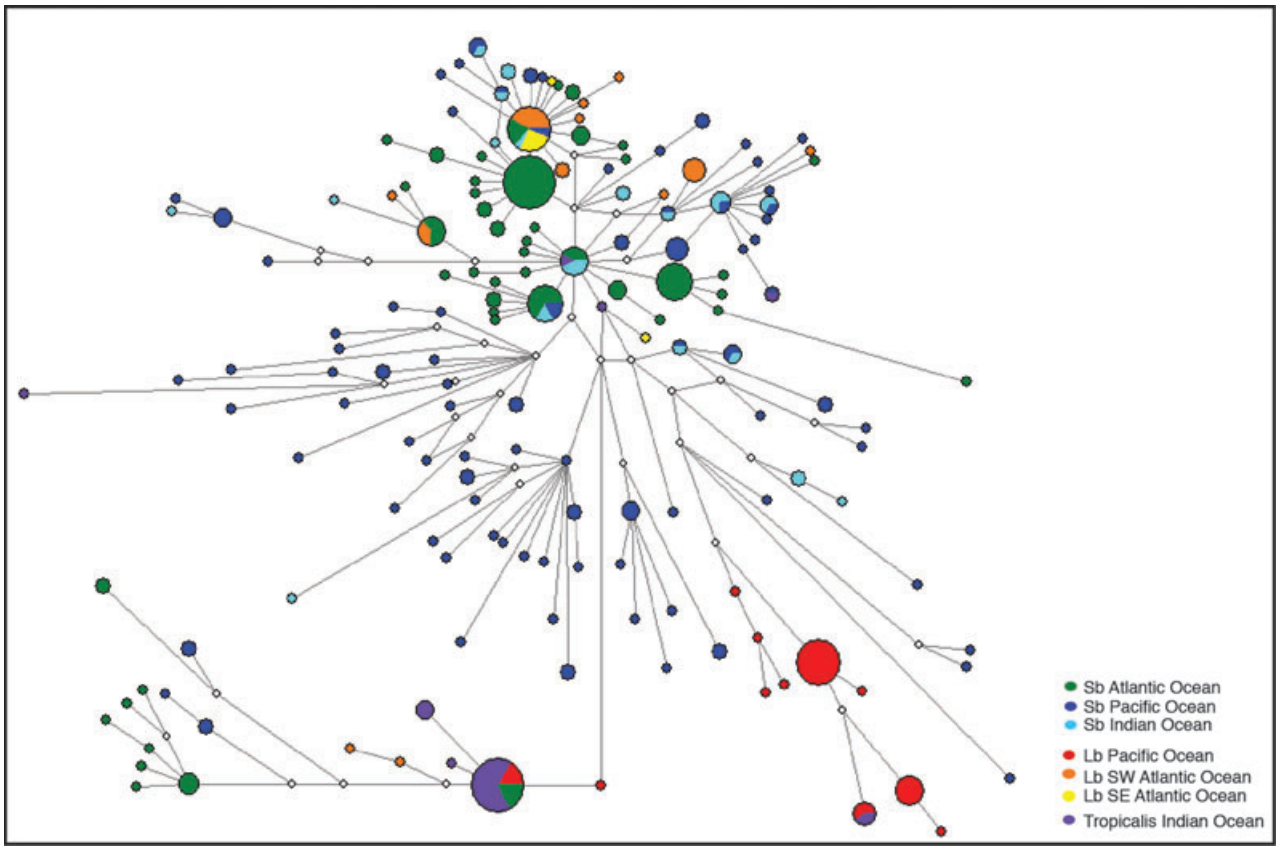

Fig. 2 Median-joining network of cytochrome *b* gene haplotypes of common dolphins. Circle size is proportional to the number of individuals exhibiting the corresponding haplotype. Each geographical region and morphotype within each haplotype is coloured according to the legend. Length of lines is proportional to the number of mutational steps separating haplotypes. White circles indicate missing, intermediate haplotypes. Sb, short-beaked morphotype; Lb, long-beaked morphotype; Tropicalis, *tropicalis* morphotype.

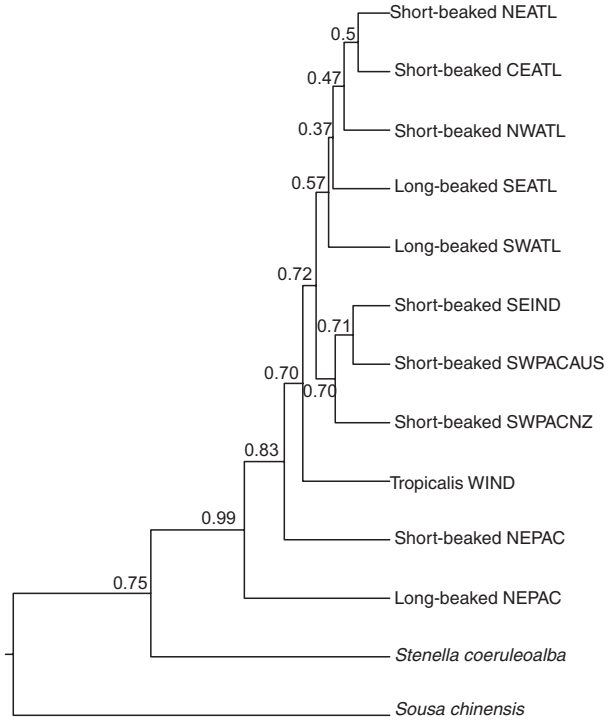

Fig. 3 Species tree phylogeny of combined mitochondrial and nuclear data sets estimated with the *BEAST method. Bayesian posterior probability values are above nodes. NEATL, Northeast Atlantic Ocean; CEATL, Central Eastern Atlantic Ocean; NWATL, Northwest Atlantic Ocean; SEATL, Southeast Atlantic Ocean; SEIND, Southeast Indian Ocean; SWPACAUS, Southwest Pacific Ocean (Australia); SWPACNZ, Southwest Pacific Ocean (New Zealand); WIND, Western Indian Ocean; NEPAC, Northeast Pacific.

(φ_{CT} = 0.0798, P = 0.014) (Table 4). Significant differences were also found among short-beaked populations within oceans (φ_{SC} = 0.0817, P = 0.000 for mtDNA and φ_{SC} = 0.0308, P = 0.027 for nuDNA). For the long-beaked populations, only the nuDNA data set supported differentiation within oceans (φ_{SC} = 0.4918, P = 0.000) (Table 4). For the hierarchical level among oceans, a negative value for the variance coefficient was obtained. Negative values in the variance coefficients of AMOVA analysis are usually an artefact of the calculations, where the value is very close to zero and indicate an absence of genetic partitioning in the data.

Genealogical and phylogenetic relationships obtained show complex phylogeographic patterns and no reciprocal monophyly of species or morphotypes (Figs 2, 3 and S1, Supporting information). For the mitochondrial network, most high-frequency haplotypes are clustered together and were mostly sampled in the Atlantic Ocean. This includes short-beaked populations inhabiting the North Atlantic and long-beaked populations inhabiting the South Atlantic. Most haplotypes sampled in the Indian Ocean short-beaked population are also found in this cluster, together with some haplotypes sampled in the Pacific short-beaked populations (NEPAC, SWPAC_AUS, SWPAC_NZ). We herein loosely refer to these as the Atlantic/Indian Ocean cluster. Several single-frequency haplotypes from this cluster are nested with the central haplotypes, forming a star phylogeny pattern generally observed in population genealogies impacted by recent demographic expansions. In marked contrast to the cluster described above, most haplotypes sampled in the Pacific short-beaked populations have long branches, are not arranged in star phylogenies and show relatively high divergence from the Atlantic/Indian Ocean cluster. A highly divergent cluster is located at a tip of the network and contains mostly haplotypes that were sampled in short- and long-beaked populations from the Atlantic and Indian Oceans, but also short-beaked individuals from the Pacific Ocean. Long-beaked dolphins from NEPAC show a distinct pattern from those described above. For these animals, most haplotypes form a divergent lineage composed of related haplotypes, except for two that cluster with the *tropicalis* population from WIND. The remaining haplotypes sampled in the *tropicalis* population from WIND are found in the Atlantic/SW Pacific-SE Indian cluster, and also in the highly divergent cluster (Fig. 2).

Although the median-joining networks based on nuclear loci are less variable and generally less informative than that obtained with mtDNA, they provide strong support for recent coalescence of lineages in the genus and historical gene flow among morphotypes and species (Fig. S1, Supporting information). Patterns of high-frequency haplotypes that show wide distribution closely linked to low-frequency haplotypes are seen in most networks (Fig. S1, Supporting information). The species tree obtained in *BEAST placed the long-beaked and short-beaked populations from NEPAC and the *tropicalis* population from WIND as basal to all other populations (Fig. 3). Two other clusters were obtained, although they were supported by low posterior probability values. These separate the short-beaked populations from the Southwest Pacific and Southeast Indian Oceans from the short-beaked and long-beaked population from the Atlantic Ocean (Fig. 3).

Divergence time estimates

Estimates obtained in the program MDIV varied from 0.036 (0.032–0.085) million years (Ma) (between short-beaked and long-beaked populations from the Atlantic Ocean) to 1.35 (1.218–2.402) Ma (between short-beaked populations from the Atlantic and Pacific Oceans), indicating that divergences within *Delphinus* took place within the Pleistocene period (Table 5). The divergence between short- and long-beaked populations from

Table 5 Divergence times between common dolphin populations obtained in MDIV. Maximum likelihood estimates of divergence times, effective population sizes and migration rates based on the mitochondrial cytochrome *b* gene [95% credible interval]. θ, effective population size; *M* (2N*m*); *T* (*t*/2N). Time divergence values (in million years, Ma) are given for a mutation rate of 9.86×10^{-9} substitutions per nucleotide site per year and a generation time of 7 years. Question marks indicate parameter values for which the likelihood surface was too flat to enable inference

Population comparison	θ	M	T	t (Ma)
SbATL-SbPAC	20.305 [18.321–36.123]	0.600 [?–3.862]	0.420	1.350 [1.218–2.402]
SbATL-SbIND	11.450 [9.971–20.993]	1.620 [?–8.133]	0.160	0.290 [0.253–0.532]
SbPAC-SbIND	25.634 [22.943–48.054]	1.500 [?–7.550]	0.280	1.136 [1.017–2.130]
LbATL-LbPAC	2.541 [2.522–7.378]	0.180 [?–0.588]	1.680	0.676 [0.671–1.962]
LbATL-TroIND	3.670 [3.466–9.712]	0.380 [?–4.546]	1.280	0.744 [0.702–1.968]
LbPAC-TroIND	2.727 [2.704–7.946]	0.480 [?–6.612]	2.100	0.908 [0.899–2.642]
SbATL-LbATL	3.779 [3.367–8.983]	0.240 [?–14.392]	0.060	0.036 [0.032–0.085]
SbPAC-LbPAC	17.574 [15.024–31.494]	0.600 [?–5.559]	0.420	1.168 [0.999–2.094]

SbATL, short-beaked morphotype from the Atlantic Ocean; SbPAC, short-beaked morphotype from the Pacific Ocean; SbIND, short-beaked morphotype from the Indian Ocean; LbATL, long-beaked morphotype from the Atlantic Ocean; LbPAC, long-beaked morphotype from the Pacific Ocean.

Table 6 Estimation of time since expansion and demographic parameters using mismatch analysis. Results are provided for each population based on cytochrome *b* gene

	SSD	*Hri*	θ_0	θ_1	t	t (9.86×10^{-9})
mtDNA						
Sb_NEATL	0.014	0.021	0.000	13.760	4.301	0.195
Sb_CEATL	0.028	0.046	0.000	7.068	5.350	0.242
Sb_NWATL	0.311*	0.008	0.000	99 999.000	0.777	0.035
Sb_NEPAC	0.005	0.009	3.683	143.203	7.666	0.347
Sb_SWPAC_AUS	0.005	0.013	0.000	67.969	8.881	0.402
Sb_SWPAC_NZ	0.003	0.011	1.113	175.859	8.777	0.397
Sb_SEIND	0.003	0.009	2.983	36.426	3.871	0.175
Lb_NEPAC	0.065	0.153	0.002	4.903	19.832	0.897
Lb_SEATL	0.041	0.047	0.000	9.478	6.682	0.302
Tro_WIND	0.398*	0.191	0.000	428.125	0.000	0.000

SSD, sum of the square deviations; *Hri*, Harpending raggedness index; θ_0 and θ_1, effective population size before and after the population expansion, respectively; τ, time in generations; and *t*, time of the expansion. Significant results are indicated by a star, $*P > 0.05$.

NEPAC was estimated at 1.168 (0.999–2.094) Ma. It should be noted that these estimates may be biased owing to the mutation rate used, generation time and also because MDIV assumes constant and equal population sizes. Nevertheless, the obtained estimates are within the range of values obtained for the divergence of *Delphinus* from other members of the subfamily Delphininae (e.g. McGowen *et al.* 2009) and are therefore broadly indicative of the period when each genetic differentiation occurred.

MDIV also generated estimates of the ancestral populations sizes (θ) and migration (*M*) for all pairwise comparisons (Table 5). Theta values varied from 2.542 to 25.634, with pairwise comparisons with high theta values involving the short-beaked population from the Pacific Ocean. Migration rates were higher between short-beaked populations from the Pacific and Indian Oceans, and lower between the long-beaked populations from the Atlantic and Pacific Oceans. Posterior probability distributions for all parameters estimated are shown in Fig. S2 (Supporting information).

Demography

As expected based on visual assessment of nuclear and mtDNA genealogies, our statistical framework used to investigate demographic history (i.e. summary statistics, mismatch analysis and Bayesian skyline plots) revealed that most common dolphin populations do not conform with a model of constant size through time. Mismatch analyses supported demographic expansions for almost every short-beaked population analysed, but only for the SEATL long-beaked population (Table 6, Fig. 4). The Bayesian skyline plot analyses, which are coalescent

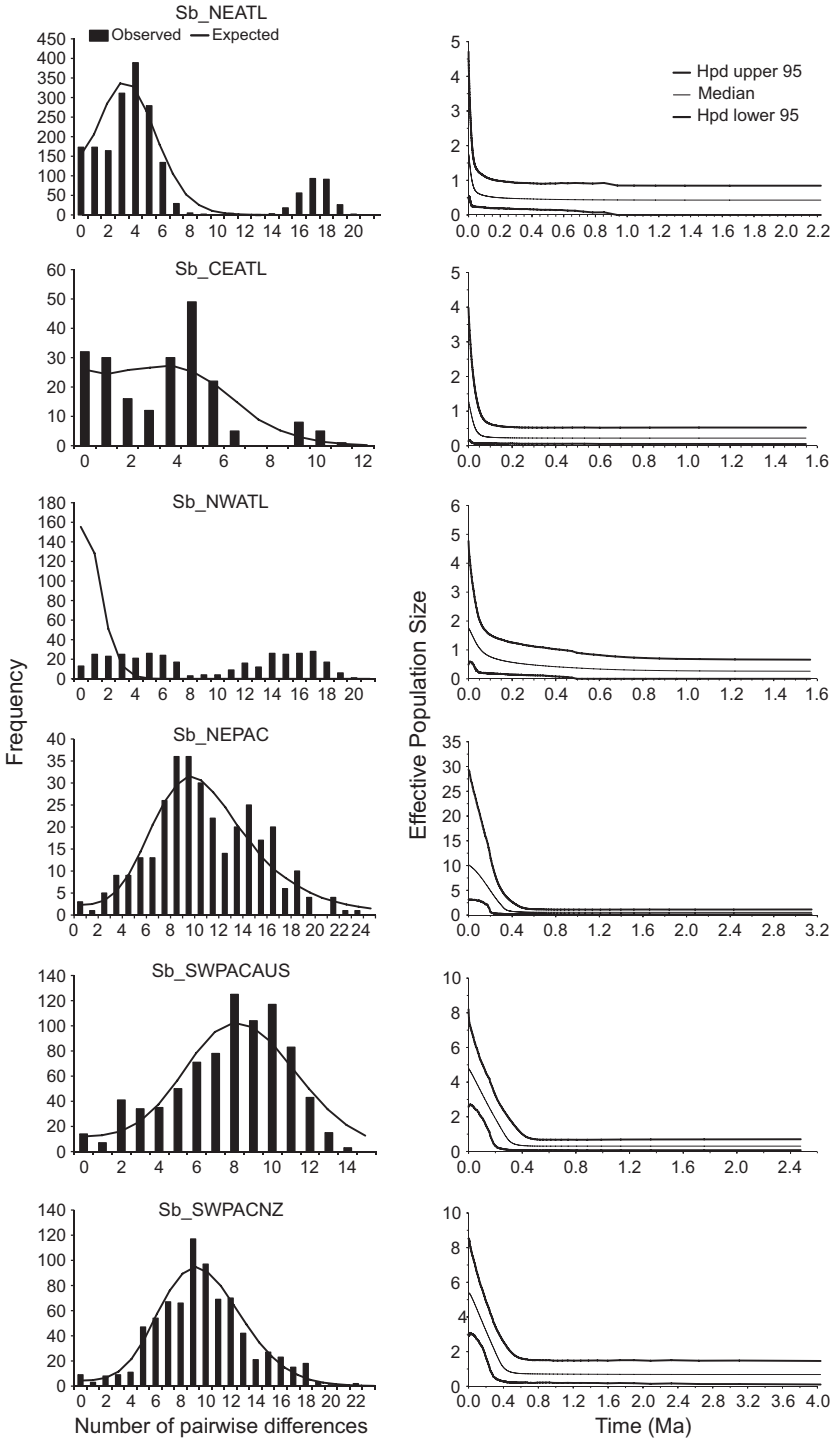

Fig. 4 Historical demography of the common dolphin populations examined in this study. Mismatch distributions obtained with the mitochondrial DNA data set (left) and Extended Bayesian Skyline Plots showing changes in population size through time (Ma) (right).

based and utilized the combined mitochondrial and nuclear data sets, showed very similar results. All skyline plot runs showed an efficient mixing of chains for the several statistics estimated, with ESS higher than 1000. Mismatch distributions and skyline plots showed differences between short-beaked populations from the

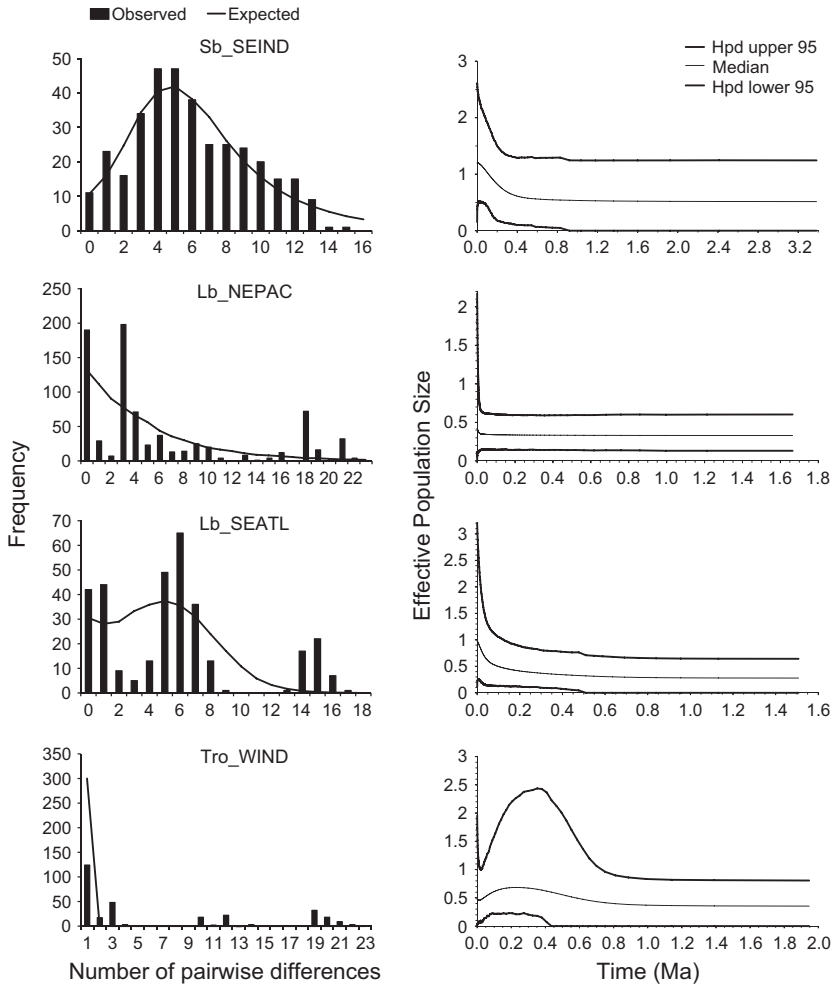

Fig. 4 (*Continued*)

Pacific and Atlantic Oceans (Fig. 4). Pacific Ocean populations showed older population expansions (starting between 0.35 and 0.40 Ma) when compared to Atlantic populations (starting between 0.24 and 0.30 Ma) (Table 6).

Estimates of effective population size were also different between oceans, being higher for populations inhabiting the Pacific Ocean, and lower for populations inhabiting the Atlantic. These results are concordant with those based on MDIV (Table 5). Long-beaked common dolphin populations showed different demographic patterns. The SEATL population was the only showing a clear sign of expansion in the mismatch distribution and the skyline plot (Fig. 4). The NEPAC population showed a constant population size through time in the skyline plot, a result consistent with the summary statistics (Table 6, Fig. 4). The SWATL population was not analysed owing to the small sample size. The skyline plot for the *tropicalis* form population from WIND showed an old population expansion that ended at around 0.2 MA, followed by a population decline that seems to be stabilizing (Fig. 4). In summary, all analyses support the notion that common dolphins are a group of marine predators with young coalescence and multiple localized demographic expansions.

Discussion

This study used a multilocus data set to reconstruct the history of diversification and population dynamics of a group of cosmopolitan marine predators, the common dolphins (genus *Delphinus*). Our analyses indicate that this widely distributed group is composed of very closely related lineages that show young age, rapid morphologic diversification and strong signatures of regional demographic expansions. Here we propose a biogeographic scenario that accounts for the origin of common dolphins and suggest that Pleistocene changes in climate and oceanography influenced the demography, dispersal and speciation in the genus *Delphinus*.

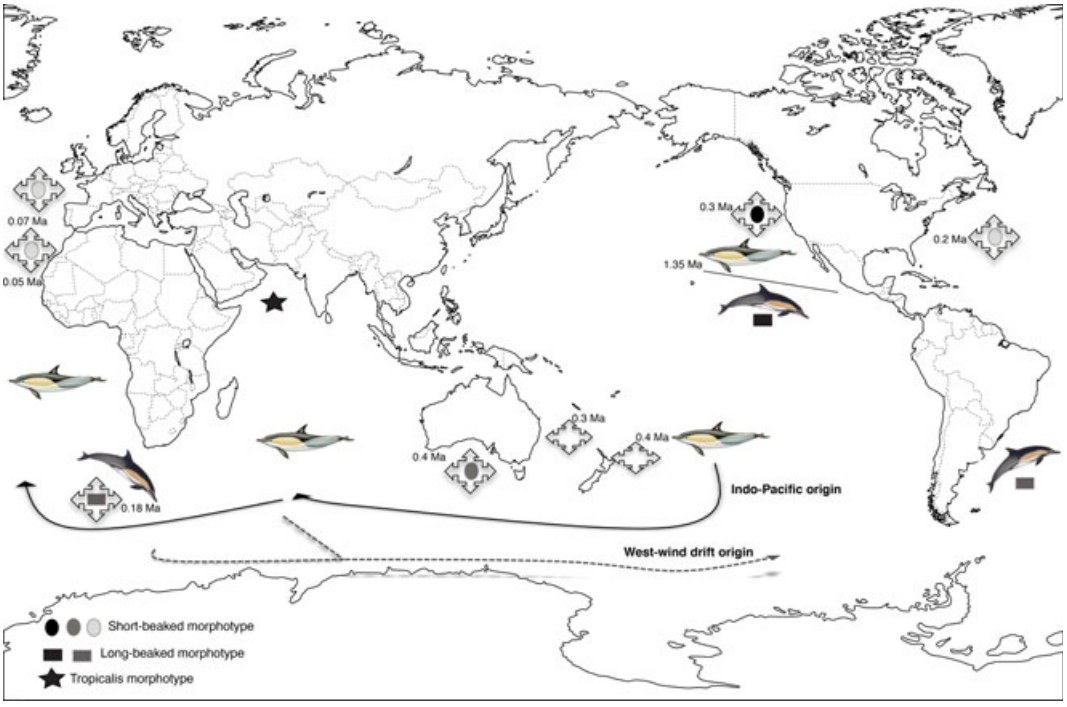

Fig. 5 Map summarizing the proposed origin, expansion and speciation of the genus *Delphinus*. The different shades of grey and blue illustrate the older (darker) and younger (lighter) populations of the short- and long-beaked morphotypes. Arrows indicate the route of colonization of the short-beaked morphotype. The dash line represents the time of speciation/origin of the long-beaked morphotype in the Northeast Pacific. Blue circles indicate the independent origin of the long-beaked populations in the Atlantic Ocean. Centred arrows represent population expansions with approximate times of expansion obtained with the Extended Bayesian Skyline Plot method in bold. The alternative route of colonization (west-wind drift) is shown in dark grey dashed arrows.

Origin, range expansion and speciation of common dolphins

Genealogical and phylogenetic relationships obtained with our multilocus data set indicate that the ancestral common dolphin populations are in the Pacific Ocean. Evidence for this hypothesis comes from the unequal frequency and distribution of haplotypes from the Atlantic and the Pacific Oceans in the mtDNA network, and the basal position of short- and long-beaked populations from the Pacific Ocean in the species tree obtained in *BEAST. We therefore suggest that common dolphins originated in the Pacific Ocean, and most likely in the Northern Hemisphere given the branching order obtained in the species tree. The North Pacific is considered a marine centre of evolutionary origin (Briggs 2003). It has originated biota able to transgress and successfully colonize the Arctic, Atlantic and South Pacific Oceans, and its biota has also remained permeable to invasions by taxa from other regions (Briggs 2003). The dispersal of common dolphins across equatorial waters to the Southern Hemisphere would be facilitated by a cooling of the tropical Pacific during the Pleistocene period (Lindberg 1991; Lee & Poulsen 2005; Lawrence *et al.* 2006). The climatic fluctuations during this period and consequent impacts on sea levels, sea temperatures and shoreline configurations are known to have impacted the distribution of several marine organisms (e.g. Taguchi *et al.* 2010; Liu *et al.* 2011). Some organisms found glacial refugia, whereas others have dispersed. Our results indicate that, from the Pacific Ocean, common dolphins may have dispersed westerly, into the Indian Ocean and later into the Atlantic Ocean, around the tip of South Africa (Fig. 5). Altogether, these results support the hypothesis we put forward for the origin and dispersal of the genus in the Indo-Pacific region, thus failing to support the alternative scenario of the west-wind drift hypothesis. The presence of haplotypes from the Pacific nested within those from the Atlantic Ocean in the mtDNA median-joining network corroborates this hypothesis (Fig. 2). Moreover, Southeast Indian Ocean haplotypes (SEIND) are mostly grouped with those from the Atlantic, and not dispersed within Pacific haplotypes. This same route of dispersal has been previously described for several marine organisms, from teleost fishes (e.g. Bremer *et al.* 1998) to marine turtles (Bowen *et al.* 1997) and sea birds (Avise *et al.* 2000). In addition, it has also been suggested for the dusky dolphin, *Lagenorhynchus obscurus* (Harlin-Cognato *et al.* 2007) and its prey, *Engraulis* sp.

(Grant & Bowen 2006), as well as for the species of *Stenella* (Perrin 2007). In fact, the phylogeography of dusky dolphins correlates to that of *Engraulis* sp., suggesting that primary productivity and prey abundance are likely to have played a role in the species history (Harlin-Cognato *et al.* 2007). Common dolphins prey on the same small schooling fish and therefore it is possible that trophic changes may also have played a role in the evolutionary history of the genus.

Although the exact timing of dispersal of common dolphins could not be estimated, according to the values obtained in MDIV, the divergence between short-beaked populations from the Pacific and Atlantic Oceans and from the Pacific and Indian Oceans occurred between 1.13 and 1.35 Ma, indicating that dispersal would have occurred at around this time. These estimates, however, should be considered with caution given the potential violation of the assumption of equilibrium when using MDIV. The divergence time between short- and long-beaked morphotypes inhabiting the Pacific Ocean was also estimated to occur at around 1.2 Ma. This period coincides with the onset of rapid climatic changes and oceanographic shifts that occurred during the mid-Pleistocene. More specifically, this period followed a stage of maximum productivity in the Pacific Ocean owing to a major cooling event (Morley & Dworetzky 1991; Lawrence *et al.* 2006). The decrease in productivity that followed this period owing to higher temperatures could have led to the dispersal of the short-beaked morphotype to other ocean basins. Concomitantly, it could also have led to niche specialization in more coastal areas that would originate the long-beaked morphotype in the Pacific Ocean. Genetic subdivisions during this period have also been reported for other marine taxa occurring in this region (Harlin-Cognato *et al.* 2007; Liu *et al.* 2011). Nevertheless, responses of marine organisms to these fluctuations in sea surface temperature and consequent effects on marine productivity and shoreline configuration have been shown to vary (e.g. Hickerson & Cunningham 2005), even in taxa with similar dispersal potentials (e.g. Marko 2004).

In the Atlantic Ocean, the long-beaked morphotype appears to have evolved much more recently, as indicated by younger estimates of divergence times (0.04 Ma) and the position of haplotypes at the tips of mtDNA and nuclear genealogies (Figs 2, 3 and S1, Supporting information). It has been previously suggested that the long-beaked morphotype evolved independently in different ocean basins through feeding specializations (Natoli *et al.* 2006). Our results support the hypothesis of independent evolutionary events; however, sampling of additional geographical regions where the morphotypes occur in sympatry is needed.

Phylogeography of common dolphins

Overall, despite some differences across loci and methods, we recovered strong signals of demographic expansion for all short-beaked populations. Estimates of the time of population expansion should, however, be interpreted cautiously as departures from the mutation rate may be expected and could cause an error in the estimation. Nevertheless, values obtained can be considered a rough approximation at which period the historical events occurred. Our estimates place all population expansions in the Pleistocene, although the actual ages since expansion differed between Atlantic and Pacific Ocean populations. Older expansions occurred in the Pacific Ocean, which is in agreement with these populations being the oldest. During the Pleistocene period, glaciations in the Northern Hemisphere caused temperature fluctuations that have influenced upwelling systems and consequently favoured the availability of resources, generating episodes of range expansions and contractions, with subsequent fluctuations in population size (Lindberg 1991; Hewitt 2000; Lawrence *et al.* 2006). This same pattern has also been described for other marine taxa in the Atlantic (e.g. Aboim *et al.* 2005; Pastene *et al.* 2007; Larmuseau *et al.* 2009; Banguera-Hinestroza *et al.* 2010) and in the Pacific Ocean, including for the harbour porpoise, which population expansions have been estimated to occur at about the same period as in common dolphins (e.g. Diaz-Jaimes *et al.* 2010; Lopez *et al.* 2010; Taguchi *et al.* 2010). By contrast, the North Atlantic was subjected to more severe temperature cycles than the North Pacific during the Pleistocene (Briggs 1974), and this may account for the different patterns of population expansion seen in short-beaked populations inhabiting these two oceans. The long-beaked populations inhabiting the Atlantic and Pacific Oceans also showed different patterns. The SEATL population showed a clear sign of a recent population expansion, which was supported by all methods used. On the contrary, the long-beaked populations from NEPAC did not appear to have experienced demographic expansions according to our analyses. Results obtained for the *tropicalis* population indicate an older expansion, followed by a population decline. Interestingly, at the estimated time of expansion (~0.5 Ma) there was an extraordinary peak in primary productivity in the Arabian Sea, which has been related to the onset of an intensive meridional overturning in the Atlantic Ocean (Ziegler *et al.* 2010).

The existence of highly divergent mitochondrial clades in marine animals has been associated with scenarios of vicariance during the Pleistocene—a period in which temperature fluctuations temporarily impeded regional migrations (Graves & McDowell 1995; Bremer *et al.* 1998; Buonaccorsi *et al.* 2001; Vinas *et al.* 2004;

Martinez *et al.* 2006). Secondary contact and subsequent unidirectional migration would result in contemporary asymmetrical distribution of mitochondrial clades (e.g. Bremer *et al.* 1998; Martinez *et al.* 2006). The intermittent isolation between the Atlantic and Indo-Pacific Ocean basins during the Pleistocene has been suggested to explain phylogeographic patterns in large migratory bony fishes such as the Atlantic big-eyed tuna (Bremer *et al.* 1998; Martinez *et al.* 2006), the Atlantic bonito (Vinas *et al.* 2004) and swordfishes (Bremer *et al.* 2005), as well as in hammerhead sharks (Duncan *et al.* 2006). A similar scenario of vicariance and secondary contact could therefore account for the highly divergent lineage observed in the mtDNA network of common dolphins, where the predominance of haplotypes is from the Atlantic and Indian Oceans.

A common phylogeographic pattern across many widespread teleost fishes and sharks is lower genetic diversity in populations inhabiting the Atlantic Ocean compared to those from the Pacific, as well as significant differences in haplotype frequencies between the two ocean basins (e.g. Vinas *et al.* 2004; Duncan *et al.* 2006; Castro *et al.* 2007). Our analyses have also disclosed a similar pattern among short-beaked common dolphins inhabiting the two ocean basins, indicating a recent colonization of the Atlantic Ocean by taxa originating in more diverse ecosystems, such as the Indo-West Pacific or the North Pacific Ocean (Briggs 2000, 2003). Moreover, temperature fluctuations in the North Pacific were not so drastic as in the North Atlantic during the Quaternary glaciations. First, the Pacific basin is larger and therefore more climatically stable and, second, glaciations were more intense in the North Atlantic (Briggs 1974). These different climatic regimes may therefore account for the markedly different phylogeographic patterns obtained in marine organisms occurring in the Atlantic and Pacific Ocean basins.

Genetic differentiation within short- and long-beaked morphotypes

In short-beaked common dolphins, fixation indices showed a pattern of higher genetic differentiation across larger geographical scales (e.g. between populations inhabiting different oceans) and lower differentiation among populations inhabiting the same ocean basin. Although including a broader geographic sampling, these results support previous findings (Natoli *et al.* 2006; Amaral *et al.* 2012). Nonetheless, AMOVA analyses also supported higher levels of partition for populations within ocean basins for both mitochondrial and nuclear markers. As for long-beaked populations, high levels of differentiation were found at both mitochondrial and nuclear markers, between the populations inhabiting SEATL and NEPAC, similar to that reported for the mitochondrial control region (Natoli *et al.* 2006). Although the presently recognized long-beaked common dolphin species (*Delphinus capensis*) may prove to be invalid, it seems unlikely, despite their close genetic relationship, that all ecologically and morphologically distinct *Delphinus* populations belong to the same species.

Conclusion

Using multilocus sequence data from a global sample and analyses based on coalescent and traditional statistical methods, we showed that the phylogeographic history, historical demography and local adaptation of common dolphins are likely to have been influenced by Pleistocene climatic oscillations. We also provided insights into the evolutionary history of the genus *Delphinus,* showing that the origin and route of dispersal from the Pacific Ocean into the Atlantic Ocean is the most plausible biogeographic scenario. This has also been proposed for other marine organisms such as teleosts, turtles, sharks and sea birds. Finally, our study highlights the role of climate change on the distribution and abundance of marine predators.

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This study forms part of A.RA.'s PhD research on evolutionary genetics of dolphins supervised by L.M., L.B. and M.C. All authors share similar research interests about evolution and conservation of aquatic animals.

Data accessibility

DNA sequences: nuclear loci GenBank Accessions nos. JX205962–JX206411; mitochondrial cytochrome *b* gene GenBank Accession nos. JX264568–JX264703. DNA sequences, separate NEXUS input files by locus: Data deposited in the Dryad repository: doi:10.5061/dryad.3pf37.

Supporting information

Additional Supporting Information may be found in the online version of this article.

Fig. S1 Median-joining networks of nuclear gene haplotypes of common dolphins: (a) CHRNA1, (b) PLP, (c) Del_12, (d) Del_15, (e) Del_17. Circle size is proportional to the number of individuals exhibiting the corresponding haplotype.

Fig. S2 Posterior probability distributions for θ (population size), *M* (migration) and *T* (time since divergence) obtained in the program MDIV under a HKY model.

Table S1 Pairwise F_{ST} values obtained for the cytochrome *b* gene (below diagonal) and for the concatenated nuclear loci (above diagonal) for the different putative populations analysed in this study.

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