Original Article

# Biogeography and temporal progression during the evolution of striped dolphin population structure in European waters

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**Running title:** Population structure of striped dolphin in European waters

**Word count of abstract + main text + references:** 6987

**Figures & Tables:** Approximately 1.5 pages

## Abstract

### Aim

We investigated the population genetic structure of a highly mobile marine species, the striped dolphin, *Stenella coeruleoalba* (Meyen, 1833), along a geographic range with habitat transitions and historical dynamics to identify the causes of genetic divergence, and to assess the effect of past climate change on demography and population connectivity.

### Location

North-east Atlantic Ocean and Mediterranean Sea.

### Methods

Twenty microsatellite loci were used in conjunction with coalescent methods to investigate the genetic structure and demographic history of striped dolphins (*Stenella coeruleoalba*) in the Mediterranean Sea and eastern North Atlantic Ocean. Approximate Bayesian modelling was used to compare the support for alternative scenarios for the pattern of divergence over time in the context of known geographic transitions and environmental change over the course of the Quaternary.

### Results

We describe a novel pattern of structure among the extant populations along north/south and east/west axes. Modern gene flow shows strong directionality from north-east to south and west in the North Atlantic, and from west to east in the Mediterranean. On a temporal scale we found evidence for a progression starting with a division between the North Atlantic and Mediterranean Sea populations during the middle Pleistocene, followed by a division within the Mediterranean between the east and west basins towards the end of the Pleistocene, and finally an east/west division in the eastern North Atlantic at the start of the Holocene.

**Main conclusions**

In the context of known population structure for other marine species along the same geographic range, our data facilitate inference of the more general processes that shaped patterns of biogeography across this region through the environmental transitions of the Quaternary.  In particular, Pleistocene era divisions apparently reflect strong physical habitat boundaries, with later divisions associated with climate warming in the Holocene.

Key words: Holocene, Mediterranean Sea, migration, North Atlantic Ocean, Pleistocene, population structure, *Stenella coeruleoalba*

## Introduction

Species biogeography is shaped by demographic processes through evolutionary and ecological time-scales, including influence from environmental instability and/or direct anthropogenic pressures. Alterations in species ecological niches can influence their demographic history, adaptation and dispersal behaviour. It is well known that climatic oscillations in the Quaternary were responsible for significant changes in species distributions and population dynamics in terrestrial environments (e.g. see Hewitt 2004). In marine systems genetic breaks (e.g. Barber *et al.* 2000) and recolonization through migration (e.g. Wares & Cunningham 2001) contributed to altering genetic structure among populations throughout the Quaternary period. During Pleistocene glaciations, sea level was reduced and environmental conditions were re-distributed sometimes creating isolated refugia, imposing at first geographical barriers to gene flow followed by post glacial dispersal and expansion (Xue *et al.* 2014). This has been reported for various fish species (e.g. Bargelloni *et al.* 2005), and this pattern of vicariance followed by recolonization of marine organisms, often associated with bottlenecks and expansions, likely shaped contemporary genetic structure for various species.

Marine mammals have reportedly experienced declines during the last Last Glacial Maximum (LGM; see de Bruyn *et al.* 2011; Moura *et al.* 2014), subsequent re-expansion (e.g. Banguera *et al.* 2010) and species-specific effects associated with habitat release and loss (e.g. de Bruyn *et al.* 2009). For example, studies report that modern harbour porpoise (*Phocoena phocoena*) populations in the eastern North Atlantic and North Sea have evolved during the late Pleistocene (Martinez-Bakker *et al.* 2013) or early Holocene (see Fontaine *et al.* 2014), including phenotypic adaptation and differential prey choice suited to different habitats (de Luna Lopez *et al.* 2012, Fontaine *et al.* 2014). A similar effect was suggested for *Lagenorhynchus* species in the North Atlantic (Banguera *et al.* 2014).

Across the geographic range extending from the Black Sea through the Mediterranean Sea and through the eastern North Atlantic to Scotland, studies have proposed habitat-related barriers to gene flow for harbour porpoise (Fontaine *et al.* 2014) and bottlenose dolphins (Natoli *et al.* 2005). In the bottlenose dolphin study there was differentiation across established oceanographic discontinuities (such as the Almeria Oran front; Tintoré *et al.* 1988) that had shown evidence for restricting gene flow for a diversity of marine species (see Natoli *et al.* 2005). This includes various fish species such as *Solea solea* (Exadactylos *et al.* 1998), *Solea vulgaris* (Guarniero *et al.* 2002), *Dicentrarchus labrax* (Bahri-Sfar *et al.* 2000) and the bivalve *Mytilus galloprovincialis* (Quesada *et al.* 1995). In contrast, common dolphins (*Delphinus delphis*) show little or no population structure through a similar range (e.g. Mirimin *et al.* 2009), and the fine scale structure shown (between the eastern and western basins of the Mediterranean Sea; e.g. Natoli *et al.* 2006) may be driven by relatively recent processes associated with anthropogenic impact (Moura *et al.* 2013a). Social coherence within local populations may be an ancillary mechanism promoting philopatry and habitat dependence, as in the extreme case of the killer whale (*Orcinus orca*), where social cohesion in kin-groups is strong enough to largely define regional population structure in this species (Hoelzel *et al.* 2007; Pilot *et al.* 2010). Social kinship associations have been investigated in other delphinid species, including the striped dolphin (*Stenella coeruleoalba* (Meyen, 1833)),, and a significant association among adult female kin in small social groups was reported (Gaspari *et al.* 2007).

Here we investigate the processes promoting population structure using data from the same eastern North Atlantic and Mediterranean geographic range for the striped dolphin. The striped dolphin is distributed world-wide in tropical and temperate waters (see Hammond *et al.* 2008). In the Mediterranean Sea it is the most common and abundant species (Notarbartolo di Sciara *et al.* 1993). Among earlier studies Galov *et al.* (2009) reported a lack of genetic differentiation for striped dolphin mtDNA control region haplotypes between the Croatian part of the Adriatic Sea and the rest of Mediterranean Sea. Another mtDNA study showed no subdivision within the broader Mediterranean Sea (Garcia-Martinez *et al.* 1999).  However microsatellite DNA revealed genetic differentiation between the Mediterranean Sea and North Atlantic (Bourret *et al.* 2007; Gaspari *et al.* 2007), between the western and eastern Mediterranean basins, and a weak pattern of isolation by distance between nearshore and offshore populations in the Ligurian Sea (Gaspari *et al.* 2007). However, these studies were based on relatively few samples, few loci (up to 8) and limited geographic range.

To test our hypotheses about historical biogeography we required greater resolution and a broader sampling range.  We use these data to undertake demographic modelling using the approximate Bayesian computational (ABC) method, permitting novel inference.  We use fine-scale sampling to test the hypothesis that the point of division between the western and eastern Mediterranean basins is across the Sicily channel as proposed for other species (e.g. Guarniero *et al.* 2002 for common sole, *Solea vulgaris*; Natoli *et al.* 2005 for bottlenose dolphins).  We use historical modelling to test hypotheses about the pattern and timing of population founding and divisions in the context of Quaternary environmental change. In particular, we consider the potential impact of periods of sea-level change during Pleistocene glaciations and the impact of warming during the Holocene.

## Material and Methods

### Samples collection and Study area

Striped dolphin samples were collected from strandings and fisheries bycatch from the Mediterranean Sea and the eastern North Atlantic Ocean. Sampling sites and sizes are shown in Fig. 1. The total sample size was 256, and all used in this study for the first time. Tissue samples were either stored in 20% DMSO NaCl 5M or in 70% ethanol. The majority of the stranded individuals from the western Mediterranean died during a morbillivirus epizootic during 1990-1992 and 2006-2008. However, further stranded samples from the same region were collected from 1989 and during 1993-2005 for which the cause of death is unknown. Overall 36 samples were collected between 1990 and 1992 and 21 between 2006 and 2008 from this region.

### DNA extraction and PCR amplification

Skin and muscle tissue were extracted following a standard phenol/chloroform extraction protocol (after Hoelzel 2009). A panel of 29 microsatellite DNA loci were tested (see Table S1 in Appendix S1 in Supporting Information). A multiplex PCR Kit (Qiagen) with hot start Taq was used for the DNA amplifications. The 29 pairs of primers were divided into 4 multiplex Groups (Table S1 in Appendix S1) according to size range and florescent primer pigment. The PCR cycling profile was: 95°C for 15 minutes; 30 cycles of 95°C for 1 minute, annealing temperature for 30 seconds and 72°C for 30 seconds; 72°C for 15 minutes. PCR products were verified by agarose gel electrophoresis. Amplified DNA products were screened on an ABI 3730 DNA Analyser (Applied Biosystems) using the ROX500 size marker. Each specimen's alleles were scored by the software STRAND 2.0 (Toonen & Hughes 2001) and10% of genotypes were redone for error checking.

## Statistical analysis

All loci were tested for the presence of null alleles or allelic dropout using the software MICROCHECKER 2.2.3 (van Oosterhout *et al.* 2004). Exact tests for Hardy-Weinberg equilibrium and Linkage Disequilibrium (using the Markov Chain Monte Carlo (MCMC) method with 10,000 dememorization steps followed 1,000 batches with 10,000 iterations per batch), were carried out using GENEPOP 3.4 (Raymond & Rousset 1995). BAYESCAN (Foll & Gaggiotti 2008) was used to identify candidate loci under natural selection, running 100,000 iterations. Expected heterozygosity ($H_{EXP}$) and observed heterozygosity ($H_{OBS}$) were estimated using GENEPOP 3.4 (Raymond & Rousset 1995). Fixation indexes $F_{ST}$ and $F_{IS}$, using the formulations described by Weir & Cockerham (1984; significance tested using10,000 permutations test) and the number of alleles per locus were calculated using ARLEQUIN 3.5 (Excoffier & Lischer 2010).

Factorial correspondence analysis (FCA) was performed using GENETIX 4.05.2 (Belkhir *et al.* 2002) and the '3D by populations' setting. Population structure was further assessed using STRUCTURE 2.3 (Pritchard *et al.* 2000) assuming correlated allele frequencies and admixture. Three independent repeats were run for each value of K ($1 \leq K \leq 10$). Following test runs, the burn-in length and length of simulation were set at 1,000,000 and 3,000,000 repetitions, respectively. STRUCTURE HARVESTER was used to assess the likelihood value of the different K values and to implement the $\Delta$K method (Evanno et al. 2005) reflecting the highest hierarchical level of structuring (Earl & von Holdt 2012).

A hierarchical analysis of molecular variance (AMOVA; Excoffier & Lischer 2010) was performed to partition variance components attributable to (1) variance between areas (the North Atlantic and the Mediterranean); (2) variance between populations within areas; (3) variance among samples within populations; and (4) within individuals. The significance of the resulting *F*-indices was considered after sequential Bonferroni correction and variance components were permutated 10,000 times. Evidence of bottleneck signatures was assessed using BOTTLENECK (Cornuet & Luikart 1996) with significance tests done for the infinite allele, two parameter and stepwise mutation models (1,000 iterations; TPM model was used with default settings of 70% variation from the SMM model and 30% from the IAM model). The Garza-Williamson *M*-ratio test was implemented to test a bottleneck signal using the software ARLEQUIN 3.5 (Excoffier & Lischer 2010). Bottleneck analyses were not undertaken for the Biscay Gulf population due to the relatively small number of samples. BAYESASS 3.0 (Wilson & Rannala 2003) was used to infer the rates and directionality of contemporary migration. In order to achieve acceptance ratios between 20%-60% values of $\Delta_M$, $\Delta_A$ and $\Delta_F$ were set to 0.10, 0.30 and 0.50, respectively using 3 x $10^6$ iterations and a burn-in of $10^6$. The software TRACER 1.6 was used (Rambaut & Drummond 2007) to check for convergence.

To compare demographic scenarios of divergence history, an approximate Bayesian computational analysis was implemented in the software DIYABC 2.0.3 (Cornuet *et al.* 2008). Different scenarios about population history were compared and their relative support assessed using direct and logistic regression analyses. Scotland, Ireland, the western Mediterranean (Gibraltar strait, Valencia, Strait of Sicily and Ionian Sea) and the eastern Mediterranean (Korinthiakos Gulf and Israel) basins were pooled (according to FCA results, see below) and compared. The Biscay Gulf sample was relatively small and differentiated from Scotland and Ireland, and so not included in this analysis. Broad log-normal priors were used (see Table 1) and multiple scenarios were tested considering alternative division times and demographics. We first test 10 unique permutations varying the number of time division points (2, 3 or 4), the identity of the ancestral population and the identity of populations dividing at different time points. This covered the main alternatives, but was not exhaustive, and so in a second analysis we retain the basic case where all split at the same time, the best supported scenarios from the first run, and add some scenarios that consider plausible alternative patterns of ancestry (for a total of 12 scenarios; see Fig. S1 in Appendix S2 in Supporting Information). $1.2 \times 10^7$ data sets were implemented for each scenario. The best fit was obtained by direct and logistic regressions of each scenario. Given a best supported scenario, we then assessed the probability of the deviation between simulated and observed summary statistics for the number of alleles, gene diversity and $F_{ST}$.

## Results

Among the 29 loci screened, only one locus showed evidence of null alleles (TexVet 5) and two of them could not be amplified for the entire data set (D08, Dde59 ), therefore 26 loci were used for the statistical analyses. These 26 loci were tested for Hardy-Weinberg equilibrium (HWE) and at four loci (KWM1b, MK3, Sco28 and Sco66) significant departures were detected in multiple populations (after Bonferroni correction, Rice 1989). There was no significant linkage disequilibrium. Furthermore, two loci (Ev37 and Sco11) showed evidence for positive selection from the assessment of outliers in BAYESCAN. Thus, a final set of 20 loci were used for further analyses. Replicate genotyping detected no differences and so no error rate based on those data. Missing data are illustrated in Table S2 in Appendix S1.

The scatter plot of FCA (Fig. 2) showed clear differentiation between Mediterranean Sea and eastern North Atlantic Ocean populations. Within the Mediterranean Sea basin, populations were divided into two separate groups (Fig. 1). Based on the FCA data, samples from GS, VL, SS and IS were clustered as western Mediterranean (WM), whereas samples from KG and IS were clustered as eastern Mediterranean (EM). The apparent boundary is east of the commonly proposed position at the Straight of Sicily (e.g. Exadactylos *et al.* 1998). In the North Atlantic there is a weaker division, roughly on an east/west axis (see Fig. 2; note that the division lines are only illustrative). Comparing individual samples by collection date showed that this had no impact on the pattern of structure shown in the FCA analysis (Fig. S2 in Appendix S2). Genetic variation at each locus for each population is reported in Table S3 in Appendix S1 (including Ho, He, $F_{IS}$, number of alleles and allelic richness). All pairwise $F_{ST}$ values were significant and highest for comparisons between the North Atlantic and Mediterranean Sea (Table 2).

For the analysis in STRUCTURE, LnP($K$) leveled off after K=2 (Fig. S3 in Appendix S2), and $\Delta$K = 2. At $K$ = 2, the two clusters separate the North Atlantic and the Mediterranean Sea (Fig. S3A and Fig. S4A in Appendix S2). Independent analyses for each of these two clusters gave a maximum LnP(K) for the North Atlantic samples of $\Delta$K = 2 (Fig. S3B and Fig. S4B in Appendix S2) and for the Mediterranean samples $\Delta$K = 3 (Fig. S3C and Fig. S4C in Appendix S2). However, the trend for LnP(K) showed little change between K=1-3 for either within region comparison, and so the support for K>1 is not strong for those analyses (see Fig. S3 in Appendix S2). The hierarchical AMOVA found significant support for differentiation both between the two main groups (North Atlantic versus the Mediterranean Sea) and among populations within groups (Table S4 in Appendix S1), consistent with the results found by FCA and STRUCTURE.

The program BOTTLENECK did not show statistical support for a bottleneck event in any of the North Atlantic regions based on heterozygote excess (Table S5 in Appendix S1) or the allele frequencies mode shift as the distribution was clearly L shaped as expected for non- bottleneck populations close to mutation-drift equilibrium (Fig. S4 in Appendix S2). The Garza-Williamson *M-ratio* index for Scotland ($M$=0.836 ± 0.152) and Ireland ($M$=0.893 ± 0.107) were both over the suggested threshold of 0.68 identified by Garza & Williamson (2001). Within the Mediterranean basin BOTTLENECK gave significant evidence for bottleneck events, but only when applying the stepwise mutation model (Table S5 in Appendix S1). However, *M-ratio* did not reveal any evidence for bottleneck events within the Mediterranean basin (WestMed: 0.823 ± 0.165, EastMed: 0.733 ± 0.174).

Estimates for contemporary rates and patterns of gene flow (based on BayesAss) are provided for comparisons among five putative populations: Scotland, Ireland, the Biscay Gulf, the western Mediterranean, and the eastern Mediterranean (Tables 3, S6 in Appendix S1, Fig. 3). There was a strong indication of directionality from the north (Scotland) into populations to the west (Ireland) and south (Biscay Gulf), and from the western into the eastern Mediterranean Sea.

The initial comparison of 10 scenarios in the DIY-ABC analysis (Fig. S1a in Appendix S2) revealed that scenario 8 best fits the observed data (Fig. 4). This scenario was also the best fit among the 12 scenarios illustrated in Fig. S1b in Appendix S2. Details of the relative support from logistic and direct regression analyses together with confidence intervals are provided in Table S6 in Appendix S1. The best supported scenario has much greater support than the tested alternatives (Fig. 4; Table S7 and Table S8 in Appendix S1), and is based on the hypothesis of a common ancestor (with effective size Na; Table 1) that was split into Mediterranean and Atlantic Ocean populations (at t3), followed by divergence within the Mediterranean Sea (t2), and a more recent divergence within the Atlantic Ocean (t1; Fig. 4). Posterior support for parameter estimates are illustrated in Fig. S6 in Appendix S2 and presented in Table 1. The time of the first divergence event (t3) was estimated at a median of 34,700 generations ago. The estimated generation time by Taylor *et al.* (2007) of 22 years for the striped dolphin, would imply this divergence occurring approximately 763 Ka during the middle Pleistocene. Following that, the Mediterranean basin divergence occurred approximately 53 ka (t2) during Late Pleistocene while divergence within the Atlantic Ocean occurred approximately 6 ka (t1) at the start of the Holocene. Effective population size estimates suggest that Scotland and the eastern Mediterranean are smallest, and that the ancestral population size was relatively small (Table 1).

## Discussion

The evolution of population structure can be influenced by both biotic and abiotic factors. Biotic interactions may be driven by competition or other frequency dependent factors that can influence patterns of diversity. Changes in environmental factors (e.g. climatic or oceanographic) may also drive patterns of diversity, and the relative contribution of biotic and abiotic factors has been discussed at some length (see Benton 2009). Our results provide chronological data that may help provide inference in this context. Environmental change over time can lead to diversification shifts (Perry *et al.* 2005) and phylogeographic breaks (Avise 2000). One well established mechanism is through climatic change, especially over the Pleistocene glacial cycles (e.g. Hewitt 2004). Perhaps at the same time competition over resources can lead to differential resource specialisation and habitat dependence, promoting divergence across habitat boundaries (e.g. Natoli *et al.* 2005). The marine environment across the geographic range from the Mediterranean Sea to the North Sea, along the southern and western coastline of Europe, is characterised by a number of transitions, and these have been dynamic in nature over time. There are boundaries that are known to be associated with reduced gene flow for a diversity of extant species (e.g. Limborg *et al.* 2012), however not all species show the same pattern.

There are seven putative phylogeographic breaks (likely including varying transition ranges and extents) from the Mediterranean Sea to the North Atlantic where barriers to gene flow have been reported for various taxa. Between the North Atlantic and the Mediterranean Sea there are putative breaks at the Strait of Gibraltar and the Almeria-Oran front (e.g. Bahri-Sfar *et al.* 2000; Guarniero *et al.* 2002; Gaspari *et al.* 2007). Within the Mediterranean Sea there are three breaks: the Dardanelle Strait which separates the Black Sea and Mediterranean Sea (e.g. Nikula & Vainola

2003), the boundary between the Adriatic Sea and Mediterranean Sea (e.g. Galov *et al.* 2009), and the Italian Peninsula separating the eastern and western Mediterranean basins (e.g. Natoli *et al.* 2006; Rolland *et al.* 2007). In the North Atlantic between the Mediterranean and the North Sea there are at least two breaks: the barrier between the Biscay Gulf and the English Channel (Jolly *et al.* 2005; Fontaine *et al.* 2014) and in the Skagerrak between the North Sea and the Baltic Sea (e.g. Johannesson & Andre 2006). Not many species have been studied across all or most of these regions, but a direct comparison can be made between the common dolphin which showed panmixia across most of the range (Natoli *et al.* 2006; Mirimin *et al*., 2009; Moura *et al.* 2013a) and the bottlenose dolphin which showed differentiation across nearly all of these boundaries (Natoli *et al.* 2005; Louis *et al.* 2014).

Our data for the striped dolphin show a north/south and east/west dimension to the pattern of population structure. However, there are also indications of dynamic interactions over the course of the Pleistocene, such that the earliest division (middle Pleistocene) is between the North Atlantic and the Mediterranean, the next division (late Pleistocene) is between the eastern and western Mediterranean, and finally between the population around Scotland and those further south and west (at around the start of the Holocene). Evidence for striped dolphin population expansion through the Pleistocene was provided from the Ne estimates in the ABC analyses, since the ancestor value was lower than for all extant estimates (Table 1). During the Pleistocene epoch, oscillations such as changes in sea level, upwelling events, temperature alterations and changes in the distribution of food resources may have played a role in the changing dynamics of delphinid populations (see Banguera *et al.* 2010; Moura *et al.* 2014). Sea level during glacial periods within the Pleistocene is estimated to have dropped by about 110 to 120 metres (Lambeck *et al.* 2005) which may have influenced population dynamics, dispersion and colonization in the Mediterranean basin. This could have promoted vicariance between the North Atlantic and the Mediterranean basins early on, and perhaps between the separate basins of the Mediterranean after that (as suggested by our analyses).

After the LGM, rapid warming affected the nature and availability of coastal marine habits. According to Boehme *et al.* (2012) investigating habitat suitability for grey seals (*Halichoerus grypus*), during the LGM the higher latitudes of the North Atlantic Ocean were isolated, and only the Biscay Gulf and Iberian Peninsula were suitable for habitation. Our data suggest that population differentiation was generated in this region following the LGM, and a post-glacial expansion associated with population structuring in the eastern North Atlantic has been discussed for other marine mammals (Banugera *et al.* 2010; 2014; Fontaine *et al*., 2014). Of course earlier glacial/ inter-glacial transitions during the Pleistocene Milankovitch cycles may have had the potential to generate structure in this region as well. It is possible that we are detecting the latest phase of what may have been a period of reticulation as populations in this region divided and re-formed.

The pattern of contemporary population structure detected was consistent for the FCA, STRUCTURE, BAYESASS analyses and measures based on summary statistics. There was division between the Mediterranean and North Atlantic, as seen for a broad range of species from invertebrates to fin whales (e.g. Quesada *et al.* 1995; Berube *et al.* 1998). The structure in the North Atlantic was more unusual. Here the magnitude of differentiation was less, though detectable, highly directional (with contemporary gene flow out of Scotland for the most part), and showed division both east to west (between Scotland and Ireland) and north to south (between Scotland and the Biscay Gulf). Scotland is near the northern range limit for the striped dolphin, which may explain a tendency for gene flow to the south, despite recent warming from anthropogenic climate change. Previous studies on microsatellite loci (Bourret *et al.* 2007) and mtDNA (Garcia-Martinez *et al.* 1999) did not reveal any differences among striped dolphin populations in this region of the Atlantic Ocean, however each provided a lower level of resolution than reported here. While other studies have described relatively fine-scale differentiation in this region for other marine mammals (Natoli *et al.* 2005; Fontaine *et al.* 2014) and fishes (Exadactylos *et al.* 1998), differentiation is more typically between northern and southern populations rather than east to west.

In the Mediterranean Sea, Gaspari *et al.* (2007) found significant differentiation between striped dolphin populations sampled from Spain (Balearic Sea) and those from the west of Italy (Ligurian Sea). A finer scale diversity pattern was also recorded between samples from the eastern north side of Italy (Croatia, Puglia, Greece) and the western side of Italy (Ligurian Sea and Tuscany). Our data suggest a division to the east of Sicily, between the Ionian Sea and Greece, though perhaps affected by post-mortem drift in currents. However, the Korinthiakos Gulf in Greece is semi-enclosed and consists of a unique water body due to deep and steep slopes along its coasts, and a systematic occurrence of wind-driven upwelling currents (Lascaratos *et al.* 1989). Although waters from the Ionian Sea enter the gulf, overall it provides an isolated habitat. Frantzis & Herzing (2002) in a study of delphinid species sightings and abundance in Korinthiakos Gulf suggested philopatry of striped dolphins there. The eastern Mediterranean basin consists of the Ionian, Aegean and Levantine Seas, which are dynamically active areas with unique oceanographic features and different water masses compared to the western Mediterranean basin (Theocharis *et al.* 1993). Different patterns of water circulation and different mass exchanges such as low salinity out-flow from the Black Sea, in conjunction with the freshwater input of the continental shelf, and the high salinity input from the Levantine Sea and Ionian Sea, create complex cyclonic and anticyclonic gyres (e.g. Kourafalou *et al.* 2004). These different systems contribute to differentiated nutrient-enriched water masses, supporting different food resources and availability (Theodorou 2004). The region represents a transition zone with respect to ecological niches for many marine species (e.g. Viñas *et al.* 2010). Therefore subtle differences in habitat structure may be expected, and the boundary point suggested by our data could be more than an artefact. This could be resolved through the collection of samples from free-ranging animals in the region.

There are now data on population genetic structure for three delphinid species across the full geographic range from the eastern Mediterranean to Scottish waters.  Common dolphins stand out as distinct showing panmixia (Moura *et al.* 2013a), even though this species shows fine-scale population structure in the Pacific (e.g. Bilgmann *et al.* 2008).  The striped dolphin shows a pattern of structure that is more similar to that seen for the bottlenose dolphin (Natoli *et al.* 2005; Louis *et al.* 2014), but these two species also differ.  For effective conservation and management, understanding what drives these differences is critical, since it will often be necessary to base strategy on transferable inference.  Given the numbers, it is impractical to instead investigate all species of concern individually in all regions of conservation concern. This particular geographic region provides a useful study system due to the complexity and known phylogeographic breaks (shared by a range of different species).  While the bottlenose dolphin apparently shows differentiation across expected habitat boundaries throughout this range (Natoli *et al.* 2005), the striped dolphin shows differentiation at some of the same boundaries, though not in exactly the same way. Data on the historical context helps us understand the process of differentiation, and the relative roles that biotic and abiotic factors may have played for each of these species.

A comparison based on mitogenome sequences between populations at either extreme of the geographic range (between Scotland and the eastern Mediterranean) suggests relatively recent radiation among bottlenose dolphin populations (Moura *et al.* 2013b), during the late Pleistocene. This may be consistent with processes associated with local habitat dependence and differential resource specialisation. In contrast, our data for the striped dolphin suggest a division between the North Atlantic and Mediterranean in the middle Pleistocene, perhaps instead associated with climate change and vicariance events. Boundaries established by abiotic factors may be reinforced by habitat dependence and competition, and the details of the division for the striped dolphin within the Mediterranean suggest that this may be the case, especially if the boundary is displaced eastward from that seen for the bottlenose dolphin. In general, habitat boundaries appear to establish divisions early on, while the more recent division in the North Atlantic may have been in response to warming climate at the start of the Holocene.

## Conflict of Interest

The authors declare no conflict of interest.

## Acknowledgements

We thank Dr S. Gaspari (University of Florence, Florence, Italy), Willy Dabin (University of La-Rochelle, La-Rochelle, France), Vasilis Podiadis (Multihull Yachting Greece, Lavrio, Hellas) for providing us with samples from Ionian Sea, Biscay Gulf, Scotland, Israel, Strait of Gibraltar and Strait of Sicily. Samples in Ireland from stranded animals were collected via funding from a number of sources and we gratefully acknowledge The Heritage Council of Ireland; European Commission ECFAIR contract FAIR-CT95-0523: Assessment and Reduction of the By-catch of Small Cetaceans of Small Cetaceans (BY-CARE); contract EVK3-2000-00027: Bioaccumulation of persistent organic pollutants in small cetaceans in European waters: transport pathways and impact on reproduction (BIOCET). Sampling along the Valencian coast has been supported by Conselleria de Medio Ambiente and Conselleria de Educación (PROMETEOII/2015/018) of the Generalitat Valenciana. This study was funded by the Hellenic State Scholarship Foundation through PhD grant awarded to Dr Georgios A. Gkafas. We thank Andrew Brownlow for helpful comments on the manuscript.

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## Data accessibility

Genotype data is archived on a Dryad database; xxx

## Supporting Information

**Appendix S1**: Tabulated molecular genetic data

**Appendix S2**: Further illustrations

## Biosketch

**George A. Gkafas** is a molecular evolutionary biologist working as a post-doctoral researcher at the University of Thessaly, Greece, and a past and recent member of the Molecular Ecology Group at Durham University, UK, which focuses on understanding the evolution of biodiversity and the historical context of biogeography for a wide range of study species.

Author contributions: study was conceived by ARH and GAG and the analyses undertaken mostly by GAG. The paper was written by GAG and ARH with feedback from all co-authors. Samples and data on regional populations were provided by ER, JAR and AE.

**Handling Editor**

Michelle Gaither

**Table 1** Prior distribution settings and parameter estimates (Mode and Median) for the DIY-ABC analyses, using 1.2 x $10^7$ data sets simulated under scenario 8 (95% confidence intervals are shown for each of the parameters) for striped dolphin populations.

| Parameter | Prior range | Mode | Median | 95% CI low | 95% CI high |
|---|---|---|---|---|---|
| *N1* (Scotland) | 10 - $10^7$ | 1,480 | 12,900 | 644 | 274,000 |
| *N2* (Ireland) | 10 - $10^7$ | 71,400 | 769,000 | 44,100 | 8,240,000 |
| *N3* (W Med) | 10 - $10^7$ | 14,200 | 34,000 | 5,340 | 700,000 |
| *N4* (E Med) | 10 - $10^7$ | 204,000 | 10,200 | 539 | 147,000 |
| *Na* (Ancestral) | 10 - $10^5$ | 10 | 64 | 10 | 2,030 |
| *t0* (generations) | 10 - $10^4$ | 1 | 26.2 | 1 | 611 |
| *t1* (generations) | 10 - $10^5$ | 44.1 | 273 | 17.4 | 3,160 |
| *t2* (generations) | 10 - $10^6$ | 248 | 2,410 | 107 | 8,690 |
| *t3* (generations) | 10 - 2 x $10^6$ | 24,400 | 34,700 | 6,250 | 127,000 |

**Table 2** $F_{ST}$ pairwise values of the striped dolphin populations. An asterisk indicates significance, with alpha set to 0.05 after Bonferroni correction.

| | Scotland | Ireland | Biscay Gulf | western Mediterranean | eastern Mediterranean |
|---|---|---|---|---|---|
| Scotland | 0 | | | | |
| Ireland | $0.012^*$ | 0 | | | |
| Biscay Gulf | $0.012^*$ | $0.010^*$ | 0 | | |
| western Mediterranean | $0.045^*$ | $0.033^*$ | $0.044^*$ | 0 | |
| eastern Mediterranean | $0.051^*$ | $0.053^*$ | 0.056* | $0.032^*$ | 0 |

**Table 3** Contemporary migration rates (± sd) of the striped dolphin populations as derived using the BAYESASS software (confidence intervals are given in parentheses). Values are given as *m*, the proportion of migrants per generation from each population on the left (row headings) into the populations on the right (column headings).

| | Scotland | Ireland | Biscay Gulf | western Mediterranean | eastern Mediterranean |
|---|---|---|---|---|---|
| Scotland | - | 0.297 ± 0.015<br>(0.267 - 0.326) | 0.249 ± 0.032<br>(0.186 - 0.312) | 0.017 ± 0.007<br>(0.003 - 0.184) | 0.041 ± 0.019<br>(0.004 - 0.078) |
| Ireland | 0.06 ± 0.006<br>(0.012 - 0.072) | - | 0.035 ± 0.023<br>(0.001 - 0.08) | 0.003 ± 0.003<br>(0 - 0.003) | 0.012 ± 0.012<br>(0.001 - 0.035) |
| Biscay Gulf | 0.006 ± 0.006<br>(0 - 0.012) | 0.007 ± 0.006<br>(0 - 0.018) | - | 0.003 ± 0.003<br>(0 - 0.008) | 0.011 ± 0.010<br>(0 - 0.03) |
| western Mediterranean | 0.018 ± 0.012<br>(0 - 0.041) | 0.008 ± 0.007<br>(0 - 0.014) | 0.016 ± 0.015<br>(0 - 0.045) | - | 0.259 ± 0.024<br>(0.012 - 0.306) |
| eastern Mediterranean | 0.006 ± 0.006<br>(0 - 0.012) | 0.007 ± 0.007<br>(0 - 0.013) | 0.018 ± 0.017<br>(0 - 0.051) | 0.003 ± 0.003<br>(0 - 0.008) | - |

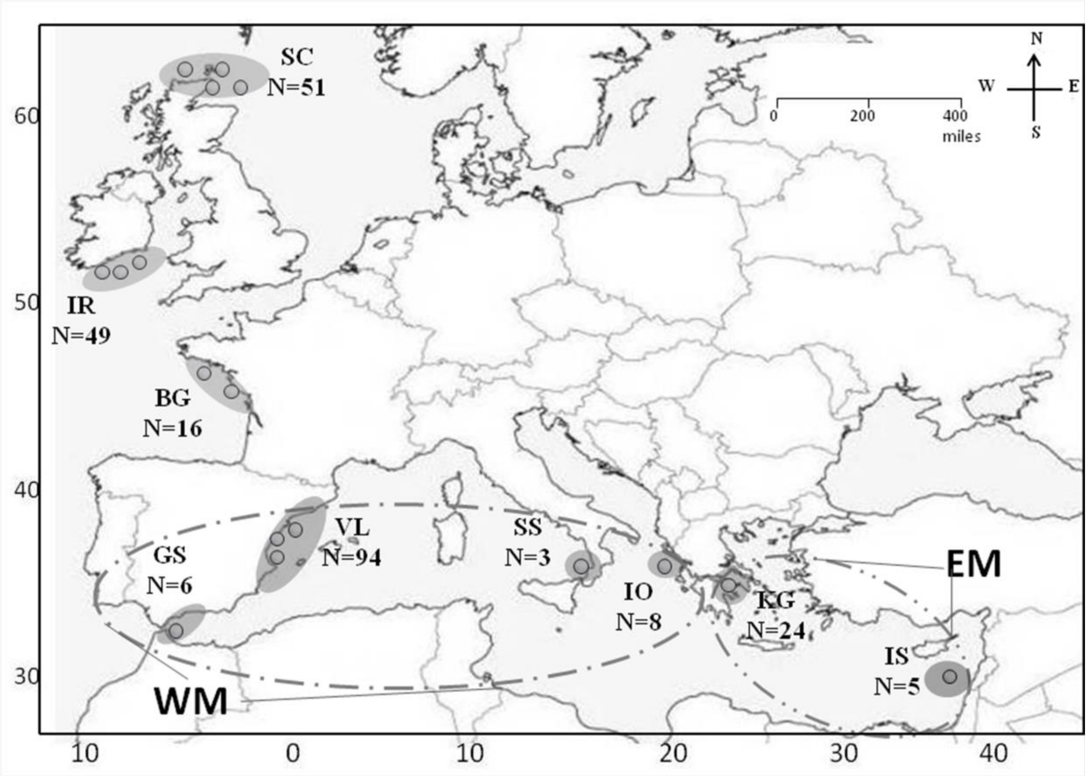
**Figure 1**. Regional sites of striped dolphin samples showing local populations and pooled sample set (dashed circles) used for analyses; WM (western Mediterranean) and EM (eastern Mediterranean). Sampling locations: northern Scotland (SC), south-east of Ireland (IR), Biscay Gulf, western France (BG), Gibraltar Strait (GS), Valencia, eastern Spain (VL), Strait of Sicily (SS), Ionian Sea, western Greece (IO), Korinthiakos Gulf, central Greece (KG) and Israel (IS).

**Figure 2**. Factorial correspondence analysis (FCA) of striped dolphin population multilocus scores computed using GENETIX. Multilocus scores are computed in the bivariate space defined by the first two factorial components (SC: Scotland, IR: Ireland, BG: Biscay Gulf, GS: Gibraltar Strait, VL: Valencia, SS: Strait of Sicily, IO: Ionian Sea, KG: Korinthiakos Gulf, IS: Israel). Lines show nominal distinctions across the east/west and north/south axes.

**Figure 3**. Circos plots of source-sink migration dynamics for striped dolphin populations as implemented in R platform (3.2.3). Plot corresponds to contemporary migration directionality (using BAYESASS software). Width of migration curves indicates amount of migration according to the scale provided (in units of the proportion of migrants per generation).

**Figure 4**. a) Logistic regression showing relative support for different scenarios for striped dolphin population ancestry (see Fig. S1a in Appendix S2). Scenarios with support greater than zero are shown. b) Illustration of the best supported scenario, scenario 8. Na = ancestral population, EM = eastern Med, WM = western Med, IR = Ireland, SC = Scotland.

Figure 1


SC
N=51
IR
N=49
BG
N=16
GS
N=6
VL
N=94
SS
N=3
IO
N=8
KG
N=24
IS
N=5
WM
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40

Figure 2

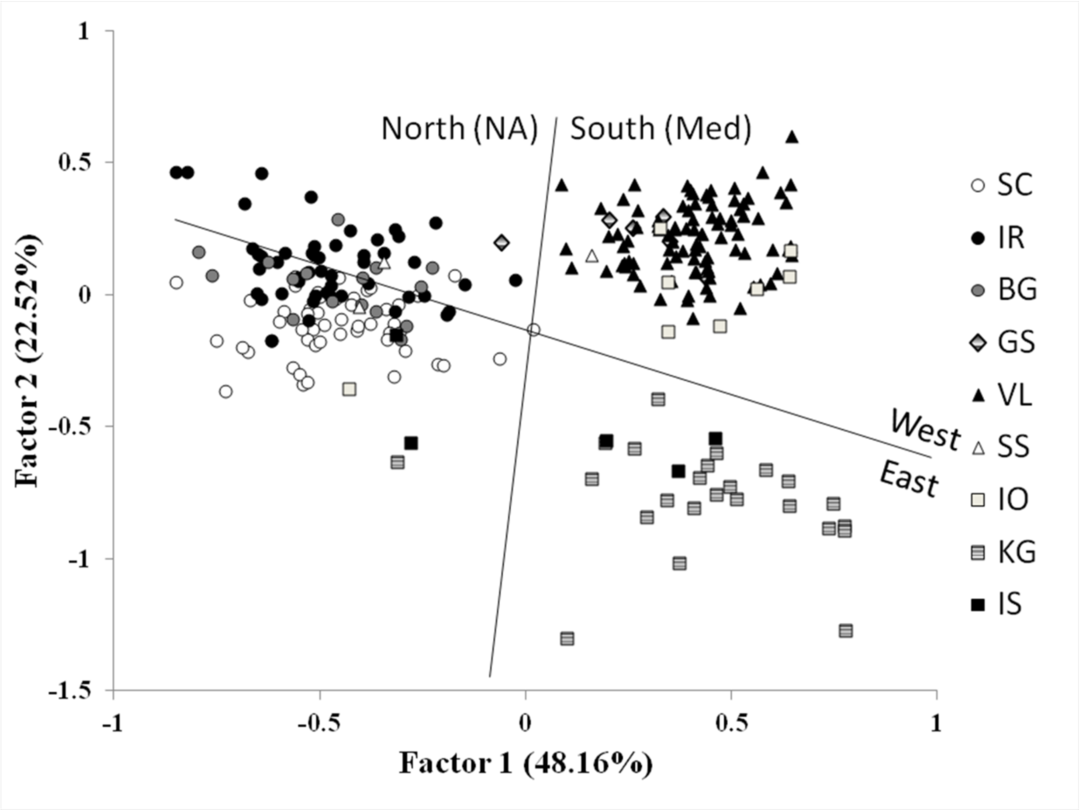
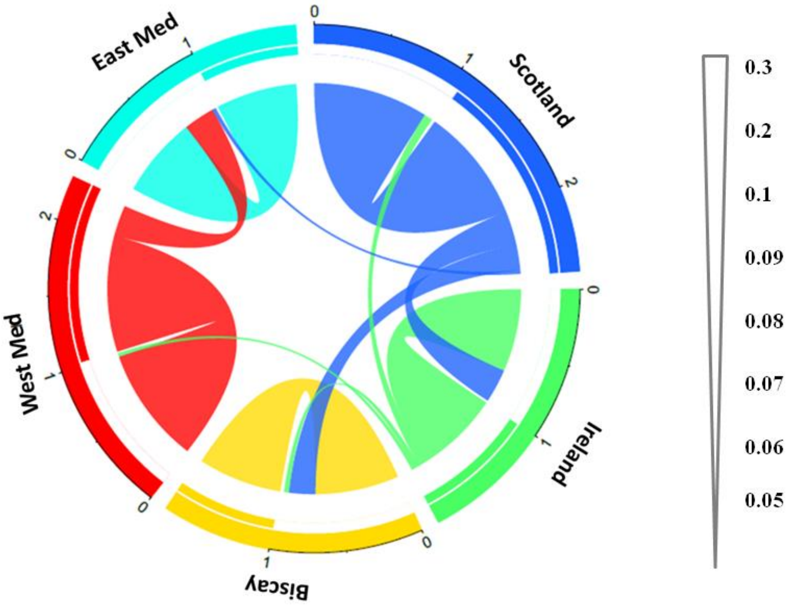

North (NA)
South (Med)
West
East
Factor 2 (22.52%)
Factor 1 (48.16%)
1
0.5
0
-0.5
-1
-1.5
-1
-0.5
0
0.5
1
SC
IR
BG
GS
VL
SS
IO
KG
IS

Figure 3


East Med
Scotland
Ireland
Biscay
West Med
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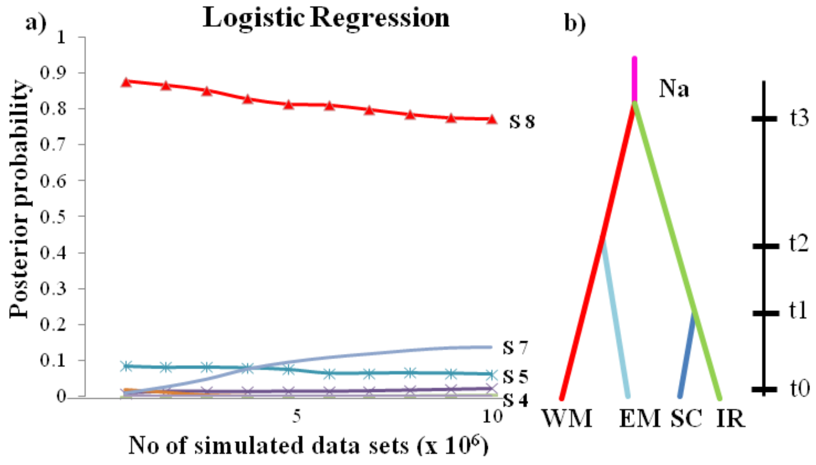
1
2
0.3
0.2
0.1
0.09
0.08
0.07
0.06
0.05

Figure 4


a)
Logistic Regression
Posterior probability
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10
No of simulated data sets (x 10⁶)
S 8
S 7
S 5
S 4
b)
Na
t3
t2
t1
t0
WM
EM
SC
IR