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Fine-scale population structure and connectivity of bottlenose dolphins, *Tursiops truncatus*, in European waters and implications for conservation

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Abstract

1. Protecting species often involves the designation of protected areas, wherein suitable management strategies are applied either at the taxon or ecosystem level. Special Areas of Conservation (SACs) have been created in European waters under the Habitats Directive to protect bottlenose dolphins, *Tursiops truncatus,* which forms two ecotypes, pelagic and coastal.

2. The SACs have been designated in coastal waters based on photo-identification studies that have indicated that bottlenose dolphins have relatively high site fidelity. However, individuals can carry out long-distance movements which suggest potential for demographic connectivity between the SACs as well as with other areas.

3. Connectivity can be studied using genetic markers. Previous studies on the species in this area used different sets of genetic markers and therefore inference on the fine-scale population structure and demographic connectivity has not yet been made at a large scale. A common set of microsatellite markers was used in this study to provide the first comprehensive estimate of genetic structure of bottlenose dolphins in European Atlantic waters.

4. As in previous studies, a high level of genetic differentiation was found between coastal and pelagic populations. Genetic structure was defined at an unprecedented fine-scale level for coastal dolphins leading to identification of five distinct coastal populations inhabiting the following areas: Shannon estuary, west coast of Ireland, English Channel, coastal Galicia, east coast of Scotland, and Wales/West Scotland. Demographic connectivity was very low among most populations with less than 10% migration rate suggesting no demographic coupling among them. Each local population should therefore be monitored separately.

Keywords: coastal, ocean, population genetics, Special Area of Conservation, mammals, bottlenose dolphins

Introduction

Protecting species and their habitats is the goal of conservation biology, and this often includes the designation of protected areas, wherein suitable management strategies are applied either at the taxon or ecosystem level. According to the definition by the World Conservation Union (IUCN), a Marine Protected Area (MPA) is "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher & Phillips, 1999, 18). The usefulness of static MPAs to preserve biodiversity or to protect a particular species or population has been debated (e.g., Agardy, di Sciara, & Christie, 2011; Hartel, Constantine, & Torres, 2015; Hooker & Gerber, 2004; Wilson, 2016), but they remain the primary spatial conservation unit worldwide and are key components of various conservation plans (e.g., the United Nations Plan for Biodiversity (2011–2020), the IUCN Worlds Parks Congress and the European Biodiversity Strategy to 2020 (European Commission, 2011)). In European waters, the Member States of the European Union are required to designate Special Areas of Conservation (SACs) for species listed in Annex II of the Habitats Directive (European Economic Community, 1992), which includes two cetacean species; the harbour porpoise, *Phocoena phocoena,* and the common bottlenose dolphin, *Tursiops truncatus*. These SACs, which are part of the European Natura 2000 strategy, should represent areas essential for the species' life and reproduction. In addition to the protection under the Habitats Directive, as top predators, bottlenose dolphins are considered as one of the indicator species for 'good environmental status' (GES) in coastal waters by the Marine Strategy Framework Directive (MSFD, Council of the European Communities, 2008). The aim of MSFD is to protect the European marine

environment by applying a comprehensive ecosystem-based approach to the management of human activities, and by maintaining or restoring the favourable conservation status of a number of species.

Previous research using photo-identification has shown that most coastal bottlenose dolphin populations in Europe comprise between 30 and 400 resident individuals with strong site fidelity to their respective coastal site (e.g., Cheney et al., 2013; Ingram & Rogan, 2002; Louis et al., 2015). However, also based on photo-identification studies, some of these individuals are highly mobile travelling distances of hundreds of kilometres around the UK and Ireland (Cheney et al., 2013; Ingram, Englund, & Rogan, 2001; Ingram & Rogan, 2003; O'Brien et al., 2009; Robinson et al., 2012). Nonetheless, the high site-fidelity and the preferential use of some geographical areas indicate that coastal bottlenose dolphins may be very sensitive to changes in local environmental conditions, ecological factors, or anthropogenic disturbance. The sensitivity of bottlenose dolphins to these threats is exacerbated by their position as an apex predator and also by their low reproductive rates (Connor, Wells, Mann, & Read, 2000; Quick et al., 2014). The main threats in coastal environments include pollutants such as xenobiotic chemicals (Jepson et al., 2016; Reif, Schaefer, Bossart, & Fair, 2017), reduced prey availability, habitat degradation, disturbance from vessel traffic (Lusseau, Bain, Williams, & Smith, 2009; Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015; Williams, Bain, Smith, & Lusseau, 2009), entanglement and incidental bycatch, direct hunting, marine construction and anthropogenic noise (Hammond et al., 2012; Meissner et al., 2015; Pirotta et al., 2015). The increased risks of demographic perturbation of dolphin populations due to human activities highlights the need for the design and management of protected areas ensuring that dolphin

habitat remains favourable and does not deteriorate. A careful investigation of the population structure and quantification of the genetic and demographic connectivity is also necessary as small isolated populations may require more protection due to their reduced genetic resilience.

An important step towards the conservation of bottlenose dolphins was taken under the Habitats Directive by designating SACs across the European North-east Atlantic and Mediterranean coastal waters. These designations were based on photo-identification and habitat use surveys showing long-term site-fidelity (Anon, 2012). Another important step towards their conservation is to evaluate population structure and connectivity of populations between the protected areas as well as with other areas. This is particularly important because of the propensity for some individuals to carry out long-distance movements, which suggests potential demographic connectivity between the populations. It is unclear if such movements can result in migration rates that could lead to correlated population dynamics. There is a paucity of studies assessing the level of migration that will lead to demographic coupling (Waples & Gaggiotti, 2006); a process by which changes in population size in one population are influenced by changes taking place in another population (Hastings, 1993). However, a simulation study by Hastings (1993) indicated that under a simple two-population density-dependent model, a migration rate of 10% or more can lead to coupled dynamics, which would require monitoring the populations as a single management/conservation unit. Thus, a threshold of 10% migration above which two local populations are considered independent management units can be used as an operational criterion to address conservation problems.

The most cost-effective approach to evaluate demographic connectivity and fine-scale

population subdivision is based on the use of genetic markers and population genetics principles. Thus, a recent workshop on bottlenose dolphin conservation (December 2016; Ó Cadhla & Marnell, 2017) concluded that one of the main priorities for implementing the afore-mentioned EU directives for this species was a fine-scale population genetics analysis of dolphins inhabiting European waters. This will allow the definition of meaningful management units (MUs), which is essential when setting up strategies for conservation and monitoring, including the estimation of population trends and the evaluation of the impacts of anthropogenic activities. Note that in the past, MUs were frequently defined in genetic terms as genetic management units (GMUs), following Moritz (1994, 374): "populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles". However, it is now accepted that MUs comprise demographically independent populations, thus estimating migration rates forms a central part of the assessment of suitable MUs (Allendorf, Luikart, & Aitken, 2013; Palsbøll, Berube, & Allendorf, 2007). Furthermore, the criterion underlying GMUs is not entirely appropriate from a demographic point of view because migration rates (m) well below 10% can still lead to an absence of significant allelic differentiation (e.g., if local population size is 100, $m > 0.01$ will lead to absence of genetic differentiation; c.f. Waples & Gaggiotti, 2006). Nevertheless, population genetics principles can be used to estimate migration rates to implement the 10% migration threshold criterion. In addition, other measures can be used in order to define MUs, such as ecological tracers (e.g., Giménez et al., 2018) or analyses of population viability (Olsen et al., 2014).

Previous genetic studies on bottlenose dolphins worldwide have identified a clear population structuring based on nuclear microsatellites and mitochondrial markers with varying geographical scales (e.g., Allen et al., 2016; Hoelzel, Potter, & Best, 1998; Rosel, Hansen, & Hohn, 2009; Vollmer & Rosel, 2017). The same has been found in European waters (Gaspari et al., 2015; Louis, Viricel et al., 2014; Mirimin et al., 2011; Natoli, Peddemors, & Hoelzel, 2003; Nichols et al., 2007; Nykänen et al., 2018; Quérouil et al., 2007), and in some areas this structuring is present even between geographically adjacent populations (e.g., between the Shannon estuary and the rest of the west coast of Ireland, Mirimin et al., 2011; Nykänen et al., 2018). Recently, Louis, Viricel et al. (2014) determined that coastal and pelagic bottlenose dolphins in European waters were genetically and ecologically distinct from each other and that further structuring within the two ecotypes existed; the coastal ecotype was divided into the Coastal South population, which included individuals from Normandy and Galicia, and the Coastal North population, consisting of coastal bottlenose dolphins around the UK and Ireland. However, these authors did not have sufficient sample sizes from each local coastal population to fully investigate fine-scale structuring and no samples were available from the population occupying the Shannon Estuary in Ireland. Therefore, it remained unclear whether further fine-scale population structure in coastal waters exists and whether the movement of mobile individuals maintains connectivity between the local populations. Furthermore, the previous studies on bottlenose dolphin population structure (Fernandez et al., 2011; Louis, Viricel et al., 2014; Mirimin et al., 2011; Natoli et al., 2003; Nykänen et al., 2018) have all employed different sets of microsatellite markers, preventing the comparison between studies, and thus giving a fragmented vision of population structure. The purpose of this study, therefore, was to evaluate the population structure of bottlenose dolphins in European

Atlantic waters at a fine-scale level, including samples from the Shannon Estuary and a larger number of samples from west of Ireland and using a common set of microsatellite markers between the studies by Louis, Viricel et al. (2014), Mirimin et al. (2011) and Nykänen et al. (2018). The demographic dispersal between the populations was estimated, and the findings are discussed in light of the conservation of the species in European waters.

Materials and methods

Ninety-six samples from Nykänen et al. (2018), were genotyped at 14 microsatellites loci used in Louis, Viricel et al. (2014) (Tut02, Ttr34, Ttr58, Ttr04, Ttr63, Tut01, Ttr19, Tut05, TtrFF6, Tut09, Ttr11, Ttr48, EV37, TexVet7, see characteristics and amplification conditions in Table S1 and Supplementary text S2 of Louis, Viricel et al. (2014). This dataset included 13 samples from Louis, Viricel et al. (2014) which were known to be duplicates based on their sample ID. Additionally, three samples previously genotyped in Louis, Viricel et al. (2014) were used as a scale, or controls, to define allele size. Nine samples from Corsica from Louis, Viricel et al. (2014) were excluded from this study as they are out of the area of interest. Further two samples from Louis, Viricel et al. (2014) and two samples from Nykänen et al. (2018), were excluded as they had less than eight loci genotyped out of 14 loci. The overall dataset used in the present study thus consists of 425 individuals; 344 samples from Louis, Viricel et al. (2014) and 81 samples (excluding the 13 duplicate samples) from Nykänen et al. (2018), with the latter originating mainly from the Shannon and West Ireland populations. The 425 samples include 228 biopsy samples and 197 samples from stranded animals.

The biopsy samples were taken in coastal Normandy (English Channel, France, N=90), West Ireland (Connemara-Mayo-Donegal area, N=30), Cork harbour (Ireland, N=4) and Shannon Estuary (Ireland, N=45), offshore Ireland (on the shelf edge, see Figure 1, N=1), the Azores (Portugal, N=19), Gibraltar and Cadiz (Spain, N=39). Fifteen samples of stranded dolphins were matches to photo-identification catalogues of coastal animals from East Scotland (N=10), Normandy (N=2), and the Arcachon estuary (Bay of Biscay, France, N=3). The rest of the stranded animals came from Ireland (N=31), Wales (N=26), Scotland (N=34), France (N=58) and Spain (N=33). The coastal or pelagic origin of all stranded animals was identified using genetic assignments to the same cluster as biopsied individuals (Louis, Viricel et al., 2014). Ecotype assignment was further confirmed for some of the individuals using photo-identification catalogues of known coastal animals as detailed above (N=15), stable isotopes (N=40, Louis, Fontaine et al., 2014) and/or drift prediction models (N=66, Louis, Viricel et al., 2014). For example, all samples of stranded animals from East Scotland were predicted to have died close to shore (Louis, Viricel et al., 2014). Individuals stranded in the English Channel in France were predicted to originate from coastal waters while individuals stranded in the Bay of Biscay were predicted to come both from the shelf and the shelf-edge (Louis, Viricel et al., 2014).

Microsatellite marker quality

The 13 identified duplicate samples between the two studies were used to calculate genotyping error rate by dividing the number of inconsistent genotypes among the duplicates (three) by the total number of genotypes (364 minus six missing genotypes, therefore 358).

All individuals were successfully amplified for at least eight loci and there was 1.80% of missing values in the dataset. Microchecker 2.2.3 was used to check for null alleles and scoring errors (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Departures from Hardy-Weinberg equilibrium (HWE) and linkage equilibrium were tested using 10 000 dememorizations, 1 000 batches and 10 000 iterations per batch in GENEPOP on the web version 4.2 (Raymond & Rousset, 1995; Rousset, 2008). Tests were conducted for the whole dataset and for the finest level of population structure identified by the clustering methods (see below).

Genetic population structure

Population delimitation and assignment of individuals was done using three genetic clustering methods, which were applied to: (i) the full microsatellite dataset (N=425), and (ii) a subset comprising only coastal individuals (N=269). The clustering methods include: two Bayesian methods implemented in STRUCTURE (Pritchard, Stephens, & Donnelly, 2000) and TESS (Durand, Chen, & Francois, 2009) and a multivariate method, Discriminant Analysis of Principal Components (DAPC) (Jombart, Devillard, & Balloux, 2010). TESS was also run considering only the pelagic individuals (N=156). For the coastal dolphins, if any cluster included several sampling locations, TESS was re-run considering only those sampling areas to determine if there was further genetic structuring among them.

The three different approaches were used to ensure the robustness of the inferred results, as determining the most likely number of clusters can be challenging (Guillot, Leblois, Coulon, & Frantz, 2009). STRUCTURE assigns individuals to clusters by minimizing HWE and linkage disequilibria (Pritchard et al., 2000). TESS implements a probabilistic model similar to STRUCTURE but is spatially explicit as it incorporates

the geographic coordinates of the sampled individuals as *a priori* information (Durand et al., 2009). In contrast to these two Bayesian approaches that use the full data, DAPC uses genetic similarity to cluster individuals and does not make any population genetic model assumptions, i.e., it does not assume clusters are in HWE (Jombart et al., 2010).

TESS was run using the conditional auto-regressive (CAR) admixture model with a burn-in of 20 000 steps followed by 120 000 Markov Chain Monte Carlo (MCMC) steps. The number of clusters (K) tested varied between two and ten when considering the whole data set and the coastal samples only, and between two and six when analysing the pelagic samples only. In these cases, ten replicate runs for each value of K were performed but six replicates were used in the analyses that excluded closely related individuals. The spatial interaction parameter was left at the default value (0.6) with a linear degree trend. To select the most likely number of clusters, the Deviance Information Criterion (DIC) values were plotted against K and plots of individual membership proportions were examined. Consistency across runs was also checked.

STRUCTURE was run using the admixture models with correlated and independent allele frequencies, without *a priori* information. Ten independent runs for number of clusters ranging from one to ten were carried out with a burn-in of 100 000 iterations followed by 500 000 MCMC steps. Convergence of each run was confirmed visually by inspecting the α-parameter and likelihood chains, and the consistency across runs was examined using pophelper (Francis, 2017), a package that implements the functions from software CLUMPP (Jakobsson & Rosenberg, 2007) in R (R Core Team, 2018). If the results between replicate runs differed (a sign of MCMC non-convergence across all runs), STRUCTURE was re-run increasing the number of MCMC steps to 500 000 burn-in followed by 1 000 000 samples. To determine the

most likely *K*, the likelihood (L(*K*)), the rate of change in the likelihood (L'(*K*) and L''(*K*)) and ΔK (Evanno, Regnaut, & Goudet, 2005) were calculated and plotted for each *K* using pophelper (Francis, 2017), and individual membership proportion plots for the run with the highest likelihood were plotted for the most likely values of *K*, following Pritchard et al., (2000).

The DAPC analysis was performed using the package adegenet 2.1.1 (Jombart, 2008) in R following the recommendations in Jombart (2012). The most likely number of clusters was determined with the *K*-means method using the decrease in Bayesian Information Criterion (BIC) value and, in the absence of an "elbow" (a clear drop followed by a sharp increase) in the BIC curve, by plotting and inspecting the membership proportions for the values of *K* with the lowest BIC values. Maximum number of clusters tested was set to ten, and the linear discriminant analysis was performed on 80% of the retained principal components. Scatter-plots were produced for varying *K*. The membership proportion plots were checked for concordance with the number of estimated clusters and whether membership proportions to those clusters were high (>80%).

Results of analyses characterizing population structure presented in the main text are based on TESS because they were the most consistent between runs, and importantly, were more concordant with photo-identification studies (see details in the Results section) than those of the two other genetic clustering methods.

The inclusion of closely related individuals can affect population structure analyses (Anderson & Dunham, 2008). Therefore the Queller and Goodnight's (Queller & Goodnight, 1989) relatedness coefficient (*R*) was estimated among individuals using COANCESTRY (Wang, 2011) within each population identified by TESS. TESS was

re-run after removing one individual from each pair of individuals showing a relatedness coefficient larger or equal to 0.45 as in Rosel et al. (2009).

Nuclear genetic differentiation and diversity

Genetic differentiation, i.e., pairwise F_{ST} (Weir & Cockerham, 1984) and Jost's D (Jost, 2008), between the populations inferred by TESS, were estimated using the R-package diveRsity (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013). The level of significance was assessed using 1 000 bootstrap samples. For each population, the mean number of alleles (NA), allelic richness (AR), inbreeding coefficient (F_{IS}), observed heterozygosity (*Ho*) and expected heterozygosity (*He*), were calculated, also in diveRsity. Program CONVERT (Glaubitz, 2004) was used to count private alleles. Diversity indices were also calculated separately for each locus.

Recent migration rates

Recent migration rates (i.e., within the last two generations) between the populations identified by TESS at the finest level of genetic structuring were estimated using BayesAss (Wilson & Rannala, 2003). Following Rannala (2013), preliminary runs were first performed to tune up MCMC parameters ensuring proposal acceptance rates around 30%. Ten runs were performed with a burn-in of 1×10^6 iterations followed by 2×10^7 MCMC iterations and a sampling frequency of 1 000. Trace files were plotted using Tracer (Rambaut & Drummond, 2007) to check for convergence and mixing. Consistency of the results between the runs was also checked.

Results

The genotyping error rate between the two datasets was 0.0084. Significant departures from Hardy-Weinberg equilibrium (HWE) were detected for loci EV37 and Ttr34 in one population each (Appendix S1). As deviation was significant in only one out of seven populations for each locus, these loci were kept in the analyses. Linkage disequilibrium was not significant for any of the pairwise comparisons within each population. No null alleles or scoring errors were found.

Individual assignment methods

The most likely number of clusters when running TESS on the whole dataset was six. The delimitation of the six clusters (see Figure 2, Appendices S2a and S2b) and the whole data set (i.e., including both coastal and pelagic individuals) is as follows. The first cluster was mainly composed of coastal dolphins from East Scotland (ten of which were identified as resident based on photo-identification catalogue), Wales and a few individuals from West Scotland and Galicia. The second cluster consisted of individuals biopsy sampled in the Connemara-Mayo-Donegal area on the west coast of Ireland (i.e., the West Ireland population). The third cluster included coastal biopsies from the Shannon Estuary and four biopsy samples from dolphins sampled in Cork harbour, Ireland (i.e., the Shannon population). The fourth cluster was composed of coastal dolphins sampled in the English Channel, in particular in the Gulf of Saint-Malo, three stranded dolphins previously photo-identified as part of a small group that used to reside in the Arcachon estuary (Bay of Biscay, France) and a few individuals from Galicia (i.e., the English Channel population). The fifth cluster included stranded samples from the west coasts of the United Kingdom, Ireland, France and northern Spain, and biopsy samples from the Northeast Atlantic and around the Azores (*i.e.* the

Pelagic Atlantic population). The last cluster was composed of individuals sampled in the Strait of Gibraltar and the Gulf of Cadiz (i.e., the Gibraltar-Cadiz population). When considering K=2, populations (e) and (f) (in Figure 2), were grouped together in one cluster and all remaining populations in the other (TESS, results not shown). This result highlights the hierarchical structuring of the species into coastal (populations (a) to (d)) and pelagic (populations (e) and (f)). Indeed, populations (e) and (f) consist of biopsies from individuals sampled in deep waters of the Azores, North Atlantic and Strait of Gibraltar (plus some samples from the Gulf of Cadiz) as well as samples from stranded animals from the West coasts of Scotland, Ireland, France and Spain.

In order to study in more detail the structuring among the coastal individuals, TESS was re-run with coastal samples only. In this case, the most likely number of clusters was five (Figure 3A). The DIC plot indicated a plateau at K=5 or K=6 (Appendix S3a) but examination of membership proportions indicated that there were actually only five clusters in all of the replicate runs with K=6 (Figure 3A, Appendix S3b). Thus, this finer scale analysis uncovered an additional cluster among the coastal dolphins. More precisely, the cluster comprising individuals sampled in Scotland, Wales and Galicia (Figure 2a) was divided into two clusters: one comprising individuals from Scotland and Wales (Figure 3A(a)) and another including individuals from Galicia (i.e., the Galicia population, Figure 3A(e)). All remaining coastal individuals (Figure 2b-d) were clustered as before (see Figure 3A(b-d)).

To further explore fine-scale structuring, TESS was re-run for only the individuals of the Scotland–Wales cluster (Figure 3A(a)), as this population encompassed several geographical areas. Further population structure was found within this area (see Figure 3B and Appendices S4a and S4b) with the first cluster including individuals from

Wales and a few individuals from West Scotland (Wales–West Scotland population, Figure 3B(a)) and a second cluster consisting of individuals from East Scotland (East Scotland population, Figure 3B(b)).

When running TESS on the pelagic samples only, no further genetic structuring was found but the best number of clusters was two, corresponding to the Pelagic Atlantic and the Gibraltar-Cadiz populations (Appendices S5a and S5b), inspection of the admixture plots for K=2 to K=6 also indicated that there were only two clusters, results shown for K=2 and K=3 in S5b.

Additional analyses with STRUCTURE and DAPC provide general support for TESS results but were either less stable due to convergence problems (STRUCTURE) or were not completely congruent with results of photo-identification studies. When all samples (N=425) were included in STRUCTURE runs, the Evanno-method (ΔK, Evanno et al., 2005) detected only the uppermost hierarchical structure i.e., the division into coastal and pelagic at K=2 (Appendix S9d). Nevertheless, using the L(K) criterion proposed by Pritchard et al. (2000), the most likely K was six (Appendix S9a), in concordance with TESS. Beyond this, no new genetic clusters emerged in the membership proportion plots (Appendix S10). The full description of STRUCTURE results when including all samples and only the coastal samples is given in Appendices S7 and S11, respectively. In contrast to TESS, STRUCTURE could not detect the samples from Galicia as a separate cluster when only coastal samples were included.

When all samples were included in the DAPC analyses, the best number of clusters was found at K=6 (Appendices S15-S16). The clusters were almost identical to those found with TESS and STRUCTURE, dividing the Irish samples into Shannon and West coast populations and separating the biopsy samples from Cadiz-Gibraltar from

the Azores biopsies and stranded samples thought to be from a pelagic origin. However, in contrast to TESS, DAPC also failed to delineate the samples from Galicia into a separate cluster when only coastal samples were included. The full description of results when including only the coastal samples is given in Appendix S17.

As mentioned previously (Methods), the inclusion of closely related individuals can bias results of genetic clustering methods. The presence of related individuals varied among the geographic areas considered in this study. They were almost inexistent among pelagic samples as no closely related individuals (with a relatedness coefficient of ≥0.45) were found in the Gibraltar-Cadiz population and only three pairs were found in the pelagic Atlantic population. In contrast, relatedness among coastal individuals varied from 1.15% in the English Channel population to 5.13% in the Galicia population. Therefore, TESS was re-run for the coastal populations only taking out one individual from each close kin pair (N=79). The results were similar to the runs including close relatives and also indicated five clusters corresponding to the Shannon, the West Ireland, the English Channel, the East and West Scotland–Wales and the Galicia populations (Appendices S6a and S6b). As the results with and without including close relatives were similar, we conclude that the results from TESS presented in Figures 2 and 3 are highly reliable and can be used to draw inferences on migration rates.

Results from genetic clustering methods such as TESS can be used as a first approach to study migration. More precisely, individuals assigned to a population different from the geographical area where they were sampled can be considered as likely migrants. One individual sampled in Galicia had a high assignment probability to the English Channel population (0.75), another individual sampled in the English Channel was

assigned to the West Ireland population (with 0.86 probability) and a third individual sampled in the Shannon estuary was assigned to the West Ireland population (with 0.77 probability). These results suggest that there is some connectivity between dolphin populations and further analyses with BayesAss are warranted.

Nuclear genetic differentiation and diversity

All nuclear F_{ST} and Jost's D pairwise comparisons between the eight populations identified with TESS were significant. The highest level of differentiation was between pelagic and coastal populations (Table 1). When considering $F_{ST,}$ the lowest level of differentiation was detected between the two pelagic populations. In terms of Jost's *D* the lowest differentiation was between Wales and East Scotland. The Shannon population was the most differentiated from the pelagic populations followed by the West Ireland population for both indices.

Nuclear genetic diversity (Allele Richness (AR) and Observed Heterozygosity (*Ho*)) was significantly lower in most coastal populations than in the pelagic populations, with Kruskal-Wallis $P<0.01$ in all AR coastal-pelagic comparisons except between English Channel and Gibraltar-Cadiz ($P=0.07$), and $P<0.05$ in all *Ho* comparisons except between Gibraltar-Cadiz and English Channel ($P=0.12$), Gibraltar-Cadiz and Galicia ($P=0.18$) and Pelagic Atlantic and Galicia ($P=0.09$) (Table 2, Appendix S20 for values per loci per populations). Among the coastal populations, allele richness was highest in the English Channel population and lowest in the Shannon population, between which the difference was significant (Kruskal-Wallis $P<0.05$). The highest number of private alleles was found in the pelagic Atlantic population (N=26), two private alleles were found in the Gibraltar/Cadiz and the English Channel populations and one private allele in the East Scotland and in the West Scotland–Wales

populations. A significant heterozygote deficiency was detected in the Shannon, West Ireland and Galicia populations (Table 2).

Recent migration rates

Estimates of recent migration rates were highly consistent between runs; therefore, the results presented here are based on a randomly chosen run (Table 3). Estimated migration rates were very low between most populations, around <1% per generation, with an upper bound for the 95% credibility interval of less than 10% and a lower bound of 0 (Table 3). The only exceptions were mean migration rate of 18.1% between Galicia and East Scotland, and mean rate of 25.7% from East Scotland to Wales–West Scotland. However, these higher migration rates need to be interpreted with caution as individuals from Scotland, Wales and Galicia consisted of stranded animals. As mentioned before, although a portion of the East Scotland individuals were matched to photo-identification catalogues of known coastal animals, there is uncertainty about the origin of strandings in Wales and West Scotland.

Discussion

This study presents, to date, the most comprehensive analysis of the genetic structure of bottlenose dolphins in the North-east Atlantic as it includes samples collected from an unprecedentedly wide geographical area, which unlike previous studies, were analysed using a common set of microsatellite markers. The results of this study, therefore, have the potential to be used to identify management units in this area and thus offer a significant contribution to the conservation of the species in European waters.

A first level of genetic differentiation was found between coastal and pelagic populations, as in a previous study (Louis, Viricel et al., 2014). The results from TESS in terms of assignments to coastal and pelagic ecotypes were identical to that of Louis, Viricel et al. (2014) with only one exception. One individual that stranded in the Bay of Biscay which belonged to the Pelagic Mediterranean population in Louis, Viricel et al. (2014) clustered with the coastal English Channel population in this study. No further genetic structure was found within the two pelagic populations (i.e., Pelagic Atlantic and Gibraltar-Cadiz).

Fine-scale population structure among coastal bottlenose dolphins from different geographical locations corresponded to the different local populations that inhabit the Shannon estuary, west of Ireland, the English Channel, Galicia, East Scotland, and Wales/West Scotland. Previous studies only identified large-scale population structure in coastal waters due to uneven sampling of each local coastal population (Louis, Viricel et al., 2014) or fine-scale population structure in small geographic regions (Fernandez et al., 2011; Mirimin et al., 2011, Nykänen et al., 2018). Thus, the results of this study highlight the need for and the power of broad scale collaboration when working on the conservation of highly mobile species that can move across national borders. The level of resolution was only possible thanks to broad international collaborations, sample sharing and careful calibration of allele scoring to overcome the difficulties of comparing genotypes across studies.

Although results of all three genetic clustering methods were generally consistent, their comparison with independent results from photo-identification studies highlighted differences in performance among them. More explicitly, the coastal population assignments inferred with TESS were concordant with photo-identification studies

indicating geographically isolated populations with site fidelity. This was not always the case for STRUCTURE and DAPC results. This highlights the power of clustering methods using *a priori* spatial information to infer complex population structure. Indeed, although STRUCTURE was able to identify the same six clusters as TESS when all samples were considered, it was unable to identify further fine-scale structuring among coastal samples. Comparing the two approaches to infer the number of clusters using STRUCTURE, supports the idea that Evanno's method is well adapted to identify the first level of structuring under hierarchical scenarios (Waples & Gaggiotti 2006) such as those observed in bottlenose dolphins. DAPC also supports the subdivision of bottlenose dolphins into six management units but assignment of individuals to populations was less consistent with those of the two other methods. In particular, one of the genetic clusters was composed of individuals sampled from many different geographic locations. As Jombart et al. (2010) indicate, DAPC uses a purely statistical criterion aimed at identifying the minimum number of groups that best explain total observed variation while at the same time maximising between group variation. Thus, as opposed to TESS and STRUCTURE, it does not take into consideration Hardy-Weinberg and linkage equilibrium, which explains the observed differences with the two other methods in the individual assignments to populations.

The use of stranded animals could be considered as a limitation of this study. However, we are relatively confident in the inferences made, even though strandings constitute almost half of all samples. Firstly, a drift-prediction model (Peltier et al., 2012) was applied in a previous study (Louis, Viricel et al., 2014), to estimate the most likely area of death. The estimated origin with the drift prediction model was consistent with the genetic results separating coastal and pelagic bottlenose dolphins (Louis, Viricel et al.,

2014). For example, in East Scotland, all individuals were estimated to have died very close to shore. The coastal and pelagic assignments of a subset of the samples were confirmed using stable isotopes (Louis, Fontaine et al., 2014). In addition, 15 stranded animals were known to be part of the resident coastal populations and their genetic assignments matched photo-identification studies (Louis, Viricel et al., 2014). Nevertheless, we acknowledge that there is uncertainty in the origin of the stranded animals when there is no further evidence such as photo-identification and drift modelling. This is the case for the coastal populations of Galicia and Wales/West Scotland and caution is therefore required when interpreting these results.

The fine-scale population structure likely results from natal philopatry, possibly driven by vertically (mother to offspring) and horizontally (between non-filial conspecifics) learned foraging behaviours during the juvenile life stage, site fidelity and social structure (Foote et al., 2016; Kopps et al., 2014; Whitehead, 2017; see further discussion in Louis, Viricel et al., 2014; Louis, Fontaine et al., 2014; Nykänen et al., 2018). Photo-identification studies indicated site fidelity to relatively restricted geographical areas (Cheney et al., 2014; Ingram & Rogan, 2002; Louis et al., 2015), however, individuals can undertake movements of a few hundreds of kilometres, i.e., around Ireland (O'Brien et al., 2009) and the East coast of Scotland (Cheney et al., 2013) but these movements can still be considered occurring at a relatively small scale. There is also some evidence of larger scale movements between the North Sea and the Atlantic, as reported in Robinson et al. (2012), and this provides further potential for genetic and demographic connectivity between the populations; seven transient dolphins were first sighted in the Moray Firth, East Scotland and later re-sighted in the Hebrides, West Scotland. Five of these animals were later recorded in coastal Irish

waters and some of these movements represent travelled distances of over 1 200 km (Robinson et al., 2012). These individuals are believed to be part of the West Ireland population based on photo-identification catalogue kept on the coastal Irish dolphins. However, photo-identification fieldwork mainly occurs during the summer in most areas. Therefore, movements outside this season may be overlooked.

Despite the above-mentioned movements, our results are consistent with a very low degree of connectivity among the studied populations. In other words, the different populations are relatively isolated from each other. Estimated migration rates among populations were very low, and less than 1% per generation for most of the pairwise comparisons. Although there is no consensus on the level of migration that leads to demographic coupling (Waples & Gaggiotti, 2006; Palsboll et al., 2007), the estimated migration rates are well below the rate of 10%, which according to a simulation study can lead to coupled dynamics (Hastings, 1993). Demographic connectivity is therefore very low among local populations. The only exceptions are the migration rates of 18% from East Scotland to Galicia and 26% from East Scotland to Wales, the latter of which could be explained by the relatively short distance between the two sites. However, as these populations included only stranded dolphins and although all the East Scotland samples were estimated to originate from the North Sea according to a drift-prediction model used in a previous study (Louis, Viricel et al., 2014), there is some uncertainty about the origin of the individuals sampled in Wales and Galicia. As migration rate estimates have been shown to be dependent on the number of clusters chosen to best represent the population structure and thus the number of individuals in each cluster (Olsen et al., 2014), great care has to be taken that the sampling strategy used is robust and the samples are representative of each population. The present study is based on

the most comprehensive set of genetic samples available but there is still a need for more biopsy samples from Wales and Scotland to further support our results.

The different populations were characterised in terms of genetic diversity, differentiation and migration rates. This information and existing estimates of abundance will help to evaluate the conservation status and vulnerability of the populations. Indeed, small isolated population are at risk of losing heterozygosity and genetic resilience due to genetic drift (Lacy, 1987) and are thus more vulnerable to stochastic environmental changes or anthropogenic stressors than larger populations. Genetic diversity was higher in the pelagic populations than coastal populations as in previous studies (Hoelzel et al., 1998; Louis, Viricel et al., 2014). This is consistent with higher abundance of the pelagic populations compared to the coastal populations. The Gibraltar-Cadiz population included around 700 photo-identified individuals (Giménez et al., 2018) and the Pelagic Atlantic abundance estimates (from Scotland to Spain) are several tens of thousands of individuals (Hammond et al., 2013, 2009) while the abundances of coastal dolphins do not exceed ~400 individuals (see below).

Genetic diversity indices for the coastal populations were concordant with abundance estimates using mark-recapture methods. The population of the English Channel, which is the largest coastal population with abundance estimates of around 400 individuals (Louis et al., 2015), had the highest genetic diversity. The Shannon population had the lowest genetic diversity and is the smallest with abundance estimated between 110 and 140 dolphins (Berrow, 2012; Englund, Ingram, & Rogan, 2008; Ingram & Rogan, 2002, 2003; Rogan, Gkarakouni, Nykänen, Whitaker, & Ingram, 2018). Abundance estimates were around 200 individuals in East Scotland

(Cheney et al., 2013), ca. 190 for the West Irish population (Nykänen, 2016) and 150 to 250 individuals in Wales (Pesante, Evans, Baines, & McMath, 2008). Any local perturbation or global change could thus have drastic negative effects on these coastal populations due to their small size, low genetic diversity and low connectivity uncovered in this study.

This study filled a major knowledge gap on the fine-scale population structure of bottlenose dolphins in European Atlantic waters, which was considered as the main research priority for the protection of this species (Ó Cadhla & Marnell, 2017). As previously found in Louis, Viricel et al. (2014), coastal and pelagic populations are distinct and should be monitored separately. In terms of the coastal populations, the high genetic differentiation and negligible migration rates found in this study highlight the need to separately monitor each local population (the English Channel, the Shannon, the West Ireland, the East Scotland, the Galicia and the Wales–West Scotland populations) as they correspond to different management units. However, we cannot rule out further fine-scale population division in Wales and West Scotland due to the small sample sizes (N=16 and N=5, respectively), and the fact that all came from stranded dolphins as the use of samples of stranded animals only may lead to under-estimated population structure (Bilgmann, Möller, Harcourt, Kemper, & Beheregaray, 2011).

The small population sizes of the coastal populations and their isolation may render them vulnerable to anthropogenic impacts. These results highlight the need to protect their habitat through protected areas such as the SACs where anthropogenic activities are appropriately managed, ensuring their ecological suitability to the populations utilizing them. Regular monitoring of population dynamics (e.g., abundance, survival,

calving rate) using photo-identification, as undertaken in some of the areas, is therefore recommended to evaluate population trends. Population viability analyses, as applied to harbour seals, *Phoca vitulina*, in Southern Scandinavia in Olsen et al. (2014), could also help inform whether the populations are of sufficient size for long-term population viability in the absence of immigration.

In this study, management units were identified by first clustering individuals into putative populations based on individuals' genotypes and then by estimating their connectivity. Populations not sampled in this study (i.e., the Sado Estuary, Portugal, and the Iroise Sea, France) could be genotyped in the future using the same set of markers as in this study to further clarify their connectivity with the other European Atlantic populations. The Atlantic pelagic population showed no genetic differentiation over a large geographical range from West Scotland to the Azores. However, pelagic bottlenose dolphin populations may show ecological differences even in the absence of genetic divergence and this should be considered when allocating management units. For example, the bottlenose dolphins of the Gibraltar Strait and of the Gulf of Cadiz, although potentially presenting no genetic structure, showed differences in ecology detected using different ecological tracers (i.e., stable isotopes and contaminant loads) and individual monitoring through photo-identification, leading to the delineation of two ecological, management units (Giménez et al., 2018). This type of ecological differentiation may be detected using next generation sequencing data covering the whole genome of the species, which would allow testing for adaptive differentiation (Funk, McKay, Hohenlohe, & Allendorf, 2012). We recommend combining genetic data with ecological data (e.g., the use of stable isotopes) and individual monitoring, where available, to determine

the geographical scales most relevant to monitoring and the protection of populations of any species.

Data accessibility: The data are available on dryad at the following link: (to be uploaded at the revisions stage).

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Tables

Table 1. Pairwise fixation indices based on 14 microsatellite loci (given as average with 95% Highest Probability Density Interval (HPDI)) between the different populations. The samples were divided into populations based on results from TESS. Values above the diagonal are F_{ST}-values and values below the diagonal are Jost's D values.

	Shannon	Wales/West Scotland	East Scotland	West Ireland	English Channel	Galicia	Gibraltar/Cadiz	Pelagic Atlantic
Shannon	-	0.136 (0.096-0.180)	0.164 (0.130-0.200)	0.129 (0.104-0.153)	0.090 (0.079-0.103)	0.226 (0.178-0.283)	0.232 (0.215-0.249)	0.227 (0.212-0.241)
Wales/West Scotland	0.090 (0.061-0.121)	-	0.066 (0.037-0.103)	0.128 (0.092-0.169)	0.082 (0.058-0.111)	0.125 (0.083-0.176)	0.173 (0.154-0.197)	0.178 (0.159-0.198)
East Scotland	0.141 (0.104-0.176)	0.036 (0.010-0.075)	-	0.149 (0.119-0.183)	0.090 (0.067-0.114)	0.091 (0.062-0.131)	0.150 (0.129-0.172)	0.164 (0.147-0.183)
West Ireland	0.074 (0.056-0.095)	0.089 (0.064-0.116)	0.115 (0.086-0.148)	-	0.115 (0.099-0.131)	0.178 (0.132-0.234)	0.208 (0.190-0.227)	0.190 (0.177-0.206)
English Channel	0.065 (0.052-0.079)	0.082 (0.054-0.115)	0.081 (0.054-0.110)	0.104 (0.085-0.125)	-	0.094 (0.065-0.134)	0.134 (0.122-0.146)	0.146 (0.136-0.157)
Galicia	0.174 (0.123-0.234)	0.098 (0.042-0.164)	0.054 (0.027-0.090)	0.111 (0.067-0.164)	0.093 (0.060-0.142)	-	0.140 (0.115-0.173)	0.139 (0.116-0.170)
Gibraltar/Cadiz	0.386 (0.346-0.426)	0.289 (0.246-0.331)	0.260 (0.220-0.310)	0.347 (0.308-0.388)	0.286 (0.254-0.320)	0.259 (0.214-0.312)	-	0.034 (0.026-0.043)
Pelagic Atlantic	0.457 (0.423-0.492)	0.359 (0.318-0.398)	0.345 (0.310-0.384)	0.379 (0.347-0.414)	0.351 (0.324-0.377)	0.335 (0.281-0.401)	0.097 (0.072-0.126)	-

1048 Table 2. Nuclear diversities over all loci for each population inferred by TESS.

Population	N (mean)	A	%	AR	*Ho*	*He*	HWE	F_{IS}	F_{IS} Low	F_{IS} High	PA
Shannon	52	52	31.19	3.06	0.44	0.42	0.997	-0.0604*	-0.1215	-0.0014	0
Wales/West Scotland	20	57	35.86	3.36	0.46	0.48	0.839	0.0362	-0.0744	0.1386	1
East Scotland	31	54	35.94	3.42	0.52	0.54	0.982	0.0297	-0.0565	0.1067	1
West Ireland	36	53	34.82	3.30	0.51	0.47	1.000	-0.0754*	-0.1358	-0.0204	0
English Channel	111	93	57.45	4.75	0.60	0.60	0.971	0.0115	-0.0244	0.0470	2
Galicia	13	58	36.90	3.76	0.60	0.55	0.419	-0.0892*	-0.2011	-0.0046	0
Gibraltar/Cadiz	49	113	72.10	6.10	0.73	0.74	0.463	0.0141	-0.0172	0.0462	2
Pelagic Atlantic	106	148	92.43	7.07	0.75	0.77	0.998	0.0266	0.0030	0.0497	26

1049 N=mean number of individuals used for each locus, A=number of alleles observed, %=percentage of total alleles, AR=allelic richness,
1050 *Ho*=observed heterozygosity, *He*=expected heterozygosity, are given as per locus per population sample. Hardy-Weinberg Equilibrium
1051 (HWE)=corrected p-values (chi-square test for goodness-of-fit), F_{IS}=F_{IS} values for each loci and population sample (overall), F_{IS} Low/High=bias
1052 corrected 0.025% and 92.5% percentiles of the confidence interval. *denotes significance in F_{IS} values as the 95% CI does not overlap zero,
1053 PA=number of Private Alleles.

1054

Table 3. Mean (and 95% Credible Interval) recent migration rates inferred using BayesAss. The migration rate is defined as the proportion of individuals in a population that immigrated from a source population per generation. Migration rates above 0.10 have been highlighted in bold.

Population \ Source	Shannon	Wales/West Scotland	East Scotland	West Ireland	English Channel	Galicia	Gibraltar/Cadiz
Shannon	0.959 (0.931 - 0.987)	0.005 (0.000 - 0.016)	0.007 (0.000 - 0.019)	0.006 (0.000 - 0.018)	0.006 (0.000 - 0.018)	0.005 (0.000 - 0.016)	0.005 (0.000 - 0.016)
Wales/West-Scotland	0.012 (0.000 - 0.036)	0.678 (0.657 - 0.700)	**0.257 (0.206 - 0.307)**	0.010 (0.000 - 0.029)	0.013 (0.000 - 0.037)	0.010 (0.000 - 0.029)	0.010 (0.000 - 0.029)
East Scotland	0.010 (0.000 - 0.030)	0.008 (0.000 - 0.025)	0.935 (0.892 - 0.978)	0.009 (0.000 - 0.027)	0.011 (0.000 - 0.030)	0.009 (0.000 - 0.025)	0.009 (0.000 - 0.026)
West Ireland	0.054 (0.000 - 0.112)	0.008 (0.000 - 0.022)	0.009 (0.000 - 0.028)	0.898 (0.833 - 0.964)	0.008 (0.000 - 0.024)	0.008 (0.000 - 0.022)	0.008 (0.000 - 0.022)
English Channel	0.008 (0.000 - 0.021)	0.003 (0.000 - 0.008)	0.007 (0.000 - 0.019)	0.005 (0.000 - 0.013)	0.969 (0.948 - 0.990)	0.003 (0.000 - 0.008)	0.003 (0.000 - 0.008)
Galicia	0.015 (0.000 - 0.043)	0.014 (0.000 - 0.041)	**0.181 (0.104 - 0.257)**	0.015 (0.000 - 0.043)	0.062 (0.000 - 0.127)	0.684 (0.652 - 0.716)	0.014 (0.000 - 0.041)
Gibraltar/Cadiz	0.006 (0.000 - 0.017)	0.006 (0.000 - 0.018)	0.006 (0.000 - 0.018)	0.006 (0.000 - 0.017)	0.006 (0.000 - 0.018)	0.006 (0.000 - 0.017)	0.941 (0.902 - 0.981)
Pelagic Atlantic	0.003 (0.000 - 0.009)	0.003 (0.000 - 0.009)	0.003 (0.000 - 0.009)	0.003 (0.000 - 0.009)	0.004 (0.000 - 0.011)	0.003 (0.000 - 0.009)	0.008 (0.000 - 0.022)

Figure legends

Figure 1. Map of samples used in the study and their origin; stranding - samples collected from stranded bottlenose dolphins, biopsy - samples collected from skin biopsies, and catalogued – samples collected from stranded animals that had been matched to a photo-identification catalogue of known coastal dolphins. The grey contours represent 200m and 1000m depth contours.

Figure 2. Map of individual assignment probabilities per population identified by TESS using the whole dataset (N=425) and *K*=6. The color scale bar indicates the assignment probabilities, (a) East and West Scotland, Wales and Galicia, (b) West Ireland, (c) Shannon estuary, Ireland, (d) English Channel, France, (e) pelagic Atlantic, (f) Gibraltar-Cadiz.

Figure 3. Results of TESS analyses involving only coastal samples. A) Map of individual assignment probabilities per population using all coastal samples (N= 269) and *K*=5: (a) East Scotland and Wales (b) West Ireland, (c) Shannon estuary, Ireland, (d) English Channel, France, (e) Galicia, Spain. (B) Map of individual assignment probabilities per population using only the samples from coastal Wales, West and East Scotland (N=53) and *K*=2: (a) West Scotland and Wales (b) East Scotland. The color scale bar indicates the assignment probabilities.

1065

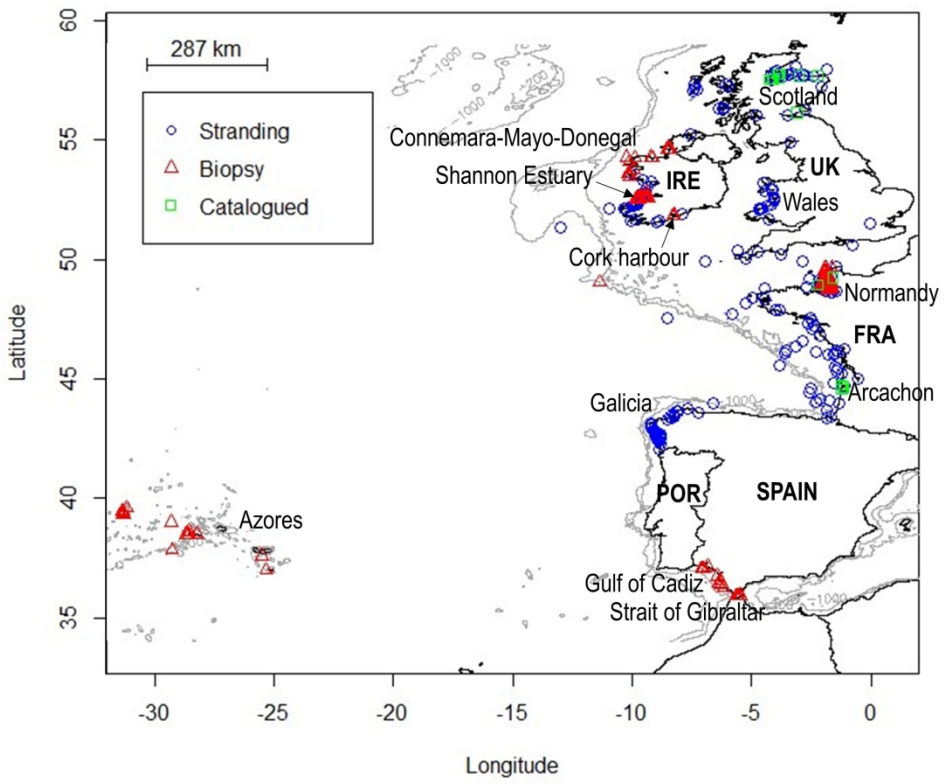
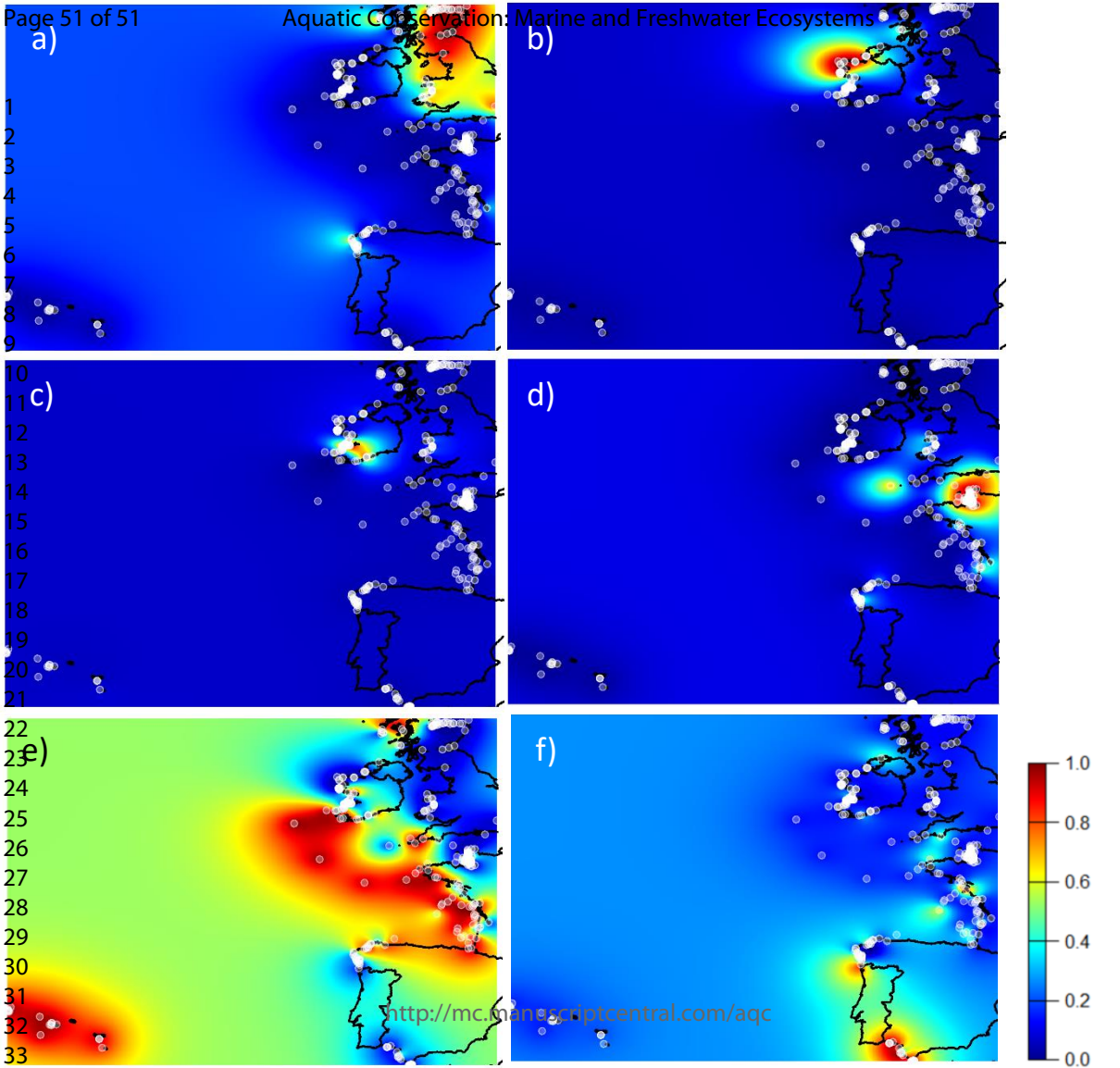


Figure 1. Map of samples used in the study and their origin; stranding - samples collected from stranded bottlenose dolphins, biopsy - samples collected from skin biopsies, and catalogued – samples collected from stranded animals that had been matched to a photo-identification catalogue of known coastal dolphins. The grey contours represent 200m and 1000m depth contours.

208x181mm (300 x 300 DPI)


a)
b)
c)
d)
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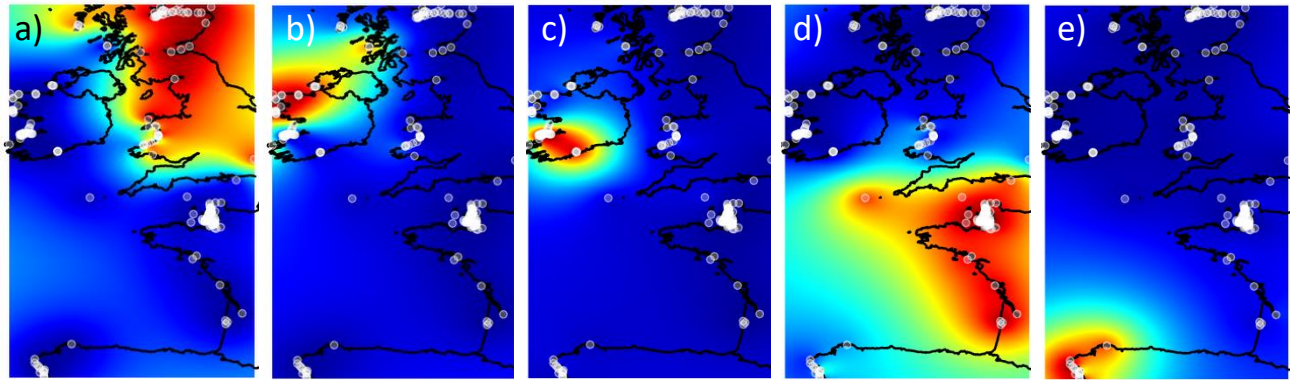
1.0
0.8
0.6
0.4
0.2
0.0

A) Coastal samples - *K* = 5



B) Wales and all Scotland coastal samples - *K* = 2