



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

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4 **1 Fine-scale population structure and connectivity of bottlenose**  
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6 **2 dolphins, *Tursiops truncatus*, in European waters and implications**  
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8 **3 for conservation**  
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## 50 **Abstract**

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39 51 1. Protecting species often involves the designation of protected areas, wherein  
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41 52 suitable management strategies are applied either at the taxon or ecosystem level.  
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43 53 Special Areas of Conservation (SACs) have been created in European waters under  
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45 54 the Habitats Directive to protect bottlenose dolphins, *Tursiops truncatus*, which  
46  
47 55 forms two ecotypes, pelagic and coastal.  
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51 56 2. The SACs have been designated in coastal waters based on photo-identification  
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53 57 studies that have indicated that bottlenose dolphins have relatively high site fidelity.  
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55 58 However, individuals can carry out long-distance movements which suggest  
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57 59 potential for demographic connectivity between the SACs as well as with other areas.  
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3 60 3. Connectivity can be studied using genetic markers. Previous studies on the species  
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5 61 in this area used different sets of genetic markers and therefore inference on the fine-  
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7 62 scale population structure and demographic connectivity has not yet been made at a  
8  
9 63 large scale. A common set of microsatellite markers was used in this study to provide  
10  
11 64 the first comprehensive estimate of genetic structure of bottlenose dolphins in  
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13 65 European Atlantic waters.  
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17 66 4. As in previous studies, a high level of genetic differentiation was found between  
18  
19 67 coastal and pelagic populations. Genetic structure was defined at an unprecedented  
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21 68 fine-scale level for coastal dolphins leading to identification of five distinct coastal  
22  
23 69 populations inhabiting the following areas: Shannon estuary, west coast of Ireland,  
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25 70 English Channel, coastal Galicia, east coast of Scotland, and Wales/West Scotland.  
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27 71 Demographic connectivity was very low among most populations with less than 10%  
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29 72 migration rate suggesting no demographic coupling among them. Each local  
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31 73 population should therefore be monitored separately.  
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36 74 Keywords: coastal, ocean, population genetics, Special Area of Conservation,  
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38 75 mammals, bottlenose dolphins  
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## 77 **Introduction**

78 Protecting species and their habitats is the goal of conservation biology, and this often  
79 includes the designation of protected areas, wherein suitable management strategies  
80 are applied either at the taxon or ecosystem level. According to the definition by the  
81 World Conservation Union (IUCN), a Marine Protected Area (MPA) is “any area of  
82 intertidal or subtidal terrain, together with its overlying water and associated flora,  
83 fauna, historical and cultural features, which has been reserved by law or other  
84 effective means to protect part or all of the enclosed environment” (Kelleher &  
85 Phillips, 1999, 18). The usefulness of static MPAs to preserve biodiversity or to protect  
86 a particular species or population has been debated (e.g., Agardy, di Sciara, & Christie,  
87 2011; Hartel, Constantine, & Torres, 2015; Hooker & Gerber, 2004; Wilson, 2016),  
88 but they remain the primary spatial conservation unit worldwide and are key  
89 components of various conservation plans (e.g., the United Nations Plan for  
90 Biodiversity (2011–2020), the IUCN Worlds Parks Congress and the European  
91 Biodiversity Strategy to 2020 (European Commission, 2011)). In European waters, the  
92 Member States of the European Union are required to designate Special Areas of  
93 Conservation (SACs) for species listed in Annex II of the Habitats Directive (European  
94 Economic Community, 1992), which includes two cetacean species; the harbour  
95 porpoise, *Phocoena phocoena*, and the common bottlenose dolphin, *Tursiops*  
96 *truncatus*. These SACs, which are part of the European Natura 2000 strategy, should  
97 represent areas essential for the species’ life and reproduction. In addition to the  
98 protection under the Habitats Directive, as top predators, bottlenose dolphins are  
99 considered as one of the indicator species for ‘good environmental status’ (GES) in  
100 coastal waters by the Marine Strategy Framework Directive (MSFD, Council of the  
101 European Communities, 2008). The aim of MSFD is to protect the European marine

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3 102 environment by applying a comprehensive ecosystem-based approach to the  
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5 103 management of human activities, and by maintaining or restoring the favourable  
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7 104 conservation status of a number of species.  
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10 105 Previous research using photo-identification has shown that most coastal bottlenose  
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12 106 dolphin populations in Europe comprise between 30 and 400 resident individuals with  
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14 107 strong site fidelity to their respective coastal site (e.g., Cheney et al., 2013; Ingram &  
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16 108 Rogan, 2002; Louis et al., 2015). However, also based on photo-identification studies,  
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18 109 some of these individuals are highly mobile travelling distances of hundreds of  
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20 110 kilometres around the UK and Ireland (Cheney et al., 2013; Ingram, Englund, &  
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22 111 Rogan, 2001; Ingram & Rogan, 2003; O'Brien et al., 2009; Robinson et al., 2012).  
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24 112 Nonetheless, the high site-fidelity and the preferential use of some geographical areas  
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26 113 indicate that coastal bottlenose dolphins may be very sensitive to changes in local  
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28 114 environmental conditions, ecological factors, or anthropogenic disturbance. The  
29  
30 115 sensitivity of bottlenose dolphins to these threats is exacerbated by their position as an  
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32 116 apex predator and also by their low reproductive rates (Connor, Wells, Mann, & Read,  
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34 117 2000; Quick et al., 2014). The main threats in coastal environments include pollutants  
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36 118 such as xenobiotic chemicals (Jepson et al., 2016; Reif, Schaefer, Bossart, & Fair,  
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38 119 2017), reduced prey availability, habitat degradation, disturbance from vessel traffic  
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40 120 (Lusseau, Bain, Williams, & Smith, 2009; Pirotta, Merchant, Thompson, Barton, &  
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42 121 Lusseau, 2015; Williams, Bain, Smith, & Lusseau, 2009), entanglement and incidental  
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44 122 bycatch, direct hunting, marine construction and anthropogenic noise (Hammond et  
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46 123 al., 2012; Meissner et al., 2015; Pirotta et al., 2015). The increased risks of  
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48 124 demographic perturbation of dolphin populations due to human activities highlights  
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50 125 the need for the design and management of protected areas ensuring that dolphin  
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3 126 habitat remains favourable and does not deteriorate. A careful investigation of the  
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5 127 population structure and quantification of the genetic and demographic connectivity is  
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8 128 also necessary as small isolated populations may require more protection due to their  
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10 129 reduced genetic resilience.

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13 130 An important step towards the conservation of bottlenose dolphins was taken under  
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15 131 the Habitats Directive by designating SACs across the European North-east Atlantic  
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17 132 and Mediterranean coastal waters. These designations were based on photo-  
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19 133 identification and habitat use surveys showing long-term site-fidelity (Anon, 2012).

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22 134 Another important step towards their conservation is to evaluate population structure  
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24 135 and connectivity of populations between the protected areas as well as with other areas.

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26 136 This is particularly important because of the propensity for some individuals to carry  
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28 137 out long-distance movements, which suggests potential demographic connectivity  
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30 138 between the populations. It is unclear if such movements can result in migration rates  
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32 139 that could lead to correlated population dynamics. There is a paucity of studies  
33  
34 140 assessing the level of migration that will lead to demographic coupling (Waples &  
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36 141 Gaggiotti, 2006); a process by which changes in population size in one population are  
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38 142 influenced by changes taking place in another population (Hastings, 1993). However,  
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40 143 a simulation study by Hastings (1993) indicated that under a simple two-population  
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42 144 density-dependent model, a migration rate of 10% or more can lead to coupled  
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44 145 dynamics, which would require monitoring the populations as a single  
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46 146 management/conservation unit. Thus, a threshold of 10% migration above which two  
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48 147 local populations are considered independent management units can be used as an  
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50 148 operational criterion to address conservation problems.

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57 149 The most cost-effective approach to evaluate demographic connectivity and fine-scale  
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3 150 population subdivision is based on the use of genetic markers and population genetics  
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5 151 principles. Thus, a recent workshop on bottlenose dolphin conservation (December  
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7 152 2016; Ó Cadhla & Marnell, 2017) concluded that one of the main priorities for  
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9 153 implementing the afore-mentioned EU directives for this species was a fine-scale  
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11 154 population genetics analysis of dolphins inhabiting European waters. This will allow  
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13 155 the definition of meaningful management units (MUs), which is essential when setting  
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15 156 up strategies for conservation and monitoring, including the estimation of population  
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17 157 trends and the evaluation of the impacts of anthropogenic activities. Note that in the  
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19 158 past, MUs were frequently defined in genetic terms as genetic management units  
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21 159 (GMUs), following Moritz (1994, 374): “populations with significant divergence of  
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23 160 allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic  
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25 161 distinctiveness of the alleles”. However, it is now accepted that MUs comprise  
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27 162 demographically independent populations, thus estimating migration rates forms a  
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29 163 central part of the assessment of suitable MUs (Allendorf, Luikart, & Aitken, 2013;  
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31 164 Palsbøll, Berube, & Allendorf, 2007). Furthermore, the criterion underlying GMUs is  
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33 165 not entirely appropriate from a demographic point of view because migration rates ( $m$ )  
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35 166 well below 10% can still lead to an absence of significant allelic differentiation (e.g.,  
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37 167 if local population size is 100,  $m > 0.01$  will lead to absence of genetic differentiation;  
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39 168 c.f. Waples & Gaggiotti, 2006). Nevertheless, population genetics principles can be  
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41 169 used to estimate migration rates to implement the 10% migration threshold criterion.  
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43 170 In addition, other measures can be used in order to define MUs, such as ecological  
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45 171 tracers (e.g., Giménez et al., 2018) or analyses of population viability (Olsen et al.,  
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47 172 2014).  
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3 173 Previous genetic studies on bottlenose dolphins worldwide have identified a clear  
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5 174 population structuring based on nuclear microsatellites and mitochondrial markers  
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8 175 with varying geographical scales (e.g., Allen et al., 2016; Hoelzel, Potter, & Best,  
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10 176 1998; Rosel, Hansen, & Hohn, 2009; Vollmer & Rosel, 2017). The same has been  
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12 177 found in European waters (Gaspari et al., 2015; Louis, Viricel et al., 2014; Mirimin et  
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14 178 al., 2011; Natoli, Peddemors, & Hoelzel, 2003; Nichols et al., 2007; Nykänen et al.,  
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16 179 2018; QuéroUIL et al., 2007), and in some areas this structuring is present even between  
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18 180 geographically adjacent populations (e.g., between the Shannon estuary and the rest of  
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20 181 the west coast of Ireland, Mirimin et al., 2011; Nykänen et al., 2018). Recently, Louis,  
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22 182 Viricel et al. (2014) determined that coastal and pelagic bottlenose dolphins in  
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24 183 European waters were genetically and ecologically distinct from each other and that  
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26 184 further structuring within the two ecotypes existed; the coastal ecotype was divided  
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28 185 into the Coastal South population, which included individuals from Normandy and  
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30 186 Galicia, and the Coastal North population, consisting of coastal bottlenose dolphins  
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32 187 around the UK and Ireland. However, these authors did not have sufficient sample  
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34 188 sizes from each local coastal population to fully investigate fine-scale structuring and  
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36 189 no samples were available from the population occupying the Shannon Estuary in  
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38 190 Ireland. Therefore, it remained unclear whether further fine-scale population structure  
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40 191 in coastal waters exists and whether the movement of mobile individuals maintains  
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42 192 connectivity between the local populations. Furthermore, the previous studies on  
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44 193 bottlenose dolphin population structure (Fernandez et al., 2011; Louis, Viricel et al.,  
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46 194 2014; Mirimin et al., 2011; Natoli et al., 2003; Nykänen et al., 2018) have all employed  
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48 195 different sets of microsatellite markers, preventing the comparison between studies,  
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50 196 and thus giving a fragmented vision of population structure. The purpose of this study,  
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52 197 therefore, was to evaluate the population structure of bottlenose dolphins in European  
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3 198 Atlantic waters at a fine-scale level, including samples from the Shannon Estuary and  
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5 199 a larger number of samples from west of Ireland and using a common set of  
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7 200 microsatellite markers between the studies by Louis, Viricel et al. (2014), Mirimin et  
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9 201 al. (2011) and Nykänen et al. (2018). The demographic dispersal between the  
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11 202 populations was estimated, and the findings are discussed in light of the conservation  
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14 203 of the species in European waters.

#### 17 18 204 **Materials and methods**

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20 205 Ninety-six samples from Nykänen et al. (2018), were genotyped at 14 microsatellites  
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22 206 loci used in Louis, Viricel et al. (2014) (Tut02, Ttr34, Ttr58, Ttr04, Ttr63, Tut01,  
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24 207 Ttr19, Tut05, TtrFF6, Tut09, Ttr11, Ttr48, EV37, TexVet7, see characteristics and  
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26 208 amplification conditions in Table S1 and Supplementary text S2 of Louis, Viricel et  
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28 209 al. (2014). This dataset included 13 samples from Louis, Viricel et al. (2014) which  
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30 210 were known to be duplicates based on their sample ID. Additionally, three samples  
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32 211 previously genotyped in Louis, Viricel et al. (2014) were used as a scale, or controls,  
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34 212 to define allele size. Nine samples from Corsica from Louis, Viricel et al. (2014) were  
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36 213 excluded from this study as they are out of the area of interest. Further two samples  
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38 214 from Louis, Viricel et al. (2014) and two samples from Nykänen et al. (2018), were  
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40 215 excluded as they had less than eight loci genotyped out of 14 loci. The overall dataset  
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42 216 used in the present study thus consists of 425 individuals; 344 samples from Louis,  
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44 217 Viricel et al. (2014) and 81 samples (excluding the 13 duplicate samples) from  
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46 218 Nykänen et al. (2018), with the latter originating mainly from the Shannon and West  
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48 219 Ireland populations. The 425 samples include 228 biopsy samples and 197 samples  
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50 220 from stranded animals.  
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3 221 The biopsy samples were taken in coastal Normandy (English Channel, France,  
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5 222 N=90), West Ireland (Connemara-Mayo-Donegal area, N=30), Cork harbour (Ireland,  
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7 223 N=4) and Shannon Estuary (Ireland, N=45), offshore Ireland (on the shelf edge, see  
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9 224 Figure 1, N=1), the Azores (Portugal, N=19), Gibraltar and Cadiz (Spain, N=39).  
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11 225 Fifteen samples of stranded dolphins were matches to photo-identification catalogues  
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13 226 of coastal animals from East Scotland (N=10), Normandy (N=2), and the Arcachon  
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15 227 estuary (Bay of Biscay, France, N=3). The rest of the stranded animals came from  
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17 228 Ireland (N=31), Wales (N=26), Scotland (N=34), France (N=58) and Spain (N=33).  
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19 229 The coastal or pelagic origin of all stranded animals was identified using genetic  
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21 230 assignments to the same cluster as biopsied individuals (Louis, Viricel et al., 2014).  
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23 231 Ecotype assignment was further confirmed for some of the individuals using photo-  
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25 232 identification catalogues of known coastal animals as detailed above (N=15), stable  
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27 233 isotopes (N=40, Louis, Fontaine et al., 2014) and/or drift prediction models (N=66,  
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29 234 Louis, Viricel et al., 2014). For example, all samples of stranded animals from East  
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31 235 Scotland were predicted to have died close to shore (Louis, Viricel et al., 2014).  
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33 236 Individuals stranded in the English Channel in France were predicted to originate from  
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35 237 coastal waters while individuals stranded in the Bay of Biscay were predicted to come  
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37 238 both from the shelf and the shelf-edge (Louis, Viricel et al., 2014).  
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#### 45 239 *Microsatellite marker quality*

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47 240 The 13 identified duplicate samples between the two studies were used to calculate  
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49 241 genotyping error rate by dividing the number of inconsistent genotypes among the  
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51 242 duplicates (three) by the total number of genotypes (364 minus six missing genotypes,  
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53 243 therefore 358).  
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3 244 All individuals were successfully amplified for at least eight loci and there was 1.80%  
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5 245 of missing values in the dataset. Microchecker 2.2.3 was used to check for null alleles  
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7 246 and scoring errors (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Departures  
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9 247 from Hardy-Weinberg equilibrium (HWE) and linkage equilibrium were tested using  
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11 248 10 000 dememorizations, 1 000 batches and 10 000 iterations per batch in GENEPOP  
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13 249 on the web version 4.2 (Raymond & Rousset, 1995; Rousset, 2008). Tests were  
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15 250 conducted for the whole dataset and for the finest level of population structure  
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17 251 identified by the clustering methods (see below).  
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### 22 252 *Genetic population structure*

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25 253 Population delimitation and assignment of individuals was done using three genetic  
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27 254 clustering methods, which were applied to: (i) the full microsatellite dataset (N=425),  
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29 255 and (ii) a subset comprising only coastal individuals (N=269). The clustering methods  
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31 256 include: two Bayesian methods implemented in STRUCTURE (Pritchard, Stephens,  
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33 257 & Donnelly, 2000) and TESS (Durand, Chen, & Francois, 2009) and a multivariate  
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35 258 method, Discriminant Analysis of Principal Components (DAPC) (Jombart, Devillard,  
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37 259 & Balloux, 2010). TESS was also run considering only the pelagic individuals  
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39 260 (N=156). For the coastal dolphins, if any cluster included several sampling locations,  
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41 261 TESS was re-run considering only those sampling areas to determine if there was  
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43 262 further genetic structuring among them.  
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48 263 The three different approaches were used to ensure the robustness of the inferred  
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50 264 results, as determining the most likely number of clusters can be challenging (Guillot,  
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52 265 Leblois, Coulon, & Frantz, 2009). STRUCTURE assigns individuals to clusters by  
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54 266 minimizing HWE and linkage disequilibria (Pritchard et al., 2000). TESS implements  
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56 267 a probabilistic model similar to STRUCTURE but is spatially explicit as it incorporates  
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3 268 the geographic coordinates of the sampled individuals as *a priori* information (Durand  
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5 269 et al., 2009). In contrast to these two Bayesian approaches that use the full data, DAPC  
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7 270 uses genetic similarity to cluster individuals and does not make any population genetic  
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9 271 model assumptions, i.e., it does not assume clusters are in HWE (Jombart et al., 2010).  
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12 272 TESS was run using the conditional auto-regressive (CAR) admixture model with a  
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14 273 burn-in of 20 000 steps followed by 120 000 Markov Chain Monte Carlo (MCMC)  
15  
16 274 steps. The number of clusters ( $K$ ) tested varied between two and ten when considering  
17  
18 275 the whole data set and the coastal samples only, and between two and six when  
19  
20 276 analysing the pelagic samples only. In these cases, ten replicate runs for each value of  
21  
22 277  $K$  were performed but six replicates were used in the analyses that excluded closely  
23  
24 278 related individuals. The spatial interaction parameter was left at the default value (0.6)  
25  
26 279 with a linear degree trend. To select the most likely number of clusters, the Deviance  
27  
28 280 Information Criterion (DIC) values were plotted against  $K$  and plots of individual  
29  
30 281 membership proportions were examined. Consistency across runs was also checked.  
31  
32 282 STRUCTURE was run using the admixture models with correlated and independent  
33  
34 283 allele frequencies, without *a priori* information. Ten independent runs for number of  
35  
36 284 clusters ranging from one to ten were carried out with a burn-in of 100 000 iterations  
37  
38 285 followed by 500 000 MCMC steps. Convergence of each run was confirmed visually  
39  
40 286 by inspecting the  $\alpha$ -parameter and likelihood chains, and the consistency across runs  
41  
42 287 was examined using pophelper (Francis, 2017), a package that implements the  
43  
44 288 functions from software CLUMPP (Jakobsson & Rosenberg, 2007) in R (R Core  
45  
46 289 Team, 2018). If the results between replicate runs differed (a sign of MCMC non-  
47  
48 290 convergence across all runs), STRUCTURE was re-run increasing the number of  
49  
50 291 MCMC steps to 500 000 burn-in followed by 1 000 000 samples. To determine the

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3 292 most likely  $K$ , the likelihood ( $L(K)$ ), the rate of change in the likelihood ( $L'(K)$  and  
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5 293  $L''(K)$ ) and  $\Delta K$  (Evanno, Regnaut, & Goudet, 2005) were calculated and plotted for  
6  
7 294 each  $K$  using pophelper (Francis, 2017), and individual membership proportion plots  
8  
9 295 for the run with the highest likelihood were plotted for the most likely values of  $K$ ,  
10  
11 296 following Pritchard et al., (2000).

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13  
14  
15 297 The DAPC analysis was performed using the package adegenet 2.1.1 (Jombart, 2008)  
16  
17 298 in R following the recommendations in Jombart (2012). The most likely number of  
18  
19 299 clusters was determined with the  $K$ -means method using the decrease in Bayesian  
20  
21 300 Information Criterion (BIC) value and, in the absence of an “elbow” (a clear drop  
22  
23 301 followed by a sharp increase) in the BIC curve, by plotting and inspecting the  
24  
25 302 membership proportions for the values of  $K$  with the lowest BIC values. Maximum  
26  
27 303 number of clusters tested was set to ten, and the linear discriminant analysis was  
28  
29 304 performed on 80% of the retained principal components. Scatter-plots were produced  
30  
31 305 for varying  $K$ . The membership proportion plots were checked for concordance with  
32  
33 306 the number of estimated clusters and whether membership proportions to those clusters  
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35 307 were high (>80%).

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41 308 Results of analyses characterizing population structure presented in the main text are  
42  
43 309 based on TESS because they were the most consistent between runs, and importantly,  
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45 310 were more concordant with photo-identification studies (see details in the Results  
46  
47 311 section) than those of the two other genetic clustering methods.

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49  
50 312 The inclusion of closely related individuals can affect population structure analyses  
51  
52 313 (Anderson & Dunham, 2008). Therefore the Queller and Goodnight's (Queller &  
53  
54 314 Goodnight, 1989) relatedness coefficient ( $R$ ) was estimated among individuals using  
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56 315 COANCESTRY (Wang, 2011) within each population identified by TESS. TESS was  
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3 316 re-run after removing one individual from each pair of individuals showing a  
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5 317 relatedness coefficient larger or equal to 0.45 as in Rosel et al. (2009).  
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7

8 318 *Nuclear genetic differentiation and diversity*  
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10  
11 319 Genetic differentiation, i.e., pairwise  $F_{ST}$  (Weir & Cockerham, 1984) and Jost's  $D$   
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13 320 (Jost, 2008), between the populations inferred by TESS, were estimated using the R-  
14  
15 321 package *diveRsity* (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013). The level  
16  
17 322 of significance was assessed using 1 000 bootstrap samples. For each population, the  
18  
19 323 mean number of alleles (NA), allelic richness (AR), inbreeding coefficient ( $F_{IS}$ ),  
20  
21 324 observed heterozygosity ( $H_o$ ) and expected heterozygosity ( $H_e$ ), were calculated, also  
22  
23 325 in *diveRsity*. Program CONVERT (Glaubitz, 2004) was used to count private alleles.  
24  
25 326 Diversity indices were also calculated separately for each locus.  
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29

30 327 *Recent migration rates*  
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32  
33 328 Recent migration rates (i.e., within the last two generations) between the populations  
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35 329 identified by TESS at the finest level of genetic structuring were estimated using  
36  
37 330 BayesAss (Wilson & Rannala, 2003). Following Rannala (2013), preliminary runs  
38  
39 331 were first performed to tune up MCMC parameters ensuring proposal acceptance rates  
40  
41 332 around 30%. Ten runs were performed with a burn-in of  $1 \times 10^6$  iterations followed by  
42  
43 333  $2 \times 10^7$  MCMC iterations and a sampling frequency of 1 000. Trace files were plotted  
44  
45 334 using Tracer (Rambaut & Drummond, 2007) to check for convergence and mixing.  
46  
47 335 Consistency of the results between the runs was also checked.  
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3 337 **Results**  
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5 338 The genotyping error rate between the two datasets was 0.0084. Significant departures  
6  
7 339 from Hardy-Weinberg equilibrium (HWE) were detected for loci EV37 and Ttr34 in  
8  
9 340 one population each (Appendix S1). As deviation was significant in only one out of  
10  
11 341 seven populations for each locus, these loci were kept in the analyses. Linkage  
12  
13 342 disequilibrium was not significant for any of the pairwise comparisons within each  
14  
15 343 population. No null alleles or scoring errors were found.  
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20 344 *Individual assignment methods*  
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22 345 The most likely number of clusters when running TESS on the whole dataset was six.  
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24 346 The delimitation of the six clusters (see Figure 2, Appendices S2a and S2b) and the  
25  
26 347 whole data set (i.e., including both coastal and pelagic individuals) is as follows. The  
27  
28 348 first cluster was mainly composed of coastal dolphins from East Scotland (ten of which  
29  
30 349 were identified as resident based on photo-identification catalogue), Wales and a few  
31  
32 350 individuals from West Scotland and Galicia. The second cluster consisted of  
33  
34 351 individuals biopsy sampled in the Connemara-Mayo-Donegal area on the west coast  
35  
36 352 of Ireland (i.e., the West Ireland population). The third cluster included coastal  
37  
38 353 biopsies from the Shannon Estuary and four biopsy samples from dolphins sampled in  
39  
40 354 Cork harbour, Ireland (i.e., the Shannon population). The fourth cluster was composed  
41  
42 355 of coastal dolphins sampled in the English Channel, in particular in the Gulf of Saint-  
43  
44 356 Malo, three stranded dolphins previously photo-identified as part of a small group that  
45  
46 357 used to reside in the Arcachon estuary (Bay of Biscay, France) and a few individuals  
47  
48 358 from Galicia (i.e., the English Channel population). The fifth cluster included stranded  
49  
50 359 samples from the west coasts of the United Kingdom, Ireland, France and northern  
51  
52 360 Spain, and biopsy samples from the Northeast Atlantic and around the Azores (*i.e.* the  
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3 361 Pelagic Atlantic population). The last cluster was composed of individuals sampled in  
4  
5 362 the Strait of Gibraltar and the Gulf of Cadiz (i.e., the Gibraltar-Cadiz population).  
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7 363 When considering  $K=2$ , populations (e) and (f) (in Figure 2), were grouped together in  
8  
9 364 one cluster and all remaining populations in the other (TESS, results not shown). This  
10  
11 365 result highlights the hierarchical structuring of the species into coastal (populations (a)  
12  
13 366 to (d)) and pelagic (populations (e) and (f)). Indeed, populations (e) and (f) consist of  
14  
15 367 biopsies from individuals sampled in deep waters of the Azores, North Atlantic and  
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17 368 Strait of Gibraltar (plus some samples from the Gulf of Cadiz) as well as samples from  
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19 369 stranded animals from the West coasts of Scotland, Ireland, France and Spain.

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23  
24 370 In order to study in more detail the structuring among the coastal individuals, TESS  
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26 371 was re-run with coastal samples only. In this case, the most likely number of clusters  
27  
28 372 was five (Figure 3A). The DIC plot indicated a plateau at  $K=5$  or  $K=6$  (Appendix S3a)  
29  
30 373 but examination of membership proportions indicated that there were actually only  
31  
32 374 five clusters in all of the replicate runs with  $K=6$  (Figure 3A, Appendix S3b). Thus,  
33  
34 375 this finer scale analysis uncovered an additional cluster among the coastal dolphins.  
35  
36 376 More precisely, the cluster comprising individuals sampled in Scotland, Wales and  
37  
38 377 Galicia (Figure 2a) was divided into two clusters: one comprising individuals from  
39  
40 378 Scotland and Wales (Figure 3A(a)) and another including individuals from Galicia  
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42 379 (i.e., the Galicia population, Figure 3A(e)). All remaining coastal individuals (Figure  
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44 380 2b-d) were clustered as before (see Figure 3A(b-d)).

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50 381 To further explore fine-scale structuring, TESS was re-run for only the individuals of  
51  
52 382 the Scotland–Wales cluster (Figure 3A(a)), as this population encompassed several  
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54 383 geographical areas. Further population structure was found within this area (see Figure  
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56 384 3B and Appendices S4a and S4b) with the first cluster including individuals from

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3 385 Wales and a few individuals from West Scotland (Wales–West Scotland population,  
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5 386 Figure 3B(a)) and a second cluster consisting of individuals from East Scotland (East  
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7 387 Scotland population, Figure 3B(b)).  
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10 388 When running TESS on the pelagic samples only, no further genetic structuring was  
11  
12 389 found but the best number of clusters was two, corresponding to the Pelagic Atlantic  
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14 390 and the Gibraltar-Cadiz populations (Appendices S5a and S5b), inspection of the  
15  
16 391 admixture plots for  $K=2$  to  $K=6$  also indicated that there were only two clusters, results  
17  
18 392 shown for  $K=2$  and  $K=3$  in S5b.  
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21  
22 393 Additional analyses with STRUCTURE and DAPC provide general support for TESS  
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24 394 results but were either less stable due to convergence problems (STRUCTURE) or  
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26 395 were not completely congruent with results of photo-identification studies. When all  
27  
28 396 samples ( $N=425$ ) were included in STRUCTURE runs, the Evanno-method ( $\Delta K$ ,  
29  
30 397 Evanno et al., 2005) detected only the uppermost hierarchical structure i.e., the  
31  
32 398 division into coastal and pelagic at  $K=2$  (Appendix S9d). Nevertheless, using the  $L(K)$   
33  
34 399 criterion proposed by Pritchard et al. (2000), the most likely  $K$  was six (Appendix S9a),  
35  
36 400 in concordance with TESS. Beyond this, no new genetic clusters emerged in the  
37  
38 401 membership proportion plots (Appendix S10). The full description of STRUCTURE  
39  
40 402 results when including all samples and only the coastal samples is given in Appendices  
41  
42 403 S7 and S11, respectively. In contrast to TESS, STRUCTURE could not detect the  
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44 404 samples from Galicia as a separate cluster when only coastal samples were included.  
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49  
50 405 When all samples were included in the DAPC analyses, the best number of clusters  
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52 406 was found at  $K=6$  (Appendices S15-S16). The clusters were almost identical to those  
53  
54 407 found with TESS and STRUCTURE, dividing the Irish samples into Shannon and  
55  
56 408 West coast populations and separating the biopsy samples from Cadiz-Gibraltar from  
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3 409 the Azores biopsies and stranded samples thought to be from a pelagic origin.  
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5 410 However, in contrast to TESS, DAPC also failed to delineate the samples from Galicia  
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7 411 into a separate cluster when only coastal samples were included. The full description  
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9 412 of results when including only the coastal samples is given in Appendix S17.

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11  
12 413 As mentioned previously (Methods), the inclusion of closely related individuals can  
13  
14 414 bias results of genetic clustering methods. The presence of related individuals varied  
15  
16 415 among the geographic areas considered in this study. They were almost inexistent  
17  
18 416 among pelagic samples as no closely related individuals (with a relatedness coefficient  
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20 417 of  $\geq 0.45$ ) were found in the Gibraltar-Cadiz population and only three pairs were found  
21  
22 418 in the pelagic Atlantic population. In contrast, relatedness among coastal individuals  
23  
24 419 varied from 1.15% in the English Channel population to 5.13% in the Galicia  
25  
26 420 population. Therefore, TESS was re-run for the coastal populations only taking out  
27  
28 421 one individual from each close kin pair (N=79). The results were similar to the runs  
29  
30 422 including close relatives and also indicated five clusters corresponding to the Shannon,  
31  
32 423 the West Ireland, the English Channel, the East and West Scotland–Wales and the  
33  
34 424 Galicia populations (Appendices S6a and S6b). As the results with and without  
35  
36 425 including close relatives were similar, we conclude that the results from TESS  
37  
38 426 presented in Figures 2 and 3 are highly reliable and can be used to draw inferences on  
39  
40 427 migration rates.

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43 428 Results from genetic clustering methods such as TESS can be used as a first approach  
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45 429 to study migration. More precisely, individuals assigned to a population different from  
46  
47 430 the geographical area where they were sampled can be considered as likely migrants.  
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49 431 One individual sampled in Galicia had a high assignment probability to the English  
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51 432 Channel population (0.75), another individual sampled in the English Channel was  
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3 433 assigned to the West Ireland population (with 0.86 probability) and a third individual  
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5 434 sampled in the Shannon estuary was assigned to the West Ireland population (with  
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7 435 0.77 probability). These results suggest that there is some connectivity between  
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9 436 dolphin populations and further analyses with BayesAss are warranted.

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13 437 *Nuclear genetic differentiation and diversity*

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15 438 All nuclear  $F_{ST}$  and Jost's  $D$  pairwise comparisons between the eight populations  
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17 439 identified with TESS were significant. The highest level of differentiation was between  
18  
19 440 pelagic and coastal populations (Table 1). When considering  $F_{ST}$ , the lowest level of  
20  
21 441 differentiation was detected between the two pelagic populations. In terms of Jost's  $D$   
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23 442 the lowest differentiation was between Wales and East Scotland. The Shannon  
24  
25 443 population was the most differentiated from the pelagic populations followed by the  
26  
27 444 West Ireland population for both indices.

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31 445 Nuclear genetic diversity (Allele Richness (AR) and Observed Heterozygosity ( $H_o$ ))  
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33 446 was significantly lower in most coastal populations than in the pelagic populations,  
34  
35 447 with Kruskal-Wallis  $P < 0.01$  in all AR coastal-pelagic comparisons except between  
36  
37 448 English Channel and Gibraltar-Cadiz ( $P = 0.07$ ), and  $P < 0.05$  in all  $H_o$  comparisons  
38  
39 449 except between Gibraltar-Cadiz and English Channel ( $P = 0.12$ ), Gibraltar-Cadiz and  
40  
41 450 Galicia ( $P = 0.18$ ) and Pelagic Atlantic and Galicia ( $P = 0.09$ ) (Table 2, Appendix S20  
42  
43 451 for values per loci per populations). Among the coastal populations, allele richness  
44  
45 452 was highest in the English Channel population and lowest in the Shannon population,  
46  
47 453 between which the difference was significant (Kruskal-Wallis  $P < 0.05$ ). The highest  
48  
49 454 number of private alleles was found in the pelagic Atlantic population ( $N = 26$ ), two  
50  
51 455 private alleles were found in the Gibraltar/Cadiz and the English Channel populations  
52  
53 456 and one private allele in the East Scotland and in the West Scotland–Wales  
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3 457 populations. A significant heterozygote deficiency was detected in the Shannon, West  
4  
5 458 Ireland and Galicia populations (Table 2).  
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8 459 *Recent migration rates*  
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10 460 Estimates of recent migration rates were highly consistent between runs; therefore, the  
11  
12 461 results presented here are based on a randomly chosen run (Table 3). Estimated  
13  
14 462 migration rates were very low between most populations, around <1% per generation,  
15  
16 463 with an upper bound for the 95% credibility interval of less than 10% and a lower  
17  
18 464 bound of 0 (Table 3). The only exceptions were mean migration rate of 18.1% between  
19  
20 465 Galicia and East Scotland, and mean rate of 25.7% from East Scotland to Wales–West  
21  
22 466 Scotland. However, these higher migration rates need to be interpreted with caution as  
23  
24 467 individuals from Scotland, Wales and Galicia consisted of stranded animals. As  
25  
26 468 mentioned before, although a portion of the East Scotland individuals were matched  
27  
28 469 to photo-identification catalogues of known coastal animals, there is uncertainty about  
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30 470 the origin of strandings in Wales and West Scotland.  
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40 472 **Discussion**  
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42 473 This study presents, to date, the most comprehensive analysis of the genetic structure  
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44 474 of bottlenose dolphins in the North-east Atlantic as it includes samples collected from  
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46 475 an unprecedentedly wide geographical area, which unlike previous studies, were  
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48 476 analysed using a common set of microsatellite markers. The results of this study,  
49  
50 477 therefore, have the potential to be used to identify management units in this area and  
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52 478 thus offer a significant contribution to the conservation of the species in European  
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54 479 waters.  
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3 480 A first level of genetic differentiation was found between coastal and pelagic  
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5 481 populations, as in a previous study (Louis, Viricel et al., 2014). The results from TESS  
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7 482 in terms of assignments to coastal and pelagic ecotypes were identical to that of Louis,  
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9 483 Viricel et al. (2014) with only one exception. One individual that stranded in the Bay  
10  
11 484 of Biscay which belonged to the Pelagic Mediterranean population in Louis, Viricel et  
12  
13 485 al. (2014) clustered with the coastal English Channel population in this study. No  
14  
15 486 further genetic structure was found within the two pelagic populations (i.e., Pelagic  
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17 487 Atlantic and Gibraltar-Cadiz).

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22 488 Fine-scale population structure among coastal bottlenose dolphins from different  
23  
24 489 geographical locations corresponded to the different local populations that inhabit the  
25  
26 490 Shannon estuary, west of Ireland, the English Channel, Galicia, East Scotland, and  
27  
28 491 Wales/West Scotland. Previous studies only identified large-scale population structure  
29  
30 492 in coastal waters due to uneven sampling of each local coastal population (Louis,  
31  
32 493 Viricel et al., 2014) or fine-scale population structure in small geographic regions  
33  
34 494 (Fernandez et al., 2011; Mirimin et al., 2011, Nykänen et al., 2018). Thus, the results  
35  
36 495 of this study highlight the need for and the power of broad scale collaboration when  
37  
38 496 working on the conservation of highly mobile species that can move across national  
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40 497 borders. The level of resolution was only possible thanks to broad international  
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42 498 collaborations, sample sharing and careful calibration of allele scoring to overcome  
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44 499 the difficulties of comparing genotypes across studies.

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50 500 Although results of all three genetic clustering methods were generally consistent, their  
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52 501 comparison with independent results from photo-identification studies highlighted  
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54 502 differences in performance among them. More explicitly, the coastal population  
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56 503 assignments inferred with TESS were concordant with photo-identification studies

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3 504 indicating geographically isolated populations with site fidelity. This was not always  
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5 505 the case for STRUCTURE and DAPC results. This highlights the power of clustering  
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7 506 methods using *a priori* spatial information to infer complex population structure.  
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9  
10 507 Indeed, although STRUCTURE was able to identify the same six clusters as TESS  
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12 508 when all samples were considered, it was unable to identify further fine-scale  
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14 509 structuring among coastal samples. Comparing the two approaches to infer the number  
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16 510 of clusters using STRUCTURE, supports the idea that Evanno's method is well  
17  
18 511 adapted to identify the first level of structuring under hierarchical scenarios (Waples  
19  
20 512 & Gaggiotti 2006) such as those observed in bottlenose dolphins. DAPC also supports  
21  
22 513 the subdivision of bottlenose dolphins into six management units but assignment of  
23  
24 514 individuals to populations was less consistent with those of the two other methods. In  
25  
26 515 particular, one of the genetic clusters was composed of individuals sampled from many  
27  
28 516 different geographic locations. As Jombart et al. (2010) indicate, DAPC uses a purely  
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30 517 statistical criterion aimed at identifying the minimum number of groups that best  
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32 518 explain total observed variation while at the same time maximising between group  
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34 519 variation. Thus, as opposed to TESS and STRUCTURE, it does not take into  
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36 520 consideration Hardy-Weinberg and linkage equilibrium, which explains the observed  
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38 521 differences with the two other methods in the individual assignments to populations.  
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45 522 The use of stranded animals could be considered as a limitation of this study. However,  
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47 523 we are relatively confident in the inferences made, even though strandings constitute  
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49 524 almost half of all samples. Firstly, a drift-prediction model (Peltier et al., 2012) was  
50  
51 525 applied in a previous study (Louis, Viricel et al., 2014), to estimate the most likely area  
52  
53 526 of death. The estimated origin with the drift prediction model was consistent with the  
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55 527 genetic results separating coastal and pelagic bottlenose dolphins (Louis, Viricel et al.,  
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3 528 2014). For example, in East Scotland, all individuals were estimated to have died very  
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5 529 close to shore. The coastal and pelagic assignments of a subset of the samples were  
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7  
8 530 confirmed using stable isotopes (Louis, Fontaine et al., 2014). In addition, 15 stranded  
9  
10 531 animals were known to be part of the resident coastal populations and their genetic  
11  
12 532 assignments matched photo-identification studies (Louis, Viricel et al., 2014).  
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14 533 Nevertheless, we acknowledge that there is uncertainty in the origin of the stranded  
15  
16 534 animals when there is no further evidence such as photo-identification and drift  
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19 535 modelling. This is the case for the coastal populations of Galicia and Wales/West  
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21 536 Scotland and caution is therefore required when interpreting these results.

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23  
24 537 The fine-scale population structure likely results from natal philopatry, possibly driven  
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26 538 by vertically (mother to offspring) and horizontally (between non-filial conspecifics)  
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28  
29 539 learned foraging behaviours during the juvenile life stage, site fidelity and social  
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31 540 structure (Foote et al., 2016; Kopps et al., 2014; Whitehead, 2017; see further  
32  
33 541 discussion in Louis, Viricel et al., 2014; Louis, Fontaine et al., 2014; Nykänen et al.,  
34  
35 542 2018). Photo-identification studies indicated site fidelity to relatively restricted  
36  
37 543 geographical areas (Cheney et al., 2014; Ingram & Rogan, 2002; Louis et al., 2015),  
38  
39 544 however, individuals can undertake movements of a few hundreds of kilometres, i.e.,  
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41 545 around Ireland (O'Brien et al., 2009) and the East coast of Scotland (Cheney et al.,  
42  
43 546 2013) but these movements can still be considered occurring at a relatively small scale.  
44  
45 547 There is also some evidence of larger scale movements between the North Sea and the  
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47 548 Atlantic, as reported in Robinson et al. (2012), and this provides further potential for  
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49 549 genetic and demographic connectivity between the populations; seven transient  
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51 550 dolphins were first sighted in the Moray Firth, East Scotland and later re-sighted in the  
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53 551 Hebrides, West Scotland. Five of these animals were later recorded in coastal Irish  
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3 552 waters and some of these movements represent travelled distances of over 1 200 km  
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5 553 (Robinson et al., 2012). These individuals are believed to be part of the West Ireland  
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7 554 population based on photo-identification catalogue kept on the coastal Irish dolphins.  
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9 555 However, photo-identification fieldwork mainly occurs during the summer in most  
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11 556 areas. Therefore, movements outside this season may be overlooked.  
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15 557 Despite the above-mentioned movements, our results are consistent with a very low  
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17 558 degree of connectivity among the studied populations. In other words, the different  
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19 559 populations are relatively isolated from each other. Estimated migration rates among  
20  
21 560 populations were very low, and less than 1% per generation for most of the pairwise  
22  
23 561 comparisons. Although there is no consensus on the level of migration that leads to  
24  
25 562 demographic coupling (Waples & Gaggiotti, 2006; Palsboll et al., 2007), the estimated  
26  
27 563 migration rates are well below the rate of 10%, which according to a simulation study  
28  
29 564 can lead to coupled dynamics (Hastings, 1993). Demographic connectivity is therefore  
30  
31 565 very low among local populations. The only exceptions are the migration rates of 18%  
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33 566 from East Scotland to Galicia and 26% from East Scotland to Wales, the latter of which  
34  
35 567 could be explained by the relatively short distance between the two sites. However, as  
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37 568 these populations included only stranded dolphins and although all the East Scotland  
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39 569 samples were estimated to originate from the North Sea according to a drift-prediction  
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41 570 model used in a previous study (Louis, Viricel et al., 2014), there is some uncertainty  
42  
43 571 about the origin of the individuals sampled in Wales and Galicia. As migration rate  
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45 572 estimates have been shown to be dependent on the number of clusters chosen to best  
46  
47 573 represent the population structure and thus the number of individuals in each cluster  
48  
49 574 (Olsen et al., 2014), great care has to be taken that the sampling strategy used is robust  
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51 575 and the samples are representative of each population. The present study is based on  
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3 576 the most comprehensive set of genetic samples available but there is still a need for  
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5 577 more biopsy samples from Wales and Scotland to further support our results.  
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11 579 The different populations were characterised in terms of genetic diversity,  
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13 580 differentiation and migration rates. This information and existing estimates of  
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15 581 abundance will help to evaluate the conservation status and vulnerability of the  
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17  
18 582 populations. Indeed, small isolated population are at risk of losing heterozygosity and  
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20 583 genetic resilience due to genetic drift (Lacy, 1987) and are thus more vulnerable to  
21  
22 584 stochastic environmental changes or anthropogenic stressors than larger populations.  
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25 585 Genetic diversity was higher in the pelagic populations than coastal populations as in  
26  
27 586 previous studies (Hoelzel et al., 1998; Louis, Viricel et al., 2014). This is consistent  
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29 587 with higher abundance of the pelagic populations compared to the coastal populations.  
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31  
32 588 The Gibraltar-Cadiz population included around 700 photo-identified individuals  
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34 589 (Giménez et al., 2018) and the Pelagic Atlantic abundance estimates (from Scotland to  
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36 590 Spain) are several tens of thousands of individuals (Hammond et al., 2013, 2009) while  
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38 591 the abundances of coastal dolphins do not exceed ~400 individuals (see below).  
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41 592 Genetic diversity indices for the coastal populations were concordant with abundance  
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43 593 estimates using mark-recapture methods. The population of the English Channel,  
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45 594 which is the largest coastal population with abundance estimates of around 400  
46  
47 595 individuals (Louis et al., 2015), had the highest genetic diversity. The Shannon  
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49 596 population had the lowest genetic diversity and is the smallest with abundance  
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51 597 estimated between 110 and 140 dolphins (Berrow, 2012; Englund, Ingram, & Rogan,  
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53 598 2008; Ingram & Rogan, 2002, 2003; Rogan, Gkarakouni, Nykänen, Whitaker, &  
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55 599 Ingram, 2018). Abundance estimates were around 200 individuals in East Scotland  
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3 600 (Cheney et al., 2013), ca. 190 for the West Irish population (Nykänen, 2016) and 150  
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5 601 to 250 individuals in Wales (Pesante, Evans, Baines, & McMath, 2008). Any local  
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7 602 perturbation or global change could thus have drastic negative effects on these coastal  
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9 603 populations due to their small size, low genetic diversity and low connectivity  
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11 604 uncovered in this study.  
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15 605 This study filled a major knowledge gap on the fine-scale population structure of  
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17 606 bottlenose dolphins in European Atlantic waters, which was considered as the main  
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19 607 research priority for the protection of this species (Ó Cadhla & Marnell, 2017). As  
20  
21 608 previously found in Louis, Viricel et al. (2014), coastal and pelagic populations are  
22  
23 609 distinct and should be monitored separately. In terms of the coastal populations, the  
24  
25 610 high genetic differentiation and negligible migration rates found in this study highlight  
26  
27 611 the need to separately monitor each local population (the English Channel, the  
28  
29 612 Shannon, the West Ireland, the East Scotland, the Galicia and the Wales–West  
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31 613 Scotland populations) as they correspond to different management units. However, we  
32  
33 614 cannot rule out further fine-scale population division in Wales and West Scotland due  
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35 615 to the small sample sizes (N=16 and N=5, respectively), and the fact that all came from  
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37 616 stranded dolphins as the use of samples of stranded animals only may lead to under-  
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39 617 estimated population structure (Bilgmann, Möller, Harcourt, Kemper, & Beheregaray,  
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41 618 2011).  
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48 619 The small population sizes of the coastal populations and their isolation may render  
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50 620 them vulnerable to anthropogenic impacts. These results highlight the need to protect  
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52 621 their habitat through protected areas such as the SACs where anthropogenic activities  
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54 622 are appropriately managed, ensuring their ecological suitability to the populations  
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56 623 utilizing them. Regular monitoring of population dynamics (e.g., abundance, survival,  
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3 624 calving rate) using photo-identification, as undertaken in some of the areas, is therefore  
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5 625 recommended to evaluate population trends. Population viability analyses, as applied  
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7 626 to harbour seals, *Phoca vitulina*, in Southern Scandinavia in Olsen et al. (2014), could  
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9 627 also help inform whether the populations are of sufficient size for long-term population  
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11 628 viability in the absence of immigration.  
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15 629 In this study, management units were identified by first clustering individuals into  
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17 630 putative populations based on individuals' genotypes and then by estimating their  
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19 631 connectivity. Populations not sampled in this study (i.e., the Sado Estuary, Portugal,  
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21 632 and the Iroise Sea, France) could be genotyped in the future using the same set of  
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23 633 markers as in this study to further clarify their connectivity with the other European  
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25 634 Atlantic populations. The Atlantic pelagic population showed no genetic  
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27 635 differentiation over a large geographical range from West Scotland to the Azores.  
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29 636 However, pelagic bottlenose dolphin populations may show ecological differences  
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31 637 even in the absence of genetic divergence and this should be considered when  
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33 638 allocating management units. For example, the bottlenose dolphins of the Gibraltar  
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35 639 Strait and of the Gulf of Cadiz, although potentially presenting no genetic structure,  
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37 640 showed differences in ecology detected using different ecological tracers (i.e., stable  
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39 641 isotopes and contaminant loads) and individual monitoring through photo-  
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41 642 identification, leading to the delineation of two ecological, management units  
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43 643 (Giménez et al., 2018). This type of ecological differentiation may be detected using  
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45 644 next generation sequencing data covering the whole genome of the species, which  
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47 645 would allow testing for adaptive differentiation (Funk, McKay, Hohenlohe, &  
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49 646 Allendorf, 2012). We recommend combining genetic data with ecological data (e.g.,  
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51 647 the use of stable isotopes) and individual monitoring, where available, to determine  
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3 648 the geographical scales most relevant to monitoring and the protection of populations  
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5 649 of any species.  
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10 651 Data accessibility: The data are available on dryad at the following link: (to be  
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12 652 uploaded at the revisions stage).  
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1040 **Tables**

1041

1042 Table 1. Pairwise fixation indices based on 14 microsatellite loci (given as average  
 1043 with 95% Highest Probability Density Interval (HPDI)) between the different  
 1044 populations. The samples were divided into populations based on results from TESS.  
 1045 Values above the diagonal are  $F_{ST}$ -values and values below the diagonal are Jost's  $D$   
 1046 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)	-

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

Population	N (mean)	A	%	AR	$H_o$	$H_e$	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  $H_o$ =observed heterozygosity,  $H_e$ =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.

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7 1055 Table 3. Mean (and 95% Credible Interval) recent migration rates inferred using BayesAss. The migration rate is defined as the proportion of  
8 1056 individuals in a population that immigrated from a source population per generation. Migration rates above 0.10 have been highlighted in bold.  
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Population \ Source	Shannon	Wales/West Scotland	East Scotland	West Ireland	English Channel	Galicia	Gibraltar/Cadiz
11 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)
12 Wales/West-Scotland	0.012 (0.000 - 0.036)	0.678 (0.657 - 0.700)	<b>0.257 (0.206 - 0.307)</b>	0.010 (0.000 - 0.029)	0.013 (0.000 - 0.037)	0.010 (0.000 - 0.029)	0.010 (0.000 - 0.029)
13 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)
14 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)
15 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)
16 Galicia	0.015 (0.000 - 0.043)	0.014 (0.000 - 0.041)	<b>0.181 (0.104 - 0.257)</b>	0.015 (0.000 - 0.043)	0.062 (0.000 - 0.127)	0.684 (0.652 - 0.716)	0.014 (0.000 - 0.041)
17 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)
18 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)

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## 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.

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For Peer Review

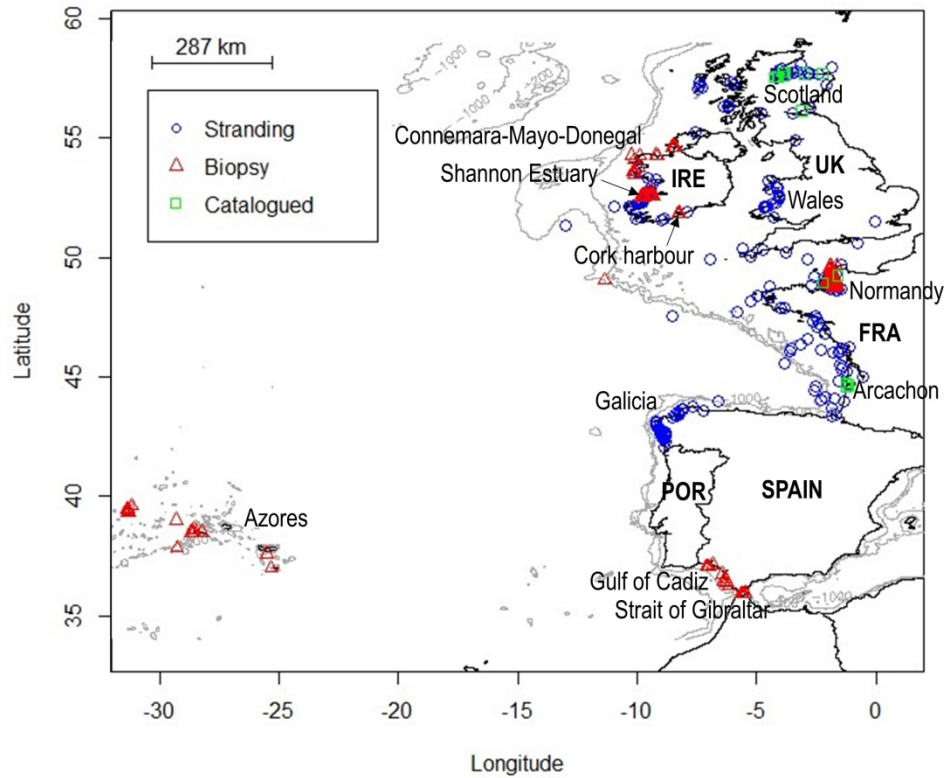
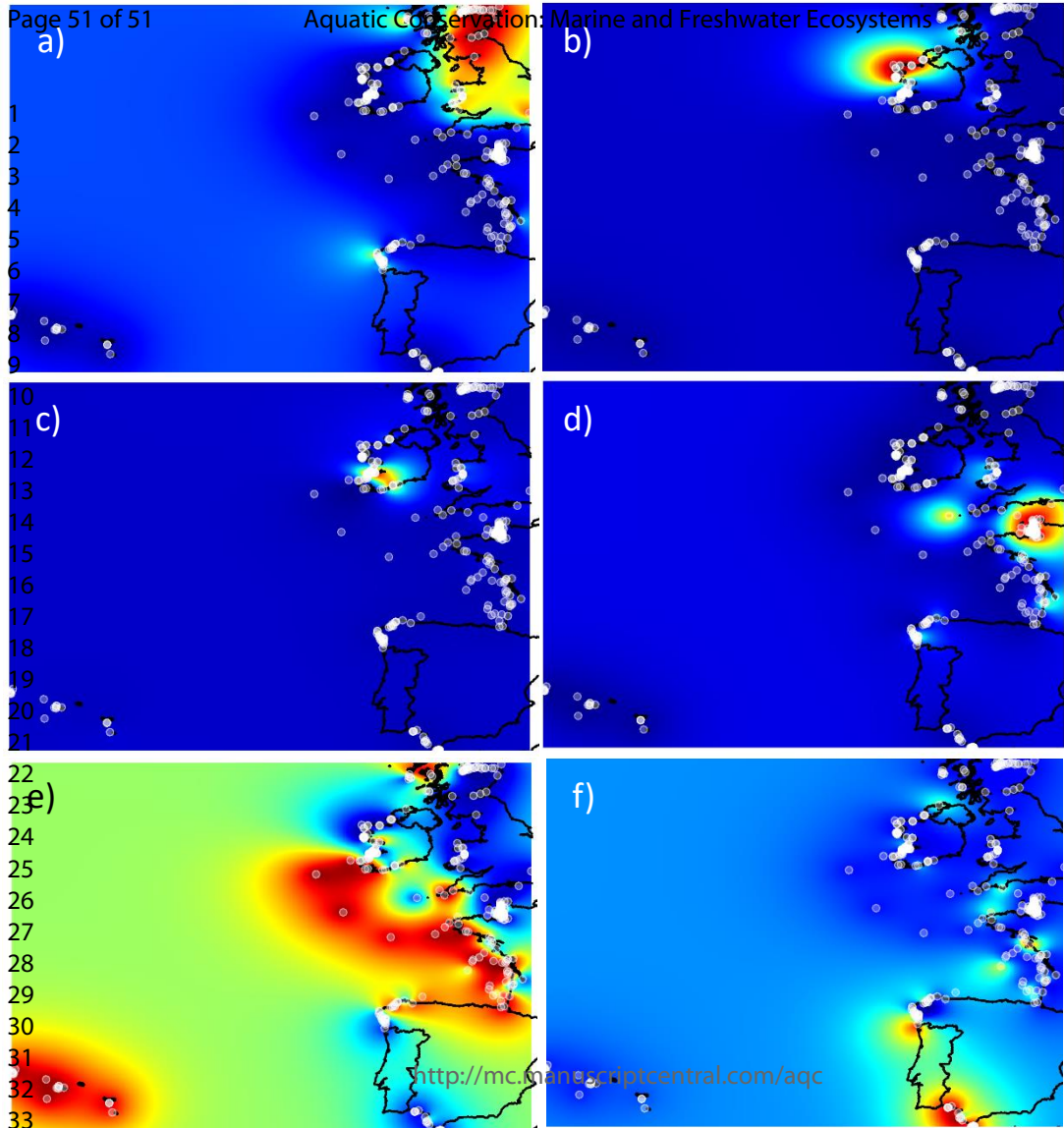


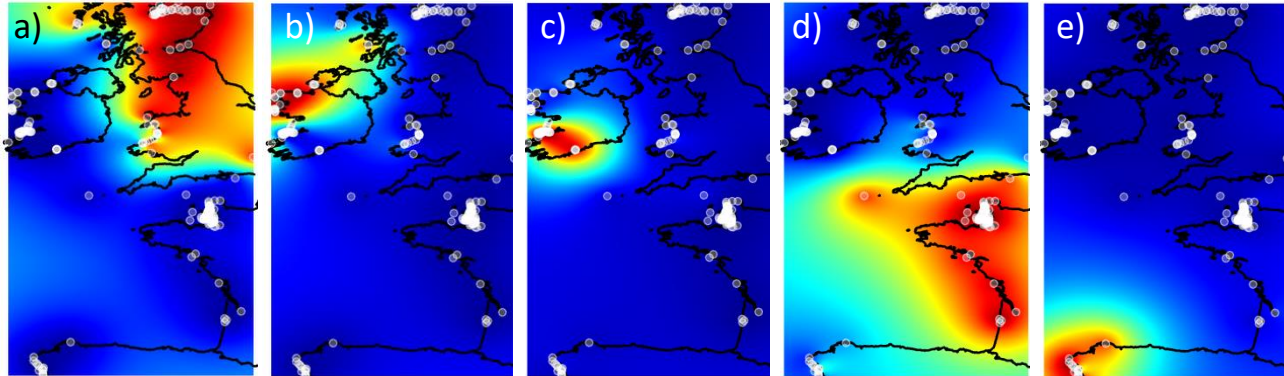
Figure 1. Map of samples used in the study and their origin; stranding - samples collected from stranded bottlenose dolphins, biopsy - samples collected from skin biopsies, and catalogued - samples collected from stranded animals that had been matched to a photo-identification catalogue of known coastal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

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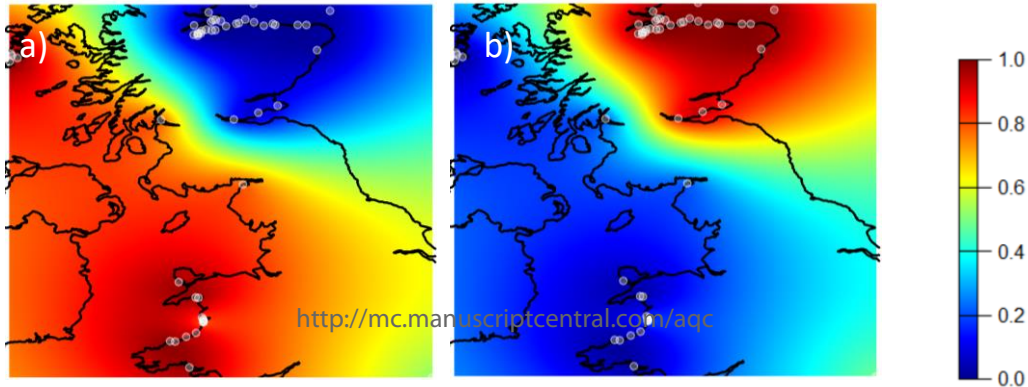


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### A) Coastal samples - $K = 5$



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



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