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Quantifying dispersal between marine protected areas by a highly mobile species, the bottlenose dolphin, *Tursiops truncatus*

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Running title: Dispersal of bottlenose dolphins between MPAs

Abstract

The functioning of Marine Protected Areas (MPAs) designated for marine megafauna has been criticized due to the high mobility and dispersal potential of these taxa. However, dispersal within a network of small MPAs can be beneficial as connectivity can result in increased effective population size, maintain genetic diversity and increase robustness to ecological and environmental changes making populations less susceptible to stochastic genetic and demographic effects (*i.e.* Allee effect). Here, we use both genetic and photo-identification methods to quantify gene flow and demographic dispersal between MPAs of a highly mobile marine mammal, the bottlenose dolphin *Tursiops truncatus*. We identify three populations in the waters of western Ireland, two of which have largely non-overlapping core coastal home ranges and are each strongly spatially associated with specific MPAs. We find high site-fidelity of individuals within each of these two coastal populations to their respective MPA. We also find low levels of demographic dispersal between the populations, but it remains unclear whether any new gametes are exchanged between populations through these migrants (genetic dispersal). The population sampled in the Shannon Estuary has a low estimated effective population size and appears to be genetically isolated. The second coastal population, sampled outside of the Shannon, may be demographically and genetically connected to other coastal subpopulations around the coastal waters of the UK. We therefore recommend that the methods applied here should be used on a broader geographically sampled dataset to better assess this connectivity.

Introduction

The conservation and management of wild animal populations is often achieved through designation of protected areas that are thought to represent important habitats for foraging, breeding and other fitness-related activities (Palumbi 2001; Reeves 2000). Demographic connectivity, defined as the linking together of local fragmented populations through the dispersal of individuals as larvae, juveniles or adults (Sale *et al.* 2005), is an important factor to consider when designating marine protected areas (MPAs), since it has implications for the persistence of meta-populations (reviewed in Botsford *et al.* 2009). For example, in many marine fish species, larval dispersal and population connectivity determine whether a MPA (or a network of MPAs) contributes to the overall survival and reproduction of the species, thus maintaining sustainable population sizes (Burgess *et al.* 2014). Dispersal is thus a key variable that conservation biologists need to quantify and consider in order to assess the effectiveness of protected areas (Reeves 2000). This is particularly relevant in highly mobile and wide ranging marine species, whose management provision is often restricted to small fixed areas of protection and for which the low cost of movement can facilitate long-range dispersal (reviewed in Forcada 2009). High levels of mobility can result in substantial gene flow and the homogenization of genetic diversity across a geographic range (*e.g.* Ryman *et al.* 1986; Winkelmann *et al.* 2013). However, whilst in most marine fish meta-populations dispersal during the larval stage facilitates greater connectivity among habitat patches and reduces the risk of local extinctions (Burgess *et al.* 2014), marine mammals typically have much lower reproductive rates and their offspring can exhibit a high degree of natal philopatry (Baird 2000; Sellas *et al* 2005; Amos *et al.* 1993). This can lead to small isolated populations and a system that is sensitive to changes in environmental conditions, ecological factors or anthropogenic disturbance.

Lowe and Allendorf (2010) distinguished demographic connectivity from genetic connectivity by defining the former as the relative contribution of net immigration and local recruitment to the population growth rate, and the latter as the degree to which evolutionary processes within (sub)populations are affected by gene flow. Population genetic approaches may provide a tool to measure and quantify the rate and scale of dispersal (*i.e.* migration) when it is not feasible to assess the movement of individuals by non-genetic capture-recapture methods (Gagnaire *et al.* 2015). However, when combined together, genetic and non-genetic methods are highly complementary and can provide invaluable information for management of populations. Photo-identification is a cost-effective technique commonly used by marine mammal researchers to identify individuals of several species using the unique natural markings on their body and thus enabling, for example, the estimation of their distribution, association patterns or abundance via capture-recapture methods (see review by Würsig & Jefferson 1990). If natural markings cannot be used because of insufficient individual variation, molecular genotyping may provide a usable alternative to photo-identification methods in estimating animal movements (see Palsbøll *et al.* 1997). Here, both these approaches were applied to quantify the demographic and genetic connectivity between marine protected areas designated for bottlenose dolphins in an area in the north-east Atlantic.

Bottlenose dolphins are widely distributed, being found in the Atlantic, Indian and Pacific oceans (Leatherwood & Reeves 1990). Throughout much of its range, the common bottlenose dolphin (*Tursiops truncatus*) exhibits hierarchical population structure, with the greatest divergence found between pelagic and coastal populations (Curry & Smith 1998; Hoelzel *et al.* 1998; Louis *et al.* 2014a,b; Lowther-Thieleking *et al.* 2015). Genetic differentiation is often correlated with ecological and/or morphological differences (Hoelzel *et al.* 1998; Louis *et al.* 2014a; Natoli *et al.* 2004; Hersh & Duffield 1990). Further fine-scale structuring has been found among coastal populations in several locations (Natoli *et al.* 2005; Parsons *et al.* 2002;

2006; Baird *et al.* 2009; Rosel *et al.* 2009; Fernández *et al.* 2011; Martien *et al.* 2011; Mirimin *et al.* 2011; Caballero *et al.* 2012; Gaspari *et al.* 2013, 2015; Louis *et al.* 2014a,b; Martinho *et al.* 2014). The driving force(s) behind fine-scale population structuring among coastal populations of bottlenose dolphins are not fully resolved, but have been suggested to include isolation following a historical founding event; habitat preferences; differences in social structure and site fidelity; learned foraging specializations; natal philopatry; limited dispersal of both sexes; and habitat discontinuity linked to prey availability (Krützen *et al.* 2004a,b; Natoli *et al.* 2005; Parsons *et al.* 2006; Rosel *et al.* 2009; Martien *et al.* 2011; Louis 2014a,b; Gaspari *et al.* 2015).

Common bottlenose dolphins are listed in Annex II of the European Union's Habitats Directive requiring the member states to designate Special Areas of Conservation (SACs) as part of an overall European strategy (Natura 2000) to maintain or restore the species at "favourable conservation status". Consequently, SACs (or Natura 2000 sites) have been designated in the coastal waters of several areas in EU Member States. Around the British Isles such SACs are located in Moray Firth (Scotland), Cardigan Bay (Wales) and in two areas on the west coast of Ireland; the Shannon Estuary and in western parts of Counties Galway and Mayo (West Connacht Coast) (see Fig. 1). However, it is unclear how much connectivity (genetic or demographic) there is between the different groups of bottlenose dolphins inhabiting these areas.

Bottlenose dolphins using the Shannon Estuary SAC have been found to be genetically differentiated from another population inhabiting the coastal waters off counties Galway and Mayo (Mirimin *et al.* 2011). However, these findings were based on a limited number of samples collected in a relatively small area (ranging about 70km along the Galway/Mayo coastline) and it is not known whether additional fine-scale structuring exists. Photo-

identification studies of dolphins using the Shannon Estuary SAC suggest that these individuals have a high degree of site fidelity (*e.g*. Ingram & Rogan 2003; Englund *et al.* 2008), however, the extent of the range of dolphins using Ireland's coastal waters is not yet fully understood. Previous research has shown that at least some of these coastal animals move over great distances (Ingram *et al.* 2001, 2003; O'Brien *et al.* 2009; Oudejans *et al.* 2010; Robinson *et al.* 2012; Cheney *et al.* 2013), which could indicate some potential for genetic connectivity between adjacent sub-populations using neighbouring coastal SACs, but this has not previously been demonstrated or quantified.

Genetic clustering and kinship-based methods are used here to re-examine the population structure in Irish waters using a larger dataset supplemented with samples collected from a wider coastal area. The contribution of demographic and genetic dispersal to the connectivity between neighbouring SACs within Irish waters is quantified using a combination of photo-identification and genetic techniques. In addition, the role of possible drivers for population structuring, including social structure, relatedness, site-fidelity and sex-biased dispersal are examined. The findings are discussed in the context of conservation and management.

Materials and Methods

Photo-identification surveys and photograph selection

Boat-based photo-identification surveys were conducted within the Lower River Shannon SAC, Ireland, every year between 1996 to 2008 with the exception of 2004, and in other coastal areas of Ireland (including the West Connacht Coast SAC), in 2001-2005, 2007-2010 and 2013-2014 (Figs. 1 and 2). These surveys were mostly conducted during the summer months (May–September), however, some were done in autumn or winter (see Table S1 in dryad for the survey information). A bottlenose dolphin 'group' was defined as all dolphins within a 100m radius of each other as per Irvine *et al.* (1981) and hereafter 'encounters' refer to periods

of data collection whilst with dolphin groups. Best effort was made to photograph every individual in the group, and identification photographs of bottlenose dolphins' dorsal fins were examined. For each encounter, the best quality photograph was chosen of each identifiable dolphin and the quality of the photograph was graded from 1 to 4 (1 being the highest quality, 4 being the lowest, see Appendix 1) with no consideration concerning the degree of marking of the individual. Each photographed individual was then assigned one of three grades of mark-severity (Fig. 3), and visually matched against the full catalogue of dolphins photographed during previous encounters.

Skin tissue sample collection and analysis

The dataset comprising of altogether 97 unique samples included 85 samples already genotyped by Mirimin *et al.* (2011). This set of 85 genotypes included 45 skin tissue samples collected from animals in the Shannon Estuary SAC in 2005 and 2007, four samples from animals encountered in Cork Harbour in 2008 and 12 samples collected from animals ranging in coastal waters of Galway and Mayo (part of West Connacht Coast SAC) during 2009 (Fig. 1). The previously genotyped dataset also included samples collected from 23 individuals stranded along the west coast of Ireland, including two dolphins found dead within the Shannon Estuary, between 1993 and 2009. This dataset was supplemented by ten skin biopsies collected from free-ranging animals in coastal waters of Co. Mayo and Co. Donegal during 2013-2014, a sample from a dolphin that stranded in Co. Cork in 2014, and a sample collected from an animal that was by-caught by a fishing vessel on the continental shelf off south-west of Ireland in 1996. All of the skin biopsy samples in this study were taken using a modified 0.22 calibre rifle (see Krützen *et al.* 2002) and sampling was carried out during the summer months. The gender of stranded individuals was recorded by inspection of the genital area and reproductive organs, while the sex of free-ranging biopsied individuals was determined by multiplex amplification of sex chromosome-specific DNA fragments, following the method described in

166 Rosel (2003).

167 *DNA Extraction, PCR Amplification and Genotyping*

168 DNA was extracted from 12 new skin samples using the DNeasy Blood and Tissue kit from
169 Qiagen. A total of 15 nuclear microsatellite loci (see Appendix 2) were amplified following
170 polymerase chain reaction (PCR) conditions described in Mirimin *et al.* (2011). The amplified
171 products were separated on 6% polyacrylamide gels on a LICOR 4300 DNA analyser (Li-Cor
172 Inc, Lincoln, NE, USA) and allele sizes determined by eye in comparison to a 50–530 size
173 standard (LI-COR) and allele cocktails from reference samples. These allele cocktails consisted
174 of mixtures of PCR products from 4-5 individuals previously genotyped for each locus and
175 allowed alleles in this study to be consistently sized across runs and in line with the samples of
176 Mirimin *et al.* (2011). Due to the possibility that the same individual dolphin may have been
177 unintentionally biopsied more than once, the uniqueness of the new genotypes was confirmed
178 by calculating the percentage of similarity between the samples in program GIMLET 1.3.3.
179 (Valière 2002). The same program was also used to calculate the probability of identity (PI),
180 which estimates the power of the set of microsatellite markers to differentiate between two
181 distinct individual samples (Waits *et al.* 2001). The error rate involved in genotyping had
182 already been estimated as negligible (<0.01%) by Mirimin *et al.* (2011), therefore, re-
183 estimation of the error was not performed for the new samples because of their low number (*n*
184 = 12).

185 The 15 microsatellite loci were checked for null alleles, allelic dropout and stuttering, using
186 MICRO-CHECKER 2.2.3 (Van Oosterhout *et al.* 2004) and selecting the Bonferroni adjusted 95%
187 confidence interval option with 1,000 simulations. Additionally, MICRODROP 1.01 (Wang *et al.*
188 2012) was used to further check for allelic dropout due to low DNA concentration or poor
189 sample quality. The microsatellite loci were inspected for significant deviations from Hardy-

Weinberg equilibrium (HWE) using GENEPOP (Raymond & Rousset 1995; Rousset 2008) and linkage equilibrium using ARLEQUIN (Excoffier & Lischer 2010) with 10,000 iterations and applying sequential Bonferroni corrections. The above analyses were performed considering the whole dataset as a single unit and separately at population level (identified with Bayesian clustering methods, see below).

Individual assignment tests

All samples were included in a cluster analysis using STRUCTURE (Pritchard *et al.* 2000). The admixture model was run with correlated allele frequencies without including any prior information on the sampling location. Ten independent runs were carried out for each value of K (the number of theoretical populations), with K set to vary from 1 to 6, using 1,000,000 Markov Chain Monte Carlo (MCMC) iterations preceded by 1,000,000 burn-in steps. Convergence of chains (traces of alpha and F_{ST} values) was confirmed visually and the consistency of runs was checked by confirming that the variance in estimated ln Pr(X|K) was smaller within each K compared to the variance between the different Ks, and calculating the average posterior probability for each K. ΔK, which has been argued to be a better predictor of the number of populations, was also calculated following Evanno *et al.* (2005) in STRUCTURE HARVESTER web-version 0.6.94 (Earl & vonHoldt 2012). Once K was determined, each individual was assigned to a cluster based on its maximum membership proportion.

Since relatedness between individuals can affect population assignment (*i.e.* including samples of closely related individuals can lead to artificial structuring of populations (Guinand *et al.* 2006; Anderson & Dunham 2008), the relatedness coefficient, r, (Queller & Goodnight 1989) was calculated between all possible dyads within the putative populations identified by the clustering methods using KINGROUP (Konovalov *et al.* 2004). Subsequently, one member of each dyad with a relatedness coefficient of 0.45 or greater was removed (according to Rosel *et*

214 *al.* 2009) and STRUCTURE re-run with this reduced dataset.

215 In addition, population structuring was inferred using a discriminant analysis of principal
216 components (DAPC) that clusters individuals together based on genetic similarity to find the
217 most likely number of populations. DAPC does not rely on any population genetic model (*i.e.*
218 does not assume HWE) and is efficient at detecting hierarchical structure (Jombart *et al.* 2010).
219 DAPC using the package adegenet (Jombart 2008) in R (R Core Team 2016) was run following
220 the recommendations in the tutorial (Jombart & Collins 2015), and cluster membership
221 probabilities were calculated for each individual.

222 A third clustering method was implemented in program TESS (Durand *et al.* 2009a,b) which
223 uses GPS-coordinates along with genetic markers in order to infer population structure;
224 therefore only biopsy samples were used in this analysis since stranded and by-caught
225 individuals had unknown geographic origins. The conditional autoregressive (CAR) model was
226 used with admixture using 20,000 burn-in followed by 120,000 MCMC steps with the number
227 of clusters, *K*, varying 2–10, with 10 replicates per each run. The most probable number of
228 clusters was selected by plotting Deviance Information Criterion (DIC) values against different
229 values of *K* and by examining individual assignment probability plots. Consistency of the runs
230 was checked by examining the convergence of MCMC chains in TRACER 1.6. (Rambaut *et al.*
231 2014). TESS cannot directly test for $K = 1$ but we checked this by examining individual
232 assignment probabilities. When the most likely *K* was determined, the run with the lowest DIC
233 was used and individuals were assigned to clusters based on maximum assignment
234 probabilities.

235 The results from clustering methods when all samples were included (*i.e.* STRUCTURE and
236 DAPC, see below) were highly consistent in their inference of the most likely number of
237 clusters and the individual assignment probabilities so the data set was divided into three

putative populations, *Coastal Shannon*, *Coastal mobile* and *Pelagic*, for the remaining genetic analyses. There is uncertainty associated with the geographic range of the *Pelagic* population since the samples consist mostly of stranded animals, but based on the fact that these animals have not been photographed in coastal waters coupled with their genetic divergence, and for consistency with previous publications, *e.g*. Louis *et al.* (2014a), this population is referred to as the *Pelagic* population.

Population differentiation was estimated by calculating pairwise F_{ST} (Weir & Cockerham 1984) and Jost's *D* (Jost 2008) values using the R package diveRsity (Keenan *et al.* 2013) between populations identified by STRUCTURE, with the whole and the reduced dataset after the removal of close relatives, and the 95% confidence intervals were obtained using 10,000 bootstrap replicates. Population specific F_{IS}-values, expected and observed heterozygosity, mean number of alleles and allele richness were also calculated using package diveRsity in order to examine the level of inbreeding. Heterozygote deficiency and excess in each population was tested using Fisher's method implemented in GENEPOP (Raymond & Rousset 1995; Rousset 2008) with 10,000 iterations. As a further check that differentiation was not solely driven by sampling of related individuals or uneven sampling of populations (see Puechmaille 2016), 10 individuals were randomly selected from each of the two putative coastal populations and the pairwise F_{ST}-values (with 95% CI) estimated using the R package diveRsity and repeated 10 times. These pairwise values were compared to F_{ST}-values calculated for two sets of ten individuals randomly drawn from within a single coastal population, *Coastal Shannon* or *Coastal mobile*. To supplement this analysis, the power to detect a significant moderate population differentiation, based on an F_{ST} value of $\geq$0.1 in a sample consisting of the allele frequencies from both coastal populations and using a sample size of ten individuals per 'subpopulation' (*i.e. Coastal Shannon* and *Coastal mobile*), was calculated by running 1,000 simulations in POWSIM 4.1 (Ryman & Palm 2006; see also Ryman

263 *et al.* 2006; Morin *et al.* 2009).

264 Sex-biased dispersal between the three populations identified by clustering methods was tested
265 by comparing assignment indices, relatedness, F_{ST} and F_{IS} values separately for males and
266 females using 1,000 permutations in FSTAT 2.9.3 (Goudet 2001). Following Goudet (2001), it
267 was assumed that sex-biased dispersal within the sampled populations could be detected from
268 gender differences in genetic structuring with the more philopatric sex showing more structure.

269 *Migration rates*

270 Recent migration rates (the proportion of migrants per population) within the last two
271 generations were estimated using BAYESASS (Wilson & Rannala 2003). The migration rates
272 were calculated between the populations identified by STRUCTURE and DAPC, and then re-
273 estimated with the individual biopsied in the Shannon Estuary but genetically assigned to
274 *Coastal mobile* population grouped together with the Shannon dolphins. The MCMC mixing
275 parameters of migration rates, allele frequencies and inbreeding coefficients, were adjusted as
276 recommended by Rannala (2007), during preliminary runs in order to obtain acceptance rates
277 of around 30%. Ten runs with a burn-in of 1,000,000 iterations followed by 10,000,000 MCMC
278 iterations sampling every 1,000 iterations were performed. Convergence and mixing of chains
279 were confirmed by plotting trace files using TRACER (Rambaut *et al.* 2014) and the consistency
280 of runs was checked.

281 *Effective population size*

282 An estimate of contemporary effective population size (N_e) for the *Coastal Shannon* population
283 was derived using LDNe, a method that uses linkage disequilibrium (Waples & Do 2008). This
284 method has performed best in situations with little to no migration (<1%) (Gilbert & Whitlock
285 2015) and adequately with migration rates of up to ~5–10% (Waples & England 2011). Allele

frequencies of <0.02 were excluded from the analyses to avoid bias caused by rare alleles (Waples & Do 2010; Louis *et al.* 2014a). As some of the samples were collected over a 15-year time period (in the Shannon estuary) and the data are thus likely to be biased downwards due to overlapping generations (Waples 2010), the estimate of N_e was inflated by 15% as in Louis *et al.* (2014a). N_e could not be calculated for the *Coastal mobile* or the *Pelagic* populations, due to small sample size (Tallmon *et al.* 2010).

Analyses of social structure and site fidelity

To test possible drivers of population structure and connectivity, indices of social structure, site fidelity and kinship were examined among the coastal bottlenose dolphins (*Shannon* and *Mobile*). Long-term photo-identification data are not available for the 'pelagic' dolphins in this area. Social structure analyses were performed in SOCPROG 2.4 compiled version (Whitehead 2009). The dataset was limited to photographs of sufficient quality (grades 1-3) and to individuals with permanent and obvious markings (mark severity grade M1, Fig. 3) in order to identify individuals between several years, and only dolphins photographed in at least five separate encounters were included to reduce bias caused by rarely seen individuals (Whitehead 2008). Individuals photographed together during an encounter were considered associated with each other, so an encounter was chosen as the grouping variable in SOCPROG. "Day" was chosen as the sampling period.

The strength of association between pairs of individuals (*i.e.* dyads) was measured using two indices of the frequency of co-occurrence: the half-weight association index (HWI) and the simple ratio (Cairns & Schwager 1987; Ginsberg & Young 1992). The simple ratio index is suitable when association is defined by presence in the same group during a sampling period (Ginsberg & Young 1992). However, the half-weight index (HWI) can be more appropriate when not all individuals within a group have been identified (Ginsberg & Young 1992), as is

often the case with dolphin photo-identification studies due to individuals reacting differently to the presence of the research vessel. Since both indices gave almost identical results and were considered good representations of social structure by the high cophenetic correlation coefficient (CCC) values (CCC HWI: 0.874, CCC simple ratio: 0.887), only the results derived using the HWI are presented. NETDRAW (Borgatti 2002) was used to visualize a social network diagram using the network statistics calculated in SOCPROG. Permutation tests (Bejder *et al.* 1998; Whitehead 1999) with 20,000 steps were used to test whether the observed association patterns were different than expected from random associations and to identify dyads with significantly larger or smaller association indices.

The standardized lagged association rate (SLAR) was used to test if temporary or long-lasting social bonds existed between individuals, and compared to the null association rate (expected if all individuals are associating at random). The SLAR was fitted separately to the individuals encountered within and outside of the Shannon Estuary since the data showed that these groups did not associate with each other. Mathematical models representing simulated social structures, *i.e.* whether individuals had constant companionships or casual associates during the study (Whitehead 1995), were fitted to the SLARs. The best-fitting models were chosen based on the lowest quasi Akaike's Information Criterion (QAIC) value (see Whitehead 2007). To investigate movements of dolphins between different coastal areas and to estimate the amount of time identified individuals resided within each area, Lagged Identification Rates (LIRs) within and between all study areas were calculated in SOCPROG (Whitehead 2009). Markov movement models (expected LIRs) of emigration/mortality and emigration + re-immigration (Whitehead 2001) were fitted to estimate the probabilities of individuals moving from one area to another, and QAIC-values were used to identify the best fitting model. 100 bootstrap replicates were used to estimate the standard error for the LIRs.

Relatedness, associations and spatial overlap

A Mantel-test in R-package ade4 (Dray & Dufour 2007) was used to investigate whether associations reflected kinship bonds, and whether a correlation existed between the strength of pairwise association (HWI) and relatedness between all biopsied dyads that had been encountered at least three times. To examine whether there was a correlation between spatial overlap and relatedness kernel utilization distribution (KUD) was calculated for individually identified dolphins that were encountered at least five times using R-package adehabitatHR (Calenge 2006), and the overlap in the areas used by two dolphins was then estimated by calculating the volume of intersection (VI) index (Fieberg & O'Kochanny 2005; Podgórski *et al.* 2014) of KUD. This index takes values between 0 and 1, and it quantifies the similarity between two KUDs thus comparing the area shared and the intensity of use by two individuals. These correlation tests were performed for the combined dataset and also separately for each of the two coastal populations, and significance tested in the correlations by performing randomization tests with 10,000 MCMC permutations.

Results

Twelve new individuals, including ten coastal biopsies and two stranded dolphins, were genotyped for this study and analysed together with 85 previously genotyped unique individuals from Mirimin *et al.* (2011). The dataset consisted of 32 females, 64 males and one individual for which the sex could not be determined. Genotyping was successful in over 96% of cases with just 54 genotypes missing from the entire dataset of 1455. The probability (PI) of two of the 97 individuals sharing the same genotype over the 15 microsatellite loci was 4.5×10^{-14} for any two random unrelated individuals and 5.9×10^{-6} for siblings. This indicates that the set of markers used in this study has a high power to discriminate between identical genotypes that may have originated by chance alone. No identical genotypes were found among

the samples genotyped in this study. When all the samples were pooled and tested for deviations from HWE across all microsatellite loci, eleven out of the fifteen loci were found to be out of HWE. Further tests using MICRODROP (Wang *et al.* 2012) indicated no correlation between the amount of homozygotes and the amount of missing data across individuals (Pearson r = -0.091, p = 0.85) or across loci (Pearson r = 0.178, p = 0.26), suggesting that homozygosity was not due to allelic dropout. Therefore, the observed deviations from HWE across all populations and loci are most likely attributed to the structuring of the populations, *i.e.* Wahlund effect (Wahlund 1928). When deviations from HWE were inspected for each population separately, only two loci (*Dde*66 and *Dde*72) within the *Coastal mobile* population and one locus (*Dde*61) within the *Pelagic* population were out of HWE (Appendix 2). STRUCTURE was therefore run with and without these three loci.

Individual assignment tests

The most likely number of clusters (*i.e.* populations), K, identified by STRUCTURE based on the highest Pr($X|K$) and using the *ad-hoc* method by Evanno *et al.* (2005) was three when all the coastal biopsies and stranded samples were included in the analysis (Appendix 3a). The majority of the individuals (92 out of 97) were strongly assigned (with probability >90%) to one of these three clusters (Fig. 4a). Removing the three loci that were out of HWE did not have an effect on the most likely number of clusters or the assignment of individuals into the three clusters. However, when considering assignments at K = 2, the *Coastal mobile* dolphins clustered together with the *Pelagic* dolphins with high (>80-90%) assignment probabilities instead of clustering together with the *Coastal Shannon* as was the case when all loci were included (latter presented in Appendix 4a). This may have resulted from the large number of unique alleles only found in the pelagic samples (altogether 13 unique alleles) being left out of the analysis.

382 One individual (DNA sample code 'tt-05-03' and photo-id number 18, see Fig. 5) biopsy
383 sampled inside the Shannon Estuary was assigned to the *Coastal mobile* cluster with 79%
384 probability by STRUCTURE (individual indicated in Fig. 4a, and in Appendix 5, as a possible
385 migrant; this was also found by Mirimin *et al.* (2011)). Four dolphins sampled in Cork harbour
386 were strongly assigned (>80% probability) to the same cluster as the *Coastal Shannon* dolphins
387 (Fig. 4a and Appendix 5), consistent with Mirimin *et al.* (2011). Two individuals found dead-
388 stranded outside of the Shannon estuary (~30km and ~50km north of the mouth of the estuary)
389 were assigned to the *Coastal Shannon* population (Fig. 4a); this may be a result of carcass
390 drifting or an indication that at the least some of the *Coastal Shannon* population are using
391 areas beyond the estuary.

392 DAPC, which does not assume HWE, also identified three clusters when all the samples were
393 included (Appendix 6) with a mild hierarchical structure among them; the distance between
394 the clusters of *Coastal Shannon* and *Coastal mobile* samples is shorter than the distance
395 between either of the coastal clusters and the *Pelagic* cluster (Fig. 4b). Individual assignments
396 were high (>99%) and highly consistent compared to STRUCTURE with 99% of the individuals
397 assigned to the same cluster across the methods. In fact, only one stranded individual (sample
398 code ‘bnd204’, an outlier in Fig. 4b) was assigned to the *Coastal mobile* cluster by DAPC
399 whereas it was clustered together with stranded pelagic samples by STRUCTURE when all the
400 samples were included (Fig. 4a).

401 These results were consistent with clustering probabilities calculated in TESS when only the
402 biopsy samples of coastal dolphins (n = 71) were considered; the most likely number of coastal
403 populations identified was two (Fig. 4c) as indicated by the DIC-values reaching a plateau
404 (Appendix 7). The individual assignment probabilities were also 100% consistent with
405 STRUCTURE and DAPC with all the same individuals assigned with >90% probability to either

406 the *Coastal Shannon* or the *Coastal mobile* cluster (excluding the individual sampled in the
407 Shannon Estuary that assigned to the *Coastal mobile* cluster with 59% certainty).

408 The samples assigned to the *Coastal Shannon* population had the largest percentage (2.4%) of
409 dyads that were close relatives, with the Queller and Goodnight (1989) relatedness coefficient
410 $r \geq 0.45$ indicating possible parent-offspring or full sibling relationships among these
411 individuals. Relatedness was also found in the *Coastal mobile* cluster, with 2.0% of all possible
412 dyads assigned as being close relatives; no close relatives were found among the *pelagic*
413 samples. The mean relatedness coefficient varied from -0.02 (SD = 0.23) among individuals
414 assigned to the *Coastal Shannon* population, -0.04 (SD = 0.25) among the *Coastal mobile*, to
415 -0.06 (SD = 0.13) among the *Pelagic* dolphins. The mean relatedness values within the *Coastal*
416 *Shannon* (1431 possible dyads) and the *Coastal mobile* (300 dyads) were also significantly
417 higher compared to the relatedness of dyads when individuals were selected randomly, one
418 from each of the two coastal populations (1350 dyads, Kruskal-Wallis $p < 0.0001$, Appendix
419 8).

420 Removing one individual from a dyad with relatedness coefficient $r \geq 0.45$ led to the removal
421 of 22 individuals from the *Coastal Shannon* and six individuals from the *Coastal mobile*
422 cluster. When considering only these 'coastal' samples, the most likely number of clusters
423 identified by STRUCTURE and the Evanno-method was still two (Appendix 3b,d) and the
424 majority of individuals (49 out of 51) were assigned to either of the two coastal populations
425 with >80% certainty (Appendix 4b). However, when including samples from all three
426 populations after removing close relatives, the most likely number of populations was two with
427 a division of samples to coastal and pelagic clusters (Appendices 3c and 4b), indicating that
428 relatedness may be a significant driver of finer-scale population structuring.

Population differentiation and effective population size

No evidence of significant heterozygote deficiency was found across all loci in any of the populations (*Coastal Shannon p* = 0.998, *Pelagic p* = 0.469, *Coastal mobile p* = 0.061). Allele richness (AR) and observed heterozygosity (H_O) were lower in the two *coastal* populations compared to the *pelagic* population (Appendix 2). Inbreeding coefficients were low in all populations. The mean estimate for effective population size in the *Coastal Shannon* population was 32 (with 95% CI of 22 – 43).

There was significant differentiation in allele frequencies (based on both F_{ST} and Jost's *D*) between the *pelagic* and the two *coastal* populations and between the two coastal populations (defined with STRUCTURE), and this difference persisted after removing close relatives from the dataset (Table 1). The Jost's *D* values revealed a hierarchical population structure, with largest differences observed between the *pelagic* and the two *coastal* populations (Table 1). The pairwise comparisons of F_{ST} values for randomized *coastal* populations showed no population differentiation when two sets of 10 individuals were randomly drawn from within the same population, *i.e.* consisting of only *Coastal Shannon* (mean: -0.0005, 95% CI: -0.0086 – 0.0080) or *Coastal mobile* (mean: 0.0021, 95% CI: -0.0074 – 0.0115) individuals (Appendix 9). However, significant population differentiation was observed in comparisons of 10 individuals randomly drawn from one population with 10 individuals randomly drawn from the other (mean F_{ST}: 0.1820, 95% CI: 0.1589 – 0.2051) indicating a true population differentiation that was not driven by the sampling of closely related individuals or uneven sampling. The simulations run in POWSIM 4.1 (Ryman & Palm 2006) indicated that the power to detect a differentiation of $F_{ST} \geq 0.1$ between the two coastal populations was >0.99 with the set of 15 microsatellite markers used in the present study, even with a low sample size of 10 individuals drawn from each population.

453 *Sex-biased dispersal and migration rates*

454 No evidence of sex-biased dispersal was found in any of the indices used (Appendix 10). The
455 inferred migration rates (the proportion of migrants per population) calculated with BAYESASS
456 were non-significant as zero was included in the range of 95% confidence intervals in each
457 comparison (Table 2).

458 When looking at individual posterior probabilities of migrant ancestry, two individuals from
459 the *Coastal mobile* population and one from the *Pelagic* population had >50% probability of
460 being either 1st or 2nd generation migrants from other populations. Two individuals from the
461 *Coastal mobile* population ('tt-09-12' and '12-09-2014_Tt2') were 2nd generation migrants from
462 the *Coastal Shannon* population with 64% and 79% probability, respectively. One individual
463 assigned to the *Pelagic* population by STRUCTURE ('bnd204') had a 37% probability of being a
464 1st generation migrant and a 46% probability of being a 2nd generation migrant from the *Coastal*
465 *mobile* population. When the individual that was biopsied in the Shannon Estuary but
466 genetically assigned to *Coastal mobile* population ('tt-05-03') was grouped together with other
467 Shannon individuals, it had a 19% probability of being a 1st generation migrant and a 70%
468 probability of being a 2nd generation migrant from the *Coastal mobile* population.

469 *Social structure and site fidelity*

470 When testing for preferred and avoided companionships between and within the two coastal
471 populations, the mean HWI in the real data was found to be significantly higher compared to
472 the HWI of a permuted random data set (mean: $p < 0.01$, SD: $p < 0.0001$ and CV: $p < 0.0001$)
473 indicating significant preferred short- (within sampling period) and long-term (between
474 sampling periods) companions. Moreover, the proportion of non-zero elements was larger in
475 the random data compared to real data which suggests that some individuals may avoid others
476 (Whitehead 2009), both within each population and between the two coastal populations (Fig.

6). The latter comes as no surprise since the two populations have not been documented associating with each other. Pairwise associations within the *Coastal Shannon* population were best described by the Standardized Lagged Association Rate (SLAR) model 'casual acquaintances' (Appendix 11a), by which dyads remain associated for a period of time, dissociate and may, or may not, re-associate (Whitehead *et al.* 1991; Whitehead 2015). Within the *Coastal mobile* population, on the other hand, the model 'constant companions and casual acquaintances' best explained the data, with 'constant companions' remaining associated with each other throughout the length of the study (Whitehead *et al.* 1991; Whitehead 2015) (Appendix 11b). The mean HWI within the *Coastal Shannon* was 0.08 (SD = 0.09) and within the *Coastal mobile* population it was 0.23 (SD = 0.21). The difference in the association indices between the two populations and especially the higher variation associated with the *Coastal mobile* may be linked to the lower number of encounters included in the social analysis (48 with the *Coastal mobile* and 315 with the *Coastal Shannon*).

Bottlenose dolphins that were first photographed in the Shannon Estuary were not photographed anywhere else during 1996-2008 except once in Brandon Bay, Co. Kerry (approximately 15km south from the mouth of the Shannon Estuary), hence their annual average Lagged Identification Rate (LIR) was zero to any other study area, except to Brandon Bay where it was 0.0263 (SE = 0.0128). Likewise, dolphins belonging to the *Coastal mobile* population were never photographed in the Shannon Estuary during the study period so their LIR in the Shannon Estuary was also zero. The LIR within the Shannon stayed fairly constant for approximately 100 days, followed by some fluctuations in the rate (Fig. 7a). Two competing models had substantial support explaining the data, with the emigration/mortality model having the lowest AIC value, followed by emigration+reimmigration+mortality model (Appendix 12). LIR associated with the *Coastal mobile* population was best explained by the emigration/mortality model (Fig. 7b, Appendix 12).

Relatedness, spatial overlap and associations

When only the biopsied individuals with a sufficient number of photo-ID encounters (≥3) were considered, a significant correlation was found between the relatedness coefficient (Queller & Goodnight 1989) and HWI (r = 0.345, p = 0.0001) when the data from the two coastal populations were combined. However, this is likely attributed to the correlation of zero values in the combined data set since no correlation was found between the two indices when testing for this separately for each population (*Coastal Shannon:* r = 0.028, p = 0.363; *Coastal mobile:* r = 0.0004, p = 0.480). Out of fifteen dyads with significant associations (*i.e*. who associated with each other significantly more or less than with other individuals), none had relatedness coefficient ≥ 0.45, but three dyads had coefficient values close to 0.25 indicating possible half-siblings or cousins. No correlation was found between relatedness and spatial overlap within the *Coastal Shannon* (r = 0.076, p = 0.193) or the *Coastal mobile* population (r = 0.042, p = 0.417). Overall, these results indicate that close kinship may not strongly promote overall social associations in these two populations.

Discussion

Understanding the scale of dispersal is an important consideration for the conservation and management of marine species (Lotterhos 2012). By combining genetic and photo-identification data, spatial and genetic dispersal over both short and long temporal scales have been elucidated in unprecedented detail for bottlenose dolphins in Irish waters. Dispersal can be gametic, *i.e.*, via gene flow during temporary interactions and spatial overlap, and therefore only detected by genetic methods. Dispersal can also be demographic, *i.e.*, the permanent movement of individuals from one location to another, detectable over the short-term using photo-identification of naturally marked individuals and over the past few generations using genetic methods (relatedness, migration and admixture proportions; Iacchei *et al.* 2013). The

combined results indicate social and reproductive isolation between the three identified populations, with only low levels of demographic and potential genetic connectivity *sensu* Lowe and Allendorf (2010). The accumulation of differentiation, estimated with fixation indices, indicates that this relative isolation has persisted over longer timescales.

Among the bottlenose dolphin samples, large and significant F_{ST} and Jost's *D* values between the populations, comparison of F_{ST} values from randomized 'coastal populations', the individual assignment methods and kinship methods were all in agreement, supporting the division of the samples into one '*pelagic'* and two *'coastal'* clusters. In addition, Jost's *D* values and DAPC indicated the presence of a hierarchical population structure with the largest genetic difference occurring between the '*pelagic*' and '*coastal*' populations. Furthermore, social structure analyses using long-term photo-identification data revealed that the two coastal populations were not only genetically, but also socially, distinct. This kind of social separation has been previously reported between the '*pelagic*' and '*coastal*' bottlenose dolphins (Oudejans *et al.* 2015).

The results also suggest that both coastal populations show a similar degree of site fidelity to their respective areas and are likely to have non-overlapping core home ranges, at least during the seasons that photo-id work was conducted. The gradual decline in the Lagged Identification Rates (LIRs) towards the end of the study period reflects a decrease in site-fidelity that is likely explained by mortality and/or emigration. These results highlight that a high degree of site-fidelity, especially evident in the Shannon Estuary SAC where data have been collected for over 12 years, is a key driver of fine-scale population structure among coastal populations. A high degree of site-fidelity among resident populations of bottlenose dolphins to certain local areas has been found in other parts of the world (Simoes-Lopez & Fabian 1999; Bristow & Rees 2001; Möller *et al.* 2002). This residency, found especially in embayments, coupled with

genetic differentiation between dolphins residing in adjacent coastal habitats, has led a number of authors to suggest that variability in these habitats accompanied by the ability of local populations to accommodate it by the development of different foraging strategies (*e.g.* Smolker *et al.* 1997; Barros & Wells 1998), may have shaped the fine-scale population structure among these dolphins (Hoelzel *et al.* 1998; Chilvers & Corkeron 2001; Natoli *et al.* 2005; Möller *et al.* 2007; Sargeant *et al.* 2007; Richards *et al.* 2013; Allen *et al.* 2016). In addition, there is growing evidence that cultural transmission occurs within dolphin social communities in the form of social learning (*e.g.* Krützen *et al.* 2005; Mann *et al.* 2012) which may facilitate the evolution of specialist foraging behaviours, which in turn has the potential to maintain population structure between adjacent communities.

In this study, there is evidence of significant companionships within the two coastal populations, and it is possible that social bonds promote and maintain the observed social and genetic separation of these populations. The observed companionships did not seem to be linked to relatedness, but close associates were found both among kin and non-kin individuals, similar to a recent study by Louis *et al.* (2018) In contrast, close associations were linked to relatedness among females in a population of Indo-Pacific bottlenose dolphins (Möller *et al.* 2006), and support for relatedness in male groups has been documented in alliances of this genus (Krützen *et al.* 2003), as well as among short-beaked common dolphins (*Dephinus delphis*) in southern Australia, with greater relatedness found between males within schools than between schools (Zanardo *et al.* 2016). Unfortunately, there were insufficient combined photo-ID and genetic data to fully investigate possible sex-specific patterns in the relatedness and associations among the two coastal Irish populations, partly due to genetic sampling being biased towards males (especially in the *Coastal Shannon* population) and partly because of the fact that the biopsy sampled animals did not necessarily have enough photo-ID encounters for further social analyses.

Lowe and Allendorf (2010) described genetic connectivity as the exchange of alleles through gene flow between populations, and demographic connectivity as the dispersal of individuals from one population to another thus contributing to underlying population demographic processes and parameters (*e.g*. survival, mortality, abundance). Gene flow maintains genetic variation in populations, enhancing adaptive potential to environmental variation (Yamamichi & Innan 2012). Even small amounts of gene flow can prevent the accumulation of large genetic differences between populations of low effective size (Slatkin 1987; Palumbi 2003). Hastings (1993), on the other hand, suggested that populations become demographically isolated if the exchange between populations stays below 10%, *i.e.*, less than 10% of the population growth is contributed by migrants from other populations regardless of whether they contribute to the gene flow or not. Recent migration rates between the different Irish bottlenose dolphin populations were non-significant (*i.e*. zero) in all comparisons inferred using BAYESASS. However, one individual ('tt05-03') encountered over nine years in the Shannon Estuary, was genetically assigned to the *Coastal mobile* population. Interestingly, this dolphin has never been photographed associating with the *Coastal mobile* population, but no close kin were found among the sampled individuals assigned to the *Coastal Shannon* population. Given that ~40% of the *Coastal Shannon* population have been biopsied (and genotyped) based on abundance estimates derived for this population varying between 114–140 (Berrow *et al.* 1996, 2012; Ingram & Rogan 2002, 2003; Englund *et al.* 2007, 2008), it is possible that this dolphin has not (yet) genetically contributed to dispersal of gametes into the *Coastal Shannon* population. In contrast, close kinship was found between 'tt05-03' and an individual sampled within the *Coastal mobile* population. Thus, 'tt05-03' appears to be an example of demographic dispersal from the *Coastal mobile* population to the *Coastal Shannon* population. Nonetheless, considering that this individual (one out of 46 biopsied dolphins in the Shannon estuary) represents <3% demographic dispersal between the coastal Irish populations, it seems unlikely

that the contribution to the demographic processes are significant. However, this largely depends on the management targets set to the population in question and the power to detect changes in abundance, survival, or other demographic processes.

No evidence for sex-biased dispersal was found in this study. However, the sampling was biased towards males (due to efforts to sample marked animals), with more than double the amount of samples compared to females; thus these results should be treated with caution. Both Mirimin *et al.* (2011) and Louis *et al.* (2014a) found two haplotypes that were shared between 'coastal' and 'pelagic' dolphins based on the mitochondrial control region, but the sequencing of the entire mitochondrial genome revealed no shared haplotypes between these two 'ecotypes' suggesting limited female dispersal between coastal and pelagic populations (Moura *et al.* 2013; Nykänen 2016). However, two mitogenome haplotypes were shared between the *Coastal Shannon* and *Coastal mobile* populations (Nykänen 2016), suggesting either that some movement between these populations exists via female mediated gene flow, or that the shared haplotypes are a consequence of shared ancestry and recent divergence between the two populations.

Two individuals strongly assigned to the *Coastal mobile* population were identified as likely 2nd generation migrants originating from the *Coastal Shannon* population. However, whilst individual assignment methods, such as STRUCTURE, are believed to perform well at identifying migrant individuals (Putman & Carbone 2014), BAYEASS was found to be less reliable in calculating individual migrant probabilities (Faubet *et al*. 2007); thus, these results should be interpreted with caution. Nevertheless, BAYEASS was found to perform well at estimating overall migration rates between populations over a few generations at migration rates up to 0.1 (Faubet *et al*. 2007). Whether these dispersal events further translated into gene flow is uncertain and warrants more sampling effort especially within the *Coastal mobile*

624 population. To date, only ~12% of this population occurring in Irish waters has been sampled,
625 based on a median multi-site abundance estimate of 189 dolphins derived for a wide area
626 extending to the west and north-west coast of Ireland (Nykänen 2016). Overall, despite some
627 evidence for low levels of demographic dispersal, it appears that connectivity between
628 populations is too low to prevent the build-up of genetic differentiation.

629 Nichols *et al.* (2007) and Louis *et al.* (2014a) suggested that coastal bottlenose dolphins in
630 northern European waters may form a wider meta-population (the '*Coastal North*' meta-
631 population, Louis *et al.* 2014a) consisting of inter-connected local populations around the
632 British Isles. However, these studies did not have samples from the *Coastal Shannon*
633 population, which is, based on this study, both genetically and demographically isolated.
634 Coupled with the relatively small effective population size, this makes *Coastal Shannon*
635 especially vulnerable to any environmental or anthropogenic stressors. The *Coastal mobile*
636 population occurring in Irish waters, on the other hand, may belong to this '*Coastal North*'
637 meta-population, and previous research has shown that at least some of these mobile coastal
638 animals travel over distances at the scale of hundreds of kilometres (Ingram *et al.* 2001, 2003;
639 O'Brien *et al.* 2009; Robinson *et al.* 2012, Cheney *et al.* 2013). If they do indeed comprise part
640 of the '*Coastal North*' meta-population extending beyond Irish waters, trans-national co-
641 operation, monitoring and management may be needed. Six individuals from the west coast of
642 Ireland have been matched on an *ad-hoc* basis to photo-ID catalogues comprised of animals
643 ranging in the coastal waters of Scotland (Robinson *et al.* 2012) but there is a need for a
644 consistent collaborative effort to better integrate photo-ID catalogues from different
645 regions/countries (*e.g.* Ireland, Wales, Scotland, France, Cornwall). Such collaboration would
646 provide better insights into demographic dispersal, ranging patterns and the abundance of this
647 putative meta-population. In addition, genetic dispersal within the meta-population needs to be
648 quantified through increased sampling effort over a larger area extending beyond country

boundaries and using a common set of genetic markers that are comparable between laboratories.

The present study supports the delineation of the three populations occurring in Irish waters as separate management units based on the low genetic, social and demographic dispersal between the populations thus validating the current designation of separate SACs for the two coastal populations. The study also highlights the importance of distinguishing genetic and demographic connectivity so that gene flow can be differentiated from immigration that has no subsequent genetic contribution from the migrant to the local population. Even though the genetic connectivity between the different populations of bottlenose dolphins in this study was negligible and accompanied by moderate to strong genetic differentiation, quantification of migration rates and the degree of social connectivity have implications in the delineation of MUs, especially in cases where population structuring is less clear. With this information the functioning of existing marine protected areas or networks can be better assessed and the need for designating new protected areas evaluated.

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681 **Data Accessibility**

682 Analysis input files used for TESS, DAPC, STRUCTURE, diveRsity and SOCPROG are deposited
683 in Dryad.

684

Tables

Table 1. Pairwise F_{ST}-values based on 15 microsatellite loci (given as average with 95% HPDI) between the different populations *Coastal Shannon*, *Coastal mobile* and *Pelagic*. The samples were divided into populations based on results from STRUCTURE. Values above the diagonal are for the whole dataset, and values below the diagonal after removal of close relatives ($r \geq 0.45$).

F_{ST}			
	Coastal Shannon	*Pelagic*	*Coastal mobile*
Coastal Shannon	-	0.173 (0.151-0.200)	0.181 (0.147-0.218)
Pelagic	0.154 (0.131-0.181)	-	0.186 (0.154-0.222)
Coastal mobile	0.161 (0.121-0.205)	0.172 (0.139-0.209)	-

Jost's *D*			
	Coastal Shannon	*Pelagic*	*Coastal mobile*
Coastal Shannon	-	0.362 (0.304-0.426)	0.207 (0.165-0.251)
Pelagic	0.339 (0.279-0.404)	-	0.319 (0.265-0.378)
Coastal mobile	0.188 (0.137-0.244)	0.305 (0.250-0.369)	-

Table 2. Inferred (posterior) mean migration rates (with 95% HPDI) between the different Irish bottlenose dolphin populations identified by STRUCTURE and DAPC, given as proportion of migrants per population. Values for self-recruitment are given in diagonal.

		Sink		
		Coastal Shannon	*Pelagic*	*Coastal mobile*
Source	*Coastal Shannon*	0.987 (0.969-1.000)	0.006 (-0.005-0.017)	0.008 (-0.007-0.022)
	Pelagic	0.016 (-0.014-0.046)	0.948 (0.892-1.000)	0.036 (-0.014-0.086)
	Coastal mobile	0.034 (-0.011-0.078)	0.012 (-0.010-0.034)	0.955 (0.906-1.000)

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Figure Legends

Fig. 1. GPS-locations of bottlenose dolphin samples collected and used throughout this study and approximate locations of Special Areas of Conservation (SACs) around the British Isles (areas circled). Samples include coastal biopsies of free-living dolphins (n = 71), samples collected from dead stranded animals (n = 25) and one sample from a by-caught animal. Note that some sampling locations indicated by the circles overlap due to the scale of the map.

Fig. 2. GPS tracks recorded during boat surveys for bottlenose dolphins on the West coast of Ireland.

Fig. 3. Examples of bottlenose dolphin fins showing the three grades of mark severity used in photograph analysis. Each dolphin was graded from one to three as follows: (A) grade M1 marks, consisting of significant fin damage or deep scarring that were considered permanent; (B) grade M2 marking that consist of deep tooth rakes and lesions, with only minor cuts present; (C) fin with grade M3 marks, having only superficial rakes and lesions. Grade M1 and M2 are considered to last many years, enabling long-term identification of these dolphins. In contrast, 'superficial' markings (grade M3), such as tooth rakes may fade and heal within a relatively short period of time and inter-annual re-sighting probabilities of these animals are likely to be reduced.

Fig. 4. (A) Genetic assignment probabilities from STRUCTURE (n = 97) with each vertical column corresponding to an individual dolphin and the colours indicating the membership proportions to each of the three clusters. (B) DAPC scatterplot clustering the samples (n = 97) according to their first two principal components. The outlier 'bnd204' was the only sample assigned differently by DAPC and STRUCTURE. Red, green and blue colours represent *Coastal Shannon*, *Coastal Mobile* and *Pelagic* dolphins, respectively. (C) Map of individual assignment probabilities per population (I) *Coastal Shannon* (II) *Coastal mobile* identified by TESS including only coastal biopsies (n = 71). The colour scale bar indicates the assignment probabilities. The results are based on analyses run with the complete set of 15 microsatellite loci.

Fig. 5. Possible migrant dolphin (a male given photo-ID number 18) has been encountered only within Shannon estuary SAC over 9 years (encounter locations indicated with red dots) but is genetically assigned to coastal mobile population with 79% certainty (green colour in assignment probability plot from STRUCTURE). Dolphin 1276 (encounter locations indicated with green dots) is a male potentially closely related to 18 ($r \geq 0.45$), and he in turn is closely

related to 1199 (encounter locations indicated with yellow dots), also a male. Both 1276 and 1199 are strongly assigned to the coastal mobile population.

Fig. 6. Social network diagram of bottlenose dolphins encountered on at least five occasions during the data collection 1996-2014. Boxes represent a social cluster of individuals encountered in the Shannon estuary, and circles a cluster of the 'mobile' dolphins encountered on the west and north-west coast of Ireland. The length of the line in the network diagram inversely represents the strength of the association between a dyad calculated as Half-Weight Index (HWI).

Fig. 7. Lagged identification rate (LIR) for bottlenose dolphins encountered ≥5 times (A) in the Shannon Estuary, and (B) outside the Shannon Estuary in the coastal waters of Ireland during the study period 1996-2014. The graph describes the probability that a dolphin photographed at time 0 will be identified again at time X within the area. Data points are represented as green circles (with SE) and the best fitting model (see Appendix 12) is displayed as the blue line. Time lag (number of days) is given on logarithmic scale.

Author contributions

M.N., A.D.F., S.N.I. and E.R. conceptualized the work and the analyses. E.D. and M.N. performed laboratory work. M.N., L.M. and M.L analysed the genetic data. M.N., M.O., A.E. and S.N.I. analysed the photo-identification data. M.N., S.N.I., E.R., A.D.F., M.O., and A.E. collected the genetic samples and photo-identification data. M.N. wrote the paper. All authors approved the final manuscript.