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Ingram, Simon

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Challenges in monitoring mobile populations - Applying Bayesian multi-site mark-recapture abundance estimation to the monitoring of a highly mobile coastal population of bottlenose dolphins

Milaja Nykänen[1*], Machiel G. Oudejans[2], Emer Rogan[1], John W. Durban[3], and Simon N. Ingram[4]

[1] School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland
[2] Kelp Marine Research, Hoorn, The Netherlands
[3] Protected Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California, USA
[4] School of Biological and Marine Sciences, University of Plymouth, Plymouth UK

[*] Correspondence to be sent to: Milaja Nykänen, School of Biological, Earth and Environmental Sciences, the Butler Building, North Mall, University College Cork, Cork, Ireland, E-mail: m.nykanen@ucc.ie, Tel: +353 (0)21 4904

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Abstract

1. Monitoring the abundance of mobile and wide-ranging cetacean populations for conservation management is challenging, especially when the management is focused on static protected areas. Where abundance estimates are derived from mark-recapture data, such as photo-identification of naturally marked individuals, unpredictable movements of animals in and out of the survey area can reduce ‘capture’ probabilities and affect the precision and accuracy of resulting estimates.

2. Bayesian hierarchical log-linear likelihood was applied to photo-identification data collected in summer 2014 to derive a multi-site abundance estimate for a population of bottlenose dolphins, *Tursiops truncatus*, ranging widely throughout coastal waters of western Ireland. In addition, the effects of varying levels of sampling effort on the minimum detectable decrease in population size was examined.

3. The abundance of dolphins was estimated as 189 (coefficient of variation: 0.11, 95% highest-posterior density interval: 162–232). Over 50% of the well-marked dolphins encountered throughout the study were sighted in more than one distinct coastal area thus displaying high mobility. In addition, it was found that in order to detect a 25% decline in abundance within the six-year reporting period of the EU’s Habitats Directive would require biennial surveys.

4. Given that the Special Area of Conservation designated for these dolphins consists of two separate areas covering a substantial portion of the west coast of Ireland, the multi-site approach is appropriate for monitoring this population. It produces a precise estimate and is well-suited for sparse recapture data collected opportunistically at multiple sites, when the lack of resources prevent large scale surveys, or when concentrating surveys on smaller localized areas fail to capture the broad range and unpredictable occurrence of the animals. The Bayesian multi-site approach could be applied to the management of other wide-ranging marine or terrestrial taxa.

Keywords: coastal, mammals, monitoring, Special Area of Conservation, survey, modelling

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1. Introduction

1.1. General background

Bottlenose dolphins (*Tursiops truncatus*) are widely distributed throughout tropical and temperate seas and found in pelagic oceanic environments, on the continental shelf, as well as in coastal inshore waters (Wells and Scott, 2009). Their minimum worldwide abundance is estimated to be approximately 600,000 individuals (Wells and Scott, 2009) and numbers in European Atlantic continental shelf waters have been estimated to be around 16,000 (Hammond et al., 2013) although results from recent aerial surveys suggests that there may be strong inter-annual variation in this area (Rogan et al., 2018). Whilst the bottlenose dolphin as a species is not considered to be globally endangered, some populations, especially those inhabiting coastal areas, are small and often genetically and/or geographically isolated (e.g. Caballero et al., 2012; Fernández et al., 2011; Louis et al., 2014; Mirimin et al., 2011; Nykänen et al., 2018). This puts them at risk of losing heterozygosity and genetic resilience due to genetic drift (Lacy, 1987) placing them at greater risk to local extinctions with increased vulnerability to anthropogenic pressures. The main threats to delphinids in coastal environments include pollutants such as xenobiotic chemicals (especially PCBs and DDTs), reduced prey availability due to coastal fisheries, habitat degradation, noise and disturbance from vessel traffic, entanglement and incidental bycatch, direct hunting, marine construction and anthropogenic noise (Jepson et al., 2016; Lusseau et al., 2009; Pirotta et al., 2015; Williams et al., 2009; Williams et al., 2014). The sensitivity of bottlenose dolphins to these threats is further exacerbated by their position as apex predators in coastal ecosystems and by their low reproductive rates (Arso Civil et al., 2017; Baker et al., 2018a; Quick et al., 2014).

1.2. Conservation and monitoring requirements of bottlenose dolphins in Europe

The conservation of wild animal populations is often implemented through designation and management of protected areas that are considered to represent important habitats for foraging, breeding and other important activities (Palumbi, 2001; Reeves, 2000). This is usually followed by regular monitoring of some demographic parameters, such as abundance, survival or age structure of the individuals inhabiting these areas. In European waters, bottlenose dolphins are protected through Annexes II and IV of the European Union's Habitats Directive (European Economic Community, 1992), and the Member States are required to designate Special Areas of Conservation (SACs) as part of a European strategy to maintain or restore 'favourable conservation status' for the species. In practice, this means that in order to be classed as

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‘favourable’, the species (or population) should not decline from the reference level (defined by the Member States individually) by more than 25% over a six-year reporting period, alternatively, annual decline should not exceed 1%. In addition to the Habitats Directive, as top predators, bottlenose dolphins are included as one of the indicator species for ‘Good Environmental Status’ in European coastal waters in the Marine Strategy Framework Directive (MSFD; Council of the European Communities, 2008).

Some bottlenose dolphin populations have a strong site-fidelity to bays and estuaries (Bearzi et al., 2008; Connor et al., 2000; Ingram and Rogan, 2002; Read et al., 2003), and their conservation monitoring has been focused on discrete, local areas such the SACs. Recent studies have found that bottlenose dolphins using the coastal waters of Ireland belong to two genetically, demographically and socially distinct populations (Mirimin et al., 2011; Nykänen et al., 2018, 2019), with a resident population using the Shannon estuary, hereafter referred to as the ‘Shannon population’. Residency is determined here by individuals occurring in the area at least 50% of the months in a given year over multiple years or decades, adapted from Rosel et al. (2011). The second population, hereafter the ‘west coast population’, is more widely distributed using other coastal areas of western Ireland (Ingram et al., 2003; Oudejans et al., 2010). Consequently, two discrete SACs have been designated to ensure the protection of these populations; the Lower River Shannon Estuary SAC and the West Connacht Coast SAC (see inset map in Figure 1). While the area-based monitoring of the Shannon population has been successful, capturing majority of the individuals inhabiting the estuary (based on discovery curves) and producing precise abundance estimates (Englund et al., 2008; Ingram and Rogan, 2003), this approach may not be suitable for more mobile and dispersed populations that have spatially and temporally variable use of large areas of habitat, presenting a challenge for monitoring. For example, on the east coast of Scotland, the effectiveness of the Moray Firth SAC, designated based on high site-fidelity exhibited by a population of bottlenose dolphins to the area, has recently been questioned due to the population extending their range to areas outside the SAC over the past decade (Wilson, 2016; Wilson et al., 2004). Similarly, in Irish waters, the range of the west coast population extends beyond the designated SAC. Conservation efforts may thus need to move away from area-based management and instead focus on populations whilst considering population dynamic processes such as dispersal (genetic and demographic) that affect the dynamics and the overall viability of populations. Moreover, in order to achieve efficient monitoring appropriate for the MSFD and to ensure that

For Peer Review

effective conservation of dispersed coastal populations is achieved, it is crucial to design an appropriate monitoring strategy suitable for the population in question.

Compared to the Shannon estuary population that has been the focus of most research on bottlenose dolphins in Ireland (Baker et al., 2018a; 2018b; Berrow et al., 2012; Englund et al., 2008; Foley et al., 2010; Ingram and Rogan, 2002; 2003), much less is known about the west coast population. Preliminary studies identified a significant number of bottlenose dolphins inhabiting the waters off the west coast of Ireland (Ingram et al., 2001; 2003) with an estimated mean abundance of 171 dolphins using the waters around Connemara, Co. Galway (see Figure 1) (Ingram et al., 2009). However, this estimate was based on surveys over a limited length of coast within the West Connacht Coast SAC and was relatively imprecise with a coefficient of variation (CV) of 0.28. Moreover, despite multi-annual re-sightings of individuals, it appears that these animals are highly mobile and have a large home range with encounters occurring throughout the west coast (Ingram et al., 2001; 2003). The widespread distribution together with unpredictable movements make monitoring the abundance of this population especially challenging. Therefore, one of the aims of this study was to provide an abundance estimate which could be used as a baseline for long-term monitoring. Further, the distribution and the rate of individual movements were investigated and some of the possible underlying factors driving the distribution explored and discussed. Finally, the effect of different levels of survey effort on the precision of the abundance estimate was quantified using a power analysis. This will help inform a cost-effective strategy for future monitoring that is sufficiently sensitive to changes in abundance to reliably detect population decline in a timely manner.

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2. Methods

2.1. Data collection and photograph analysis

Mark-recapture is widely applied in ecological studies to estimate the number of individuals in a population or the density of animals within a surveyed area (Otis et al., 1978). Individual bottlenose dolphins can be identified from naturally occurring markings (Würsig and Würsig, 1977). These marks mostly consist of scars and nicks from interactions with conspecifics and they can be permanent, such as deep nicks or scars on the dorsal fin, or temporary, such as superficial scratches (Appendix 1). Heavily marked animals can be identified over periods of many years, whereas more superficial markings, such as tooth rake scars, may fade within a period of about a year reducing inter-annual re-sighting probabilities of less heavily marked individuals. In this study, identification photographs were taken of individual bottlenose dolphins encountered in schools during dedicated and opportunistic boat-based surveys. Here, a school is defined as "all dolphins within a 100m radius of each other" after (Irvine et al., 1981). Boat-based surveys were conducted along a 250km stretch of coastal waters in western Ireland (Figure 1) during the summer months (May–September) of 2014. Efforts were made to photograph the dorsal fins of all members of each encountered school.

The best quality photograph of each identifiable dolphin was selected from each encounter and assigned an image quality score of 1 to 4 (1 being the highest quality and 4 the poorest, see Appendix 2) with no consideration of the degree of marking of the individual dolphin. Each photographed individual was then assigned one of three grades of mark-severity (Appendix 1), and visually matched against the archived catalogue of dolphins identified during previous encounters. To minimise bias in capture probability resulting from identification errors, photographs of quality grade 4 were excluded from subsequent abundance estimation. Further, only the "well-marked" dolphins (M1, see Appendix 1), easily distinguishable and identifiable from both the left and the right side, were included in the analyses. For this study, the wider study area was divided into three discrete and geographically separated blocks where survey effort had been concentrated (see Figure 1). Photographs from encounters were compared within and between the blocks to establish whether individuals were seen across the whole study area during the study period.

2.2. Abundance analysis

Mark-recapture models that assume population closure (zero net migration and births and deaths) within a single defined area, are typically used in abundance estimation of dolphins with strong site-fidelity to specific areas (Berrow et al., 2012; Louis et al., 2015; Read et al., 2003; Wilson et al., 1999). However, when the animals are moving non-randomly into and out of the area within the sampling (survey) period, and the effective number of animals available for re-capture therefore changes, closed models become less applicable as the violation of population closure assumption can result in biased abundance estimates (Kendall, 1999). Bayes' theorem, as opposed to traditional frequentist maximum likelihood (ML) based estimation, has recently become more widely applied in mark-recapture abundance estimation (Mäntyniemi and Romakkaniemi, 2002; Michielsens et al., 2006). It has been applied to a range of cetacean species (Beck et al., 2014; Cheney et al., 2013; Durban et al., 2010; Durban et al., 2005; Fearnbach et al., 2012; Moore and Barlow, 2011) due to its utility with sparse data and/or

For Peer Review

opportunistic data collection. In this study, due to the large combined coastal area surveyed, Bayesian inference was applied to a model of hierarchical log-linear likelihood of counts of identified dolphins across three discrete blocks, and a combined abundance estimate of bottlenose dolphins using the entire survey area extending from Connemara to Donegal Bay was derived (Figure 1). This method, developed by Durban et al. (2005), is well-suited for data sets with low number of individual re-sightings and for situations when it is unfeasible to do systematic surveys covering the entire population's range. The model also takes into account different ranging patterns of individuals and geographical dependencies between multiple sites, enabling the estimation of movement rates of animals between sampling locations. An advantage of using Bayesian inference instead of traditional frequentist statistics is that prior knowledge of the parameter (prior) distribution can be incorporated into the model to produce a joint posterior distribution for the parameter in question. An example of this would be setting a realistic maximum value to the prior for the abundance of all well-marked animals in an area. This informative prior is then incorporated into the model to facilitate the convergence of Markov Chain Monte Carlo (MCMC) chains.

A contingency table of sighting histories of well-marked (M1) bottlenose dolphins was created based on their presence or absence in each of the study blocks during a single survey season (Table 1). The re-sightings of individuals among multiple sites therefore represented spatial, rather than temporal, capture-recapture events (Durban et al., 2005). The model predicts the number of animals not captured at any of the survey sites and incorporates this value to compute the estimate of the overall abundance of well-marked animals across the entire study area. The model also incorporates the proportion of well-marked individuals as a binomial sample of the total number of animals seen; therefore, it predicts the total number of individuals (including unmarked animals) in the study area (see Cheney et al., 2013). The model averaging and prediction (Durban et al., 2005) were performed using MCMC sampling in WinBUGS software (Lunn et al., 2000) with 100,000 burn-in followed by 100,000 iterations. Three independent chains were run to confirm consistency between runs and inspected visually for convergence.

2.3. Range of bottlenose dolphins encountered in 2001-2014

In order to describe the extent of movements of bottlenose dolphins sighted on the west coast of Ireland, the photographs taken in 2014 were supplemented with data collected over a longer time period, in 2001-2013, and the range of the sighting latitudes were plotted for the 39 most sighted (≥5 times) well-marked dolphins. These were the same individuals that were included in the social structure analyses. In addition, the dependency of the sighting latitude range (the

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difference between the maximum and the minimum latitude) and the encounter frequency was determined by calculating Pearson's correlation coefficient, *r*.

2.4. Analyses of social structure

To investigate whether this population of coastal dolphins could be divided into social clusters reflecting site-fidelity to their sighting locations and/or geographic range, analyses of social structure were performed in SOCPROG 2.4 compiled version (Whitehead, 2009a; 2009b). Applying the 'gambit of the group' concept (Whitehead and Dufault, 1999), the rate at which individuals were photographed within the same schools, was used as a proxy for social association. Daily sampling periods were used to ensure the independence between the sampling periods (Whitehead, 2008). The dataset was restricted to good quality photographs (Q1-3, Appendix 2) of individuals with permanent and obvious markings (mark severity grade M1, Appendix 1) in order to identify individuals over multi-annual periods, and only dolphins photographed in at least five sampling periods (days) were included to reduce bias caused by rarely seen individuals (Whitehead, 2009a). Social analyses included entire sighting histories from 2001 up until 2014, the duration of photo-ID surveys of this population.

The strength of association between pairs of individuals (i.e. dyads) was measured using the half-weight association index (HWI). This index of co-occurrence takes values between 0 (never seen together) and 1 (always observed together), and is appropriate when not all associates within a group have been identified (Cairns and Schwager, 1987). Standard deviation (SD) and CV of the HWI were also calculated. A Monte Carlo permutation test (Bejder et al., 1998; Whitehead, 1999) was used to test whether the observed association patterns (real data) were different than expected from randomly associating individuals (permutated data). The permutations were performed using 20,000 iterations with 1000 trials per iteration. A higher SD of the observed association indices compared to the SD of permutated data is considered as an indication of preferred and/or avoided associations between the sampling periods (Whitehead, 2009a).

The power of the analysis to capture a true representation of the social system was estimated as the correlation of the observed and estimated association indices using the maximum likelihood estimator (Pearson's correlation coefficient, *r*). A measure of social differentiation, *S*, calculated as the CV of real association indices, was used to describe the variability in the social system, with values >0.5 indicating a well differentiated society (Whitehead, 2009a). Standard errors (SEs) for *r* and *S* were calculated by bootstrapping with 100 replications. In

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order to determine whether the population of bottlenose dolphins could be divided into clusters where association indices are higher among members of the same cluster than expected by chance, an eigenvector-based maximum modularity coefficient, Q (Lusseau, 2007; Newman, 2004; 2006; Whitehead, 2009a), was calculated. This method accounts for different levels of gregariousness between the individuals (i.e. the average number of associates) with modularities greater than ~0.3 considered to represent effective community divisions (Newman, 2004; Whitehead, 2009a). NetDraw (Borgatti et al., 2002) was used to visualize a social network diagram using the network statistics calculated in SOCPROG.

2.5. Power to detect change in abundance

Program TRENDS (Gerrodette, 1987, 1991) was used to conduct a power analysis in order to estimate the annual rate of decline in population abundance within a six-year period (as mentioned previously, six years is the reporting interval set in the Habitats Directive) that could be detected with the level of precision (here, the CV) achieved in this study. The precision that would be required to detect an annual decline of 1% in population size over the six-year period was also estimated, as identifying this rate of annual decline is one of the requirements of the Habitats Directive.

Further, the effect of different amounts of sampling effort (here, number of years between surveys) on the minimum detectable overall decline in population size was examined using a longer theoretical study period of 25 years and a range of CVs varying from 0.01 (very high precision) to 0.30 (low precision). Specifically, scenarios were tested when abundance surveys were conducted every six years (five years between surveys), every three years (two years between surveys), every two years (one year between surveys) or every year, over the 25-year period. In all the power analyses, the desired power was set to 80%, the probability of Type I and II errors to 0.05, and a one-tailed test was used, as the purpose was to detect a decrease and not a general change in abundance. A linear population model was used for a non-recovering population as in Fruet et al. (2015).

3. Results

3.1. Data collection

In 2014, 146 survey hours yielded six encounters with bottlenose dolphin schools around Connemara, seven around Mullet peninsula and eight in Donegal Bay (Figure 1). School size ranged from 9 to 95 with the largest schools encountered in Donegal Bay (median school size

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of 36). In total, nearly 10,000 photographs were analysed. From these, 169 new dolphin identifications from photographs obtained from either the left, the right, or both sides of the animal were added to the archive of dolphin images collected since 2001. Note that due to the fact that bottlenose dolphin markings can change over time and that some individuals are known only from one side, the number of identifications in the archive does not equal the number of individuals in the population, especially when considering the gaps in the years when photo-ID surveys were conducted. Nevertheless, 71 animals were matched to individuals identified from encounters made in previous years with seven identifications dating back to 2001.

3.2. Abundance and movements

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From the photographs taken during May–September 2014, a total of 91 well-marked dolphins, identified or identifiable from both sides, were included in the abundance analysis (Table 1). Forty-nine (54%) of these animals were seen in more than one study block, and eight (9%) were encountered in all the study sites. The highest overlap of individuals occurred between Mullet peninsula and Donegal Bay with 28 dolphins (31%) sighted in both of these areas. Donegal also had the highest number (n = 23) of animals seen in only one of the three study sites. The average proportion of well-marked dolphins (to all dolphins, marked and unmarked) was 0.57 across all encounters in 2014. The Bayesian multi-site median abundance estimate of the total number of dolphins for the whole study area for the summer 2014 was 189 (CV = 0.11, 95% HPDI = 162–232). The non-significant P-value (P = 0.158) from the closure test of Otis et al. (1978) suggested that the closure assumption was not violated.

3.3. Range of bottlenose dolphins encountered in 2001-2014

The range of sighting latitudes of the most sighted (≥5 times) well-marked dolphins is presented in Figure 2a; it appears that while most of these animals were sighted from Donegal Bay to Connemara, with the distance between the areas of more than 250km (over water), there were four animals (IDs 1056, 1094, 1038 and 1049) that had even wider distribution having been sighted from Co. Cork to Donegal Bay between 2001 and 2014 with >500km between these sites. In contrast, there were also a number of individuals with much narrower latitudinal range, that were encountered only in two of the sites; two individuals were only encountered in Connemara and around the Mullet peninsula (IDs 1099 and 1244, Figure 2a), and 12 individuals were only recorded around the Mullet peninsula and in Donegal Bay (for example, IDs 1444 and 1468) during 2001-2014. The range of the sighting latitudes was not dependent on the number of times the animal was encountered (Pearson's $r = 0.180$, P = 0.125, see Appendix 3).

3.4. Social structure

When including only good quality photographs of well-marked (M1) individuals encountered in at least five sampling periods, 39 bottlenose dolphins were included in the analyses of social structure. These data were collected during 51 encounters over 48 days in 2001-2014. The mean number of observations per dolphin was 7.21 (SE = 1.95) and the maximum number of times that an individual was encountered was 13. The individuals had, on average, 63 associations with other individuals.

The mean HWI was 0.226, which did not differ significantly from the permuted random data (mean = 0.226, $P > 0.05$). However, the SD (0.206) and CV (0.910) in the real data were significantly higher than in the random data (SD = 0.203, $P < 0.001$; CV = 0.898, $P < 0.001$), suggesting that individuals did not associate completely randomly but that short- or long term preferred companionships exist within the community (Whitehead, 2009a). Moreover, the proportion of non-zero elements was significantly larger ($P < 0.01$) in the permuted data (proportion = 0.732) compared to the real data (proportion = 0.729) which suggests that some individuals may avoid others (Whitehead, 2009a).

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The correlation coefficient (r) between the true and estimated HWIs was 0.695 (SE = 0.042), indicating that the estimated association indices adequately represented the underlying social structure (Whitehead, 2009a). The estimate of social differentiation, S, was 0.633 (SE = 0.091), which indicates a well differentiated social system. However, a cophenetic correlation coefficient of 0.787 (less than the threshold of 0.8 for an effective social structure representation), combined with a maximum modularity (Q) of 0.264 (below the cut-off value of 0.3), shows a lack of evidence for the existence of social clusters within the community (Whitehead, 2009a) and therefore insufficient evidence for spatial segregation between individuals (Figure 2b).

3.5. Power to detect trends in abundance

According to the power analysis, detecting an annual decline of 1% in the population abundance with 80% certainty over a six-year period could only be achieved with CV of ≤ 0.01 whilst surveying every year. With the CV of 0.11 (the precision achieved in this study), on the other hand, an annual decline of 6% could be detected but only if surveys were conducted every year.

When considering a longer theoretical sampling period of 25 years and using a CV of 0.11, abundance surveys would have to be conducted every other year in order to detect an overall 25% decline (threshold in the Habitats Directive) in abundance (Figure 3). Surveying every three years with this level of precision would enable the detection of a decline of 26% and a survey frequency of every six years would only enable the detection of a larger 35% decrease in the population. On the other hand, if surveys were taking place every six years and the target was to detect the 25% decline, the CV around the estimate would have to be as low as 0.07 (Figure 3).

4. Discussion

4.1. Abundance and movements of bottlenose dolphins on the west coast of Ireland

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During summer 2014, the number of bottlenose dolphins using a 250km stretch of coastal waters between Connemara, Co. Galway and Co. Donegal on Ireland's west coast was estimated as 189 individuals (95% HPDI: 162–232). This estimate makes this the largest bottlenose dolphin population known to use Irish coastal waters, exceeding the numbers of animals estimated to inhabit the Shannon estuary (Berrow et al., 2012). Over 70 animals were matched with an existing catalogue with seven dolphins identified as far back as 2001. Such long-term re-identifications indicate that at least some of the animals using the coastal waters off the west and north-west of Ireland show a degree of site-fidelity, and it appears that the combined area between Connemara, Mullet peninsula and Donegal Bay form an important part of the home-range for a large number of bottlenose dolphins. While some of the members of this population were seen in only one of the coastal sites in 2014, several individuals exhibited high levels of mobility undertaking movements of over 250km during a single summer season. This high mobility presents challenges to the monitoring of the population, as wide-scale habitat use results in patchy temporal site occupancy with individuals and schools ranging freely over considerable distances around the Irish coast and further afield. Overall, the estimate derived in this study is remarkably similar to the cumulative number of animals (n = 179) identified around the Mullet peninsula in 2008-2009 (Oudejans et al., 2010) and to a previous abundance estimate of 171 (95% CI: 100–294) for dolphins using the waters around Connemara in 2009 (Ingram et al., 2009). However, the precision reached in this study (CV = 0.11) far exceeds the precision around the previous abundance estimate (CV = 0.28), making the 2014 estimate more robust for monitoring purposes, as shown by the power analysis. Nevertheless, biennial surveys would be required to detect the 25% overall decline in the population, and even in this case, the precision would have to remain at or below the CV of 0.11 which may not be realistic year after year.

The impacts of anthropogenic habitat degradation on coastal dolphins require detailed understanding of the demographic parameters of the populations and the ranging behaviour and site-fidelity of individuals within the populations. Efficient and regular long-term monitoring of abundance is thus a vital part of the management of protected areas designated for bottlenose dolphin conservation. Studies in some other areas around the British Isles appear to show a high degree of site-fidelity to a single confined area (e.g. Shannon estuary and Sound of Barra) simplifying conservation management planning, but in other areas, such as the Moray Firth, changes in habitat use and distribution of bottlenose dolphins have been reported over the past 15 years (Arso Civil et al., 2019; Wilson et al., 2004). Similarly, the high degree of mobility of the coastal population in this study presents challenges in designing effective spatial management plans and implementing robust monitoring strategies. This study provides a benchmark for long-term monitoring of the population and its use of the West Connacht Coast SAC and illustrates how methods need to be adapted for monitoring more mobile populations.

It is essential that bespoke monitoring strategies are designed to provide accurate and precise data on the status of populations that are sensitive to changes in abundance, population viability and survival rates. The Bayesian multi-site approach used here suits the transient behaviour of the west coast bottlenose dolphin population and provides a precise and comprehensive estimate of the abundance of animals in this large and variable habitat. A multi-site estimate is likely to better reflect the true abundance of the population than previous localised estimates due to the wider-scale sampling over a larger coastal area which increases the probability of encountering more of these animals as reflected in the lower CV value obtained in this study. Furthermore, it accounts for pseudoreplication of individuals sampled at different sites and is robust to unpredictable and unknown inter-annual variability in the distribution or occupancy of the animals. In contrast, a single site approach to monitoring this population could produce biased and highly variable abundance estimates if sections of the population were not encountered within a single site during a survey season. Further, it would be unfeasible to survey the entire known coastal range used by these animals as part of a routine monitoring strategy. With unpredictable and wide ranging movements of the animals, multi-site analysis of data enables simultaneous surveys of coastal areas by multiple research teams, and photo-identification surveys could be done opportunistically with help from a citizen science sightings network whilst maximising weather windows and keeping the costs low.

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The Bayesian multi-site approach assumes population closure with no births, deaths, immigration or emigration occurring in the area during the study period (Durban et al., 2005) as does more conventional closed maximum likelihood estimation frequently used in cetacean abundance studies (Bearzi et al., 2008; Brown et al., 2014; Gnone et al., 2011; Vermeulen and Cammareri, 2009). It is likely that although this assumption may be susceptible to violation due to the large scale of the animals' ranges, the inclusion of multiple sites over a broad geographical area should improve this model's performance. Furthermore, the short duration of the annual survey season (May–September in 2014) likely reduces the probability of migration of individuals out of the wider study area thus increasing the likelihood of effective closure of the sampled population. This is supported by the non-significant result of the closure test.

The bottlenose dolphins used the entire study area during 2014, with over half (54%) of all well-marked animals sighted in more than one of the three survey blocks, and 9% sighted in all of the study blocks with over 250km between the furthest sighing locations. Similarly, Cheney et al. (2013) found a large percentage of dolphins (58%) using more than one study site on the east coast of Scotland, however, the percentage of animals photographed in all of the sites was much smaller (only up to 1%) compared to this study, despite similar distances between the sites in both studies. In addition, up to 44% of the dolphins on the west coast of Scotland had similar long-range movements, with individuals ranging between the north and south of Skye (Cheney et al., 2013), even though the dolphins in the Sound of Barra did not exhibit movements outside this area. Some of the bottlenose dolphins in the present study that were encountered during surveys in 2014 had previously been recorded as far south as Co. Cork and appear to range widely around the west coast of Ireland and possibly beyond (Figure 2a). For example, a dolphin that was encountered in Donegal Bay in the summer of 2014 had previously been photographed in the Moray Firth in 2001 and around the Scottish Hebrides in 2004 (but is not one of the individuals regularly inhabiting these areas) (Robinson et al., 2012), thus providing further evidence of the long distance movements and transient behaviour of at least some of these animals. However, despite the large scale movements, the Irish west coast population appears to be genetically differentiated from the individuals sampled in east or west of Scotland (Nykänen et al., 2019).

4.2. Social structure

Even though different individuals showed varied ranging patterns with some dolphins ranging over 500km and others encountered more locally, there was no evidence that the bottlenose

For Peer Review

dolphins occupying the waters of western Ireland form spatially segregated social clusters, unlike the social segregation previously documented between the coastal and offshore bottlenose dolphins (Oudejans et al., 2015). In fact, the west coast dolphins in this study seem to lack social groupings altogether, and it appears that the community consists of fluid social ties where individuals have a large number of associates, even though evidence of some short and long term companions and non-preferred associates was found. Bottlenose dolphins generally live in fluid "fission-fusion" societies (Connor et al., 2000), which means that animals usually form small social groups whose composition can change rapidly within the scale of a few hours. However, division into social clusters is common in some bottlenose dolphin societies (e.g. Chilvers and Corkeron, 2002), and this clustering has been linked to sex (Connor et al., 2011; Connor and Krützen, 2015; Frère et al., 2010; Smolker et al., 1992), specialized foraging techniques (Chilvers and Corkeron, 2001; Daura-Jorge et al., 2012; Krützen et al., 2005; 2014; Mann and Sargeant, 2003; Mann et al., 2008; Simões-Lopes et al., 1998; Smolker et al., 1997) and differential ranging patterns and spatial segregation (Louis et al., 2015; Lusseau et al., 2006). For example, Louis et al. (2015) found that individuals belonging to a social cluster were mainly observed within a specific area of the wider Normano-Breton Gulf, France. However, this clustering did not reflect genetic structuring as these dolphins were part of the same genetic population (Louis et al., 2014), so at least some spatial overlap is required to prevent genetic differentiation. In contrast, social separation was accompanied by genetic isolation between two adjacent populations of bottlenose dolphins occupying the Shannon estuary and the Irish west coast waters outside the estuary in a recent study (Nykänen et al., 2018). However, the lack of social clustering found in the present study may also be an artefact of the low number of re-sightings ($n \geq 5$) compared to some other studies; for example Frère et al. (2010) used a minimum of 30 identifications to estimate the social system of female Indo-Pacific bottlenose dolphins, *Tursiops aduncus*.

4.3. Monitoring populations rather than protected areas?

Most current marine conservation management requires the designation of some form of fixed marine protected area (MPA). However, MPAs have been criticised for being too small and failing to incorporate much of the range of the animals that they were designated for (Agardy et al., 2011; Hooker and Gerber, 2004; Wilson, 2016). Furthermore, the size, distribution and ranging behaviour of wild animal populations can alter as a consequence of changes in prey density and distribution (Angerbjorn et al., 1999; Friedlaender et al., 2006; Walton et al., 2001), habitat degradation or changes in environmental conditions linked to anthropogenic climate

For Peer Review

change (Harley et al., 2006; MacLeod et al., 2005; Parmesan and Yohe, 2003; Walther et al., 2002). Therefore, MPAs with static boundaries advocated for the conservation of marine top predators may not be the most appropriate method to protect mobile species. However, there are a few examples where designation of static MPAs have been linked to improved survival probability and increased population growth rate (Cheney et al., 2019; Gormley et al., 2012), or the MPA has been large enough to encompass the majority of the range of most of the animals (White et al., 2017).

There have been calls for more dynamic MPAs where the boundaries can be adjusted in response to changing species distributions or site use (Hartel et al., 2015; Hooker et al., 2011; Hooker and Gerber, 2004). However, it is likely that shifting of MPA boundaries would present such logistical and economic difficulties that the managing bodies and stakeholders may be reluctant to adopt this strategy. An alternative strategy could be to protect multiple clearly defined areas within a population's range where specific anthropogenic threats represent 'risk hot-spots' where impacts can be closely monitored and mitigated. Another proposed approach has been the development of more comprehensive marine spatial plans and ecosystem based management (Agardy et al., 2011; Halpern et al., 2010; MacLeod et al., 2005; Wilson, 2016) emphasizing integrated protection of the ecosystem as a whole while acknowledging connectivity among systems (MacLeod et al., 2005). In this context, the Great Barrier Reef Marine Park in Australia has been described as a success story of a large scale network of MPAs with its integrated and adaptive management (McCook et al., 2010). In Europe, the MSFD, where bottlenose dolphins are listed as one of the indicator species of good environmental status of coastal habitats, and the Natura 2000 network of SACs designated for the species seem to be a step in the right direction due to the potential of a network of MPAs enhancing connectivity among populations. However, transnational co-operation in the monitoring of these areas is required since the individual Member States are responsible for reporting on the status of species only in their own national SACs, and mobile populations can have ranges extending beyond country boundaries.

If protection were focused on a population instead of a protected area, this protection could extend over the population's entire range (Reeves, 2000) rather than arbitrary portions of the population's range lying within an MPA. SACs designated for bottlenose dolphins in Irish coastal waters were designated based on limited spatial data from wide-scale and patchy surveys, and it is highly likely that the current SAC designations do not encompass the entire ecological needs of this species in the coastal waters of western Ireland. Moreover, monitoring

For Peer Review

a population only within a designated area that covers only a portion of a population or species' habitat could give a biased view of the status of the population, if its range has expanded to other areas (Wilson et al., 2004) and a considerable part of the population is using areas outside the SAC (Arso Civil et al., 2019). However, the authorities responsible for the assessment of the conservation status of the Moray Firth SAC bottlenose dolphins have taken the recent range expansion and high mobility of the individuals into account in the monitoring of the population and with the advice that planned developments will need to be considered in assessments if they have potential impacts on bottlenose dolphins anywhere within the population's range, as they are likely to have a significant effect on the conservation objectives of the SAC (Arso Civil et al., 2019; SNH Natura Casework Guidance, 2019). This provides a good example of how governments can adjust previously set restricted management schemes under changing conditions, and that successful monitoring of mobile populations requires data collection across the population's range (Arso Civil et al., 2019).

4.4. Recommendations for future monitoring

The current approach to species conservation in the EU and other parts of the world is largely reliant on fixed area based protection and monitoring. While this approach may be applicable to some species in certain areas, this study provides an interesting contrast to studies of populations with higher site fidelity to coastal sites and illustrates how monitoring methods need to be adapted for more mobile populations.

Regular monitoring with at least biennial surveying on multiple known key sites across the population's range is recommended as the most appropriate monitoring strategy for the highly mobile bottlenose dolphins in this study, and a similar approach could be applied to other mobile marine and terrestrial populations worldwide. The multi-site approach maximises sighting probabilities at selected high-use sites throughout a large part of the population's range and produces accurate and precise estimates that are robust to temporary changes in ranging behaviour whilst delivering a cost-efficient way to monitor the population. Moreover, it offers great potential to be used as a tool for monitoring abundance in networks of connected MPAs, such as the Natura 2000 network of SACs designed to protect species across the EU. Indeed, evidence suggests that these coastal bottlenose dolphins have large ranges (Ingram et al., 2001) extending beyond national boundaries (O'Brien et al., 2009; Robinson et al., 2012). Even though genetic dispersal may be limited between the populations (Nykänen et al., 2019),

For Peer Review

increased transnational cooperation may be necessary for wide-scale monitoring in order to deliver on shared obligations under the MSFD and to some extent also the Habitats Directive.

Clearly, further research is required to uncover the entire ranging patterns and year-round habitat use of the bottlenose dolphins inhabiting coastal areas of western Ireland. Since unpredictable weather conditions on the west coast make surveying difficult and even unfeasible in the winter leading to data gaps in the populations' seasonal habitat use, photo-ID surveys could be supplemented with other methods, such as passive acoustic monitoring (PAM), to monitor temporal and spatial habitat use. In fact, preliminary PAM data suggests that bottlenose dolphins use key sites (outside and within the SAC) on the Irish west coast year round (Garagouni, 2019; Nykänen, 2016). Regular assessment of small mobile populations, such as the one in this study, is imperative to ensure that any deterioration in the conservation status of the population will be detected early, allowing for responsive mitigation measures to be put in place in a timely manner.

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Conflict of interest

The authors declare no conflict of interest.

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Tables

Table 1. Contingency table of the counts of well-marked (M1) bottlenose dolphins present (Y) or absent (N) in each of the study blocks Connemara, Mullet peninsula and Donegal Bay in 2014.

	Block		
Count	Connemara	Mullet peninsula	Donegal Bay
8	Y	Y	Y
2	Y	Y	N
13	N	Y	N
6	Y	N	N
28	N	Y	Y
11	Y	N	Y
23	N	N	Y
NA†	N	N	N

† The missing value (NA) represents the number of individuals that were not seen in any of the study blocks (i.e., “missed” well-marked dolphins)

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Figure legends

Figure 1. The three coastal 'blocks' (circled areas), Donegal Bay, Mullet Peninsula and Connemara surveyed during summer 2014. The red areas in the inset map show the location of the two bottlenose dolphin SACs in Irish waters, and the hatched area in the large map shows the extent of the West Connacht SAC. Triangles denote the location of encounters with bottlenose dolphin schools during the study period.

Figure 2. The 39 most sighted well-marked bottlenose dolphins and a) the geographic range of their sighting locations, and b) their social network diagram. The bottlenose dolphins were encountered at least on five occasions during the data collection period 2001-2014 on the west coast of Ireland. The individual ID numbers are given on the x-axis in figure a) and next to the circles in figure b). The outline of Ireland has been scaled to correspond with the sighting latitudes. The centre line in the boxplot and the bottom and top of the box represent the 50th, 25th and 75th percentiles, respectively, and the whiskers the 5th and 95th percentile in figure a). The dots represent rarely visited latitudes. The data has been arranged by increasing median latitude. The length of the line in the network diagram in figure b) inversely represents the strength of the association between a dyad calculated as half-weight association index.

Figure 3. The effect of coefficient of variation (CV) on the minimum detectable decline in the abundance of a theoretical population with different survey frequency; surveys conducted every six years (five years between surveys), every three years (two years between surveys), every other year or annually, over a theoretical 25-year period.

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Appendices

Appendix 1. 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 to some extent, 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.

Appendix 2. Scoring criteria for the quality of bottlenose dolphin identification photographs.

Appendix 3. Range of sighting latitude (difference between maximum and minimum latitude) plotted against the number of times each individual well-marked bottlenose dolphin was sighted on the west coast of Ireland 2001–2014. A Loess smooth curve is fitted through the observations.

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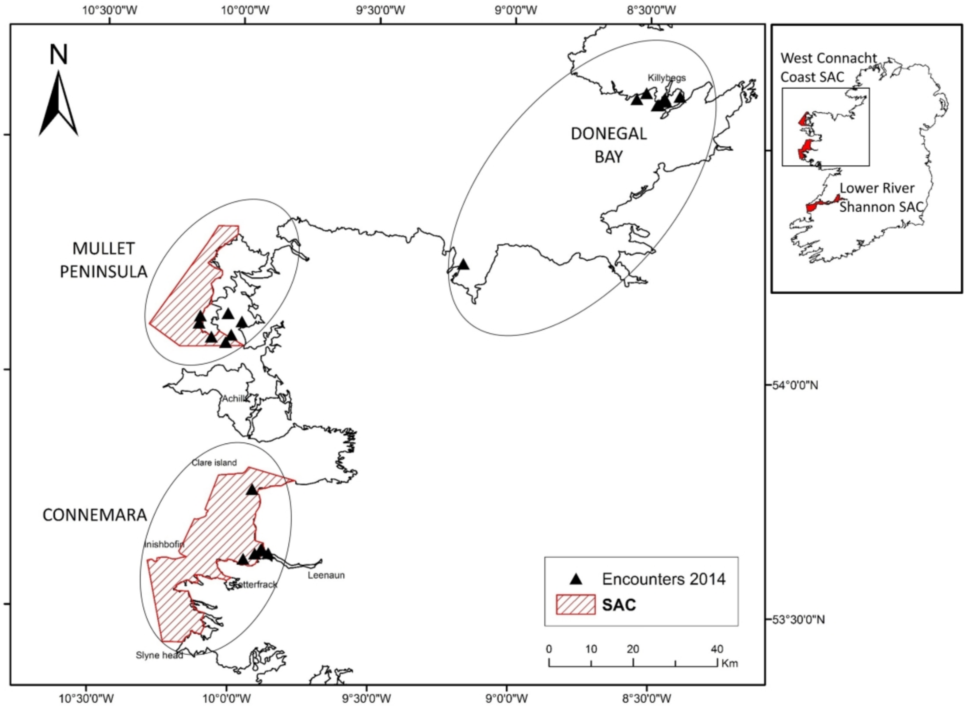

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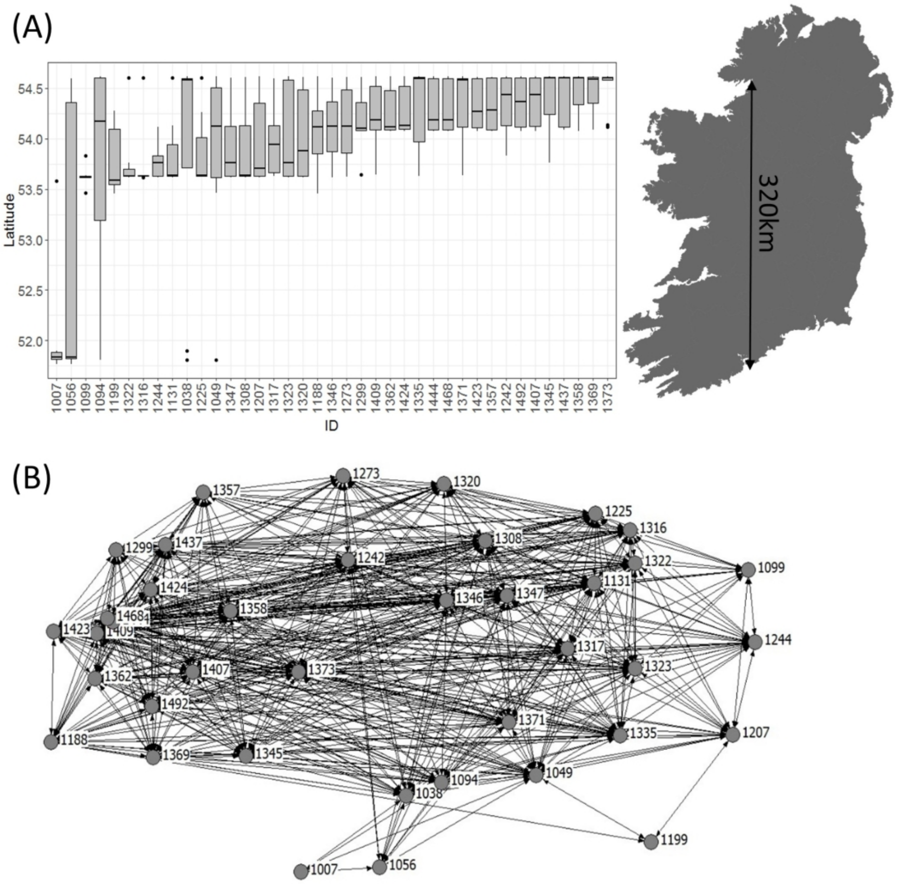

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208x201mm (300 x 300 DPI)

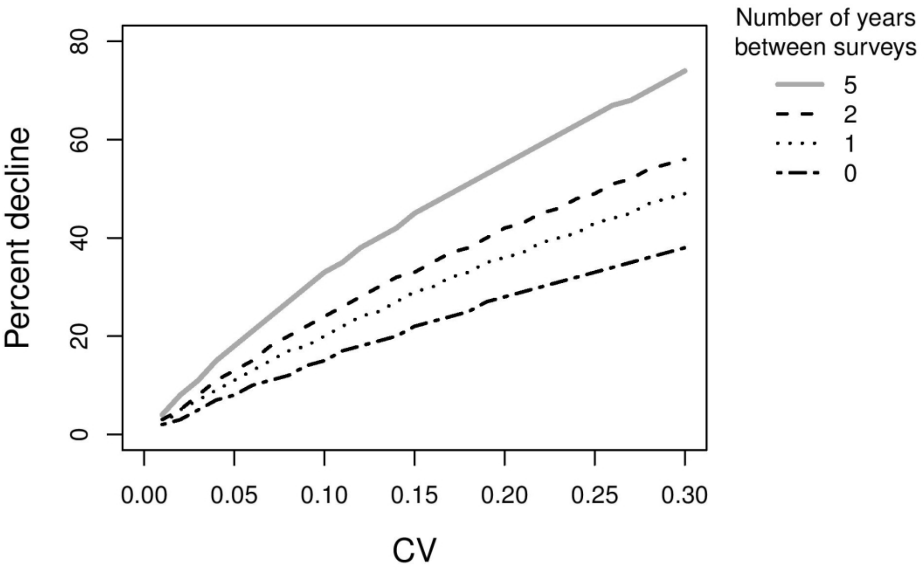

Figure 3. The effect of coefficient of variation (CV) on the minimum detectable decline in the abundance of a theoretical population with different survey frequency; surveys conducted every six years (five years between surveys), every three years (two years between surveys), every other year or annually, over a theoretical 25-year period.

172x119mm (300 x 300 DPI)