# TEMPORAL VARIATION IN THE DEMOGRAPHICS AND DYNAMICS OF A BOTTLENOSE DOLPHIN POPULATION

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A thesis presented for the degree of Doctor of Philosophy in Ecology
at the University of Aberdeen

**September 2017**

# THESIS CONTENTS

# AUTHOR'S DECLARATION

I declare that the work presented in this thesis is my own, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged below and in each chapter.

Data used in this thesis include over two decades of individual based data collected as part of a collaborative project by the University of Aberdeen and the University of St Andrews. Since 2006 I have managed the photo-identification research programme carried out by the University of Aberdeen, collecting and processing data from within the Moray Firth, and collating the photo-ID data from all other research groups. All other data contributors are acknowledged in each of the chapters.

As this thesis is comprised of chapters that have been published, submitted, or will be submitted for publication in peer-reviewed journals, each includes suggestions to the text from co-authors. In addition, my supervisor, Paul Thompson advised on modelling approaches, analyses and provided suggestions to the text of the manuscripts for all chapters. Phil Hammond provided advice on the analyses for Chapter 3. I prepared and analysed all the data, incorporating analyses code and advice from John Durban (Bayesian multi-site model, Chapter 2), Ross Corkrey (Bayesian state-space model, Chapter 3), Holly Fearnbach (Richard's growth curve analyses, Chapter 4), (David Lusseau (social structure analyses, Chapter 5) and Line Cordes (open robust design multistate model with state uncertainty and seasonal effects, Chapter 6). The references for chapters already published or in review appear as footnotes at the beginning of the respective chapters.

No part of this work has been accepted in any previous application for a degree. All quotations have been distinguished by quotation marks and all sources of information have been specifically acknowledged.

*Barbara Jean Cheney, 2017*

# ABSTRACT

Long-term individual-based studies can be central to collecting data on aspects of individual and population biology and ecology. Photo-identification often underpins long-term individual based studies, particularly for cetaceans. Bottlenose dolphins (*Tursiops truncatus*) are long-lived with low reproductive rates and complex social structures, while showing plasticity in their behaviour, biology and ecology. As such long-term individual based studies are key to investigating the complexities of their population dynamics.

My aim for this thesis was to synthesise over two decades of photo-identification data with the intention of exploring the value and contribution of a long-term individual based photo-identification study and answer key questions about the ecology and biology of bottlenose dolphins in Scottish waters.

This thesis provides the first data on distribution and status of bottlenose dolphins around Scotland. Results highlighted the smaller population on the west coast split into two discrete communities with different ranging patterns and provided the first evidence that the highly mobile east coast population may be increasing. For the east coast of Scotland bottlenose dolphin population, laser photogrammetry identified morphological differences (larger size, no sexual dimorphism, no sex differences in growth) and highlighted fitness consequences to variation in early calf growth (calves that died over their first winter were significantly shorter). This thesis also identified differences in social structure over two decades at the two extremes of the population's range, potentially caused by or a consequence of, range expansion. Finally, this study provided empirical evidence of increasing trends in population abundance, reproductive rate and calf survival. This is a rare example of empirical evidence of a positive trend in demographic parameters of a cetacean population using a marine protected area.

This work highlights the need for long-term individual based data to detect biologically meaningful change and suggests this small bottlenose dolphin population is a conservation success story.

# ACKNOWLEDGEMENTS

First, I want to thank Professor Paul Thompson for giving me the opportunity to work at the Lighthouse Field Station – not only on this amazing project but also on both the northern fulmar and harbour seal projects and even for encouraging (or should I say pushing) me to do this PhD. I appreciate all his advice on fieldwork, analysis and comments on PhD chapters, multiple drafts of manuscripts and many other things too many to mention. I really could not have done this without him.

In addition, I cannot thank Susan Lusseau enough for believing I could do the bottlenose dolphin photo-ID job and training an enthusiastic honours student with little experience. A huge thanks to Tim Barton who is second to none skippering ‘Rona’, driving around the dolphins, solving technical problems and for building the laser photogrammetry equipment - without him the fieldwork would have been much more of a challenge and definitely not as much fun. An equally massive thanks to Becky Hewitt who has been the best office mate and stand in on photo-ID trips and to Isla Graham who is always available to chat through ideas and problems. A further thanks to both for being friends and seeing me through the rough and smooth times with help and support and a laugh every so often.

Of course, I need and want to thank everyone who has ever been one of the ‘Lighthouse Crew’. Including all of those who came before me and collected this great dataset, especially Ben Wilson, John Durban, Kate Grellier, David Lusseau and Nicola Quick who have always been supportive in talking about the brilliance of photo-ID research. To all those that have passed through this amazing place during my time here and made it an interesting and great place to work, especially Kate Brookes, Line Cordes, Kelly More, Helen Bailey, Simon Ingram, Ross Culloch and Enrico Pirotta – friends for life I hope! And all the staff, students and volunteers that have helped out on the project whether it was spotting dolphins in challenging Scottish weather, writing boat notes and/or grading pictures – couldn’t have done it without you. Not forgetting ‘honorary crew’ Charlie Phillips and Sarah Pern for always being happy to talk about photography and ‘the dolphins’.

Data used in this thesis is part of a collaborative project with the University of St Andrews, so of course I cannot forget another huge thank you to Phil Hammond and his SMRU team especially Monica Arso for allowing me to use their photo-ID data. Also, a big thank you to Bob Reid, Andrew Brownlow and the SMASS team for adding blowhole to dorsal fin measurements to their strandings protocol and to Randy Wells and his amazing team for allowing me to join them on surveys and providing health assessment data.

I have to finish where it all started. Of course, I couldn’t have done any of this without the folks. Thank you just isn’t enough for a Mum and Dad who have supported me in an infinite number of ways throughout this crazy career change and have never seemed to doubt my decision.

# CHAPTER 1

## GENERAL INTRODUCTION

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Long-term individual-based studies of animal populations can be central to answering a number of key ecological questions (Clutton-Brock and Sheldon 2010a, Sutherland *et al.* 2013). Repeatedly identifying individuals through time and space provides unique opportunities to collect data on aspects of biology and ecology that otherwise would be difficult or impossible to obtain. Specifically, when ecological processes occur over years or decades (Clutton-Brock and Sheldon 2010a, Sutherland *et al.* 2013); for long-lived species with delayed maturity and low reproductive rates (Bossley *et al.* 2017) and/or for animals that are difficult or impossible to capture, widely distributed, cryptic or highly mobile.

Arguably the first ecological questions to investigate relate to estimating and monitoring population abundance and trends. A variety of approaches are used depending on the population being studied (Schwarz and George 1999). One of the commonly used methods are capture mark recapture techniques where individuals are marked (e.g. tag, brand or photographically) and in simple terms abundance is estimated from the proportion of marked animals recaptured on subsequent occasions (see Buckland *et al.* 2000, Hammond 1986 for further details). Combining the sightings of recognisable individuals collected during individual-based studies with mark recapture techniques can provide accurate and precise abundance estimates, especially for animal populations that cannot be censused. However, some assumptions need to be met to ensure data collection during the study is appropriate, for example capturing as many individuals as possible to provide a representative sample, aiming for an equal probability of capture for all individuals, choosing marks that will be recognised if the animal is seen again and marking in a way that does not affect recapture probability (e.g. photo-identification) (Evans and Hammond 2004). In addition, the long time series of data collected during these studies is often required to provide sufficient power to detect significant trends (Frederiksen *et al.* 2014, Taylor *et al.* 2007, Thompson *et al.* 2000).

Subsequent questions often focus on understanding the mechanisms driving changes or trends in abundance (Frederiksen *et al.* 2014). This requires information on demographic parameters (e.g. survival and fecundity) and how they vary spatially and temporally (Frederiksen *et al.* 2014, Sutherland *et al.* 2013). The most detailed information on these parameters are data from identifiable individuals (Frederiksen *et al.* 2014, Gaillard *et al.* 2010). Specific questions can be answered once age is estimated either by following known individuals from birth (e.g. Albon *et al.* 1987, Mann *et al.* 2000) or capturing known animals and aging through other methods (e.g. teeth, Wells *et al.* (2004)). For example, understanding age-related effects on reproduction and survival, investigating lifetime fitness and how this differs between individuals and age, and linking life stage events to examine variation in growth, reproduction and survival (Clutton-Brock and Sheldon 2010a, Gaillard *et al.* 2010). It took Jane Goodall and her collaborators 50 years to obtain enough data to fully describe chimpanzee life history and answer important ecological questions. For instance, although female reproductive success declined with age there is no evidence of menopause and male dominance is related to number of offspring but younger and less dominant males are more successful than predicted as a result of priority of access (Clutton-Brock and Sheldon 2010b).

The goal is then to identify the drivers of demographic changes to understand the links between environmental variability and population abundance (Frederiksen *et al.* 2014). Long-term individual based studies are key to this as they can help identify the factors affecting individual variation in demographic parameters, whether they are extrinsic (e.g. food availability, environmental conditions) or intrinsic (e.g. density, age, body mass, sex) (Clutton-Brock and Sheldon 2010a, Frederiksen *et al.* 2014). For example, Clutton-Brock *et al.* (1987) found first year red deer (*Cervis elaphus*) survival was related to birth date and weight, but this effect increased with increasing population density. Also, Lindström (1999) discusses how environmental conditions experienced during early development in both bird and mammal species can affect individuals' long-term survival and reproduction. Furthermore, populations' sensitivity and ability to recover from impacts can be predicted with information on life history parameters (Frederiksen *et al.* 2014). Again, long-term studies increase the statistical power to identify drivers of change (Frederiksen *et al.* 2014) and are more likely to include periods with contrasting environmental conditions which allow the investigation of links between demographic and environmental variability (Clutton-Brock and Sheldon 2010a, Frederiksen *et al.* 2014). Although the costs and benefits of primate reproductive strategies can vary due to the availability of food, this can be affected by extreme, but rare, events (e.g. droughts, disease epidemics) and therefore comparing results for only a few years can be misleading (Clutton-Brock and Sheldon 2010b).

Both cross-sectional and population-level studies can provide some answers to some ecological questions (Clutton-Brock and Sheldon 2010a, Lindenmayer *et al.* 2011). Cross-sectional studies tend to be more affordable and take less time than long-term studies. They can also investigate short-term behavioural responses to anthropogenic or environmental change, although demographic responses require longer term studies (Lindenmayer *et al.* 2011). Population-level studies have allowed ecologists to study the effects of environmental variation on populations' abundance, distribution and reproductive timing (Clutton-Brock and Sheldon 2010a). For example, sightings of animals can provide information on distribution and abundance (e.g. Durant *et al.* 2011, Hammond *et al.* 2006). Still, information on effort and sightability is required, quality control can be challenging due to differences in observer experience and it is difficult to infer the drivers of change (Evans and Hammond 2004). Also, monitoring dead animals (e.g. cetacean strandings) have provided information on life history parameters, taxonomy, diet and contaminant loads although even with information on effort, changes could be the result of many factors including both increases or decreases in abundance or changing distribution (Evans and Hammond 2004). However, unlike cross-sectional and population-level studies, long-term individual based studies have greater power to investigate temporal and spatial changes within individuals and populations; distinguish the demographic parameter causing change in population abundance; understand individual variability and account for individual differences (Clutton-Brock and Sheldon 2010a) (e.g. measure how individual heterogeneity affects vital rates or responses to environmental variation (Festa-Bianchet *et al.* 2017)); determine the drivers of variability (Clutton-Brock and Sheldon 2010a, Lindenmayer *et al.* 2011); gain understanding of the long-term fitness consequences of internal changes (e.g. age, body condition) in relation to changing environmental conditions (e.g. environmental or anthropogenic change) (Festa-Bianchet *et al.* 2017); investigate social relationships and structure and determine their effects on reproduction, survival and population dynamics (Clutton-Brock and Sheldon 2010a, Wells 2014).

Even in long-term individual based studies significant changes in abundance and demographic rates can be difficult to detect (Maxwell and Jennings 2005, Taylor *et al.* 2007, Tyne *et al.* 2016). Therefore, more recently questions are being asked about the shorter term responses of individuals to environmental change and anthropogenic affects, the individual fitness consequences of this disturbance and then ultimately the effect on population dynamics (King *et al.* 2015, New *et al.* 2013, Pirotta *et al.* 2015a). For example, a framework has been developed to model the population consequences of disturbance (PCoD) in marine mammals (King *et al.* 2015). Integrating information from long-term individual based studies on individuals' health (e.g. body condition), habitat use, reproductive history and survival can help predict the effect of disturbance on vital rates (Pirotta *et al.* 2015a). This information may facilitate detection of negative impacts of environmental change before they affect population processes (Pirotta *et al.* 2015a).

As such long-term individual based studies often play a key role in conservation and management programmes. They can answer the ecological questions fundamental for effective conservation and management (Baker 2006, Currey *et al.* 2011, Frederiksen *et al.* 2014), allow the evaluation of conservation measures (Baker 2006) and provide reliable estimates of demographic parameters required to inform Population Viability Analyses (PVA), a key tool to identify the effects of different management scenarios (Coulson *et al.* 2001, Thompson *et al.* 2000). Finally, good long-term studies can provide opportunities to broaden research goals, moving the study in new directions and facilitate the introduction of innovative techniques.

However, long-term individual based studies can be challenging to run and maintain. Ensuring consistent funding from existing and new avenues can be problematic. Conservation and management organisations often require consistent research and can be sceptical of funding research that doesn't provide clear and direct management guidance (Clutton-Brock and Sheldon 2010a). However, new funding often requires the research to be productive, push boundaries and open up new areas (Clutton-Brock and Sheldon 2010a). Although, this in itself can be challenging as just maintaining a long time series of data can be all consuming, making it difficult to take time to review priorities and methods, learn from the data already collected and subsequently initiate new analyses and research (Baker 2006). Finally, it can be exacting to keep consistency and quality over time as priorities and researchers change (Clutton-Brock and Sheldon 2010a).

## PHOTO-IDENTIFICATION

Photo-identification (photo-ID, taking photographs of animals and recognising individuals from their naturally occurring marks) is a non-invasive and central research tool in studies in both terrestrial (e.g. Goswami and Madhusudan 2011, Kelly *et al.* 1998) and marine (e.g. Hammond *et al.* 1990, Holmberg *et al.* 2009, Thompson and Wheeler 2008) ecosystems. This technique has been particularly useful for widely distributed, highly mobile, long-lived species that are difficult to or cannot be captured. As such it has been well utilised, particularly for cetaceans, to underpin long-term individual based studies and support both conservation and management. In larger cetaceans the shape, colouration and nicks in tail flukes, skin colouration or callosities (Hammond *et al.* 1990) are used to identify individuals, whereas for small cetaceans nicks in their dorsal fins are generally used (Würsig and Jefferson 1990). Additional marks such as tooth rakes and skin lesions can be used, however the longevity of these marks must be considered (Wilson *et al.* 1999b). This technique in combination with long-term individual based studies has allowed researchers to address fundamental ecological and conservation questions including understanding distribution and movement (e.g. Baird *et al.* 2008, Wilson *et al.* 1997a), abundance (e.g. Calambokidis 2009, Wilson *et al.* 1999b), survival (e.g. Currey *et al.* 2009b, Gormley *et al.* 2012), life history (e.g. Mann *et al.* 2000, Matkin *et al.* 2014) and social structure (e.g. Elliser and Herzing 2013, Lusseau *et al.* 2003, Parsons *et al.* 2009). In addition, photo-ID has been used to explore individual attributes, for example, inferring predation risk from shark wounds (Fearnbach *et al.* 2012) and monitoring epidermal lesions (Wilson *et al.* 2000, Wilson *et al.* 1997b) and body condition (Schick *et al.* 2013). More recently photogrammetry (taking measurements from photographs) has been developed and integrated into photo-ID studies to measure cetacean morphometrics (Durban and Parsons 2006, Rowe *et al.* 2010, Webster *et al.* 2010). This technique can permit quantitative investigation into health and fitness for populations of conservation concern where individuals cannot be captured.

## BOTTLENOSE DOLPHINS

Bottlenose dolphins (*Tursiops spp*.) are arguably one of the most studied terrestrial or marine species and likely the most studied cetacean species. They are highly adaptable and can be found in a variety of different habitats from coastal (e.g. Wilson *et al.* 2004) to offshore (e.g. Hoelzel *et al.* 1998) and fiords (e.g. Currey *et al.* 2009a) to bays (e.g. Nicholson *et al.* 2012). Much of what was initially known about the ecology of bottlenose dolphins came from captivity (e.g. Leatherwood and Reeves 1990, Urian *et al.* 1996), bycatch (Fernandez and Hohn 1998, Leatherwood and Reeves 1990), strandings (e.g. Hohn 1980, Urian *et al.* 1996) and a capture release programme in Sarasota, Florida (Wells 2014). However, individuals within a species and even in the same population can show variability in much of their ecology from home range, movement and connectivity to survival, reproduction and growth (Bowler and Benton 2005). Long-term individual based studies (e.g. Currey *et al.* 2007, Mann *et al.* 2000, Wells 2014, Wilson *et al.* 2004) have shown that bottlenose dolphins are no exception and their plasticity has resulted in variation in many aspects of their ecology both within and between populations. For example, variability in range and movement (e.g. Wilson *et al.* 2004), foraging behaviour (e.g. Connor *et al.* 2000), difference in life history and vital rates (e.g. Currey *et al.* 2011, Henderson *et al.* 2014, Mann *et al.* 2000, Wells *et al.* 1987), female size (e.g. Mann *et al.* 2000), sexual dimorphism (e.g. Hersh *et al.* 1990, Read *et al.* 1993) and social structure (e.g. Ansmann *et al.* 2012, Wells 2014).

Despite being well studied, bottlenose dolphins can be challenging to study. They spend the majority of their time underwater so only certain aspects of their lives can often be observed and studied. They are long-lived, making it difficult to understand their biology and ecology during one or two field season and long-term individual based research has been recognised as a valuable approach for their study (Wells 1991). Also, they tend to be highly mobile and wide ranging, often resulting in only part of a population being researched. However, they can be an important species to study. They can be indicator species for coastal ecosystems (Moore 2008, Wells *et al.* 2004), as their health and population status can reflect both natural and anthropogenic impacts on the species but also on lower trophic levels (Wells *et al.* 2004). For example, as top predators with an opportunistic diet of a variety of fish species and squid they can bioaccumulate contaminants (Wells *et al.* 2004). Extensive studies and widespread distribution has resulted in them being used as model systems. For example, the PCoD framework has been developed to work with bottlenose dolphins populations due to the availability of data on some life history parameters and increasing understanding of the potential impacts of natural and anthropogenic factors on this species (New *et al.* 2013, Pirotta *et al.* 2015a, Pirotta *et al.* 2014). They have also been used as a model system to investigate the complexity of communication and cognition (Janik 2013). In addition, bottlenose dolphins can often be found in habitats that are close to a number of concurrent, possibly cumulative, anthropogenic activities including oil and gas (Thompson *et al.* 2013), marine renewable energy (Bailey *et al.* 2010b), coastal developments (Graham *et al.* 2017, Pirotta *et al.* 2015a); shipping (Bossley *et al.* 2017, Pirotta *et al.* 2015b); fisheries (Cox *et al.* 2004, Read 2008); pollution (Wells *et al.* 2005) and tourism (Bejder *et al.* 2006, Lusseau 2003). Similar to other species with comparable life history traits (e.g. long lived, late reproduction, low fecundity, high adult survival) bottlenose dolphins can be particularly vulnerable to these activities, especially in small populations (Merrick *et al.* 2009). Anthropogenic activities can have direct and indirect effects including death (Cox *et al.* 2004); impacts on health (Schwacke *et al.* 2014, Wells *et al.* 2004), reproduction (Kellar *et al.* 2017, Wells *et al.* 2005) and survival (Currey *et al.* 2009b, McDonald *et al.* 2017); decreases in relative abundance (Bejder *et al.* 2006); short-term behavioural effects (e.g. avoidance and increased dive time, Janik and Thompson 1996, Lusseau 2003) and displacement from habitat (Bejder *et al.* 2006, Graham *et al.* 2017). All of which can be variable in the extent and severity depending on many intrinsic (e.g. population size, health) and extrinsic (e.g. available habitat, exposure amount and distance, confounding variables such as food availability) factors. In addition, the long-term consequences for individuals and populations can be difficult to determine and tend not to be fully understood (New *et al.* 2013). Therefore, there is still much to learn about this species in different areas and populations and information is still required to inform conservation and management.

## STUDY POPULATION

In Scotland conservation and management action is required for bottlenose dolphins (*Tursiops truncatus*) as a result of a number of legal frameworks including the EU

Habitats Directive, the Conservation (Natural Habitats, &c.) Regulation 1994, the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS), the Nature Conservation (Scotland) Act 2004 and the Marine (Scotland) Act 2010. Bottlenose dolphins have been observed and studied around the Scottish coastline with broad scale surveys (Hammond *et al.* 2002), anecdotal reports and dedicated effort based sightings (Anderwald *et al.* 2010, Evans *et al.* 2003), short (Grellier and Wilson 2003, Mandleberg 2006, Stockin *et al.* 2006) and longer term projects (Wilson *et al.* 2004). However, research, conservation and management has focussed on the east coast of Scotland bottlenose dolphin population.

On the east coast of Scotland bottlenose dolphin research began in 1989 (Hammond and Thompson 1991). In 2005 the Moray Firth Special Area of Conservation (SAC) was created under the European Union Habitats Directive (92/43/EEC), one of only two SACs in the UK specifically designated for bottlenose dolphins. This population is of particular interest, both in terms of its position at the edge of the species range and the fact that it is the only resident population in the North Sea (Wilson 1997). There has been concern about this population due to its geographic isolation (Parsons et al 2002), small population size (c. 130) and proximity to human activity (Wilson et al 1999). Previous research predicted an annual decline of 5.7% and approximately 45 years to quasi-extinction (less than 10 dolphins) (Sanders-Reed *et al.* 1999), highlighting the need for a precautionary approach for conservation and management (Thompson *et al.* 2000). Research on this population has included visual surveys from land to investigate fine scale habitat use and behaviour (Bailey *et al.* 2013, Hastie *et al.* 2003); boat-based visual and acoustic line transect surveys to explore habitat use (Bailey and Thompson 2009) and passive acoustic monitoring to study behaviour (Hastie *et al.* 2006, Janik 2000, Pirotta *et al.* 2015b), occurrence and distribution (Bailey *et al.* 2010a, Thompson *et al.* 2011). However, in this long-term study photo-ID has been a key tool for both research (Lusseau *et al.* 2006, Wilson *et al.* 1999a, Wilson *et al.* 1999b, Wilson *et al.* 2004, Wilson *et al.* 1997a) and for conservation and management as part of the SAC site condition monitoring requirements for the EU Habitats Directive (Thompson *et al.* 2009, Thompson *et al.* 2004).

## AIMS AND OBJECTIVES

In ecology, conservation and management countless questions can be asked. However, there are some highly relevant areas that are fundamental to long-term individual based studies where conservation and management is a key objective. These include identifying populations, characterising distribution, monitoring trends in population abundance, documenting social structure, examining health and estimating demographic rates. Each contributes to our knowledge of individuals within a population and to the population itself. With more than two decades of individual based data from a small bottlenose dolphin population on the east coast of Scotland I aim to explore these questions with the objective of discovering what we can learn about the ecology of a population using a long-term photo-ID dataset. This long-term study has previously produced information on abundance (Corkrey *et al.* 2008, Wilson *et al.* 1999b), distribution (Wilson *et al.* 2004, Wilson *et al.* 1997a) and social structure (Lusseau *et al.* 2006). I intend to expand and extend these studies, focusing on specific questions to assist in conservation and management (see below) and taking advantage of over two decades of long-term photo-ID data. Recent work has highlighted the need to measure body condition and monitor vital rates to identify potential impacts before they affect population trends. Therefore, additionally, I aim to add new techniques to fulfil these research requirements and expand this long-term study. Finally, I hope to provide insights into the ecological variability of this population, within and between populations, enabling species comparisons.

Krebs (2001) described ecology as the study of interactions that determine distribution and abundance. Therefore, in Chapter 2 I aim to, for the first time, investigate the distribution, abundance and movements of bottlenose dolphins in Scottish waters. Previously, the east coast had been the focus of research, although, even here information from before the long-term study was scattered. To explore distribution I review Scotland wide sightings data from historical and current records. To estimate abundance and movements I integrate photo-ID data from all existing studies, members of the public and a collaborative study on the west coast, set up as part of a Scottish Government and Scottish Natural Heritage project.

The remainder of my thesis focusses on the bottlenose dolphins on the east coast of Scotland, where annual photo-ID data are available for over two decades. The aim of Chapter 3 is to understand the conservation status of the bottlenose dolphin population that uses the Moray Firth SAC by investigating trends in abundance within the SAC and the wider population that uses this protected area, and explore changing use of the SAC over 21 years. It is an EU requirement to report on the condition of SACs, including the number of animals using the SAC and population trends (Thompson *et al.* 2004), and therefore vital to properly estimate these parameters. The previous estimate of abundance for this population was from the early 90s using a 3 year dataset (Wilson *et al.* 1999b) and further research suggested the population was declining (Corkrey *et al.* 2008, Sanders-Reed *et al.* 1999). Precise and accurate abundance estimates are essential for early detection of a decline (Baker 2006), while small populations are thought to be at a higher risk of extinction (Purvis *et al.* 2000), as there is a greater effect of environmental and demographic stochasticity (Begon *et al.* 2009). For consistency I base the methods on those previously used to estimate both SAC (Wilson *et al.* 1999b) and population trends in abundance (Corkrey *et al.* 2008), with amendments to investigate sampling variation, uncertainty over the proportion of well-marked animals and include data from across the population's home range.

In Chapter 4 I develop and test a laser photogrammetry method that could be easily integrated into standard photo-ID surveys to remotely monitor growth in a wild population. Chapter 3 focuses on monitoring changes in population abundance. However, significant changes can be difficult to detect (Maxwell and Jennings 2005, Taylor *et al.* 2007) potentially delaying conservation initiatives (Thompson *et al.* 2000, Turvey *et al.* 2007). Recognising shorter term changes in growth may allow quicker identification of environmental or anthropogenic impacts, potentially enabling faster implementation of mitigation or conservation. Therefore, I aim to use this method to collect total length measurements of known age individuals to investigate sexual dimorphism, population and individual growth and the impact of early growth on survival.

Social interactions can change spatially and temporally in response to intrinsic and extrinsic factors (Pinter-Wollman *et al.* 2014). Changes in the spatial ecology of this population (Wilson *et al.* 2004) provided a natural experiment to investigate temporal and spatial variation in the population's social structure during a range expansion. In

Chapter 5 I aim to investigate temporal changes in social structure by comparing over two decades of data concurrent with the range expansion from individual dolphins using the SAC. To investigate spatial variation I use more recent data from across the range of the population. Changes to social structure may be used to monitor the health of a population (Parsons *et al.* 2009) and this chapter is a first step in identifying the causes and consequences of changes in social structure.

For conservation and management it is important to reliably estimate demographic rates, to identify those that contribute to changing trends in population abundance and to recognise critical life stages (Manlik *et al.* 2016). In Chapter 6 I aim to use a new method, accounting for imperfect detections and misclassification (i.e. uncertainty in breeding status) (Kendall *et al.* 2003), to investigate trends in reproduction and early survival and identify the probable demographic factors affecting changes in population abundance.

The general discussion summarises the key findings; examines the consequences; discusses how this work can inform conservation and management; and presents the value of continuing this study and ideas to add new research opportunities that can work within the existing study.

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# CHAPTER 2

## INTEGRATING MULTIPLE DATA SOURCES TO ASSESS THE DISTRIBUTION AND ABUNDANCE OF BOTTLENOSE DOLPHINS *TURSIOPS TRUNCATUS* IN SCOTTISH WATERS

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### ABSTRACT

The distribution, movements and abundance of highly mobile marine species such as bottlenose dolphins *Tursiops truncatus* are best studied at large spatial scales, but previous research effort has generally been focused on relatively small areas, occupied by populations with high site fidelity. We aimed to characterise the distribution, movements and abundance of bottlenose dolphins around the coasts of Scotland, exploring how data from multiple sources could be integrated to build a broader-scale picture of their ecology. We reviewed existing historical data, integrated data from ongoing studies, and developed new collaborative studies to describe distribution patterns. We adopted a Bayesian multi-site mark-recapture model to estimate abundance of bottlenose dolphins throughout Scottish coastal waters, and quantified movements of individuals between study areas. The majority of sightings of bottlenose dolphins around the Scottish coastline are concentrated on the east and west coasts, but records are rare before the 1990s. Dedicated photo-identification studies in 2006 and 2007 were used to estimate the size of two resident populations: one on the east coast from the Moray Firth to Fife, population estimate 195 (95% highest posterior density intervals, HPDI: 162-253) and the second in the Hebrides, population estimate 45 (95% HPDI: 33-66). Interaction parameters demonstrated that the dolphins off the east coast of Scotland are highly mobile whereas those off the west coast form two discrete communities. We provide the first comprehensive assessment of the abundance of bottlenose dolphins in the inshore waters of Scotland. The combination of dedicated photo-identification studies and opportunistic sightings suggest that a relatively small number of bottlenose dolphins (200

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[1] This chapter has been published as: Cheney, B., Thompson, P. M., Ingram, S. N., Hammond, P. S., Stevick, P. T., Durban, J. W., Culloch, R. M., Elwen, S. H., Mandleberg, L., Janik, V. M., Quick, N. J., Islas-Villanueva, V., Robinson, K. P., Costa, M., Eisfeld, S. M., Walters, A., Phillips, C., Weir, C. R., Evans, P. G. H., Anderwald, P., Reid, R. J., Reid, J. B. & Wilson, B. (2013) Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. *Mammal Review*, 43, 71-88.

to 300 individuals) occur regularly in Scottish coastal waters. On both east and west coasts, re-sightings of identifiable individuals indicate that the animals have been using these coastal areas since studies began.

## INTRODUCTION

The widespread distribution of bottlenose dolphins *Tursiops truncatus* has made them an iconic species throughout many countries and cultures. Their tendency to inhabit both oceanic and coastal habitats has also brought them into conflict with a broad range of human activities (Bailey *et al.* 2010, Dawson and Slooten 2005, Lusseau 2003, Palka and Rossman 2001, Wilson *et al.* 2000). Consequently, most of the research currently being conducted on the species (http://www.iwcoffice.org/sci_com/scprogress.htm) is focused towards gathering data to inform conservation and management. For obvious reasons, the majority of this research has been carried out on the more accessible populations (Connor *et al.* 1992, Wells *et al.* 1987, Wilson *et al.* 1999). Conversely, populations that are at lower densities, have unpredictable distributions, are highly mobile or live in inaccessible locations have tended to receive less attention.

Distribution, movements and abundance of highly mobile marine species such as bottlenose dolphins are clearly best studied at relatively large spatial scales, but this can present enormous challenges. In North America the US Mid-Atlantic Bottlenose Dolphin Catalog project (Urian *et al.* 1999) and in Europe the Pelagos Sanctuary Marine Protected Area project (Gnone *et al.* 2011) are excellent but rare examples of a large-scale approach. In the US study, data from individually identified bottlenose dolphins have been shared between independent research projects and at least sixteen field sites to understand distribution and abundance of the dolphins that range along the western Atlantic coast of the United States (www.ml.duke.edu/faculty/read/mabdc.html; Urian *et al.* 1999). This approach has revealed a complex mixture of movements among different components of the population(s), informing federal management and leading to the development of seasonally variable management units (Hohn 1997). In Europe, photo-identification data from 10 different research groups were analysed to estimate abundance, distribution and movements of bottlenose dolphins in the Mediterranean Sea Pelagos Sanctuary. Again, differences in movements were found: most dolphins showed high site fidelity but a few ranged widely. Two (sub) populations were identified and designation of Special Areas of Conservation (SAC) was recommended (Gnone *et al.* 2011).

There is a potentially analogous scenario for populations of bottlenose dolphins off the Atlantic coasts of western Europe. As with the coastlines of the eastern United States, dolphins can be found along almost the entire coastline from Spain to the British Isles (Reid *et al.* 2003). The north of Scotland appears to be the northern extreme of the coastal range; instances of this species occurring at higher latitudes are rare (Wilson 1995). Some bottlenose dolphins occur further north but, being encountered off the shelf edge, these animals presumably belong to offshore rather than coastal populations (Skov *et al.* 1995). Within the coastal environment, our knowledge of the ecology of bottlenose dolphin populations in western Europe is more fragmented than knowledge of the populations mentioned above. This is because key long-term research projects to date have been focused on a series of apparently isolated populations with high site fidelity to relatively small coastal areas (notably: the Sado Estuary, Portugal, Harzen 1998, dos Santos *et al*. 2005; Western Brittany, Guinet *et al*. 1993, Liret *et al*. 1995; Cardigan Bay, Pesante *et al*. 2008, Pierpoint *et al*. 2009; Shannon Estuary, Ireland, Ingram and Rogan 2002; and the Moray Firth, Scotland, Wilson *et al.* 1997, 2004, Hastie *et al*. 2006, Culloch and Robinson, 2008, Bailey and Thompson 2009). These populations typically range in size from the low tens of individuals to the low hundreds (Liret *et al.* 1995, Wilson *et al.* 1999). However, while the majority of research effort has focussed on these populations, the western European coastal waters are also frequented by a number of less well known groupings. Some of these have been seen regularly, others sporadically or over a number of years before disappearing (examples include groups in south west England, Wood 1998; Sound of Barra, Scotland, Grellier and Wilson 2003; southern North Sea, Kayes 1985; English Channel, Williams *et al*. 1997). In addition, records from national sighting reporting schemes or other survey efforts suggest that other dolphins lack clear links to particular areas or recognised populations (Evans 1980, Reid *et al.* 2003).

Bottlenose dolphins in European waters are protected by a series of legislative agreements, particularly the European Union Habitats Directive (92/43/EEC), the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) and, in the United Kingdom, the Biodiversity Action Plan for Small Cetaceans

(Anonymous 1995, Baxter 2001). In particular, the European Union Habitats Directive has focused effort to protect this species by spatial designations of SACs. Several of these have been set up in European waters and are located around the best known and most site-faithful groupings of dolphins (for example Wales: Anonymous 2008a, Scotland: Anonymous 2009b). Because of the monitoring requirements for these sites, conservation research has been focused into these areas. Thus on-going conservation efforts and research are biased against areas where the animals are more mobile, dispersed or typically only occur in small groups.

In this manuscript, we characterise the distribution, movements and abundance of bottlenose dolphins around the coasts of Scotland. In doing so, we aim to explore how data from multiple sources can be integrated to build a picture of the contemporary ranging patterns and abundances of several potential populations of dolphins inhabiting the area. To achieve this, we built upon what were previously unconnected research programmes and extended these with wider ranging research effort that was actively informed by opportunistic sightings from the public and boating communities.

## METHODS

### Study Area

Scotland has a long and convoluted coastline with over 750 islands (Anonymous 2003). The largest island groups are Shetland and Orkney to the north, and the Hebrides to the west. The islands feature complex coastlines, separated by sounds and firths with strong tidal currents. The north and west coast of Scotland have a fjordic coastline with a number of deep, narrow, sheltered sea lochs. The east coast features long stretches of coastline with little shelter and is dominated by two major estuarine embayments, the Firth of Forth and the Moray Firth (Baxter *et al.* 2008). The Moray Firth has the only SAC for bottlenose dolphins in Scotland, as designated in 2005 under the European Habitats Directive (92/43/EEC). The SAC encompasses the waters of the Moray Firth west of a line drawn from Helmsdale on the northern coast to Lossiemouth on the south coast (Figure 1).

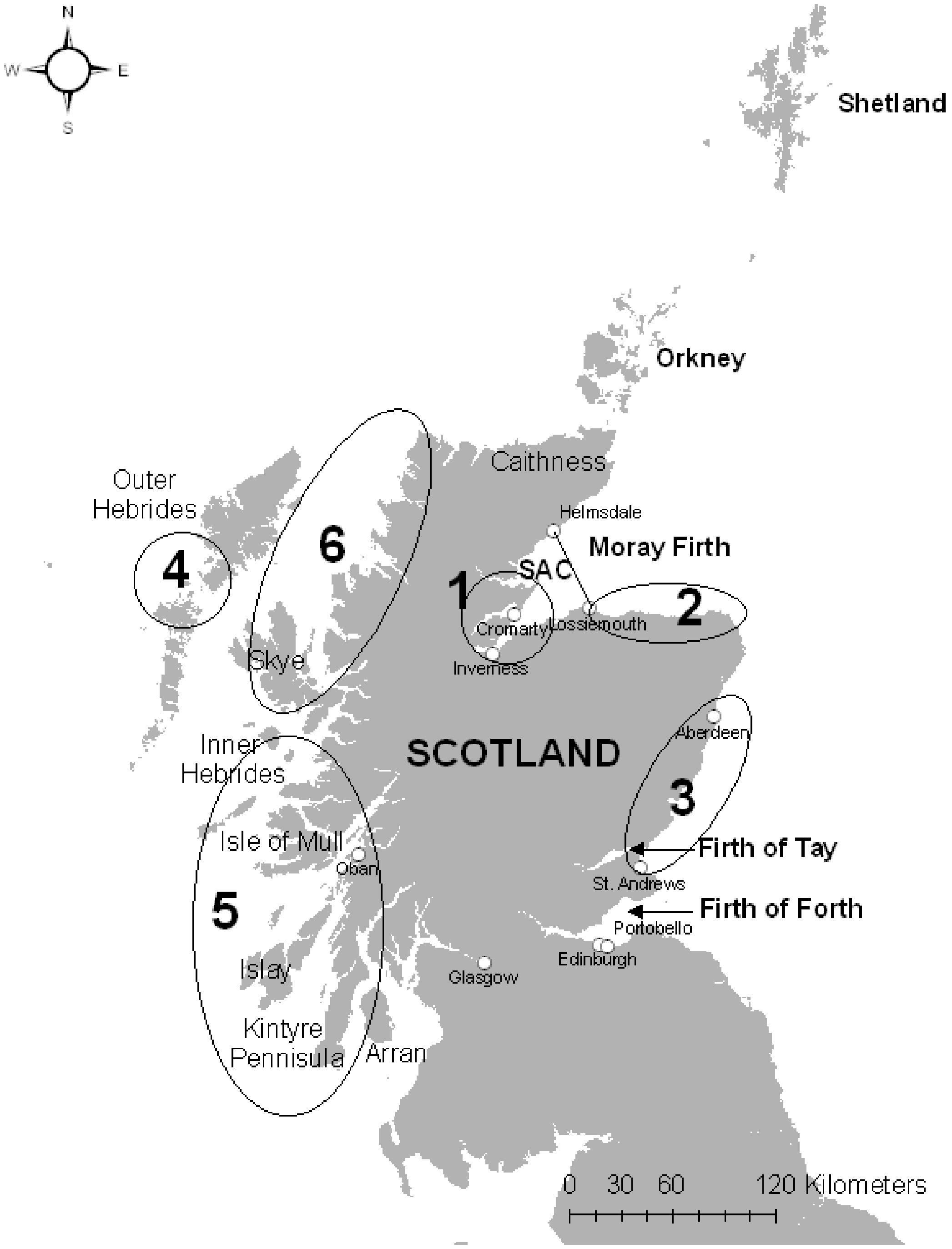

Figure 1. Map of Scotland showing the key locations mentioned in the text and the areas used for the multi-site mark-recapture analysis of bottlenose dolphins (Area 1-Inner Moray Firth, Area 2-Southern Moray Firth, Area 3-Grampian/Fife Coast, Area 4-Sound of Barra, Area 5-South of Skye and Area 6-Skye and North).

**Data Sources for Historical Review**

Our review of the historical distribution of bottlenose dolphins around Scotland was based upon the collation of records from a wide variety of published and unpublished sources. Early sightings were sought from antiquarian books by naturalists describing Scottish fauna and flora. Since 1913, the Natural History Museum of London has recorded cetacean strandings, including bottlenose dolphins, around the coasts of England, Scotland and Wales (Fraser 1934, 1946, 1953, 1974, Harmer 1927, Sheldrick 1989, Sheldrick *et al.* 1994). The National Stranded Whale Recording Scheme was set up in April 1990 for a co-ordinated investigation of the ecology and biology of cetaceans around Britain (http://www.nhm.ac.uk/research-curation/research/projects/strandings/). Since 1992, this scheme's work within Scotland has been carried out by the Scottish Agricultural College Veterinary Services (Inverness).

The Joint Nature Conservation Committee (JNCC) has integrated data from three main sources to produce an atlas of cetacean distribution (Reid *et al.* 2003). Firstly, this draws upon the European Seabirds at Sea database which contains year round cetacean records collected by JNCC and sister organisations in other European countries (Reid *et al.* 2003). Secondly, it includes effort-based data collected by the Sea Watch Foundation (see below). Finally, it includes data from the Small Cetacean Abundance in the North Sea (SCANS) surveys (Hammond *et al.* 2002). To create each of the distribution maps in the JNCC atlas, all data from 1979 to 1997 were converted to a common format, adjusted for effects of sea state upon detection rates, and only sightings which were related to effort were included (Reid *et al.* 2003).

The Sea Watch Foundation (formerly the UK Mammal Society Cetacean Group) has been collecting marine mammal sightings in UK and Irish waters since the mid 1960s from their network of observers including zoologists, ornithologists, fishermen, yachtsmen and the coastguard (Evans 1980, 1992, Evans *et al.* 2003). All sightings are entered into the Sea Watch National Database.

The Hebridean Whale and Dolphin Trust (HWDT) have been collecting bottlenose dolphin sightings from members of the public dating back to 1989. These records include casual sighting data that were collected from a number of different sources (Jeewoonarain *et al.* 1999, Mandleberg 2006) and sightings obtained from dedicated cetacean surveys conducted by the HWDT (see Embling *et al.* 2010).

In 2005, the SCANS-II survey was carried out to repeat and extend the SCANS survey conducted in 1994 (Anonymous 2008b, Hammond *et al.* 2002). This survey provided coverage of offshore as well as inshore areas of the continental shelf around Scotland. Additional data on offshore sightings were also available from JNCC through the Marine Mammal Observer programme that has been conducted since 1997 during seismic operations (Stone 2003).

## Current Abundance

Estimates of the abundance of bottlenose dolphins in Scottish coastal waters for 2006 and 2007 were obtained from mark-recapture analyses of an integrated dataset, comprising individual recognition data from photo-identification studies by all the groups conducting dedicated research programmes in Scotland.

### *Photo-Identification Data Collection, Processing and Quality Assurance*

Data were available from studies conducted along the east coast of Scotland from 1) the University of Aberdeen in the inner Moray Firth (see Wilson *et al.* 1999, Wilson *et al.* 2004, Wilson *et al.* 1997, Wilson 1995 for survey details), 2) the Cetacean Research and Rescue Unit along the southern coast of the Moray Firth (see Culloch and Robinson 2008, Eisfeld 2003, Robinson *et al.* 2007 for survey details), 3) the South Grampian Regional Group of the Sea Watch Foundation along the Aberdeen coast (see Stockin *et al.* 2006, Weir *et al.* 2008 for survey details) and 4) the University of St Andrews around the Firth of Tay (see Islas-Villanueva 2010, Quick and Janik 2008 for survey details). Additional data from the Moray Firth were also available from the Whale and Dolphin Conservation Society surveys that were made from land-based observation points in the inner Moray Firth and from commercial dolphin watching vessels along the southern coast of the Moray Firth (Thompson *et al.* 2011).

Although details of data collection varied among research groups, all researchers carried out targeted photo-identification surveys during the summer months aimed at obtaining high quality photographs from as many bottlenose dolphins as possible within their respective study areas. Systematic review and filtering of data (see below) minimised any differences in data quality resulting from differences in these studies' protocols.

In an additional collaborative study, the University of Aberdeen, University of St Andrews, Scottish Association of Marine Science and HWDT extended photo-identification efforts to coastal waters off the west and north coasts of Scotland in May to September, 2006 and 2007. Searching for animals was initially directed by our review of historic sightings, but sightings in these areas have typically been patchy in both space and time. To maximise the chance of obtaining photo-identification pictures of animals in these areas, we developed the existing HWDT sightings network to encourage real time reporting of bottlenose dolphin sightings by the public and other marine users. We targeted promotion of the sightings network particularly in the less frequently surveyed parts of the west and north coasts of Scotland. Members of the public and wildlife tour operators were also encouraged to send in photographs of bottlenose dolphins. Although data quality can be a concern, photographs are verifiable and were subjected to rigorous quality control (see below).

All collaborators provided the best quality picture of each side of each of the well-marked dolphins (i.e. animals with dorsal fin nicks that could be identified from either the left or right side) photographed in 2006 and 2007. All pictures were graded for photographic quality according to criteria adapted from Wilson *et al.* (1999). Only high quality photographs in which the dorsal fin comprised more than 10% of total image height, was in focus, was parallel to the photographer, and photographs in which the complete trailing edge of the fin was visible, were used in this analysis.

Photographs of animals identified during 2006 and 2007 were compared within and among studies to determine whether individuals had been seen in multiple study areas. The unique combination of nicks, tooth rake scars and pigmentation patterns on each dolphin were used to identify individuals (Würsig and Würsig 1977). A catalogue of individually recognisable bottlenose dolphins seen on the east coast of Scotland has been maintained by the University of Aberdeen and the University of St. Andrews since 1989. Each of the dorsal fin pictures obtained from other groups working on the east coast was initially compared with this catalogue by one experienced researcher. On the west coast of Scotland, the HWDT had also maintained a bottlenose dolphin photo-identification catalogue between 2001 and 2005 (Mandleberg 2006). Individuals were also identified during surveys conducted in the Sound of Barra in 1995 and 1998 (Grellier and Wilson 2003). Both these catalogues were reviewed, and individuals for which there were high quality pictures (as defined above) were kept for matching to more recent pictures obtained in all these areas during 2006 and 2007. Finally, these catalogues from the east and west coast were compared. All matches between research groups were confirmed by at least two experienced researchers (Table 1).

Table 1. Number of well-marked individual bottlenose dolphins *Tursiops truncatus* identified in high quality photographs by each collaborating research group and by members of the public in Scotland, UK, in photo-identification surveys in 2006 and 2007.

| Group | 2006 | 2007 |
|---|---|---|
| **East Coast of Scotland** | | |
| University of Aberdeen | 45 | 47 |
| University of St. Andrews | 48 | 44 |
| Cetacean Research and Rescue Unit | 51 | 29 |
| Whale and Dolphin Conservation Society | 39 | 43 |
| Sea Watch Foundation (South Grampian Regional Group) | 8 | 26 |
| **West Coast of Scotland** | | |
| University of Aberdeen | 18 | 22 |
| Hebridean Whale and Dolphin Trust | 5 | 3 |
| Members of the public | 4 | 13 |

In addition, archive photographs of some particularly well-marked animals were made available by all collaborators. These data provided an opportunity to detect long-range movements that could be occurring over longer time-scales (Robinson *et al.* 2012). We compared archive photographs of well-marked animals from west coast and east coast studies, to determine whether individuals had been seen in multiple study areas in earlier years.

### *Estimation of Abundance and Study Area Interactions*

The multi-site mark-recapture framework described by Durban *et al.* (2005) was used to estimate abundance and movements of animals between study areas from data stratified into three areas on the east coast and three areas on the west coast of Scotland. A Scotland-wide analysis was not possible because of the lack of exchange of animals between the east and west coasts in 2006 and 2007 (see results). On the east coast: Area 1, the inner Moray Firth, included data from the University of Aberdeen boat-based surveys and the Whale and Dolphin Conservation Society land-based observations; Area

2, the southern Moray Firth coast, included data from the Whale and Dolphin Conservation Society boat-based surveys and the Cetacean Research and Rescue Unit; and Area 3, the Grampian and Fife coast, included data from the Sea Watch Foundation and the University of St Andrews (see Figure 1). On the west coast, data from our collaborative photo-identification study in 2006 and 2007 were integrated with those provided by the public, and assigned to three areas: Area 4, the Sound of Barra; Area 5, all waters to the south of Skye; and Area 6, all waters around Skye and to the north (see Figure 1). Areas were chosen based on each collaborating group's established research sites, which represented good geographical separation throughout the known home range of bottlenose dolphins around Scotland.

Following Durban *et al.* (2005), simple contingency tables were constructed for the east and west coasts separately, the cells of which referred to discrete categories formed by the combination of the three study areas on each coast (Figure 1). The corresponding cell counts denoted the number of well-marked individuals that were photographed in each combination of study areas (Table 2). A Bayesian statistical approach was used to fit hierarchical log-linear models for the cell counts in order to predict an estimate into the empty cell for the count of the number of missed individuals that were not identified at any of the areas, and therefore estimate overall abundance of well-marked animals (Durban *et al.* 2005). The general log-linear model contained effects for each study area, describing the relative number of individuals identified in each area, and parameters for the interaction between study areas, reflecting relatively high or low levels of movement of individuals between areas. Only study area interaction terms with significant deviation from zero interaction were incorporated in model selection. Different models could be produced by omission of one or more of these interaction effects and we produced a model averaged estimate for the total number of well-marked individuals ($N$), weighted by the relative plausibility of the candidate models. Model averaging and prediction was accomplished using Gibbs sampling Markov chain Monte Carlo (MCMC) methods implemented in WinBUGS software (Lunn *et al.* 2000). This approach allows for data collected opportunistically and concurrently by different groups at different study sites based on practicalities rather than random design, as it estimates the geographical dependencies between sites (Durban *et al.* 2005).

To expand this estimate to the total abundance (*P*), data on the number of individuals with and without dorsal fin nicks in each trip were used to estimate the proportion of well-marked individuals in the population. Specifically, the number of well-marked individuals was treated as a binomial sample of the total number of individuals seen on each trip, with a common (average) binomial probability representing the proportion of well-marked individuals ($\theta$). A flat Beta (1,1) prior distribution was adopted for $\theta$ with probability mass equally spaced between 0 and 1. The mark-recapture model for well-marked individuals *N* and proportion of well-marked individuals $\theta$ were linked to form a single probability model through the relationship $P = N/\theta$, and rounded to the nearest whole number (Durban *et al.* 2010). In this way, the uncertainty from both the mark-recapture and mark-rescaling components was combined by jointly sampling from each in the same MCMC run. The 95% highest posterior density intervals (HPDI) were also calculated directly from the MCMC output. In the absence of sufficient data on the proportion of well-marked animals from all areas, we estimated this proportion from the most comprehensive datasets collected by the University of Aberdeen within the Moray Firth and west coast, and assumed this was constant on each coast.

Table 2. East and west coast cross-area contingency table used in the multi-site mark-recapture model showing the number of well-marked individual bottlenose dolphins identified each year (2006 and 2007) in different combinations of the three study areas (Y means that the individuals were seen in the areas; N means not seen, so for example, in 2006, 13 individuals were seen in areas 2 and 3, but these individuals were not seen in any other area). No dolphins were seen in both the east and west coasts of Scotland, UK, in 2006 or 2007. For locations of areas, see Figure 1.

| **East Coast** | | | | | **West Coast** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Inner Moray Firth (Area 1)** | **Southern Moray Firth (Area 2)** | **Grampian / Fife Coast (Area 3)** | **Number of well-marked Dolphins 2006** | **Number of well-marked Dolphins 2007** | **Sound of Barra (Area 4)** | **South of Skye (Area 5)** | **Skye and North (Area 6)** | **Number of well-marked Dolphins 2006** | **Number of well-marked Dolphins 2007** |
| Y | N | N | 7 | 20 | Y | N | N | 7 | 8 |
| N | Y | N | 2 | 1 | N | Y | N | 0 | 0 |
| N | N | Y | 28 | 40 | N | N | Y | 3 | 5 |
| Y | Y | N | 28 | 17 | Y | Y | N | 0 | 0 |
| Y | N | Y | 1 | 0 | Y | N | Y | 0 | 0 |
| N | Y | Y | 13 | 5 | N | Y | Y | 8 | 9 |
| Y | Y | Y | 9 | 10 | Y | Y | Y | 0 | 0 |
| **Total number of well-marked dolphins** | | | 88 | 93 | **Total number of well-marked dolphins** | | | 18 | 22 |

## RESULTS

### Historical Literature

Historical records confirm that bottlenose dolphins have been present in Scottish waters since at least the late 1800s (Herman 1992). However, until the late twentieth century sightings of this species appear to have been relatively rare. Running anti-clockwise around the Scottish coast, reports of this species on the south east coast of Scotland were absent (Sim 1903). Evans (1892) recorded five to seven museum specimens from the Firth of Forth, including one stranded at Portobello in 1833-34. Most of the records from the Moray Firth area also suggest that bottlenose dolphins were seen less often than other species, particularly harbour porpoises *Phocoena phocoena* (Harvie-Brown and Buckley 1895, Smiles 1876, Taylor 1898, 1899). The first documented bottlenose dolphin stranding in the Moray Firth occurred in 1897 (Taylor 1899); another stranding of six individuals was reported in 1901 (Taylor 1902). Bottlenose dolphins are simply listed as present in lists of fauna from Caithness (Harvie-Brown and Buckley 1887). In Orkney, one stranding of two probable bottlenose dolphins was recorded in 1888 (Buckley and Harvie-Brown 1891). Neither Evans and Buckley (1899) nor Venables and Venables (1955) report this species as occurring in Shetland. In the Outer Hebrides (Harvie-Brown *et al.* 1888), bottlenose dolphins are included in a list of mammals occurring in the area. Similarly in the Inner Hebrides, there is only mention of a single sighting in contrast to frequent sightings of harbour porpoises (Harvie-Brown and Buckley 1892). A single stranding was recorded in a west coast sea loch in 1879 (Herman 1992).

### Contemporary Information

#### ***Strandings***

Since regular stranding records have been kept by the Natural History Museum of London, there have been 72 bottlenose dolphins reported stranded around the coast of Scotland between 1929 and 2008 (Figure 2). Most of these animals were reported in the Moray Firth and the Hebrides, and the majority (78%) were in the 1990s and 2000s.

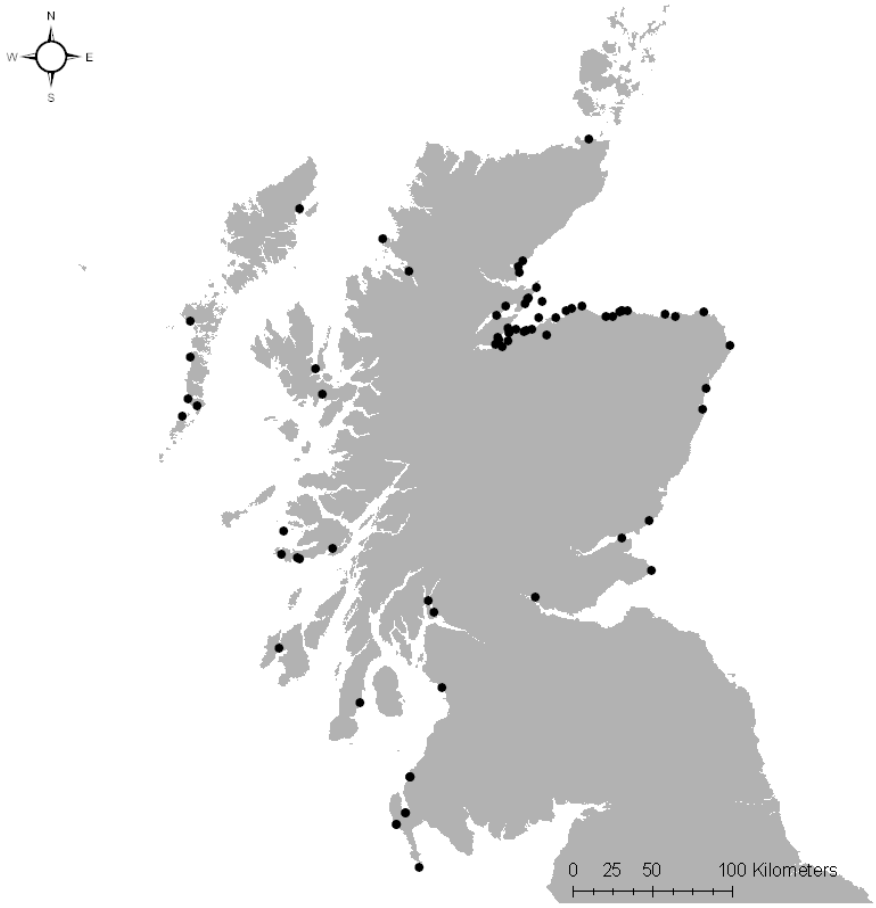

Figure 2. Locations of strandings of bottlenose dolphins around Scotland from 1929 to 2008, as recorded by the Scottish Agricultural College in Inverness and the Natural History Museum, London, UK.

***Sightings***

The JNCC cetacean atlas presents the distribution of bottlenose dolphins in north-west Europe from 1979 to 1997. In Scotland the highest sightings rates were in the north-east, specifically around the Moray Firth (Figure 3). However, there were also sightings on the west coast (especially the Outer Hebrides) and a few south of Shetland.

Three sightings of bottlenose dolphins were recorded in Scottish waters during SCANS-II (Figure 4). Marine Mammal Observers have also observed bottlenose dolphins in more offshore waters to both the west and east of Scotland during seismic operations (Figure 4).

The Sea Watch Foundation and the HWDT provided sightings of bottlenose dolphins around the Scottish coast from July 1966 to October 2007 (Figure 5).

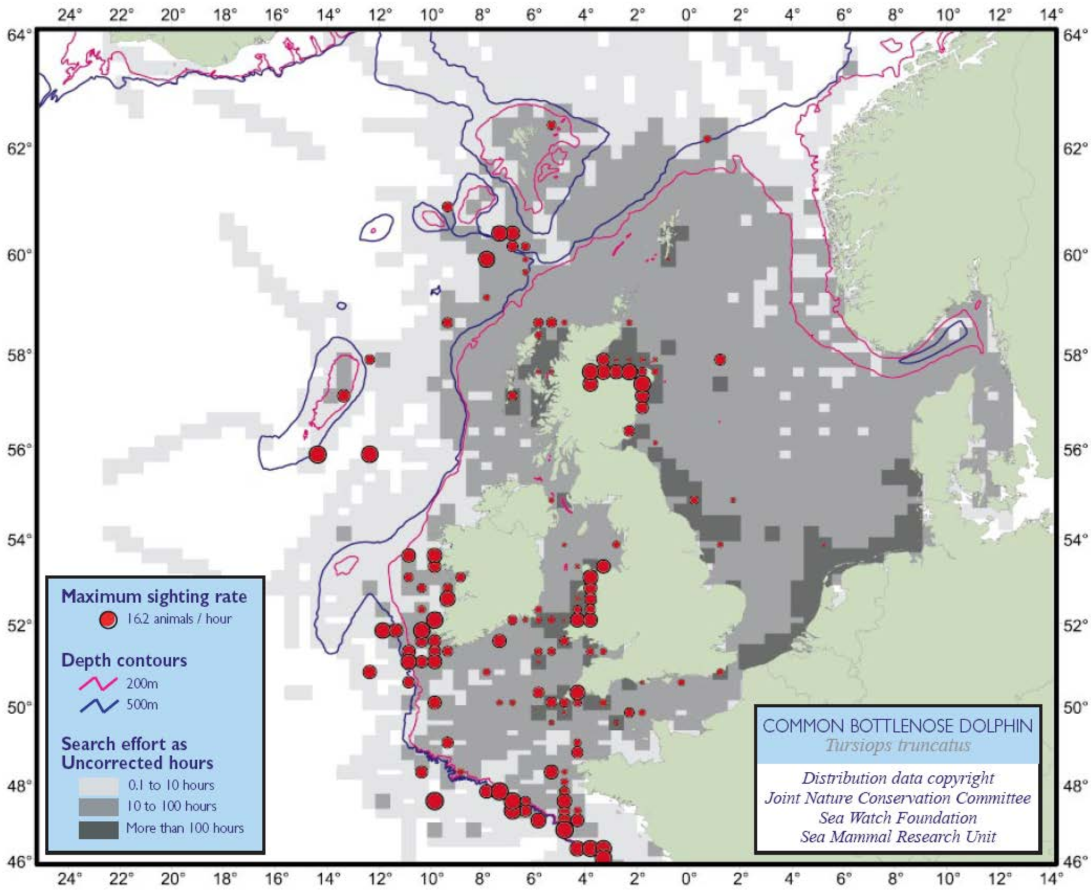

Figure 3. Bottlenose dolphin distribution in north-west Europe, from the JNCC Cetacean Atlas. The map depicts grid cells ($^1/_4$ International Council for the Exploration of the Seas rectangles, 15' latitude x 30' longitude) that are shaded, the greater the survey effort in the cell the darker the shading. The size of the red dots (which represent sightings) indicates the relative sighting rate (reproduced from Reid et al. 2003).

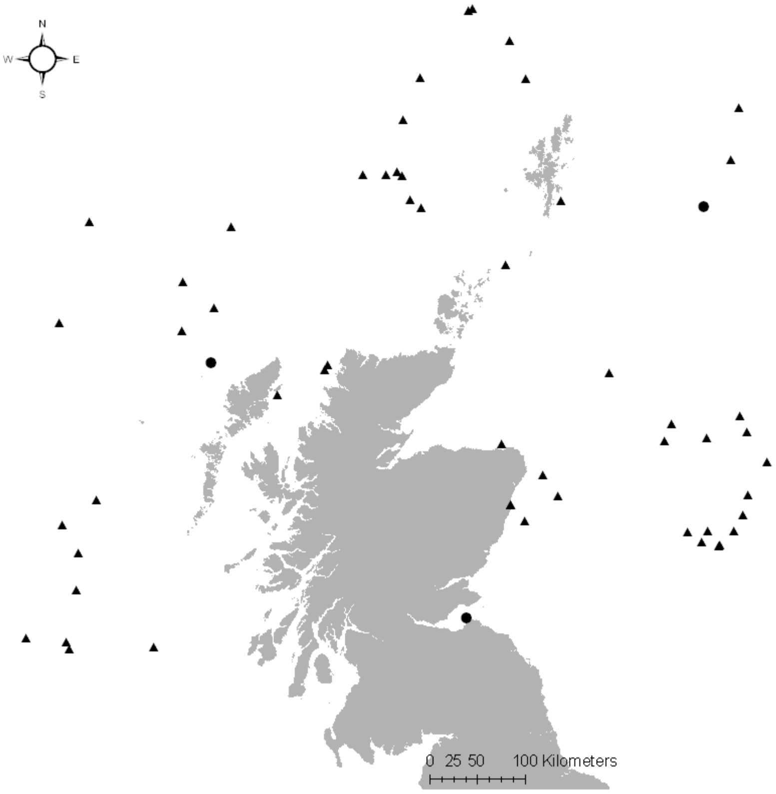

Figure 4. Sightings of bottlenose dolphins around Scotland recorded during SCANS-II (Small Cetacean Abundance in the North Sea) in 2005 (circles) and during seismic surveys conducted between 1994 and 2006 (triangles).

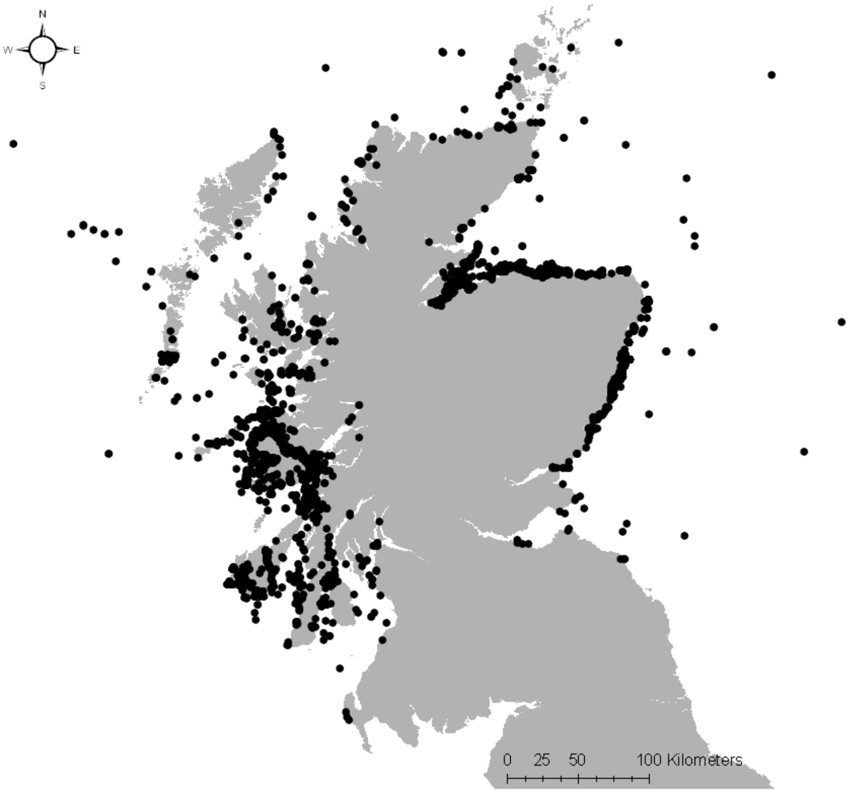

Figure 5. Sightings of bottlenose dolphins around Scotland from 1966 to 2007, recorded by the Sea Watch Foundation and the Hebridean Whale and Dolphin Trust.

## Abundance Estimates

### *East coast*

Totals of 88 and 93 well-marked individuals were identified from the highest quality photographs in the summers of 2006 and 2007, respectively. In both 2006 and 2007 a high proportion of individuals (57%) were recorded in more than one of the three study areas (Table 2). Model-averaged posterior estimates of the total number of well-marked individuals in 2006 and 2007 were 104 and 136 (Table 3). Estimates of the proportion of well-marked animals in the population in 2006 and 2007 were 0.53 (95% HPDI: 0.48-0.58) and 0.60 (95% HPDI: 0.55-0.65), giving estimates of total abundance of 195 and 227, respectively, with 95% HPDI ranging between 162 and 384 (Table 3).

Of the 98 well-marked individuals identified in either 2006 or 2007, 36% were seen in the first two years of research carried out by the University of Aberdeen and University of St. Andrews in 1989 and 1990. Two individuals were seen in all 19 years of the study and 65% were seen in at least 10 individual years.

Table 3. Model averaged estimates of a) the number of well-marked individuals (N) and b) the total number of all individual (P) bottlenose dolphins using the east and west coast of Scotland in the summers of 2006 and 2007. 95% highest posterior density intervals (HPDI) are shown for each estimate.

| | **2006** | | **2007** | |
|---|---|---|---|---|
| | **Median** | **95% HPDI** | **Median** | **95% HPDI** |
| a) Well-marked individuals (*N*) | | | | |
| East Coast | 104 | 89-132 | 136 | 107-231 |
| West Coast | 25 | 19-37 | 30 | 23-42 |
| b) All individuals (*P*) | | | | |
| East Coast | 195 | 162-253 | 227 | 175-384 |
| West Coast | 45 | 31-71 | 45 | 33-66 |

### *West coast*

Totals of 18 and 22 well-marked individuals were identified from the highest quality photographs in the summers of 2006 and 2007, respectively (Table 2). Of the 22 well-marked individuals seen in 2007, eight were from the Sound of Barra, and 14 were seen in the Inner Hebrides. Model-averaged estimates of the total number of well-marked individuals in 2006 and 2007 were 25 and 30 (Table 3). Estimates of the proportion of well-marked animals in the population in 2006 and 2007 were 0.56 (95% HPDI: 0.43-0.69) and 0.67 (95% HPDI: 0.57-0.77), giving estimates of 45 in both years, with 95% HPDI ranging between 31 and 71 (Table 3).

Around the Sound of Barra, four of the individuals seen in 2006 and 2007 were first seen in 1995/1998 by Grellier and Wilson (2003). The first bottlenose dolphin photo-identification pictures we have from the Inner Hebrides were taken in 2001. Although three individuals seen in 2006 and 2007 in the Inner Hebrides were also seen in 2001 and 2002, these were in poorer quality photographs, and the majority of animals were identified from 2004 onwards.

### Study Area Interactions

#### *East coast*

There were notable movements of individuals between areas: 51 and 33 well-marked individuals were seen in more than one area in each year (2006 and 2007), and 9 and 10 individuals were seen in all three areas. In both years, the movement of individuals was greatest between the inner and southern Moray Firth (37 and 27 individuals), as indicated by the positive estimated interaction effects for these areas in the model (Table 4). There was a weaker positive interaction between the southern Moray Firth and the Grampian/Fife coast, but less movement of individuals between the two areas (22 and 15 individuals in 2006 and 2007, respectively). Conversely, there was a strong negative estimated interaction effect between the inner Moray Firth and Grampian/Fife coast, indicating relatively low levels of movement (10 individuals) between these most geographically separate of areas. For 2007 there was a high probability of all the interaction effects being selected for inclusion in the model, but in 2006 there was little support for the southern Moray Firth and the Grampian/Fife coast interaction. The posterior distribution for this interaction effect overlapped zero, in contrast to the other interactions where the distribution covered only positive and only negative values (Table 4). The multi-site mark-recapture model incorporated these interaction terms and inclusion probabilities when using MCMC sampling to predict overall abundance (Durban *et al.* 2005).

***West coast***

There was movement of individuals only between Skye and north and south of Skye: 8 and 9 well-marked individuals were seen in both of these areas in 2006 and 2007, as indicated by the positive interaction between them. Conversely, there was a negative interaction between Skye and north and the Sound of Barra, with no movement between these areas (Table 5). Both these interactions had a high probability of inclusion in the model, but there was little utility to adding an interaction between the south of Skye and Sound of Barra areas, as the low numbers of dolphins identified in both these areas led to very imprecise estimates of the distributions for interaction effects, which significantly overlapped with zero.

Table 4. East coast of Scotland estimates of all study area interactions in the multi-site mark-recapture model describing the study area counts (Table 1). Estimates are presented as the median (95% highest posterior density intervals) of the posterior distribution for each parameter, and the probability (p) of each possible interaction being selected for inclusion in the model. The upper diagonal denotes interactions for 2006 and the lower for 2007.

| | **Inner Moray Firth (Area 1)** | **Southern Moray Firth (Area 2)** | **Grampian/Fife Coast (Area 3)** |
|---|---|---|---|
| **Inner Moray Firth (Area 1)** | | 1.4<br>(0.5, 3.4)<br>*p* = 0.99 | -1.3<br>(-3.3, -0.5)<br>*p* = 1.0 |
| **Southern Moray Firth (Area 2)** | 2.0<br>(0.9, 6.0)<br>*p* = 1.0 | | -0.2<br>(-1.9, 0.5)<br>*p* = 0.3 |
| **Grampian/Fife Coast (Area 3)** | -0.2<br>(-1.7, -0.2)<br>*p* = 0.8 | 1.0<br>(0.2, 3.4)<br>*p* = 0.95 | |

Table 5. West coast of Scotland estimates of all study area interactions in the multi-site mark-recapture model describing the study area counts (Table 1). Estimates are presented as the median (95% highest posterior density intervals) of the posterior distribution for each parameter, and the probability (p) of each possible interaction being selected for inclusion in the model. The upper diagonal denotes interactions for 2006 and the lower for 2007.

| | **Sound of Barra (Area 4)** | **South of Skye (Area 5)** | **Skye and North (Area 6)** |
|---|---|---|---|
| **Sound of Barra (Area 4)** | | -1.2<br>(-9.8, 6.6)<br>*p* = 0.4 | -5.9<br>(-17.9, 0.2)<br>*p* = 0.8 |
| **South of Skye (Area 5)** | -0.9<br>(-9.6, 6.9)<br>*p* = 0.3 | | 6.5<br>(0.3, 17.9)<br>*p* = 0.8 |
| **Skye and North (Area 6)** | -6.7<br>(-18.7, -0.4)<br>*p* = 0.8 | 6.4<br>(0.2, 17.5)<br>*p* = 0.8 | |

## DISCUSSION

Historic and contemporary sightings from naturalists and members of the public can provide a useful indication of the broad scale distribution of bottlenose dolphins around the Scottish coast. However, inferences from these data are constrained both by uncertainty over the reliability of species identification, and by spatial and temporal variation in sightings effort. Data on strandings are generally less vulnerable to misidentification issues, but are also potentially biased due to the lower likelihood of reporting on remote coasts and the relevance of the location of stranding relative to living distribution.

Historical literature sources provide little evidence for the occurrence of bottlenose dolphins in Scottish waters. There are no known archaeological sites in Scotland, and naturalists' reports suggest that the occurrence of bottlenose dolphins in the late 1800s was sporadic compared with that of other species such as harbour porpoise, killer whales *Orcinus orca* and pilot whales *Globicephala* sp. Nevertheless, it is clear from our review of more recent strandings and sightings that bottlenose dolphins are now present both in offshore waters and throughout most Scottish inshore waters. Reid *et al.* (2003) provide the most robust effort-corrected data set for comparing density in different areas, although their analysis is restricted to data collected before 1998. Their data (Figure 3) highlight the high relative densities along the east coast of Scotland and the occurrence of dolphins further offshore along the shelf edge. Sightings around the rest of the Scottish coastline were rare in this dataset (Figure 3), but search effort was also relatively low. Additional sightings from the Sea Watch Foundation and the HWDT (Figure 5), many of them reported since 1997, provide evidence of widespread occurrence of bottlenose dolphins in the Inner Hebrides. There have been relatively few reports of bottlenose dolphins on the north coast of mainland Scotland or around Orkney and Shetland (Figs. 4 and 5) and some of these sightings are by members of the public (Figure 5) where there is less certainty over species identification. Confusion with species such as Risso's dolphin *Grampus griseus* and white-beaked dolphin *Lagenorhynchus albirostris* that are more commonly seen in these areas (Reid *et al.* 2003) is of particular concern. Despite efforts to solicit additional reports from the north coast, only one sighting was reported from this area during 2006 and 2007. Photographs submitted by members of the public confirmed that individuals that we recorded on the west coast in 2006 and 2007 were subsequently recorded on the north coast in 2008 (University of Aberdeen unpublished data).

Variation in the effort underpinning these sightings constrains the extent to which these data truly indicate geographical variation in the density of bottlenose dolphins. Similarly, temporal variation in sighting effort makes it difficult to assess how the occurrence of dolphins in different areas may have changed over time. Over the last two decades, sightings have only been consistently reported from two areas: the east coast of Scotland (Anderwald *et al.* 2010, Wilson *et al.* 2004) and the Sound of Barra (Grellier and Wilson 2003). The east coast has one of the highest human population densities of the Scottish coast, but the Sound of Barra is one of its most remote areas. Regular reports of sightings in both these areas from members of the public provide some support for the assumption that the regular occurrence of dolphins in any part of the Scottish coast is now unlikely to remain undetected. Bottlenose dolphins have also been reported in many other remote areas of Scotland (see Figure 5), but the temporal pattern of these sightings appears much more patchy, and there is no evidence of predictable sightings at the same location either within or between years.

## Estimates of Abundance

We draw together all available photo-identification data to produce the first comprehensive estimates of abundance of bottlenose dolphins in inshore waters of mainland Scotland and the Western Isles.

### *East coast*

Our 2006 estimate (195, 95% HPDI: 162-253) provides the most precise indication of the current size of the Scottish east coast bottlenose dolphin population (Table 3). This result is similar to that produced by Durban *et al.* (2005), who used a smaller data set from the same areas to demonstrate the methodology used here, and estimated this population as 85 (95% HPDI: 76-263) well-marked dolphins in 2001, compared to our estimate of 104 (95% HPDI: 89-132) well-marked dolphins in 2006.

Previous studies of bottlenose dolphins in Scottish coastal waters have been focused on the east coast population, particularly in the Moray Firth. The integration of photo-identification data collected by all research groups working on this population has provided an abundance estimate that was higher than the first, and most commonly used, estimate for this population, of 129 in 1992 (Wilson *et al.* 1999). However, it is important not to over-interpret the significance of this difference. Wilson *et al.* (1999) used Chao *et al.* (1992) $M_{th}$ model, implemented in the programme CAPTURE (Rexstad and Burnham 1991). Also, the 95% confidence intervals of the 1992 estimate (110-174) overlap with the 95% HPDI for our most precise recent estimate (162-252). Unfortunately, data collection methods in each collaborating research group did not allow a direct comparison of methodologies. Further work is required to determine whether or not the overall size of the east coast population has changed over this period. However, assessment of this is complicated by the fact that the geographical range of this population has changed over the last 20 years (Wilson *et al.* 2004) and survey effort in different areas has also changed in response to this. Consequently, these two sets of estimates differ both in the detail of data collection and in the statistical approach to estimation. The 2006 estimate may be higher because survey design in the earlier studies resulted in an estimate that was negatively biased, because of differences in the mark-recapture model used for the two estimates, because our new estimate covers more of the home range of this population, or because the population has increased over the last two decades.

### *West coast*

For the west coast, our estimates for 2006 (45, 95% HPDI: 31-71) and 2007 (45, 95% HPDI: 33-66) are identical but the estimate for 2007 is slightly more precise and we consider this to be the best estimate of the number of bottlenose dolphins in the area. The only previous estimate for this area is from the Sound of Barra, where Grellier and Wilson (2003) estimated 6-15 individuals from data collected in 1995 and 1998. This compares well with our data from 2006 and 2007, which indicated that a total of 13-15 individuals used the waters around the Sound of Barra.

### *Scottish bottlenose dolphin abundance in a wider context*

Estimates from larger-scale surveys illustrate that our estimates for mainland Scotland and the Western Isles are a small proportion of the populations living in European waters. The SCANS-II line transect survey estimate of bottlenose dolphin abundance in European Atlantic continental shelf waters from 62ºN to the Straits of Gibraltar in 2005 was 12645 (95% CI: 7500-21300; Anonymous 2008b). This survey was not designed to estimate abundance in small areas, so no direct comparison is possible with our estimates. However, SCANS-II estimates from survey blocks that included Scottish waters (including Orkney and Shetland) were of the same order of magnitude (100s) as our estimates. In 2007, offshore surveys of waters (deeper than 200m) to the west of the SCANS-II survey area produced an estimated 19295 (95% CI: 11842-31440) bottlenose dolphins, 5700 (95% CI: 2900-11100) in waters north of 53ºN, including offshore Scottish waters (Anonymous 2009a). In both these surveys, researchers were unable to correct for animals missed on the transect line in analyses, so the estimates are negatively biased.

This estimate of just 200-300 bottlenose dolphins in Scottish coastal waters contrasts with the estimates of the number of offshore animals, an order of magnitude larger, that have been obtained through these large-scale surveys. The relationship between offshore groups and those occurring in coastal waters remains uncertain, although more detailed studies in the NW Atlantic suggest that inshore and offshore populations are often ecologically and genetically discrete (Hoelzel *et al.* 1998). Nevertheless, some offshore animals may occasionally strand on Scottish coasts and this is a potential confounding factor when using samples from stranded individuals to explore population structure.

### Study Area Interactions

#### *East coast*

There was significant movement of individuals between all the east coast study areas, and a number of individuals were seen in all three areas. However, the results show a higher rate of exchange of dolphins between the two geographically closest areas (inner and southern Moray Firth).

Although these results do not provide information on the ranging patterns of individual dolphins, they clearly demonstrate that the population of bottlenose dolphins off the east coast of Scotland is highly mobile: individuals range from the inner Moray Firth to Fife. However, one confirmed sighting in 2007 of a group near Whitley Bay and the Tyne river mouth suggests that individuals occasionally range further south (Thompson *et al.* 2011). This population cannot, therefore, be subdivided into separate units based on area alone. The results of genetic analyses (Parsons *et al.* 2002, Thompson *et al.* 2011) show some but not complete isolation between animals found on the east and west coasts and elsewhere in Britain and Ireland. Together, these results confirm that the east coast population should continue to be considered as a single separate unit for management purposes.

#### *West coast*

In both years the majority of individuals were observed in waters around Skye and to the north, and few individuals were seen south of Skye and in the Sound of Barra. Despite observations of significant movements of dolphins throughout the west coast, none of the individuals identified in the Sound of Barra was seen elsewhere. This suggests that there are two discrete communities of bottlenose dolphins on the west coast of Scotland, which we recommend should be considered as separate units for management purposes, pending further study.

### *Scottish bottlenose dolphin movement*

Photographs of well-marked dolphins from 2006 and 2007 from all collaborating organisations and comparisons of the east and west coast catalogues, maintained by the University of Aberdeen and the HWDT respectively, produced no matches, suggesting that there is no movement of bottlenose dolphins between the east and west coast of Scotland. However, archive photographs from previous years did provide evidence for such movement. Seven individuals that were photographed along the southern shore of the outer Moray Firth by the Cetacean Research and Rescue Unit in 2001 were later recorded on the west coast by the HWDT between 2002 and 2005 and by the University of Aberdeen in 2006 and 2007 (Robinson *et al.* 2012). Furthermore, subsequent comparisons have shown that 5 of these dolphins could also be matched with bottlenose dolphins photographed around the coasts of the Republic of Ireland (Robinson *et al.* 2012). These photographic matches support the results of the genetic analysis in showing only partial isolation between dolphins found around the Scottish coasts (Parsons *et al.* 2002, Thompson *et al.* 2011).

## CONCLUSIONS

Existing data indicated a wide but patchy distribution of bottlenose dolphins in Scottish waters. This review based on the combination of historical records, dedicated photo-identification studies and third party reports has allowed us to expand our research efforts, and examine distribution and abundance even in areas with low density, where animals are unpredictable and highly mobile. Our study suggests that a relatively small number of bottlenose dolphins (200-300 individuals) occur regularly in Scottish coastal waters. Multi-site mark-recapture estimates indicate that the numbers on the east coast are approximately five times higher than those on the west coast. On both coasts, re-sightings of identifiable individuals indicate that some of the animals recorded during our surveys in 2006 and 2007 have been using these coastal areas since studies began in 1989 on the east coast and 1995 on the west coast. The number of animals using other parts of the Scottish coastline, for example the north coast, appears to be low, but further investigation of the occurrence of dolphins on this coast may now be justified given recent evidence of movement between east and west coasts and the strategic importance of this area for marine renewable energy developments.

Our study suggests that there are 3 parapatric communities of bottlenose dolphins in Scottish coastal waters, each of a different size and with marked contrasts in their ranging patterns. On the west coast there are two small and socially segregated communities of dolphins, one of which includes approximately 15 individuals that have only been recorded in the waters around the Sound of Barra, whereas the other is double that size and ranges more widely throughout the Inner Hebrides and mainland coasts. On the east coast there is a population of nearly 200 interacting dolphins between the Moray Firth and Fife, with individual differences in ranging behaviour and site fidelity.

Analyses of photo-identification data from multiple studies have also shown that bottlenose dolphins can make long-distance movements between the east and west coasts of Scotland, and further exchange between Scottish and Irish waters has recently been revealed (Robinson *et al.* 2012). Whether these movements represent exchange between different coastal communities or interaction with more widely ranging offshore animals remains uncertain, but this finding suggests that it would be worthwhile to continue making comparisons between photo-identification catalogues from Scottish and other European waters. Importantly, this finding also highlights the value of maintaining long-term research effort in each of these areas. Without the long-term archives available through previous projects, these rare movements would not have been detected. However, considerable resources would be required to maintain long-term photo-identification studies throughout Scottish coastal waters, and monitoring programmes of this kind are only likely to be sustainable if they are integrated into broader research projects and collaborations, education programmes, or ecotourism operations.

## ACKNOWLEDGEMENTS

This project depended upon collaboration with a range of different organisations, and we thank all our colleagues who have contributed to the challenging field work required to collect the data. The success of field work on the remoter coasts of Scotland was also dependent upon input from members of the public living, working and taking holidays in these areas. We are indebted to all those who responded to the call for information, and particularly thank those who contributed photographs that could be used for photo-identification. The information coming from these contributions surpassed all our expectations. The core project was funded jointly by Scottish Natural Heritage and the Scottish Government, and we thank Elaine Tait, Louise Cunningham, Karen Hall, Fiona Manson, Katie Gillham, Sam Kelly, Evanthia Karpouzli and Ian Walker who supported this project through its steering group. Many aspects of the project have also benefited from close integration with related studies that have been funded from a variety of sources. In particular we thank the Whale and Dolphin Conservation Society, Talisman Energy (UK) Ltd., Earthwatch Europe, Chevron, the European Union, and the Natural Environment Research Council for additional support. Thanks also to the South Grampian group of the Sea Watch Foundation and everyone who contributed to the Aberdeen Cetacean Catalogue. We thank JNCC, the public body that advises the UK Government and devolved administrations on UK-wide and international nature conservation. The St Andrews Bay efforts were funded by a Royal Society University Research Fellowship, a fellowship of the Wissenschaftskolleg zu Berlin and studentships from NERC and the Mexican National Council for Science and Technology (CONACYT).

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# CHAPTER 3

## LONG-TERM TRENDS IN THE USE OF A PROTECTED AREA BY SMALL CETACEANS IN RELATION TO CHANGES IN POPULATION STATUS

# CHAPTER 3

## LONG-TERM TRENDS IN THE USE OF A PROTECTED AREA BY SMALL CETACEANS IN RELATION TO CHANGES IN POPULATION STATUS [2]

### ABSTRACT

The requirement to monitor listed species in European designated sites is challenging for long-lived mobile species that only temporarily occupy protected areas. We use a 21 year time series of bottlenose dolphin photo-identification data to assess trends in abundance and conservation status within a Special Area of Conservation (SAC) in Scotland. Mark-recapture methods were used to estimate annual abundance within the SAC from 1990 to 2010. A Bayesian mark-recapture model with a state-space approach was used to estimate overall population trends using data collected across the populations' range. Despite inter-annual variability in the number of dolphins within the SAC, there was a >99% probability that the wider population was stable or increasing. Results indicate that use of the SAC by the wider population has declined. This is the first evidence of long-term trends in the use of an EU protected area by small cetaceans in relation to changes in overall population status. Our results highlight the importance of adapting the survey protocols used in long-term photo-identification studies to maintain high capture probabilities and minimise sampling heterogeneity. Crucially, these data demonstrate the value of collecting data from the wider population to assess the success of protected areas designated for mobile predators.

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[2] This chapter has been published as: Cheney, B., Corkrey, R., Durban, J. W., Grellier, K., Hammond, P. S., Islas-Villanueva, V., Janik, V. M., Lusseau, S. M., Parsons, K. M., Quick, N. J., Wilson, B. & Thompson, P. M. (2014) Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status. Global Ecology and Conservation, 2, 118-128.

## INTRODUCTION

Estimation of abundance and trends underpins population ecology and is essential to inform management and conservation efforts (Krebs 2001). In some countries, regular assessments of abundance are also a legislative requirement to support conservation of protected species (e.g. Wade and Angliss 1996) or areas (Cowx *et al.* 2009). In Europe, the Habitats Directive (92/43/EEC) requires the designation of Special Areas of Conservation (SACs) as a measure to help protect species listed in Annex II. The Directive requires Member States to report on the conservation status of these species on a six year cycle, including information on their abundance within the protected area (European Union 1992). However, it is challenging to design cost-effective survey programmes that can assess population status, particularly for mobile species that commonly range across the boundaries of protected areas (Hammond *et al.* 2013).

This problem is particularly acute for cetaceans as they are often widely distributed, highly mobile and spend a high proportion of time underwater, making it difficult to obtain accurate and precise abundance estimates. A long time series of data is typically needed to provide sufficient statistical power to detect trends from estimates of abundance (Taylor *et al.* 2007, Thompson *et al.* 2000, Wilson *et al.* 1999). For example, Taylor *et al.* (2007) highlight that most marine mammal stocks in the USA have inadequate data to detect a 50% decline in abundance over 15 years. While some studies have used sightings surveys to identify long-term trends in large whale populations (Branch and Butterworth 2001, Buckland and Breiwick 2002, Moore and Barlow 2011), published data on abundance trends in coastal small cetaceans are rare (see Fearnbach *et al.* 2012 for a recent exception). Nevertheless, information on abundance is available from many small cetacean populations through photo-identification based mark-recapture methods (Berrow *et al.* 2012, Currey *et al.* 2011, Durban *et al.* 2000, Gormley *et al.* 2012, Nicholson *et al.* 2012, Pesante *et al.* 2008). These long-term studies can provide time series of abundance estimates for evaluating trends and informing the management of protected areas established for these populations. However, there are two issues that need to be considered when developing survey programmes for small cetaceans in these areas.

First, whilst standardised survey protocols are preferred in long-term ecological studies (Currey *et al.* 2007, Magurran *et al.* 2010), these can overlook the dynamic way in which populations use their range, introducing bias and increasing uncertainty in abundance estimates (Forney 2000). In mark-recapture studies, both short term (e.g. Nicholson *et al.* 2012, Parra *et al.* 2006) and long-term (e.g. Wilson *et al.* 2004) temporal changes in distribution or ranging patterns may introduce heterogeneity in capture probabilities along otherwise standardised survey routes, resulting in biased abundance estimates. Where these changes occur during a longer-term study, survey protocols may need to be adapted to reduce sampling heterogeneity. Similarly, developments in technology, statistical techniques, changing research priorities, logistics or financial constraints may all lead to modifications to survey protocols over time (Lindenmayer and Likens 2009, Ringold *et al.* 1996). The consequences of such flexible approaches must be explored before drawing inference from a long-term time series. Of particular concern to photo-identification mark-recapture studies, where some individuals do not have markings that can be reliably identified between annual survey seasons, are potential changes in the proportion of distinctive or well-marked animals. An accurate estimate of this proportion is required to account for non-distinct animals when estimating total abundance (e.g. Durban *et al.* 2010, Gormley *et al.* 2005, Lukoschek and Chilvers 2008, Read *et al.* 2003, Wilson *et al.* 1999). Longer-term temporal changes in this proportion may have an underlying biological basis, for example if age or sex differences in the occurrence of distinctive marks exist, a trend may reflect changes in population age or sex structure. However, it may also be affected by survey protocols. For example, photo quality and mark distinctiveness can be correlated due to photographer bias if more time is spent obtaining quality pictures of well-marked animals (Read *et al.* 2003).

Secondly, survey effort is typically focused on monitoring abundance trends within only part of the overall range of the population. This means that monitoring programmes generally only provide information on variation in the abundance of individuals using a specific area rather than changes in the population itself (Forney 2000). In some cases, monitoring may only be conducted within a protected area (Berrow *et al.* 2012, Gnone *et al.* 2011, Gormley *et al.* 2005). Yet European Directives aim to designate networks of core sites that support the conservation status of the wider population (European European Union 1992). Robust design methods could be used to assess the extent of seasonal emigration in and out of such sites (e.g. Nicholson *et al.* 2012, Smith *et al.* 2013). However, the collection of at least some information from the wider population may be needed to assess the relative value of the protected area itself (Hooker and Gerber 2004), and this typically requires a modelling framework that can be used with much sparser data from less frequent surveys (e.g. Corkrey *et al.* 2008).

Here, we explore these issues using a continuous 21 year time series of data from photo-identification surveys of bottlenose dolphins (*Tursiops truncatus*) off north-east Scotland. Our aim was firstly to use core annual survey data to assess trends in abundance within an SAC over the last two decades, thereby allowing the UK government to contribute to their reporting requirements under the EU Habitats Directive. We then go on to use Corkrey *et al.* (2008) state-space mark-recapture model which incorporates other data sources to estimate overall trends across the entire population range, and combine these data to investigate temporal changes in the use of this protected area.

## METHODS

### Study Population and Photo-Identification Survey Methods

The study monitored the bottlenose dolphin population that occurs along the east coast of Scotland (Cheney *et al.* 2013, Wilson *et al.* 2004). In response to the 1992 EU Habitats Directive, part of this population’s range was designated as the Moray Firth Special Area of Conservation in 2005 (Figure 1a).

Between 1990 and 2010, multiple boat-based photo-identification surveys were carried out each summer (May to September) within the area that was subsequently designated as the Moray Firth SAC (Table 1 and Table A1 in the Appendix). From 1990 to 2000, most surveys followed a fixed route through the core areas that were used regularly by dolphins at that time (Figure 1a) (Wilson *et al.* 1997). From 2001 onwards, in response to changes in the distribution of dolphins within this area (Wilson *et al.* 2004), more flexible survey routes were chosen to maximise sighting probability both within the original core study area and other parts of the SAC (Figure 1b). All surveys were made from small (5-6m) boats with outboard engines (Thompson *et al.* 2011, Wilson *et al.* 1997). The time and position of all encounters were noted, and the boat was carefully manoeuvred at slow speed around dolphins to obtain high quality pictures of the left and right sides of the dorsal fins of as many individuals as possible. Photographs were taken with an SLR camera, with transparency film until 2001 and digital imagery thereafter.

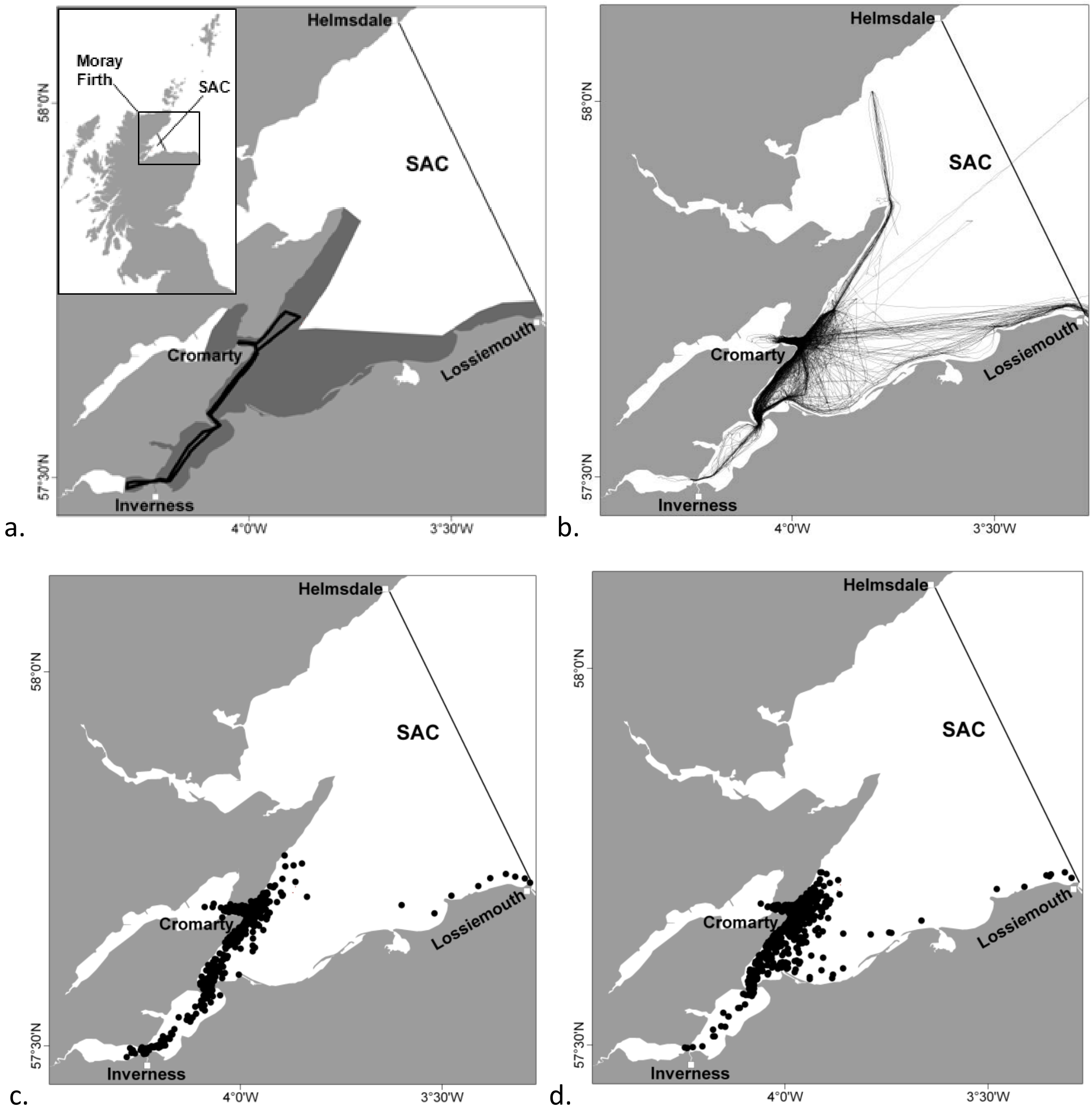


Figure 1. The Moray Firth Special Area of Conservation (SAC) with photo-identification surveys a. the fixed survey route for the majority of surveys (>80%) from 1990-2000 (black line), with occasional surveys in other areas (grey shading), b. GPS tracks of flexible surveys from 2001 onward, and the location of all bottlenose dolphin encounters in c. 1990-2000, and d. 2001-2010. Inset shows the location of the Moray Firth and the boundary of the SAC.

Table 1: Summary of the survey protocols and variables used in the generalised linear mixed models from the two decades of photo-identification surveys in the Moray Firth Special Area of Conservation. The annual mean (± standard error) are shown (full details in Table A2).

| SURVEY PROTOCOLS & VARIABLES | 1990-2000 | 2001-2010 |
|---|---|---|
| Survey Route | Fixed | Flexible |
| Camera | Film | Digital |
| Number of SAC surveys | 19 (± 2) | 29 (± 2) |
| Survey duration (hours) | 6.1 (± 0.3) | 4.2 (± 0.5) |
| Number of encounters | 58 (± 6) | 80 (± 5) |
| Encounter duration (minutes) | 31 (± 2) | 30 (±2) |
| Survey time spent with dolphins | 28% (± 2%) | 35% (± 3%) |
| Number of well-marked dolphins | 35 (± 2) | 47 (± 2) |
| Number of new calves identified | 7 (± 2) | 7 (± 1) |
| Number of capture occasions | 13 (± 2) | 24 (± 1) |
| Number of captures | 74 (± 9) | 230 (± 24) |

In most years, some data were also collected during less regular summer (May to September) surveys in other parts of the population's range (see Figure A1) (Cheney *et al.* 2013). These data were collected using standardised photo-identification procedures (Cheney *et al.* 2013, Islas-Villanueva 2010, Quick and Janik 2008, Quick *et al.* 2008, Wilson *et al.* 2004) but the design and number of surveys varied among years and survey areas (see Table A1).

All photo-identification pictures were graded for photographic quality (Wilson *et al.* 1999) and analyses restricted to the highest quality photographs (Cheney *et al.* 2013). Each image was matched against a catalogue of known individuals from the east coast of Scotland and all matches were confirmed by at least two experienced researchers.

### Trends in Abundance within the Special Area of Conservation

Annual abundance was estimated using a modification of the approach developed by Wilson *et al.* (1999). Previously, estimates were derived separately for left and right sides, but this led to high sampling variation in some years. Here, we based estimates on well-marked individuals with nicked dorsal fins that could be identified from both sides, and produced a single capture history combining left and right sides for each year. Goodness of fit tests in program CAPTURE (Rexstad and Burnham 1991) suggested that the Chao *et al.* (1992) $M_{th}$ model was the most appropriate model for the majority of years with the $M_t$ model for the remaining years. We implemented both models in CAPTURE. In all but four years the $M_{th}$ model estimates were larger, indicating that there was heterogeneity of capture probabilities in our data (Chao *et al.* 1992). Therefore the $M_{th}$ model was used to estimate the number of well-marked individuals during each summer field season and capture probabilities for each survey. This closed model was appropriate as abundance estimates were made independently for each year.

High quality pictures were used to assess the proportion of well-marked animals on each survey (θ), calculated separately for the left and right sides (because dolphins with no nicks may not be identified from both sides). Trend in θ over time was explored using a generalised linear model (GLM) with binomial error distribution and logit link. Variability in θ in relation to different biological and sampling variables was then considered using generalised linear mixed models (GLMMs) with binomial error distribution and logit link. This GLMM approach accounted for repeated measures and non-independence between the left and right side estimation of θ, using survey as a random effect. Biological variables included numbers of well-marked animals and new calves identified each year. Sampling variables included the total number of surveys, number of encounters, cumulative number of well-marked individuals identified (captures) and the number of surveys where at least one well-marked dolphin was identified in a high quality picture (capture occasions). Changes to our survey protocols were also considered, including the change from a fixed survey route to flexible surveys and from film to digital cameras (see Table A2 for details). As some of these explanatory variables were collinear, each was separately considered in its own GLMM fitted with maximum likelihood in the lme4 package (Bates *et al.* 2014). Model selection was carried out using Akaike Information Criterion (AIC) (Burnham and Anderson 2002) and all analysis was carried out in in R version 3.0.2 (R Core Team 2013).

The proportion of well-marked animals (θ) was estimated using the GLMM with the lowest AIC (see results). This was used to inflate the annual mark-recapture estimates of well-marked animals ($\widehat{N_t}$) for each year *t* 1990 to 2010 to estimate total annual abundance ($N_{t\ total} = \widehat{N}_t/\theta$ ) (see results). Assuming $N_{t\ total}$ is log normally distributed, the upper and lower 95% confidence intervals were estimated, by dividing and multiplying $N_{t\ total}$, respectively, by:

$$e^{1.96\sqrt{\ln(1+CV^2_{N_{t\,total}})}}$$

where:

$$CV^2_{N_{t\,total}} = \frac{var(\hat{N}_t)}{\hat{N}_t^2} + \frac{var(\theta)}{\theta^2}$$

A linear regression was used to determine whether there was a trend in abundance within the SAC between 1990 and 2010.

**Trends in Population Size**

Data from outside the SAC were sparser (see Table A1), especially in the early part of the time-series, and capture probabilities were often low. Therefore, a Bayesian mark-recapture model with a state-space approach (Corkrey *et al.* 2008) was used to estimate abundance and trends for the total population. Capture histories were created to record whether or not well-marked individuals were sighted anywhere in the population's known range (see Cheney *et al.* 2013) during each summer (May to September) field season. This model incorporates a series of sub-models including an underlying population model (to provide probability distributions for modelling the well-marked population), an observation model (to provide probability distributions of capture probabilities to estimate the size of the well-marked population), a model to inflate for non-distinct individuals and a Cormack-Jolly-Seber recapture model (which incorporates heterogeneity of capture probabilities across individuals). This model explicitly accounts for heterogeneity and uncertainty, can use sparse sightings data and provides a probability of whether the population is in decline or increasing (for full model details see Corkrey *et al.* 2008). Markov chain Monte Carlo (MCMC) simulation was used to obtain estimates of the posterior distribution of abundance estimates, and derive posterior means and variances. The model was fitted in Fortran compiler G95, version 0.93, for 1,000,000 iterations with a 50% burn in. This produced annual estimates from 1990 to 2010 of the total number of bottlenose dolphins using the east coast of Scotland with 95% highest posterior density intervals (HPDI).

A Bayesian linear regression model ($\mathrm{W_t}' = \mathrm{W_I} + \mathrm{W_S} \times (\mathrm{t}-1)$) was used to determine whether or not there was a trend in total population abundance between

1990 and 2010 where $W_t'$ is the predicted total population, $W_I$ and $W_S$ are intercept and slope parameters to be estimated and t is time (with t=1 corresponding to 1990). The intercept and slope parameters were assigned vague normal priors with high variance (=1000), $W_I \sim N(0,1000)$, $W_S \sim N(0,1000)$ and $W_t \sim N(W_t',1000)$ in which $W_t$ is the estimated posterior total population.

### Use of the Special Area of Conservation

To investigate trends in the proportion of the total population using the SAC from 1990 to 2010 we used a parametric bootstrap procedure to account for the uncertainty around our abundance estimates. For each year, estimates of abundance for the SAC and total population were drawn from lognormal distributions of the mean and variance of our SAC and total population abundance estimates. The annual proportion of the total population using the SAC was then calculated. A GLM with quasi-binomial error distribution to account for overdispersion in the data and logit link was fitted to these annual proportions to estimate the slope. This bootstrapping procedure was repeated 1000 times.

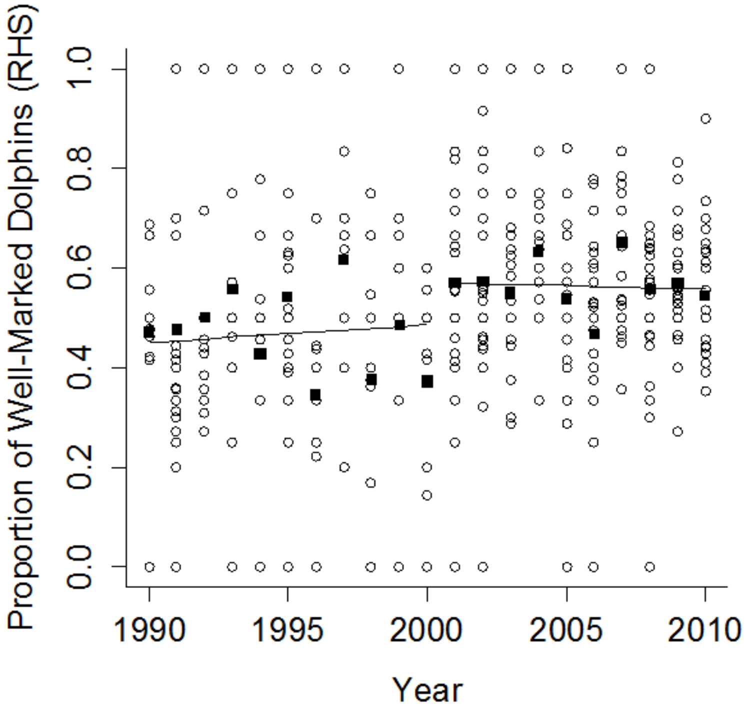
## RESULTS

### Trends in Abundance within the Special Area of Conservation

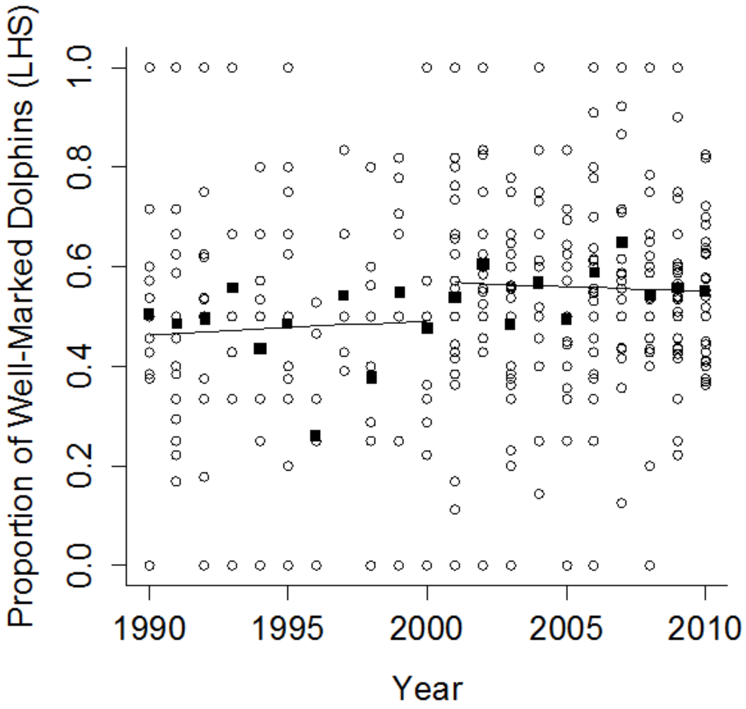
The change in survey protocols resulted in some differences in key variables between the first (1990-2000) and second decade (2001-2010) including a greater number of more frequent but shorter surveys during the second decade (Table 1).

A minimum of 21 and maximum of 60 well-marked individuals were identified in each year from high quality photographs. Mark-recapture estimates of the number of well-marked individuals ranged from 24 to 75, but there was no significant trend in the estimates of well-marked individuals using the SAC ($t_{19} = -0.738$, $p = 0.469$) (see Table A4). The coefficient of variation (CV) of estimates ranged from 0.03 to 0.28 (mean = 0.13) (see Table A4), decreasing as the number of surveys increased (linear regression, slope = -0.007, SE = 0.001, $t_{19} = -5.349$, $p < 0.0001$). Median capture probabilities for each year varied from 0.04 to 0.23, and were higher from 2001 onwards during the flexible rather than fixed survey protocol (1990-2000 median = 0.09, IQR = 0.06-0.10; 2001-2010 median = 0.17, IQR = 0.11-0.20).

Annual estimates of the proportion of well-marked animals (θ) varied among years (Figure 2), with no significant difference between sides (Pearson's Chi-squared test, $\chi^2 = 0.069$, d.f. = 1, p = 0.793). There was an increasing trend in θ between 1990 and 2010 (right side: z = 5.102, p<0.001; left: z = 3.625, p = 0.0003, Table A3), but no trend was detected within either the first or second decade of research (p>0.05, Figure 2). None of the biological variables in the GLMMs explained significant variability in θ; instead, much of the variation was accounted for by covariates relating to survey protocols (Table 2). The best model included the change in survey protocol in 2001, from the fixed survey route to flexible surveys (Table 2). This model provided two estimates of θ, one for 1990-2000 for the fixed survey route ($\theta_1 = 0.4720$, SE = 0.0345) and one for 2001-2010 for the flexible survey route ($\theta_2 = 0.5609$, SE = 0.0425), resulting in a step increase in θ coinciding with the change in survey protocol (Figure 2). There are two plausible causes for this change. One is that the population age-structure has changed in such a way that θ has increased. However, there is no evidence for this (e.g. Table 2). The other, more likely, explanation is that estimates of θ have changed as a result of changes in sampling. A priori, one might expect any sampling differences that affected the estimation of θ to also affect the estimate of well-marked animals. However, there was no increase in the mean estimate of the number of well-marked dolphins (1990-2000: 52 (SE = 5), 2001-2010: 53 (SE = 2)). Given the possibility that the change in the estimate of θ is a result of sampling bias, the higher capture probabilities and reduced capture heterogeneity in the second decade, and the absence of biological explanations for a step change in θ, we argue that the estimate of θ from the second decade probably reflects the proportion of well-marked animals in this population throughout the time series.



a.



b.

Figure 2. The proportion of well-marked individuals (θ) for each survey, a. right and b. left side from 1990 to 2010 (clear circles) and annual average estimates of θ (black squares) with binomial GLM fitted lines (black lines) for 1990 to 2000 (right side: z = 0.784, p = 0.433; left side: z = 0.533, p = 0.594) and 2001 to 2010 (right side: z = -0.379, p = 0.705; left side: z = -0.663, p = 0.507) (full GLM results in Table A3).

Table 2. The results of generalised linear mixed models to explore how the proportion of well-marked animals (θ) varied in relation to biological and sampling variables and changes to survey protocols. The model with the lowest AIC is in bold.

| **Fixed Effects** | **Coefficient** | **Std. Error** | **Z** | **P** | **Random Effects** | **Variance** | **Std. Dev.** | **AIC** |
|---|---|---|---|---|---|---|---|---|
| Intercept | -0.1557 | 0.1142 | -1.363 | 0.1730 | | | | |
| Total Surveys | 0.0111 | 0.0041 | 2.722 | 0.0065 | Survey | 0.1152 | 0.3395 | 2674.6 |
| Intercept | 0.0646 | 0.1226 | 0.526 | 0.599 | | | | |
| Encounters | 0.0010 | 0.0015 | 0.673 | 0.501 | Survey | 0.1224 | 0.3499 | 2681.4 |
| Intercept | -0.0840 | 0.0600 | -1.399 | 0.162 | | | | |
| Captures | 0.0015 | 0.0004 | 4.361 | <0.0001 | Survey | 0.1096 | 0.331 | 2663.3 |
| Intercept | -0.2915 | 0.0968 | -3.012 | 0.0026 | | | | |
| Capture Occasions | 0.0207 | 0.0044 | 4.725 | <0.0001 | Survey | 0.1045 | 0.3232 | 2660.3 |
| Intercept | -0.0451 | 0.0483 | -0.934 | 0.35 | | | | |
| Camera | 0.2956 | 0.0603 | 4.903 | <0.0001 | Survey | 0.1024 | 0.32 | 2658.8 |
| **Intercept** | **-0.1146** | **0.0533** | **-2.149** | **0.0316** | | | | |
| **Survey Route** | **0.3620** | **0.0630** | **5.750** | **<0.0001** | **Survey** | **0.0924** | **0.3039** | **2650.8** |
| Intercept | 0.0783 | 0.1068 | 0.734 | 0.463 | | | | |
| Mark-recapture Estimate | 0.0013 | 0.0020 | 0.647 | 0.518 | Survey | 0.1211 | 0.348 | 2681.5 |
| Intercept | 0.1676 | 0.0688 | 2.437 | 0.0148 | | | | |
| New calves | -0.0032 | 0.0085 | -0.370 | 0.7110 | Survey | 0.1216 | 0.3487 | 2681.7 |

Accordingly $\theta_2$ was applied to all annual mark-recapture estimates to estimate abundance within the SAC. However, given that we cannot rule out the possibility of a step-change in θ, we also explore the consequences of applying $\theta_1$ to annual abundance estimates from 1990-2000 and $\theta_2$ to estimates from 2001-2010 (see Table A4). We return to this point in the discussion.

Using $\theta_2$ throughout the time series, estimates of the number of dolphins using the SAC ranged from 43 (95% confidence interval (CI): 32-57) in 1998 to 134 (95% CI: 92-193) in 1990 (Figure 3 and Table A4), and there was no significant linear trend in annual estimates ($t_{19}$ = -0.729, p = 0.475). However, applying the two different estimates of θ to data from the first and second decades of surveys (see Table A4) resulted in significant linear decline in annual estimates (slope = -1.968, SE = 1.128, $t_{19}$ = -2.348, p = 0.03).

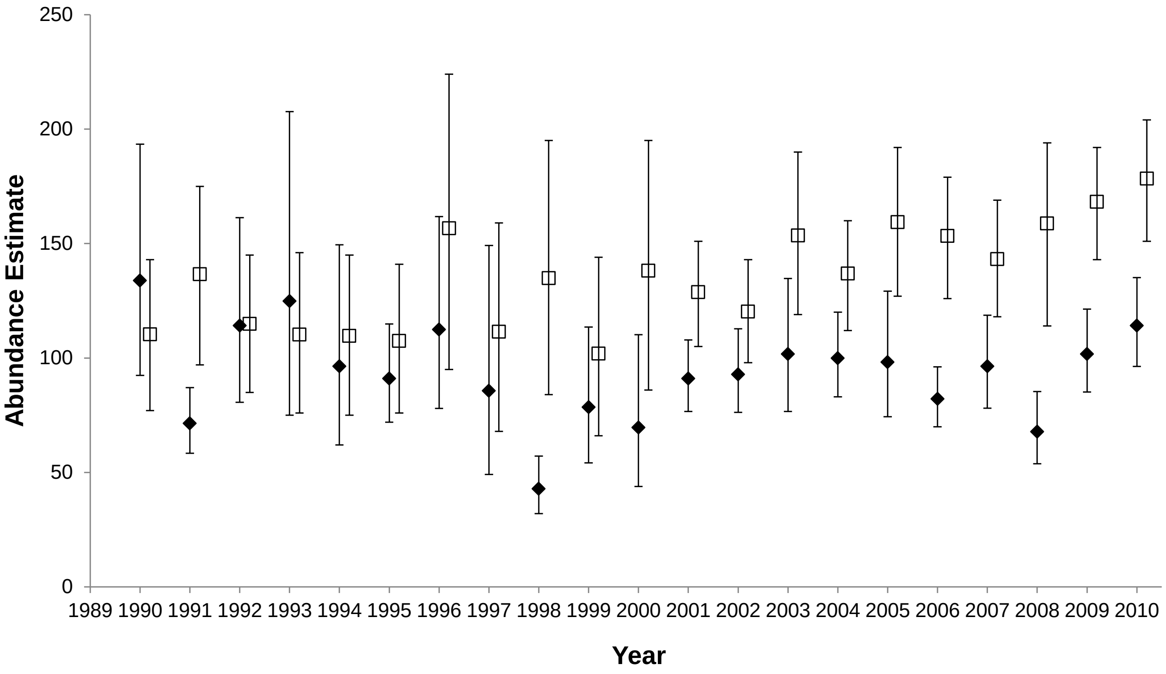


Figure 3. Annual estimates of the number of bottlenose dolphins using the Moray Firth Special Area of Conservation from 1990 to 2010 (black diamonds) with 95% confidence intervals and of the total east coast of Scotland bottlenose dolphin population with posterior means (clear squares) and 95% highest posterior density intervals.

### Trends in Population Size

Between 1990 and 2010 a minimum of 26 and maximum of 92 well-marked individuals were identified each year off the east coast of Scotland. Annual estimates of total population size using the Bayesian mark-recapture model ranged from 102 (95% HPDI: 66-144) in 1999 to 178 (95% HPDI: 151-204) in 2010 (Figure 3 and Table A5). The Bayesian linear regression suggests there is a >99% probability that this population is either stable or increasing.

### Use of the Special Area of Conservation

The proportion of the total population using the SAC was investigated using annual estimates of abundance in the SAC based upon $\theta_2$, and the estimates of population abundance. The parametric bootstrap took uncertainty around these estimates into account and provided evidence that the proportion of the population using the SAC has declined, with all the bootstrap replicate GLMs showing negative slope coefficients (mean = -0.0621, SE= 0.0007). 93% of bootstrap replicates showed that >50% of the population use the SAC.

## DISCUSSION

Protected areas are commonly promoted for *in situ* conservation, yet there is little published information on long-term abundance and trends of top predator populations to evaluate their effectiveness (Gaston *et al.* 2006, Hooker and Gerber 2004) (see Gormley *et al.* 2012 for a recent exception). We investigated some of the issues that could impact estimates of abundance, and present evidence of long-term trends in the use of a protected area for small cetaceans in relation to overall changes in population status. Results show that, despite inter-annual variability, the Moray Firth SAC has been used consistently for at least the last two decades by the majority of a stable or increasing population of bottlenose dolphins.

### Influence of changes in survey protocols on sampling variability

Survey protocols used to monitor dolphin abundance within the Moray Firth SAC were adapted primarily in response to changes in dolphin distribution (Wilson *et al.* 2004) and partly due to the development of digital photography. We investigated how these changes to survey protocols might influence trend estimates (see also Moore and Barlow 2011) and found evidence that they did affect estimates of the proportion of well-marked individuals, $\theta$. The change in this populations' distribution (Wilson *et al.* 2004) decreased sighting frequencies along parts of our original fixed survey route but, by targeting areas that were more regularly used by dolphins, we successfully increased overall capture probabilities (Table 1). Furthermore, shorter flexible surveys were less constrained by weather, resulting in an increase in the number of surveys and captures during the second decade of research (Table 1). This more intensive sampling of the dolphins using the SAC and switch to digital photography produced larger numbers of photographs, which is known to reduce capture heterogeneity (Hammond 1986). This potentially also resulted in a larger, more representative sample of animals being photographed. Sampling variability was further reduced by only using nicked animals that could be identified from both sides, allowing annual abundance to be estimated from a single capture history (see also Corkrey *et al.* 2008). This resulted in CVs that were generally lower than previous estimates that averaged left and right side estimates (Wilson *et al.* 1999).

**Trends in population size and use of the Special Area of Conservation**

There was no significant trend in mark-recapture estimates of the number of well-marked dolphins using the SAC over this study period. However, investigations of variation in the observed proportion of well-marked individuals highlight that estimates of $\theta$ are critical to any assessment of trends in the total number of animals using this protected area. Given that bottlenose dolphins are long-lived species with low recruitment, the extreme fluctuations in annual estimates of $\theta$, particularly in the first decade (Figure 2 and Table A4), are biologically implausible. Nevertheless, whilst high inter-annual variability in estimates of $\theta$ must be driven largely by sampling variation, longer term change in $\theta$ could result from gradual changes in population age or sex-structure. Our best model of variation in $\theta$ produced different estimates for the first ($\theta_1 = 0.4720$) and second ($\theta_2 = 0.5609$) decade of the study. We identified no biological reason for such a change. Instead the higher estimate of $\theta$ in the second decade was co-incident with changes in survey protocols that also resulted in higher capture probabilities and reduced capture heterogeneity. We might expect any sampling bias that affected θ to also affect the estimate of well-marked animals. However, despite observing a step change in θ we found no systematic change in the number of well-marked animals. Therefore, we suggest that $\theta_2$ more accurately reflects the actual proportion of well-marked animals in this population throughout this time-series.

At the same time, we note that inferences about whether or not there was a decreasing trend in the total number of individuals using the SAC are dependent upon the choice of using a single value of θ or the two values from the model. Applying $\theta_2$ to the complete time-series resulted in no significant trend in the number of dolphins using the Moray Firth SAC between 1990 and 2010. However, if modelled estimates of θ were used for their respective time periods ($\theta_1$ for 1990-2000 and $\theta_2$ for 2001-2012) there was a declining trend in the number of dolphins using the SAC over this period. It is well recognised that trends can be difficult to detect when sampling variability is high (Moore and Barlow 2011). Effort therefore typically focuses on reducing CVs, which in our case were relatively precise and comparable with other studies of cetaceans (Berrow *et al.* 2012, Gormley *et al.* 2005, Read *et al.* 2003, Silva *et al.* 2009). Other studies have previously highlighted how factors such as photographer behaviour can affect estimation of θ (Read *et al.* 2003). Whilst the influence of such factors can be incorporated in model based estimates of θ, our results highlight the value of conducting parallel studies that can directly investigate whether there are trends in population age, size or sex-structure (Fearnbach *et al.* 2011, Fortune *et al.* 2012).

A wider issue is that protected areas for mobile species such as this rarely encompass the entire population range. Indeed, the European Habitats Directive aims to provide a network of SACs that supports the favourable conservation status of the population. Whilst it has been recommended that broader-scale surveys are required to interpret abundance trends within SACs (Cañadas and Hammond 2006), monitoring typically occurs only within site boundaries (Berrow *et al.* 2012, Pierpoint *et al.* 2009). Our study is the first to assess trends within an SAC in relation to trends in overall population size. By updating the previous assessment by Corkrey *et al.* (2008) using data collected over the last decade (Cheney *et al.* 2013, Islas-Villanueva 2010, Quick and Janik 2008), these analyses suggest that there is a >99% probability that the overall population is either stable or increasing (Figure 3). Integration of this result with data from the more regular surveys within the SAC indicates that >50% of the population use the protected area at some point in any one year. This supports findings from intensive surveys in 2006 and 2007 that showed that > 80% of well-marked animals in the population had been observed in the SAC at some point in the previous two decades (Cheney *et al.* 2013).

Irrespective of whether the number of individuals using the SAC has remained stable or decreased, there is an indication that use of the SAC has declined over the past two decades (Figure 3); a trend that would be more pronounced if the two values of $\theta$ were used. On the one hand, this could be interpreted as a reduction in the importance of the SAC relative to surrounding areas. Alternatively, relatively stable numbers within the SAC may indicate that the area is at carrying capacity, and a decline in relative use might be expected if protective measures are facilitating the recovery and expansion of the wider population. The cause(s) of changes in habitat use or local abundance tend to be difficult to ascertain (Hartel *et al.* 2014, Tezanos-Pinto *et al.* 2013). Evaluation of these alternatives requires further research on how variation in environmental conditions (e.g. habitat and prey availability), anthropogenic disturbance (e.g. noise) and demographic parameters both in the SAC and in other parts of the population’s range, influence use of this protected area. This, in turn, serves to highlight our limited ability to predict the dynamics of coastal delphinid habitat use at larger temporal scales. There is little evidence of the presence of bottlenose dolphins in the Moray Firth before the mid-20th century (Cheney *et al.* 2013), and populations that we consider ‘resident’ may change their ranging patterns at inter-generational scales.

Even when long-time series are available, the limited power to demonstrate changes in the relative use of SACs must be recognised by conservation managers and legislators. Crucially, this dataset only provides an estimate of the number of individuals using the SAC during the summer sampling period. These investigations of the importance of protected areas should therefore be complemented by other approaches (e.g. passive acoustic monitoring) that can explore variation in the amount of time that animals spend in key areas within their range (Bailey *et al.* 2010, Pierpoint *et al.* 2009).

## CONCLUSION

The population of bottlenose dolphins inhabiting the east coast of Scotland has remained stable over the past two decades. Estimates of abundance within the Moray Firth SAC varied over that period, coinciding with changes in the way the population uses its range and expanded it. This study was underpinned by a long-term research project and it is impractical to expect this level of survey effort in and around all protected areas. However, where photo-identification is used to support monitoring of abundance trends, our results highlight the importance of adapting survey protocols to maintain high capture probabilities and minimise sampling heterogeneity and the need for accurate estimation of $\theta$ to correctly assess trends. A long time series is required to assess trends in the abundance of these long-lived mobile marine predators, and shorter-term variations in abundance within specific areas should be interpreted cautiously. Most critically, assessment of the effectiveness of protected areas for mobile predators requires at least some information on the wider population. Use of these data within a state-space modelling framework highlights how even sparse data from the wider population can help managers interpret abundance trends within a protected area.

## ACKNOWLEDGEMENTS

We thank all the colleagues who have helped collect and analyse data, and two anonymous referees for their helpful comments. The BES, ASAB, Greenpeace Environmental Trust, Scottish Natural Heritage, Scottish Government, Whale and Dolphin Conservation, Talisman Energy (UK) Ltd., Department of Energy and Climate Change, Chevron, Natural Environment Research Council and the University of Aberdeen all provided funding for annual surveys in the Moray Firth. St. Andrews Bay surveys were funded by a Royal Society University Research Fellowship to V.M.J., studentships from NERC and the Mexican National Council for Science and Technology (CONACYT), and the University of St Andrews. Survey work was conducted under Scottish Natural Heritage Animal Scientific Licences.

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## APPENDIX

Additional supporting information for the published paper.

Table A1. Summary of the location and number of photo-identification surveys.

Table A2. Summary of survey protocols and variables used in the GLMMs.

Table A3. GLM results of trends in θ.

Table A4. Annual abundance of bottlenose dolphins in the Moray Firth SAC.

Table A5. Annual abundance of the east coast of Scotland bottlenose dolphin population.

Figure A1. Map of the east coast of Scotland study area with bottlenose dolphin encounters.

Table A1: Summary of the location and number of photo-identification surveys carried out from May to September 1990 to 2010 by the University of Aberdeen, University of St. Andrews Sea Mammal Research Unit (SMRU) and Whale and Dolphin Conservation (WDC) in each of the known home range areas of the east coast of Scotland bottlenose dolphin population. Note: SAC abundance was estimated using only data from the University of Aberdeen surveys in the SAC and some surveys cover more than one area (e.g. University of Aberdeen surveys may visit the Special Area of Conservation (SAC) and outer Moray Firth on one day). See Figure A1 for details of each area.

| | **UNIVERSITY OF ABERDEEN** | | | | **SMRU** | **WDC** | |
|---|---|---|---|---|---|---|---|
| **YEAR** | **SAC** | **OUTER MORAY FIRTH** | **GRAMPIAN** | **TAYSIDE & FIFE** | **TAYSIDE & FIFE** | **SAC** | **OUTER MORAY FIRTH** |
| 1990 | 13 | | | | | | |
| 1991 | 28 | 3 | | | | | |
| 1992 | 23 | 9 | 1 | | | | |
| 1993 | 17 | 3 | | | | | |
| 1994 | 25 | 19 | 2 | | | | |
| 1995 | 36 | 7 | 1 | | | | |
| 1996 | 15 | 8 | 6 | | | | |
| 1997 | 12 | 4 | | 5 | | | |
| 1998 | 14 | 1 | | 2 | | | |
| 1999 | 14 | | | 2 | 3 | | |
| 2000 | 10 | | | 7 | 1 | | |
| 2001 | 34 | | | | 3 | | 1 |
| 2002 | 30 | | | | 10 | | 25 |
| 2003 | 27 | | | | 29 | | |
| 2004 | 23 | | | | 13 | 22 | 40 |
| 2005 | 26 | | | | | 43 | 48 |
| 2006 | 39 | 2 | | | 17 | 44 | 63 |
| 2007 | 27 | 1 | | | 21 | 59 | 32 |

| | **UNIVERSITY OF ABERDEEN** | | | | **SMRU** | **WDC** | |
|---|---|---|---|---|---|---|---|
| **YEAR** | **SAC** | **OUTER MORAY FIRTH** | **GRAMPIAN** | **TAYSIDE & FIFE** | **TAYSIDE & FIFE** | **SAC** | **OUTER MORAY FIRTH** |
| 2008 | 26 | 1 | | | | 42 | 59 |
| 2009 | 34 | 8 | | | 8 | | 54 |
| 2010 | 24 | 6 | | | 8 | | 35 |

Table A2: Summary of the survey protocols and variables used in the GLMMs from photo-identification surveys in the Moray Firth Special Area of Conservation from May to September between 1990 and 2010.

| | SURVEY PROTOCOLS & VARIABLES | | | | | | | | BIOLOGICAL | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **YEAR** | **FIXED ROUTE** | **CAMERA** | **TOTAL NUMBER OF SAC SURVEYS** | **NUMBER OF CAPTURE OCCASIONS** | | **NUMBER OF ENCOUNTERS** | **NUMBER OF CAPTURES** | | **ESTIMATE OF WELL-MARKED DOLPHINS (CAPTURE)** | | **ESTIMATED NUMBER OF NEW CALVES** |
| | | | | **LHS** | **RHS** | | **LHS** | **RHS** | **LHS** | **RHS** | |
| 1990 | Yes | FILM | 13 | 11 | 11 | 79 | 64 | 76 | 89 | 59 | 6 |
| 1991 | Yes | FILM | 28 | 20 | 19 | 106 | 73 | 84 | 35 | 39 | 12 |
| 1992 | Yes | FILM | 23 | 12 | 13 | 72 | 57 | 60 | 74 | 41 | 9 |
| 1993 | Yes | FILM | 17 | 11 | 10 | 42 | 23 | 37 | 49 | 48 | 9 |
| 1994 | Yes | FILM | 25 | 9 | 10 | 51 | 24 | 30 | 26 | 122 | 20 |
| 1995 | Yes | FILM | 36 | 17 | 20 | 69 | 39 | 89 | 40 | 40 | 6 |
| 1996 | Yes | FILM | 15 | 5 | 7 | 57 | 23 | 24 | 62 | 72 | 1 |
| 1997 | Yes | FILM | 12 | 5 | 7 | 43 | 18 | 19 | 18 | 50 | 7 |
| 1998 | Yes | FILM | 14 | 7 | 8 | 36 | 26 | 38 | 26 | 23 | 6 |
| 1999 | Yes | FILM | 14 | 7 | 9 | 42 | 36 | 30 | 43 | 44 | 3 |
| 2000 | Yes | FILM | 10 | 8 | 8 | 42 | 23 | 39 | 30 | 51 | 2 |
| 2001 | NO | FILM | 34 | 28 | 27 | 67 | 180 | 171 | 50 | 51 | 5 |
| 2002 | NO | DIGITAL | 30 | 23 | 25 | 71 | 169 | 153 | 49 | 50 | 5 |
| 2003 | NO | DIGITAL | 27 | 21 | 23 | 80 | 112 | 143 | 50 | 46 | 5 |
| 2004 | NO | DIGITAL | 23 | 21 | 20 | 70 | 94 | 97 | 62 | 59 | 4 |
| 2005 | NO | DIGITAL | 26 | 19 | 17 | 73 | 87 | 92 | 46 | 58 | 7 |
| 2006 | NO | DIGITAL | 39 | 25 | 25 | 86 | 149 | 166 | 45 | 48 | 7 |
| 2007 | NO | DIGITAL | 27 | 26 | 26 | 74 | 184 | 208 | 46 | 52 | 10 |
| 2008 | NO | DIGITAL | 26 | 23 | 23 | 75 | 159 | 166 | 35 | 36 | 3 |
| 2009 | NO | DIGITAL | 34 | 28 | 29 | 98 | 253 | 289 | 57 | 47 | 12 |
| 2010 | NO | DIGITAL | 24 | 24 | 24 | 115 | 294 | 262 | 65 | 60 | 7 |

Table A3. The results of a generalised linear model to explore trends in the proportion of well-marked animals (θ) per survey, right and left side, from 1990 to 2010, 1990 to 2000 and 2001 to 2010.

| **Variable** | **Coefficient** | **Standard error** | **Z** | **P** |
|---|---|---|---|---|
| **1990 to 2010** | | | | |
| **RIGHT** | | | | |
| Intercept | -48.9988 | 9.6327 | -5.087 | <0.0001 |
| Year | 0.0245 | 0.0048 | 5.102 | **<0.0001** |
| **LEFT** | | | | |
| Intercept | -37.6325 | 10.4249 | -3.610 | 0.0003 |
| Year | 0.0189 | 0.0052 | 3.625 | **0.0003** |
| **1990 to 2000** | | | | |
| **RIGHT** | | | | |
| Intercept | -28.6318 | 36.3326 | -0.788 | 0.431 |
| Year | 0.0143 | 0.0182 | 0.784 | 0.433 |
| **LEFT** | | | | |
| Intercept | -22.5054 | 42.0081 | -0.536 | 0.592 |
| Year | 0.0112 | 0.0211 | 0.533 | 0.594 |
| **2001 to 2010** | | | | |
| **RIGHT** | | | | |
| Intercept | 9.1204 | 23.3965 | 0.390 | 0.697 |
| Year | -0.0044 | 0.0117 | -0.379 | 0.705 |
| **LEFT** | | | | |
| Intercept | 15.6274 | 23.2123 | 0.673 | 0.501 |
| Year | -0.0077 | 0.0116 | -0.663 | 0.507 |

Table A4: Comparison of the annual abundance of bottlenose dolphins in the Moray Firth Special Area of Conservation from the mark-recapture analysis using the $M_{th}$ model when using different estimates of the proportion of well-marked animals. Including the number of well-marked individuals identified in high quality pictures (minimum number), the estimated number of well-marked individuals ($\widehat{N}$) and coefficient of variation (CV) from program CAPTURE and the estimated total number of dolphins with 95% confidence intervals (CI) applying the proportion of well-marked individuals from the GLMM for only the flexible survey route ($\theta_2$), the fixed and flexible survey route ($\theta_1\theta_2$) or annual estimate of θ based on the individuals seen on each survey.

| | Minimum | | | | | SAC Abundance | | | SAC Abundance | | | SAC Abundance | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Number | $\widehat{N}$ | 95% CI | CV | $\theta_2$ | Estimate | 95% CI | $\theta_1\theta_2$ | Estimate | 95% CI | $\theta$ | Estimate | 95% CI |
| 1990 | 47 | 75 | 59–113 | 0.17 | 0.5609 | 134 | 92–193 | 0.4720 | 159 | 110–229 | 0.4887 | 153 | 105–224 |
| 1991 | 37 | 40 | 38–50 | 0.07 | 0.5609 | 71 | 58–87 | 0.4720 | 85 | 70–103 | 0.4696 | 85 | 66–110 |
| 1992 | 43 | 64 | 52–95 | 0.16 | 0.5609 | 114 | 81–161 | 0.4720 | 136 | 96–191 | 0.5100 | 125 | 88–179 |
| 1993 | 36 | 70 | 49–124 | 0.25 | 0.5609 | 125 | 75–208 | 0.4720 | 148 | 89–246 | 0.5578 | 125 | 74–214 |
| 1994 | 34 | 54 | 41–91 | 0.21 | 0.5609 | 96 | 62–149 | 0.4720 | 114 | 74–177 | 0.4407 | 123 | 76–198 |
| 1995 | 43 | 51 | 46–66 | 0.09 | 0.5609 | 91 | 72–115 | 0.4720 | 108 | 86–136 | 0.4888 | 104 | 81–135 |
| 1996 | 39 | 63 | 50–94 | 0.17 | 0.5609 | 112 | 78–162 | 0.4720 | 133 | 93–192 | 0.2932 | 215 | 126–366 |
| 1997 | 26 | 48 | 34–92 | 0.28 | 0.5609 | 86 | 49–149 | 0.4720 | 102 | 58–177 | 0.5845 | 82 | 47–145 |
| 1998 | 21 | 24 | 22–36 | 0.13 | 0.5609 | 43 | 32–57 | 0.4720 | 51 | 38–68 | 0.3771 | 64 | 43–94 |
| 1999 | 32 | 44 | 37–69 | 0.17 | 0.5609 | 78 | 54–114 | 0.4720 | 93 | 65–135 | 0.5088 | 86 | 55–135 |
| 2000 | 26 | 39 | 31–69 | 0.23 | 0.5609 | 70 | 44–110 | 0.4720 | 83 | 52–131 | 0.4233 | 92 | 54–156 |
| 2001 | 48 | 51 | 49–59 | 0.04 | 0.5609 | 91 | 77–108 | 0.5609 | 91 | 77–108 | 0.5554 | 92 | 80–105 |
| 2002 | 47 | 52 | 49–63 | 0.07 | 0.5609 | 93 | 76–113 | 0.5609 | 93 | 76–113 | 0.5890 | 88 | 74–105 |
| 2003 | 44 | 57 | 49–79 | 0.12 | 0.5609 | 102 | 77–135 | 0.5609 | 102 | 77–135 | 0.5183 | 110 | 85–143 |
| 2004 | 52 | 56 | 54–67 | 0.06 | 0.5609 | 100 | 83–120 | 0.5609 | 100 | 83–120 | 0.6005 | 93 | 80–108 |
| 2005 | 43 | 55 | 48–75 | 0.12 | 0.5609 | 98 | 74–129 | 0.5609 | 98 | 74–129 | 0.5171 | 106 | 82–138 |
| 2006 | 45 | 46 | 46–52 | 0.03 | 0.5609 | 82 | 70–96 | 0.5609 | 82 | 70–96 | 0.5272 | 87 | 77–99 |
| 2007 | 47 | 54 | 50–67 | 0.08 | 0.5609 | 96 | 78–119 | 0.5609 | 96 | 78–119 | 0.6454 | 84 | 71–99 |

| | Minimum | | | | SAC Abundance | | | SAC Abundance | | | SAC Abundance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Number | $\widehat{N}$ | 95% CI | CV | $\theta_2$ | Estimate | 95% CI | $\theta_1\theta_2$ | Estimate | 95% CI | $\theta$ | Estimate | 95% CI |
| 2008 | 33 | 38 | 35–49 | 0.09 | 0.5609 | 68 | 54–85 | 0.5609 | 68 | 54–85 | 0.5555 | 68 | 55–84 |
| 2009 | 53 | 57 | 55–66 | 0.05 | 0.5609 | 102 | 85–121 | 0.5609 | 102 | 85–121 | 0.5631 | 101 | 90–113 |
| 2010 | 60 | 64 | 61–73 | 0.04 | 0.5609 | 114 | 96–135 | 0.5609 | 114 | 96–135 | 0.5472 | 117 | 105–130 |

Table A5: The estimated abundance of the east coast of Scotland bottlenose dolphin population from the Bayesian state-space mark-recapture model, including the number of well-marked individuals identified each year in high quality pictures (minimum estimate), the number of well-marked and total estimated abundance with 95% highest posterior density intervals (HPDI).

| Year | Minimum Estimate | Well-marked Abundance | 95% HPDI | Total Population Abundance | 95% HPDI |
|---|---|---|---|---|---|
| 1990 | 47 | 56 | 42–67 | 110 | 77–143 |
| 1991 | 37 | 54 | 45–63 | 137 | 97–175 |
| 1992 | 51 | 54 | 46–62 | 115 | 85–145 |
| 1993 | 36 | 55 | 45–67 | 110 | 76–146 |
| 1994 | 36 | 55 | 45–67 | 110 | 75–145 |
| 1995 | 47 | 56 | 45–68 | 107 | 76–141 |
| 1996 | 39 | 60 | 44–80 | 157 | 95–224 |
| 1997 | 26 | 60 | 41–82 | 112 | 68–159 |
| 1998 | 28 | 60 | 43–83 | 135 | 84–195 |
| 1999 | 34 | 60 | 44–81 | 102 | 66–144 |
| 2000 | 34 | 62 | 44–91 | 138 | 86–195 |
| 2001 | 73 | 76 | 69–83 | 129 | 105–151 |
| 2002 | 65 | 74 | 65–83 | 120 | 98–143 |
| 2003 | 72 | 80 | 69–91 | 154 | 119–190 |
| 2004 | 87 | 86 | 77–93 | 137 | 112–160 |
| 2005 | 54 | 85 | 74–93 | 159 | 127–192 |
| 2006 | 84 | 84 | 79–89 | 153 | 126–179 |
| 2007 | 88 | 85 | 78–94 | 143 | 118–169 |
| 2008 | 41 | 91 | 70–104 | 159 | 114–194 |
| 2009 | 89 | 92 | 89–95 | 168 | 143–192 |
| 2010 | 92 | 92 | 92–94 | 178 | 151–204 |

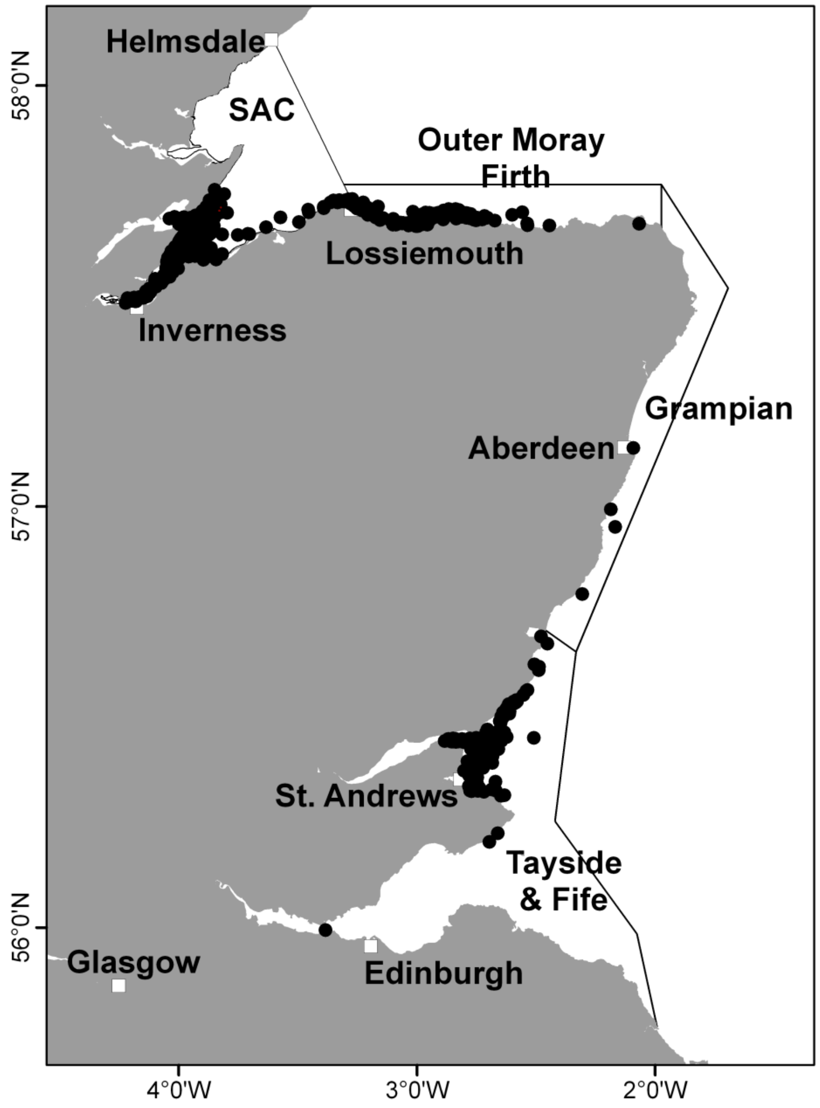

Figure A1. A map showing the study areas covered by collaborating research groups and the location of bottlenose dolphin encounters from 1990 to 2010 used in the Bayesian state-space model to estimate the abundance of bottlenose dolphins off the east coast of Scotland.

# CHAPTER 4

## LASER PHOTOGRAMMETRY REVEALS VARIATION IN GROWTH AND EARLY SURVIVAL IN FREE-RANGING BOTTLENOSE DOLPHINS

# CHAPTER 4

## LASER PHOTOGRAMMETRY REVEALS VARIATION IN GROWTH AND EARLY SURVIVAL IN FREE-RANGING BOTTLENOSE DOLPHINS [3]

### ABSTRACT

Growth and body condition can be used as indices of health and fitness, but are difficult to collect for populations of conservation concern where individuals cannot be captured. We incorporated a laser photogrammetry system into boat-based photo-identification surveys that underpin individual-based studies of cetacean populations. These data were integrated with >25 years of observations from a temperate bottlenose dolphin population in Scotland to investigate the influence of sex on growth patterns, effects of birth order on calf size and the longer term consequences of variation in early growth. Field measurements of the distance from the blowhole to the dorsal fin were made in multiple years from 87 dolphins that had been followed from birth, ranging in age from newborn to 26 years. These estimates were validated against direct measurements of 12 individuals that had previously been captured and released in Florida and two study individuals that subsequently stranded. Using relationships derived from other stranded individuals, age-specific body lengths were used to produce growth curves that were based entirely upon remote observations. Multilevel regression growth curve analyses suggested males and females showed similar patterns of growth, unlike bottlenose dolphins in sub-tropical areas, and growth was best described by a Richards' growth curve. Newborn length was unrelated to sex, however females' first calves were shorter than subsequent calves. Sample sizes remain small, yet there was evidence of fitness consequences of variation in calf length; calves that died in their first winter were significantly shorter than those that survived. The incorporation of this simple-to-use and inexpensive method into individual-based photo-identification studies provides new opportunities to non-invasively investigate drivers of variation in growth and the demographic consequences of variation in early growth in cetaceans from protected populations.

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[3] This chapter has been published as: Cheney, B., Wells, R.S., Barton, T.R. & Thompson, P.M. (2017) Laser photogrammetry reveals variation in growth and early survival in free-ranging bottlenose dolphins. Animal Conservation (online early view).

## INTRODUCTION

Conservation managers typically focus on monitoring changes in wildlife population abundance, survival and fecundity. However, significant changes in population processes can be difficult to detect (Maxwell and Jennings 2005, Taylor *et al.* 2007, Tyne *et al.* 2016), potentially resulting in delayed implementation of conservation initiatives (Thompson *et al.* 2000, Turvey *et al.* 2007). Additionally, identifying the drivers underlying these changes can be challenging (Currey *et al.* 2011, Estes *et al.* 2009). To complement these monitoring methods, data are therefore required on shorter term responses of individuals to environmental change and anthropogenic affects. One approach is to measure variation in body size, growth and individual condition. For example, changes in population size structure may inform understanding of the effects of by-catch or hunting (Holmes and York 2003), whilst information on individual condition is critical for exploring population consequences of non-lethal disturbance (McHuron *et al.* 2017, Pirotta *et al.* 2015).

When collected during individual-based studies morphometric data can help link effects of anthropogenic or environmental changes to events at multiple life history stages (Clutton-Brock and Sheldon 2010). Individual-based studies can provide opportunities for direct morphometric measurements during capture-release programmes (e.g. Coulson *et al.* 2011, Ozgul *et al.* 2010, Wells *et al.* 2004). However, captures within populations of conservation concern, particularly for some species such as cetaceans, may be impractical or unsafe. To overcome this, many individual-based studies use photographic observations of natural marks to recognise individuals (Hammond *et al.* 1990, Wells and Scott 1990, Würsig and Würsig 1977). The disadvantage is that opportunities to simultaneously obtain a time series of individual morphometric data are rare (Altmann and Alberts 2005).

Recent developments in photogrammetry highlight the potential for collecting morphological data from free-ranging terrestrial (Bergeron 2007, Rothman *et al.* 2008) and marine (Deakos 2010, Rohner *et al.* 2011) vertebrates. In particular, laser photogrammetry, where two parallel lasers provide a known length scale in photographs, can be integrated into the photo-identification techniques underpinning cetacean studies (Durban and Parsons 2006, Rowe *et al.* 2010, Rowe and Dawson 2008).

Here, we developed and tested a laser photogrammetry technique to remotely measure body length and model the growth of individuals from a protected population of wild bottlenose dolphins on the east coast of Scotland (Cheney *et al.* 2013, Wilson *et al.* 2004). We integrated these measurements with long-term demographic data to characterise growth (i.e. change in body length with age) in our study population, assess the influence of sex and birth order on growth, and explore whether variation in early growth influenced subsequent survival.

## METHODS

### Study Population

This study was conducted on bottlenose dolphins using the Moray Firth Special Area of Conservation (SAC) (92/43/EEC) on the east coast of Scotland (Cheney *et al.* 2014b) (Supporting Information Figure A1). Since 1989 individual based demographic studies have been conducted using standardised photo-identification survey procedures (for full details see Cheney *et al.* 2014a, Wilson *et al.* 1999, Wilson *et al.* 1997). The population of <200 individuals is estimated to be stable or increasing (Cheney *et al.* 2014a).

### Laser Photogrammetry

We adapted the laser photogrammetry technique used by Durban and Parsons (2006). Two Beamshot <5mW laser sights (Quarton USA INC, CA 91765, USA) were fixed horizontally, 10 cm apart, in a machined aluminium block and attached to a camera lens tripod mount (Figure 1(a) and Supporting Information Figure A2). Laser sights were adjusted using internal adjustment screws and controlled via an electronic control switch attached to the camera remote release (Supporting Information Figure A3). When the shutter was fired, lasers were projected onto the subject, providing a 10 cm scale on the photograph. Before and after each survey, calibration photographs were taken at five distances between 5 and 25 metres to ensure the lasers remained parallel and 10 cm apart (Figure 1(b)).

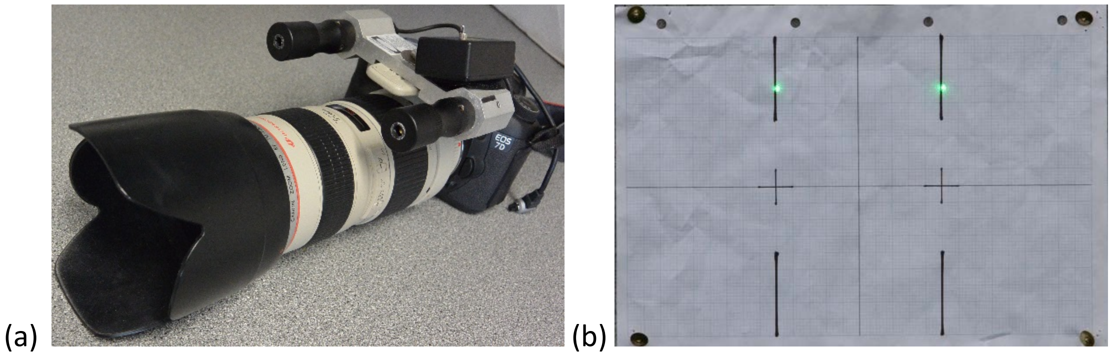

Figure 1. Laser photogrammetry equipment showing (a) two Beamshot laser sights attached to the lens tripod mount and (b) a calibration sheet with laser dots 10 cm apart.

From 2007 onwards, we applied this technique during annual photo-identification surveys (Cheney *et al.* 2014a). Only photographs where the dolphin was parallel to the photographic plane, both lasers were clear, and the individual dolphin was identifiable were used (Figure 2). We aimed to estimate body length (tip of rostrum to tail notch) of each dolphin, but the dolphins' entire body was rarely above the water. Therefore, calibrated photographs were first used to estimate the distance from the blowhole to the anterior insertion point of the dorsal fin (BH-DF), features that were often visible in photographs (Figure 2). Individual dolphin's BH-DF measurements were averaged for each month and year. Each dolphin's length was then estimated using the relationship between the BH-DF and body length derived from measurements of stranded individuals (Supporting Information Figure A4). The height of each dolphin's dorsal fin (anterior insertion point to fin tip) was also measured (Figure 2). When there were photographs of the BH-DF but no lasers visible, we used these contemporary data on the average height of an individuals' dorsal fin as an alternative scale for measuring the BH-DF. All measurements were made by BC using Image J (http://rsbweb.nih.gov/ij/). Measurement error was estimated using five repeat blind measurements of five different photographs. Statistical analyses were carried out in R version 3.3.0 (R Core Team 2016).

Figure 2. A good quality photograph, with the dolphin parallel, both lasers visible. The two green laser dots (dotted line and insert) are the scale (10 cm), the white line measures the distance between the middle of blowhole and anterior insertion point of dorsal fin (BH-DF), and the diagonal white dashed line measures the height of the dorsal fin from anterior insertion point to tip.

This study focussed on a subset of laser photogrammetry photographs from known-age individuals. Year of birth was estimated from field observations and archive photographs, based upon a newborn’s colour, size, foetal folds and behaviour (Grellier *et al.* 2003). Where possible, birth month was estimated using repeated observations of the mother without and with a calf (ensuring observations were within three months). To increase our sample of adult dolphins we also measured 23 dolphins that were first identified as adults or sub-adults between 1989 and 1996 (Supporting Information Table A1). As their age was estimated these adults were not used in the growth curve analyses. Instead these measurements were used to investigate variation in length measurements of the same individual in different photographs. Sex was determined using genital photographs or repeat associations with a calf.

## Growth Curve

Annual length measurements from each known-aged individual were first used in a multilevel regression growth curve (MRGC) analysis (Mirman 2014, Mirman *et al.* 2008) to explore sex differences in length and growth. MRGC is ideal for longitudinal data where quantifying individual differences and group level effects are required (Mirman 2014, Mirman *et al.* 2008). This method was chosen as it explicitly models time as a continuous variable and captures the non-linearity of growth (Mirman 2014). Finally, it deals with repeated measurements from individuals that are not independent and describes the group level patterns and individual variability in one analysis (Mirman 2014). This analysis used a subset of data from known sex individuals, where length estimates were available for all year classes from newborn (≤ 3 months) to 13 years old. Growth curves were modelled using the lme4 package (Bates *et al.* 2014) with third-order orthogonal polynomials, to account for age-specific changes in growth over this period (i.e. initial change from flat, increase and finally plateau) and to allow parameter estimates to be evaluated independently (Mirman 2014, Mirman *et al.* 2008). Males were treated as the baseline and parameters estimated for females. Models included random effects of individual identity on all time terms (i.e. linear, quadratic and cubic orthogonal polynomials) to account for repeated measures in different years and capture individual variability in length at birth and/or growth. Random effects were specified separately for each time term for model convergence (Mirman 2014).The fixed effect of sex on all time terms based on age was added individually. Improvements in model fit were evaluated using two times the change in log-likelihood, which is distributed as $\chi^2$ with degrees of freedom equal to the number of parameters added (for full details of MRGC analyses see Mirman 2014, Mirman *et al.* 2008).

This MRGC analysis was valuable for including repeat measures and assessing sex differences. However, these polynomial functions are less suitable for fitting asymptotic data (Mirman 2014) and could not incorporate the sparser data from older individuals. Marine mammal growth curve analyses have generally used the Gompertz (Gompertz 1825, Mattson *et al.* 2006, Read *et al.* 1993, Stolen *et al.* 2002, Webster *et al.* 2010), von Bertalanffy (Mattson *et al.* 2006, Stolen *et al.* 2002, Von Bertalanffy 1938) and/or Richards growth curves (Fearnbach *et al.* 2011, Richards 1959, Webster *et al.* 2010). However, the Richards curve has increased flexibility as the point of inflection depends on the parameter M (Fearnbach *et al.* 2011). Model selection in the drc (Ritz and Streibig 2005) and fishmethods packages (Nelson 2017) in R showed the Richards growth curve had the better fit for all our data (Supporting Information Table A2). Therefore, we fit a generalised logistic (Richards) growth curve (Richards 1959), $L_t = A\ [1 - b \text{ x } \exp(-ct)]^{M}$, where $L_t$ is the expected length at age t (years), A is the asymptotic adult length, b and c are free parameters that adjust the slope and inflection point of the curve and M describes the relative position of the inflection point relative to the asymptote. Unlike the MRGC analysis this method cannot account for repeat measurements of individuals at different ages. Therefore, we randomly selected one annual length estimate for each individual dolphin (newborn to 26 years old), maximising the number of individuals of each age while ensuring a spread of data across ages. Our full dataset is provided to allow exploration using other growth models (Supporting Information Table A6).

In addition MRGC analysis detected no significant differences in length or growth between the sexes (see results) so we combined data from both sexes in this analysis. Nevertheless, given that sex differences in growth have been found in other bottlenose dolphin populations (McFee *et al.* 2012, Read *et al.* 1993) we also fitted the Richards' growth curve to males and females separately using the drc package (Ritz and Streibig 2005).

### Calf Length and Growth

To investigate whether newborn length or growth differed between sexes we used the subset of individuals with a known sex and month of birth and with at least two measurements in the first two years of life (n=17). MRGC and Richards growth curve analyses suggested early growth was linear (Figure 3 and Supporting Information Figure A7), so we used a linear mixed-effects model with ID as a random effect, allowing for a separate intercept and slope for each individual. We also considered models with uncorrelated random effects (e.g. independent intercept and slope) and comparison with an ANOVA suggested these were the more parsimonious. Due to our small sample size we used the second order Akaike Information Criterion (AICc) (Burnham and Anderson 2002) for model selection using the AICcmodavg package (Mazerolle 2015).

To investigate individual variability in growth during this same period we used individuals with a known month of birth that had been measured both as a newborn and one year old (n=17). We used linear mixed-effects models with age as our explanatory variable, and ID as a random effect (to account for non-independence of repeat measurements) and a fixed effect (to capture individual differences and investigate individual growth). We also included whether a dolphin was a female's first calf to determine if this influenced newborn length or growth. The fixed effects of ID and first calf were modelled separately due to the limited amount of data available and model comparison was carried out using AICc (Burnham and Anderson 2002).

### First Year Survival

To investigate whether length or birth order influenced first year survival we compared first-year data from calves that were seen in their second summer with calves that were assumed to have died (based upon repeated observations of their mothers without a calf in the year after birth). Using a generalised linear model (GLM) with binomial error distribution and logit link we also included the age when the latest laser measurement was made (L_age) to account for the fact that calves could have been first measured anywhere from <1 month to 3 months old. We dropped the least significant explanatory variable, in turn, and refitted the model until only the significant variables remained. Model selection was again carried out using AICc (Burnham and Anderson 2002).

### Accuracy and Precision of Laser Photogrammetry

To confirm the accuracy and test the precision of our laser photogrammetry method we used this same technique during six photo-identification surveys in December 2011 with bottlenose dolphins in Sarasota Bay, Florida (Wells and Scott 1990). In this population, BH-DF and length measurements have been measured directly during capture-release for health assessments (Read *et al.* 1993, Wells *et al.* 2004). Only photographs of dolphins >11 years old were used to minimise growth between the dates of the health assessment measurements and laser photogrammetry photographs. Again all photographs were graded for quality and only the best photographs chosen for analysis. Laser BH-DF measurements were compared with health assessment measurements using a paired t-test and the coefficient of variation (CV) was estimated from repeated measurements of the same individuals in different photographs. We compared estimated lengths to direct measurements made during the health assessments with a paired t-test.

In addition, two known individuals stranded on the east coast of Scotland in 2010 and 2011 (SRUC 2017), permitting comparison of direct BH-DF and length measurements made after death with laser photogrammetry measurements made when alive.

## RESULTS

### Laser Photogrammetry

Photographs of sufficient quality for laser photogrammetry were available for 87 known-age individuals (88% of known-age dolphins photographed during this period and 45% of the estimated population). Ages ranged from <1 month to 26 years old with 18 males, 22 females and 47 individuals of unknown sex (Supporting Information Figure A5). The month of birth was estimated for 55 of these individuals (10 males, 13 females and 32 unknown sex) (Supporting Information Figure A6). An average of three (SE = 0.02) and maximum of eight years of photogrammetry data were available for each dolphin, with an average of four (SE = 0.26) and maximum of 15 measurements for each individual in any one year. Length was estimated using the relationship between the BH-DF and body length derived from measurements of eleven Scottish bottlenose dolphin strandings (SRUC 2017) ($F_{1,9} = 230.9$, $p < 0.0001$, $R^2 = 0.958$, $y = 3.1314x + 7.0626$). The average CV for length measurements of 20 adults (3 known-age, 17 estimated age) with multiple photographs was 1.4% (ranging from 0.2% to 3.0%). CV's for repeat measurements of the same photographs were <0.6%.

Estimated lengths of known-age dolphins ranged from 128 cm for a <1 month old calf to 326 cm for a 25-year-old female and 346 cm for a 19-year-old male. The longest dolphin was a 349 cm male and longest female was 333 cm, both identified as adults in the early 1990s. Males over 15 years old were on average longer (n=13, 335 cm, SE = 2.8 cm) than females (n=13, 321 cm, SE = 2.4 cm) (Welch Two Sample t-test: t=3.8705, df=23.554, p<0.001)

### Growth Curve

The MRGC analysis indicated that, at least up to the age of 13 years, sex did not improve model fit on the intercept ($\chi^2(1) = 0.286$, p=0.593), the linear ($\chi^2(1) = 1.315$, p=0.251) nor all time terms ($\chi^2(1) = 0.567$, p=0.753) (Supporting Information Tables A2 and A3 and Figure A7). The Richards' growth curve for this study population levelled off, but did not reach a clear asymptote (Figure 3). Separate models for males and females were similar to the growth curve for all individuals, and also showed no clear asymptote (Figure 3).

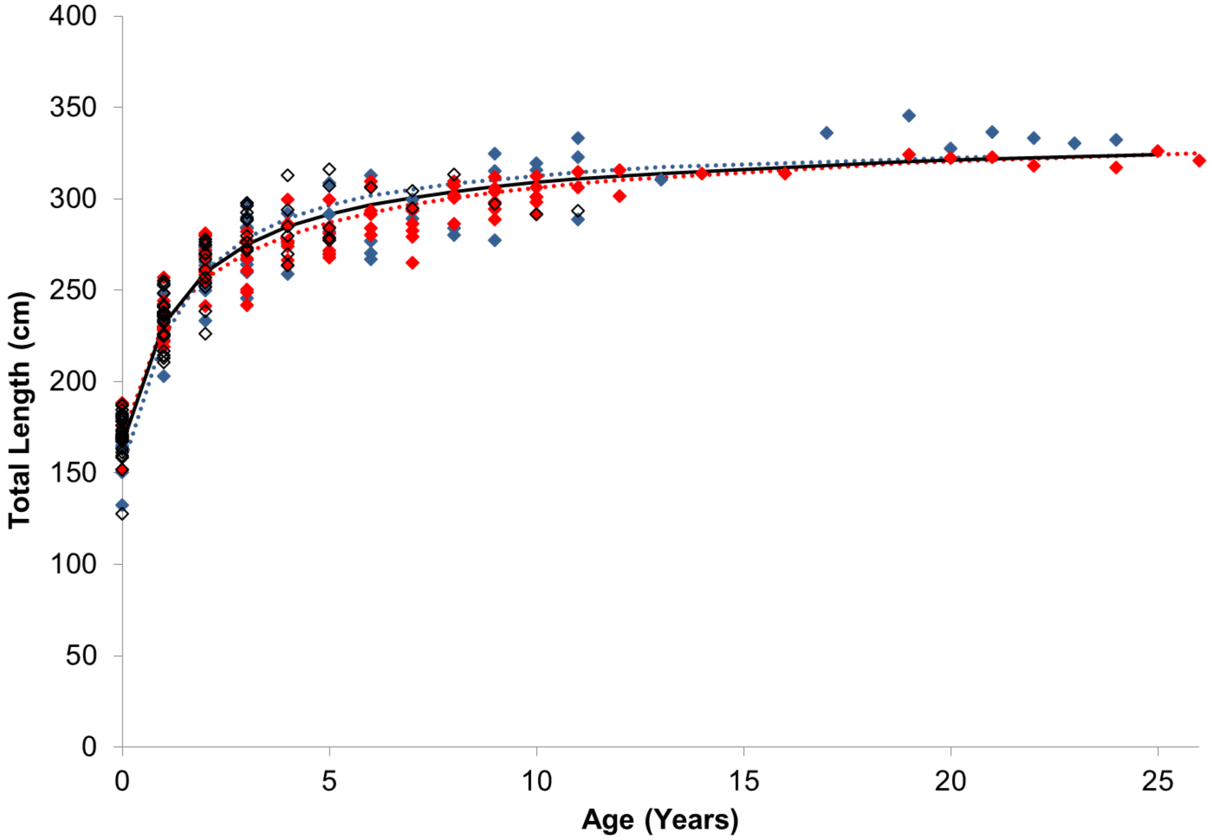

Figure 3. Annual estimates of length at age for female (red, n=22), male (blue, n=18) and unknown sex (white, n=47) known-age bottlenose dolphins from the east coast of Scotland (Appendix Table A3). The solid line represents the Richards growth curve for all individuals, females (red dotted line) and males (blue dotted line), all fitted using only one measurement per individual.

Table 1. Model selection and results of (a) linear mixed effects model to investigate the influence of sex on newborn length and growth in male (n=6) and female (n=11) calves from newborn to 1 year old; (b) linear mixed effects model to explore individual variability in newborn length and growth for all calves measured as a newborn and 1 year old (n=17) and (c) generalised linear model with binomial error distribution to investigate the best predictor of calf over-winter survival (n=36). The AICc values are shown for all models, the results are shown for the most parsimonious model with the lowest AICc (bold) and all models with some support (ΔAICc<2).

| **Model** | | **Coefficient** | **Std. Error** | **t** | **P** | **Random Effects** | **Variance** | **Std. Dev.** | **AICc** | **ΔAICc** |
|---|---|---|---|---|---|---|---|---|---|---|
| **(a)** | | | | | | | | | | |
| **Length ~ Age + Age\|ID** | **Intercept** | **160.644** | **3.149** | **51.02** | **<0.0001** | **ID** | **66.032** | **8.126** | **469.3** | **0** |
| | **Age** | **6.218** | **0.328** | **18.96** | **<0.0001** | **Age\|ID** | **0.584** | **0.764** | | |
| Length~ Age + Sex + Age\|ID | | | | | | | | | 471.6 | 2.3 |
| Length ~ Age * Sex + Age\|ID | | | | | | | | | 474.2 | 4.9 |
| **(b)** | | | | | | | | | | |
| **Length ~ Age + First Calf + Age\|ID** | **Intercept** | **167.694** | **1.901** | **88.219** | **<0.0001** | | | | **433.8** | **0** |
| | **Age** | **6.126** | **0.229** | **26.698** | **<0.0001** | **ID** | **0** | **0** | | |
| | **First Calf** | **-8.253** | **3.022** | **-2.731** | **0.011** | **Age\|ID** | **0.137** | **0.369** | | |
| Length ~ Age * First Calf + Age\|ID | Intercept | 168.293 | 2.023 | 83.179 | <0.0001 | | | | 435.7 | 1.9 |
| | Age | 6.022 | 0.259 | 23.253 | <0.0001 | | | | | |
| | First Calf | -11.371 | 4.778 | -2.380 | 0.023 | ID | 0 | 0 | | |
| | Age:First Calf | 0.459 | 0.544 | 0.844 | 0.4033 | Age\|ID | 0.129 | 0.360 | | |
| Length ~ Age + ID + Age\|ID[a] | | | | | | | | | 466.7 | 32.9 |
| Length ~ Age * ID + Age\|ID | | | | | | | | | 565.1 | 131.3 |

(a. most parsimonious model was with correlated random effects)

| Model | | Coefficient | Std. Error | t | P | Random Effects | Variance | Std. Dev. | AICc | ΔAICc |
|---|---|---|---|---|---|---|---|---|---|---|
| **(c)** | | | | | | | | | | |
| **Survival ~ Length** | **Intercept** | **10.999** | **5.771** | **1.906** | **0.057** | | | | **34.1** | **0** |
| | **Length** | **-0.0751** | **0.352** | **-2.135** | **0.033** | | | | | |
| Survival ~ Length + First Calf | Intercept | 9.860 | 6.001 | 1.643 | 0.100 | | | | 35.9 | 1.8 |
| | Length | -0.070 | 0.036 | -1.920 | 0.055 | | | | | |
| | First Calf | 0.756 | 1.012 | 0.747 | 0.455 | | | | | |
| Survival ~ Length + First Calf + L_Age | | | | | | | | | 38.3 | 4.2 |

## Calf Length and Growth

Sex also did not appear to influence newborn length or growth (Table 1(a)). Measurements made during the first two years of each dolphin's life (<1 to 14 months old) indicate that first-born calves were slightly shorter (Figure 4 and Table 1(b)). However, overall there was little individual variability in newborn length or growth (Table1 (b)).

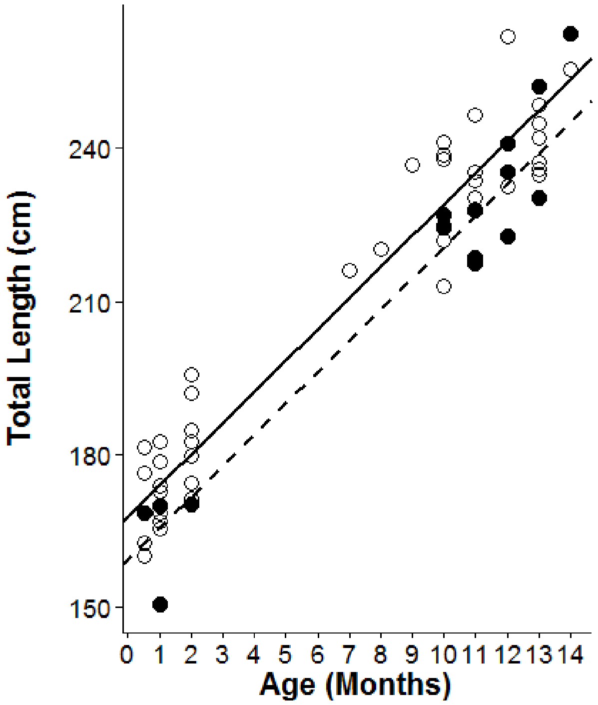

Figure 4. Length measurements of calves from <1 month to 14 months old with fitted lines from the most parsimonious linear mixed-effects model, showing estimated length of females' first calves (n=3, black circle, dashed line) and subsequent calves (n=14, white circle, solid line).

## First Year Survival

Generalised linear modelling indicated that first year survival was linked to body length (Table 1(c)). Sample sizes were small, but newborn bottlenose dolphins that died over their first winter were significantly shorter (n=7, median=159 cm) than those that survived (n=29, median=171 cm) (Mann-Whitney U test: W=165.5, p=0.01) (Figure 5). In addition, there may be some influence of birth order on first year calf survival (ΔAICc=1.8, Table 1(c)). 38% of first calves died over their first winter, whereas only 14% of subsequent calves died.

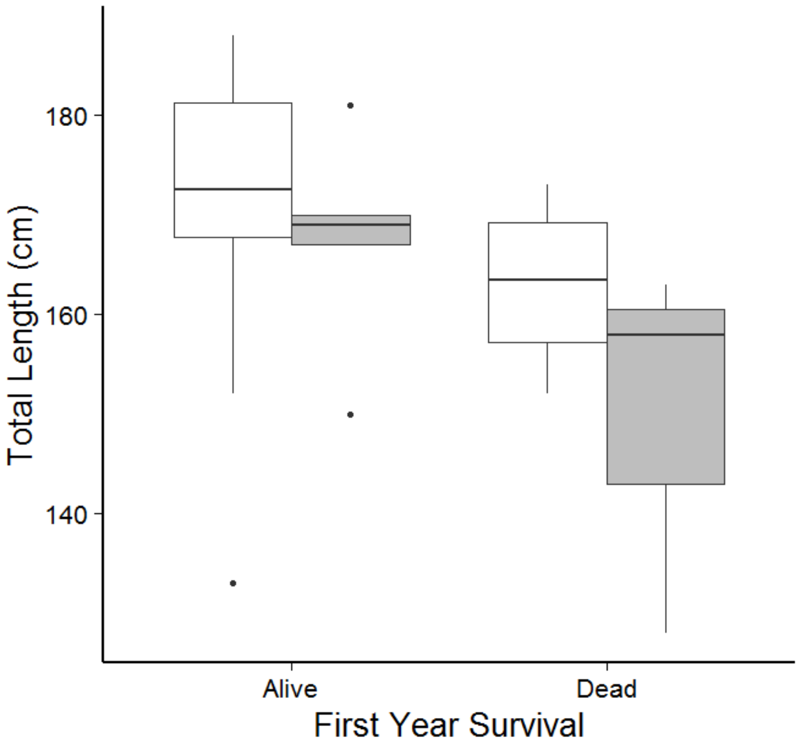

Figure 5. Length of newborn bottlenose dolphin calves during their first summer that either survived or died over their first winter, showing females' first (grey) or subsequent (white) calves.

**Accuracy and Precision of Laser Photogrammetry**

Laser photogrammetric measurements were obtained from 78 photographs of 12 dolphins from Sarasota that had previously been captured, measured directly, and released. There was no significant difference between the BH-DF measurements made during health assessments and laser photogrammetry (paired t-test, $t_{51}$=-0.767, p=0.447). Differences between the BH-DF laser and health assessment measurements ranged from -7.5 to 8 cm (mean = 3 cm, SE = 0.3 cm). The mean CV from different photographs of the same individual was 1.7% (range 0.2% to 2.7%). For Sarasota dolphins, body length was estimated using the relationship between the BH-DF and length of a subset of 42 individuals measured during health assessments ($F_{1,40}$ = 438.4, p<0.0001, $R^2$ = 0.916, y = 2.9846x + 17.9155). There was also no significant difference between the length measured during health assessments and estimated by laser photogrammetry (paired t-test: $t_{11}$ = 0.052, p = 0.9597). Differences ranged from -23 to 17 cm (mean = 5.9 cm, SE = 2.0 cm) which equated to -8.5% to 6.9% (mean = 2.3%) of the health assessment length.

The direct BH-DF measurements of the two adult male dolphins stranded in Scotland were both within 3 cm of mean laser photogrammetry estimates. The estimated length of each male were 9 cm (2.7%) shorter and 18 cm (5.2%) longer than the directly measured length.

## DISCUSSION

Growth and body condition can provide important indices of health and fitness, yet can be difficult to collect alongside studies using remote observations of natural marks to monitor populations of conservation concern. Our findings illustrate how laser photogrammetry can be successfully integrated into boat-based photo-identification studies. Repeat measurements of free-ranging bottlenose dolphins were routinely made over eight years, and the accuracy and precision of estimates characterised through comparison with direct measurements from free-living and stranded individuals. In combination with long-term observations that established the age of individuals, we developed a growth curve for individuals in this study population that was based entirely upon measurements from remote observations. While sample sizes currently remain small, these data were used to explore the causes and consequences of variation in early growth. This highlights the potential for collecting data that can explore the energetic requirements and dynamics of protected cetacean populations.

### Methodological considerations

A number of studies have developed approaches for the remote measurement of cetaceans using boat-based stereo-photogrammetry (Growcott *et al.* 2012), aerial surveys (Perryman and Lynn 1993, Sweeney *et al.* 2014) or unmanned aerial vehicles (UAVs) (Christiansen *et al.* 2016, Durban *et al.* 2016). However, when using small boats stereo-cameras generally require dedicated survey effort limiting their integration into monitoring programmes. Aerial data can only be linked to long-term individual-based data for larger species with distinct marks (Best and Rüther 1992, Fearnbach *et al.* 2011), with financial and safety considerations limiting this approach. Finally, UAVs can present technical and permitting challenges for many populations. Laser photogrammetry provides a simpler approach, which requires less investment in equipment, and can be fully integrated into the camera systems used for photo-identification.

Working with known-length bottlenose dolphins in Sarasota (Wells *et al.* 2004) we demonstrated that laser photogrammetry can provide robust estimates of body length. Laser photogrammetric measurements of BH-DF and the resulting estimates of length both compared well with existing direct measurements from health assessments. Errors around BH-DF measurements were comparable to results using laser photogrammetry to measure primate tail length (mean difference of 1.7%) (Rothman *et al.* 2008) and aerial photogrammetry (mean difference of 1.2%, based upon measurements of known length boats) (Fearnbach *et al.* 2011). Estimates of length showed greater differences, as these incorporated uncertainty in the relationship between BH-DF and length. Laser photogrammetry and physical measurements of stranded dolphins from our Scottish study population were also similar, and closest for the individual where the length estimate was based on an average of two photogrammetric measurements. Blackwell *et al.* (2006) highlight that at least two repeats should ideally be made, even with direct physical measurements. This is a reminder that some errors could result from variation in direct measurements, as significant differences in inter-researcher length measurements can occur (e.g. Waite and Mellish 2009). CVs of repeat measurements were comparable to other laser photogrammetry studies (1.5% to 3.7%) (Deakos 2010, Rowe and Dawson 2008, Webster *et al.* 2010) but were slightly higher than CVs for repeat physical measurements of adult dolphins (0.705%) (Read *et al.* 1993). One possible reason for the slightly higher CVs in this study, is that these incorporate horizontal axis error (i.e. when the dolphin is not parallel to the camera). Similar to Webster *et al.* (2010), who found deviations of $<20^o$ resulted in laser photogrammetry measurements within 2% of actual values, we minimised this error by discarding all photographs where the dolphin was considered to be nonparallel. Given the level of body size variation in these populations, measurements with this level of error and repeatability should provide valuable additional information on study individuals. Nevertheless, estimates should wherever possible be based upon multiple measurements.

## Growth Curve

Measurements of stranded and bycaught bottlenose dolphins highlight that this species exhibits marked variation in adult body size, with the largest individuals occurring in colder environments at the extremes of their global range. However, datasets of sufficient size to generate growth curves are rare, and previously restricted to populations inhabiting warmer waters (Fernandez and Hohn 1998, Read *et al.* 1993, Stolen *et al.* 2002). Our remote estimates of length at age were used to provide the first growth curve for a bottlenose dolphin population inhabiting temperate waters. The mean length of males and females over 15 years old was approximately 30% longer than estimates of adult size for populations in sub-tropical waters (Fernandez and Hohn 1998, Read *et al.* 1993, Stolen *et al.* 2002).

We also found that males and females in our population showed similar patterns of growth, in contrast to studies in sub-tropical waters (Fernandez and Hohn 1998, McFee *et al.* 2010, Read *et al.* 1993, Stolen *et al.* 2002). This may be a result of only including individuals up to 13 years old in our MRGC analysis, as Read et al. (1993) found that male bottlenose dolphins from Sarasota continued to grow after females reach asymptotic length (~ age 10). However, Richards' growth curves for males and females were very similar and there was overlap in lengths of all ages, although adult males were on average longer than females. Read *et al.* (1993) also found that females were longer and grew quicker than males at an early age, but this was not seen in our temperate population. Bottlenose dolphins in Scotland are at the northern extreme of the coastal range of this species, and colder water temperatures may require both sexes to maximise early growth as thermoregulation costs increase with decreasing body size (Harding *et al.* 2005). Although our growth curves did not reach an asymptote, they did level off and appeared close to asymptote. The absence of an asymptote may be a consequence of fewer known-age older individuals or continued somatic growth throughout life, as found in pinnipeds (Trites and Bigg 1996). Alternatively, there may be cohort variation in growth due to trends in food availability (Fearnbach *et al.* 2011). This technique provides opportunities to explore these questions through continued longitudinal studies of the size of known individuals in relation to intrinsic and extrinsic drivers.

### Causes and consequences of variation in newborn size and early growth

Our results were consistent with previous studies of stranded and bycaught dolphins indicating that male and female newborn calves are a similar size (Cockcroft and Ross 1990, Hohn 1980). We also found that sex did not affect initial calf growth, and there was little individual variability in growth. Although the combined dataset from both sexes remained small, there was evidence that first-born calves were shorter than calves of experienced mothers, as previously reported for large whales (Best and Rüther 1992). Size and growth can be affected by maternal characteristics in various species (Altmann and Alberts 2005, Bernardo 1996, Bowen *et al.* 1994). Thus, first-born dolphin calves may be smaller because mothers were younger and less experienced and/or of smaller size.

Importantly, results indicate that observed variation in calf length has fitness consequences. Calves that died over their first winter were significantly shorter than those that survived. It seems likely that variation in calf length provides a proxy for maternal investment or measures of body mass and condition (Cockcroft and Ross 1990, Reed and Plante 1997). Individual-based studies in both terrestrial (Clutton-Brock *et al.* 1987) and marine (Hall *et al.* 2001, Harding *et al.* 2005) species have illustrated how direct measures of early mass or condition may be related to subsequent survival. This is especially important in a conservation context, as the consequences of exposure to non-lethal stressors (e.g. noise, boat disturbance) are expected to act through changes in foraging energetics, and likely to be detected through variation in early growth and survival (Pirotta *et al.* 2015). There is also some evidence that birth order affects early survival in other bottlenose dolphin populations (Henderson *et al.* 2014, Mann *et al.* 2000), but this may be confounded by variation in female size, small sample sizes and environmental contaminant concentrations (Wells *et al.* 2005). Laser photogrammetry offers the potential to disentangle these effects by non-invasively integrating repeat measurements of recognisable individuals into routine monitoring of protected cetacean populations.

## ACKNOWLEDGEMENTS

Many thanks to the Chicago Zoological Society team for their assistance during photo-identification surveys in Sarasota, Florida and the Scottish Marine Animal Stranding Scheme and University of North Carolina Wilmington Marine Mammal Stranding Program for providing measurements of stranded bottlenose dolphins. Thanks to Holly Fearnbach and Isla Graham for statistical advice, to Hera Sengers and all our fieldwork assistants for their fieldwork support and to four anonymous reviewers who kindly provided comments on the manuscript. Scottish Natural Heritage, Beatrice Offshore Windfarm Ltd., Moray Offshore Renewables Ltd., Marine Scotland, The Crown Estate and Highlands and Islands Enterprise all provided funding for photo-identification surveys. Survey work was conducted under Scottish Natural Heritage Animal Scientific Licences.

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## APPENDIX

Additional supporting information for the published paper.

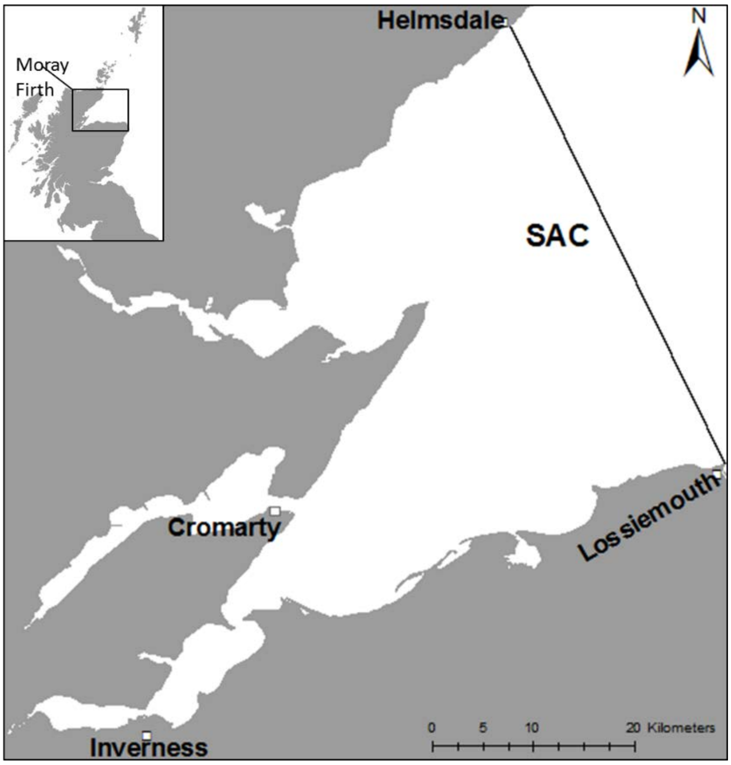

Figure A1. The Moray Firth Special Area of Conservation, with a map of Scotland inset.

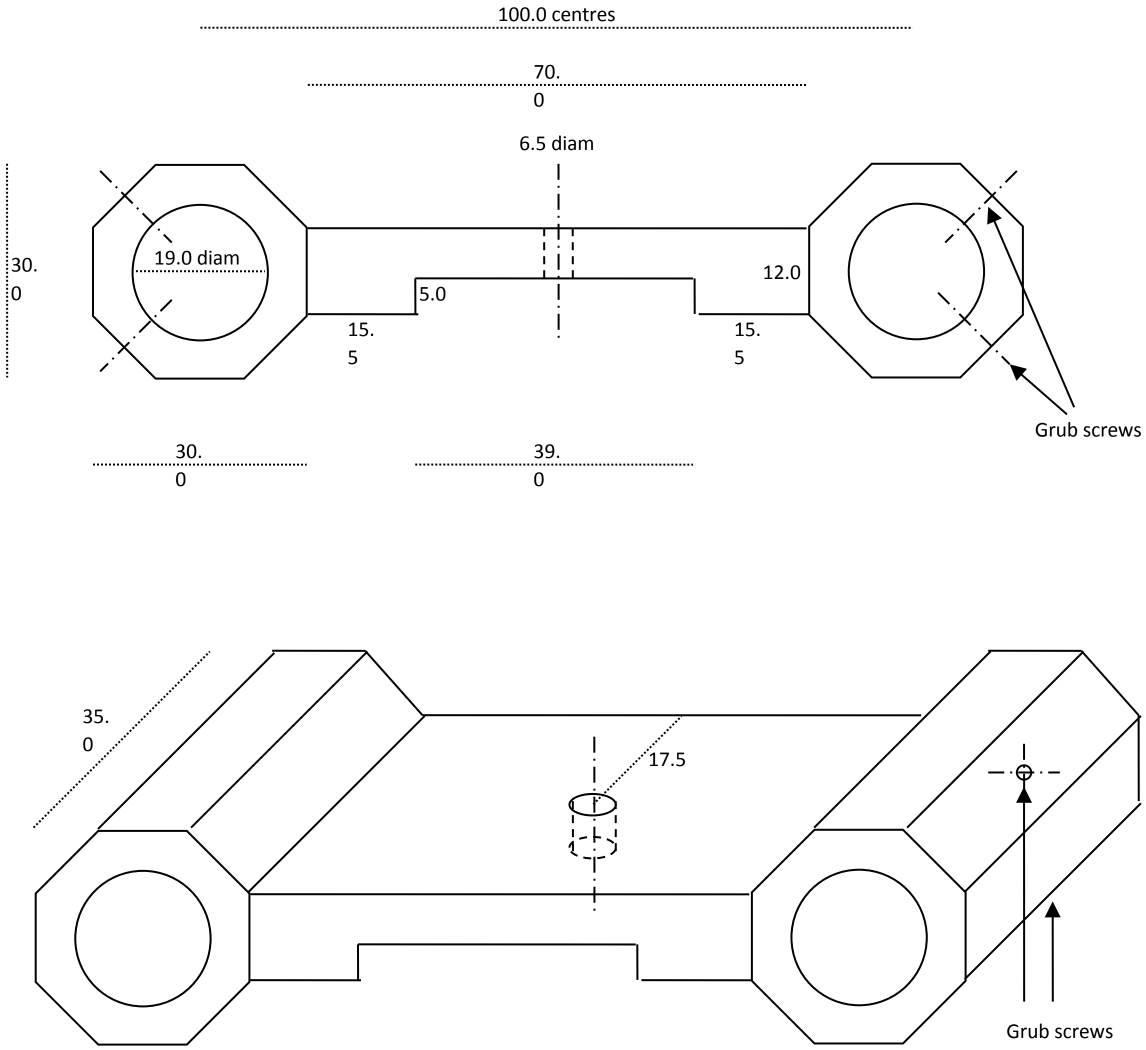

Figure A2. Diagram of the laser photogrammetry machined aluminium block with dimensions (mm). Laser separation at 100mm centres and grub screws to hold the laser sights in position.

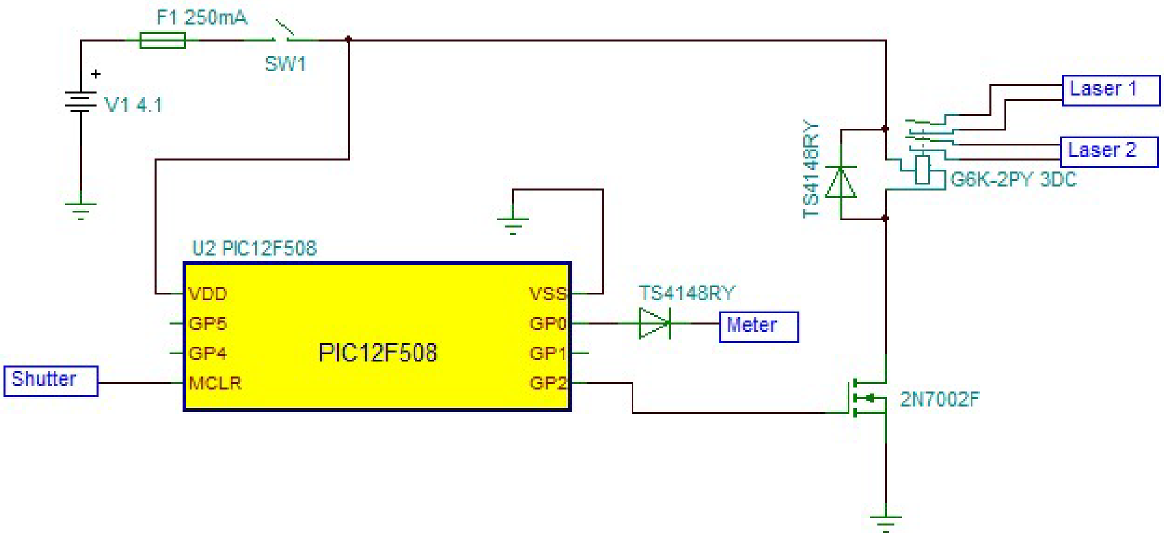

Figure A3. Diagram of the electronic control switch for the laser sights, with the connection to the camera remote release shutter, showing the microcontroller unit (PIC 12F508), relay (G6K-2PY), field effect transistor and diodes.

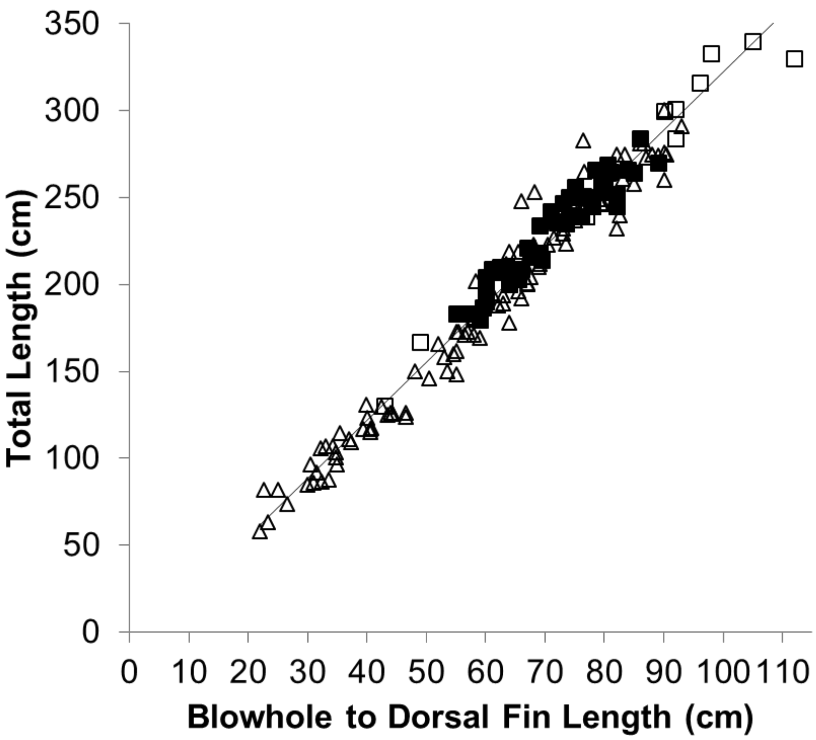

Figure A4. Relationship between the blowhole to dorsal fin distance and body length of bottlenose dolphins, from stranded individuals in the mid-Atlantic (clear triangles, n = 111) from the University of North Carolina Wilmington Marine Mammal Stranding Program, around Scotland from the Scottish Marine Mammal Stranding Scheme (clear squares, n = 11) and a selection of individuals captured during health assessments in Sarasota, Florida (black squares, n = 47) ($F_{1,166}$ = 4563, p <0.0001, $R^2$ = 0.964).

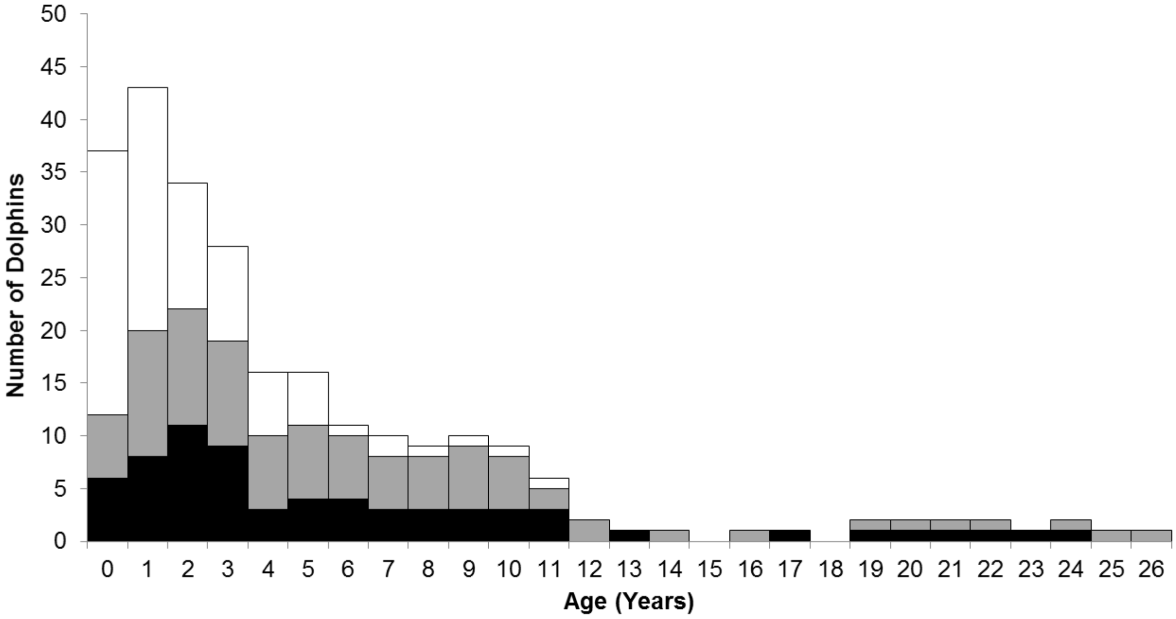

Figure A5. Number of dolphins by age and gender (males = black, females = grey, unknown sexes = white). Includes the same individuals at different ages.

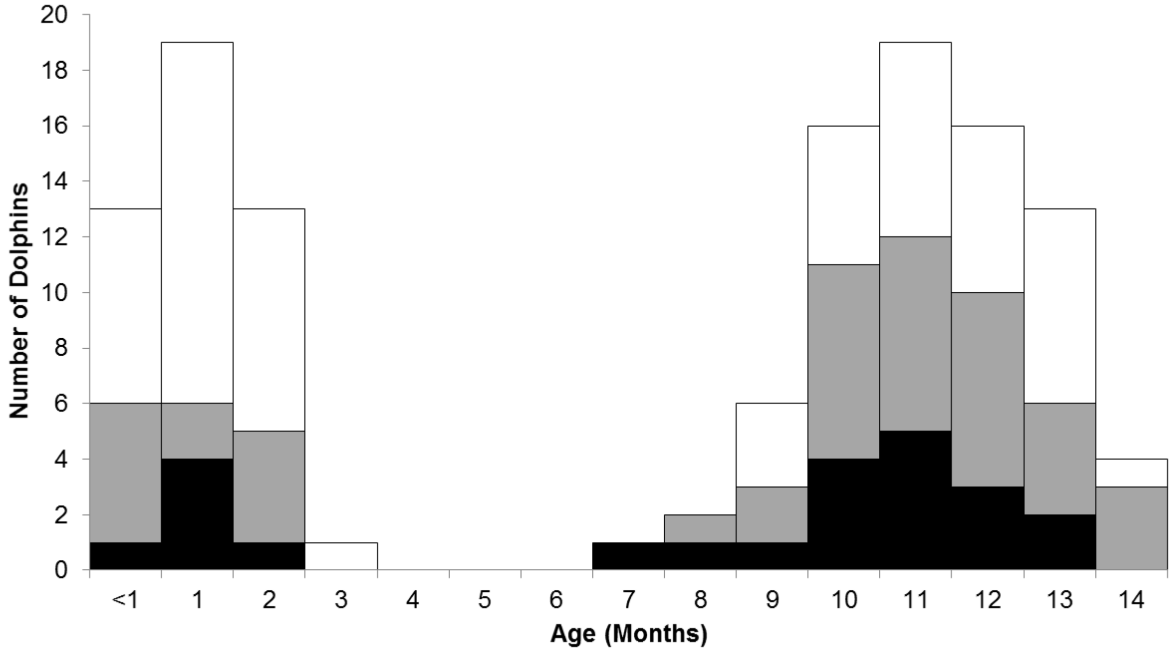

Figure A6. Number of dolphins of different estimated ages to the month (black = male, grey = female, white = unknown sex). Includes the same individuals at different ages.

### Multilevel Regression Growth Curve (MRGC) Analyses

MRGC modelling is a generalisation of standard regression approaches, however rather than a single model there are multiple (two or more) hierarchically related submodels. The first (level 1, below) captures the effect of time where the intercept and slope are allowed to vary across individuals ($_i$):

Third-order polynomial growth curve level 1 model:

$Y_{ij} = \beta_{0i} + \beta_{1i} \cdot Time_j + \beta_{2i} \cdot Time_j^2 + \beta_{3i} \cdot Time_j^3 + \varepsilon_{ij}$

Where:

$Y_{ij}$ = length of individual i at *Time* j

$\beta_{0i}$ = intercept

$\beta_{1i}$ = linear slope

$\beta_{2i}$ = quadratic curvature

$\beta_{3i}$ = cubic curvature

$\varepsilon_{ij}$ = residual error

Variation is then captured in the set of level 2 models (example below) for each parameter which can include experimental condition or group level effects (Mirman *et al.* 2008). See Mirman (2014) and Mirman *et al.* (2008) for full details of level 2 models.

Level 2 model for the intercept:

$\beta_{0i} = \gamma_{00} + \gamma_{0c} \cdot C + \zeta_{0i}$

Where:

$\gamma_{00}$ = population average for the intercept

$\gamma_{0c}$ = fixed effect of condition C on the intercept

$\zeta_{0i}$ = random deviation of an individual from the baseline/average intercept

*C* = effect of condition on the intercept (e.g. sex)

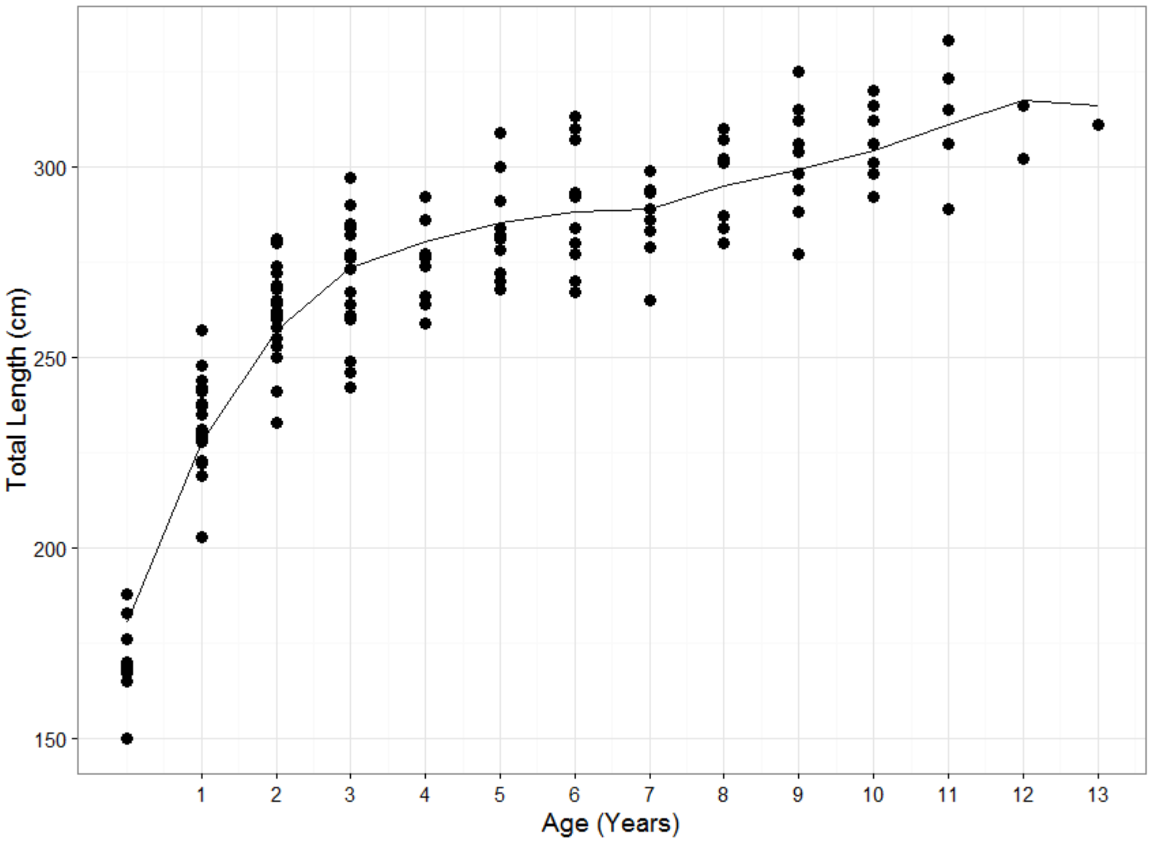

Figure A7. Annual laser photogrammetry measurements of males (n=14) and females (n=17) from newborn to 13 years old, with multilevel regression growth curve fitted line showing the average growth.

Table A1. Length (cm) and sex of bottlenose dolphins first identified as adults or sub-adults between 1989 and 1996 with their minimum age when their first laser photogrammetry picture was taken, assuming they were at least 4 years old when first seen. The stranding date and length of two identified individuals are also shown.

| ID | SEX | AVERAGE LASER LENGTH (cm) | FIRST SEEN | ESTIMATED AGE | FIRST LASER PHOTO | MINIMUM ESTIMATED AGE | STRANDED | BODY LENGTH (cm) |
|---|---|---|---|---|---|---|---|---|
| 1 | M | 348 | 1989 | Adult | 2010 | 25 | - | - |
| 8 | M | 339 | 1989 | Adult | 2009 | 24 | - | - |
| 23 | M | 331 | 1989 | Adult | 2010 | 25 | - | - |
| 30 | F | 322 | 1989 | Adult | 2010 | 25 | - | - |
| 31 | F | 312 | 1989 | Sub-adult | 2007 | 22 | - | - |
| 36 | M | 324 | 1989 | Adult | 2008 | 23 | 06/09/2010 | 333 |
| 42 | M | 332 | 1989 | Adult | 2009 | 24 | - | - |
| 49 | M | 348 | 1989 | Adult | 2009 | 24 | - | - |
| 52 | F | 317 | 1989 | Adult | 2010 | 25 | - | - |
| 60 | M | 322 | 1989 | Adult | 2009 | 24 | - | - |
| 64 | F | 319 | 1989 | Adult | 2010 | 25 | - | - |
| 79 | F | 333 | 1989 | Adult | 2012 | 27 | - | - |
| 102 | M | 322 | 1989 | Sub-adult | 2009 | 24 | - | - |
| 129 | M | 331 | 1990 | Adult | 2009 | 23 | - | - |
| 157 | M | 348 | 1990 | Adult | 2009 | 23 | 23/04/2011 | 330 |
| 192 | F | 318 | 1991 | Adult | 2008 | 21 | - | - |
| 307 | F | 333 | 1992 | Adult | 2009 | 21 | - | - |
| 430 | F | 324 | 1994 | Sub-adult | 2011 | 21 | - | - |
| 435 | M | 334 | 1994 | Adult | 2009 | 19 | - | - |
| 440 | F | 328 | 1994 | Sub-adult | 2010 | 20 | - | - |
| 573 | M | 349 | 1996 | Adult | 2009 | 17 | - | - |
| 578 | F | 301 | 1996 | Adult | 2009 | 17 | - | - |
| 580 | F | 328 | 1996 | Sub-adult | 2012 | 20 | - | - |

Table A2. Results of the multilevel regression growth curve analyses (where ot = orthogonal polynomials based on age). See Table A3 for model comparison.

| Model | Parameter | Estimate | Standard Error | df | t | P | AIC | ΔAIC |
|---|---|---|---|---|---|---|---|---|
| **Base model** | | | | | | | **1139.2** | **0.0** |
| **Length~(ot1 + ot2 + ot3) + (1\|ID) + (ot1\|ID) + (ot2\|ID) + (ot3\|ID)** | | | | | | | | |
| | **Intercept** | **282.787** | **2.275** | **3.280** | **124.321** | **<0.0001** | | |
| | **Linear (ot1)** | **129.826** | **7.890** | **1.740** | **16.454** | **<0.01** | | |
| | **Quadratic (ot2)** | **-23.623** | **6.455** | **31.160** | **-3.659** | **<0.001** | | |
| | **Cubic (ot3)** | **51.924** | **7.972** | **32.600** | **6.513** | **<0.0001** | | |
| Fixed effect of sex | | | | | | | 1141.0 | 1.8 |
| Length~(ot1 + ot2 + ot3) + Sex + (1\|ID) + (ot1\|ID) + (ot2\|ID) + (ot3\|ID) | | | | | | | | |
| | Intercept | 283.888 | 2.819 | 24.860 | 100.697 | <0.0001 | | |
| | Linear (ot1) | 131.391 | 8.400 | 31.810 | 15.642 | <0.0001 | | |
| | Quadratic (ot2) | -22.897 | 6.542 | 81.380 | --3.500 | <0.001 | | |
| | Cubic (ot3) | 52.756 | 8.013 | 32.780 | 6.584 | <0.0001 | | |
| | Sex (Female) | -2.102 | 3.635 | 21.870 | -0.578 | 0.569 | | |
| Fixed effect of sex on linear term | | | | | | | 1141.7 | 2.5 |
| Length~(ot1 + ot2 + ot3) + Sex + ot1:Sex + (1\|ID) + (ot1\|ID) + (ot2\|ID) + (ot3\|ID) | | | | | | | | |
| | Intercept | 282.185 | 2.806 | 30.400 | 100.578 | <0.0001 | | |
| | Linear (ot1) | 122.165 | 8.952 | 50.810 | 13.646 | <0.0001 | | |
| | Quadratic (ot2) | -24.740 | 6.376 | 89.160 | -3.880 | <0.001 | | |
| | Cubic (ot3) | 51.402 | 8.039 | 32.610 | 6.394 | <0.0001 | | |
| | Sex (Female) | 1.229 | 4.319 | 27.000 | 0.284 | 0.778 | | |
| | ot1:Sex (F) | 15.333 | 12.328 | 45.590 | 1.244 | 0.220 | | |

| **Model** | **Parameter** | **Estimate** | **Standard Error** | **df** | **t** | **P** | **AIC** | **ΔAIC** |
|---|---|---|---|---|---|---|---|---|
| Full model (fixed effect of sex on all time terms) | | | | | | | 1145.1 | 5.9 |
| Length~(ot1 + ot2 + ot3) * Sex + (1\|ID) + (ot1\|ID) + (ot2\|ID) + (ot3\|ID) | | | | | | | | |
| | Intercept | 281.814 | 2.841 | 33.320 | 99.200 | <0.0001 | | |
| | Linear (ot1) | 121.587 | 9.598 | 44.730 | 12.667 | <0.0001 | | |
| | Quadratic (ot2) | -25.574 | 8.475 | 96.060 | -3.018 | <0.01 | | |
| | Cubic (ot3) | 46.195 | 10.627 | 32.110 | 4.347 | <0.001 | | |
| | Sex (Female) | 1.891 | 4.381 | 33.050 | 0.432 | 0.669 | | |
| | ot1:Sex (F) | 16.879 | 14.314 | 47.510 | 1.179 | 0.244 | | |
| | ot2:Sex (F) | 1.907 | 12.870 | 85.650 | 0.148 | 0.883 | | |
| | ot3:Sex (F) | 12.121 | 16.150 | 32.170 | 0.751 | 0.458 | | |

Table A3. Comparison of the multilevel regression growth curve models using Anova (see Table A2 for full model details).

| **Model** | **Df** | **AIC** | **BIC** | **logLik** | **Deviance** | **Chisq** | **P** |
|---|---|---|---|---|---|---|---|
| Base model | 15 | 1139.2 | 1183.3 | -554.62 | 1109.2 | | |
| Fixed effect of sex | 16 | 1141.0 | 1187.9 | -554.48 | 1109.0 | 0.25836 | 0.593 |
| Fixed effect of sex on linear term | 17 | 1141.1 | 1191.5 | -553.82 | 1107.7 | 1.3154 | 0.251 |
| Full model (fixed effect of sex on all time terms) | 19 | 1145.1 | 1200.8 | 553.54 | 1107.1 | 0.5668 | 0.753 |

Table A4. Model selection results for Richards, Gompertz (‘drc’ R package) and von Bertalanffy (‘fishmethods’ R package) growth curves for known age individuals.

| **Data** | **Growth Curve** | **Log Likelihood** | **AIC** | **Lack of Fit** | **Residual Variance** | **Residual Standard Error** | **Residual Sum of Squares** |
|---|---|---|---|---|---|---|---|
| All Individuals | Richards | -354.21 | 720.42 | 0.9292 | 213.60 | 14.62 | 17515 |
| | Von Bertalanffy | - | 728.15 | - | - | 15.45 | 20043 |
| | Gompertz | -471.36 | 952.72 | 0.0000 | 3118.16 | 55.84 | 258808 |
| Males | Richards | -76.00 | 164.00 | 0.4102 | 376.92 | | |
| | Gompertz | -77.26 | 164.52 | 0.3626 | 402.68 | | |
| Females | Richards | -86.01 | 184.02 | 0.9870 | 188.53 | | |
| | Gompertz | -89.32 | 188.64 | 0.8683 | 240.53 | | |

Table A5. Length (cm) of known age bottlenose dolphins seen within the SAC between 2007 and 2014 with the number of males, females and unknown sex, range, mean (± SE) and prediction from the Richards growth curve analysis for all individuals.

| Age (Years) | Sex | N | Range | Mean (± SE) | Prediction |
|---|---|---|---|---|---|
| Newborn | Male | 6 | 133-183 | 160 (6.92) | |
| | Female | 6 | 152-188 | 171 (4.86) | 165 |
| | Unknown | 25 | 128-187 | 171 (2.57) | |
| 1 | Male | 8 | 203-248 | 230 (4.75) | |
| | Female | 12 | 219-257 | 233 (3.08) | 231 |
| | Unknown | 23 | 211-255 | 234 (2.62) | |
| 2 | Male | 11 | 233-280 | 264 (4.17) | |
| | Female | 11 | 241-281 | 264 (3.41) | 260 |
| | Unknown | 12 | 226-278 | 260 (4.60) | |
| 3 | Male | 9 | 246-297 | 275 (5.61) | |
| | Female | 10 | 242-282 | 265 (4.39) | 275 |
| | Unknown | 9 | 274-298 | 285 (3.31) | |
| 4 | Male | 3 | 259-292 | 275 (9.67) | |
| | Female | 7 | 264-300 | 278 (4.63) | 285 |
| | Unknown | 6 | 264-313 | 284 (7.23) | |
| 5 | Male | 4 | 270-309 | 288 (8.22) | |
| | Female | 7 | 268-300 | 279 (4.16) | 292 |
| | Unknown | 5 | 277-316 | 293 (7.94) | |
| 6 | Male | 4 | 267-313 | 282 (10.57) | |
| | Female | 6 | 280-310 | 294 (4.84) | 297 |
| | Unknown | 1 | 306 | - | |
| 7 | Male | 3 | 289-299 | 294 (3.02) | |
| | Female | 5 | 265-294 | 281 (4.77) | 301 |
| | Unknown | 2 | 295-304 | 300 (4.67) | |
| 8 | Male | 3 | 280-307 | 290 (8.41) | |
| | Female | 5 | 287-310 | 301 (4.00) | 304 |
| | Unknown | 1 | 313 | - | |
| 9 | Male | 3 | 277-325 | 306 (14.47) | |
| | Female | 6 | 288-312 | 300 (3.46) | 307 |
| | Unknown | 1 | 297 | - | |
| 10 | Male | 3 | 301-320 | 312 (5.69) | |
| | Female | 5 | 292-312 | 302 (3.48) | 309 |
| | Unknown | 1 | 292 | - | |
| 11 | Male | 3 | 289-333 | 315 (13.52) | |
| | Female | 2 | 306-315 | 310 (4.29) | 311 |
| | Unknown | 1 | 293 | - | |
| 12 | Female | 2 | 302-316 | 309 (7.10) | 313 |
| 13 | Male | 1 | 311 | - | 314 |
| 14 | Female | 1 | 314 | - | - |
| 16 | Female | 1 | 314 | - | - |
| 17 | Male | 1 | 336 | - | - |
| Age (Years) | Sex | N | Range | Mean (± SE) | Prediction |

| | | | | | |
|---|---|---|---|---|---|
| 19 | Male | 1 | 346 | - | 320 |
| | Female | 1 | 324 | - | |
| 20 | Male | 1 | 328 | - | - |
| | Female | 1 | 322 | - | |
| 21 | Male | 1 | 337 | - | 322 |
| | Female | 1 | 323 | - | |
| 22 | Male | 1 | 333 | - | - |
| | Female | 1 | 318 | - | |
| 23 | Male | 1 | 330 | - | - |
| 24 | Male | 1 | 332 | - | - |
| | Female | 1 | 317 | - | |
| 25 | Female | 1 | 326 | - | 324 |
| 26 | Female | 1 | 321 | - | - |

Table A6. Data set of estimated length (cm) of all bottlenose dolphins measured using laser photogrammetry, by age (years, months (mths) or adult) and sex (1 = male, 2 = female, 3 = unknown sex), including the number of photographs measured and the type of laser photogrammetry photo used (i.e. lasers used as a scale to measure the distance from the blowhole to dorsal fin (Lasers + BH-DF) and/or lasers used as a scale to measure the height of the dorsal fin and this height used as a scale to measure the distance from the blowhole to dorsal fin (DF + BH-DF)). In all cases length was estimated using the relationship between BH-DF and body length of stranded individuals.

| **ID** | **Sex** | **Age** | **Length (cm)** | **Number of Photos** | **Lasers + BH-DF** | **DF + BH-DF** |
|---|---|---|---|---|---|---|
| 1 | 1 | ADULT | 346 | 8 |  | ✓ |
| 8 | 1 | ADULT | 339 | 7 | ✓ | ✓ |
| 11 | 2 | 20 | 322 | 6 |  | ✓ |
| 11 | 2 | 21 | 323 | 11 | ✓ | ✓ |
| 11 | 2 | 22 | 318 | 10 | ✓ | ✓ |
| 11 | 2 | 24 | 317 | 4 |  | ✓ |
| 11 | 2 | 25 | 326 | 4 |  | ✓ |
| 11 | 2 | 26 | 321 | 7 | ✓ | ✓ |
| 23 | 1 | ADULT | 330 | 9 | ✓ | ✓ |
| 30 | 2 | ADULT | 320 | 8 |  | ✓ |
| 31 | 2 | ADULT | 311 | 11 | ✓ | ✓ |
| 36 | 1 | ADULT | 324 | 4 | ✓ | ✓ |
| 42 | 1 | ADULT | 332 | 3 |  | ✓ |
| 49 | 1 | ADULT | 350 | 3 | ✓ |  |
| 52 | 2 | ADULT | 317 | 9 |  | ✓ |
| 60 | 1 | ADULT | 322 | 4 |  | ✓ |
| 64 | 2 | ADULT | 320 | 9 | ✓ | ✓ |
| 79 | 2 | ADULT | 332 | 8 | ✓ | ✓ |
| 102 | 1 | ADULT | 322 | 4 |  | ✓ |
| 105 | 1 | 17 | 336 | 2 |  | ✓ |
| 105 | 1 | 19 | 346 | 7 |  | ✓ |
| 105 | 1 | 20 | 328 | 3 |  | ✓ |
| 105 | 1 | 21 | 337 | 6 |  | ✓ |
| 105 | 1 | 22 | 333 | 3 |  | ✓ |
| 105 | 1 | 23 | 330 | 5 | ✓ |  |
| 105 | 1 | 24 | 332 | 6 |  | ✓ |
| 192 | 2 | ADULT | 318 | 7 |  | ✓ |
| 307 | 2 | ADULT | 334 | 4 | ✓ | ✓ |
| 430 | 2 | ADULT | 324 | 7 | ✓ | ✓ |
| 433 | 2 | 14 | 314 | 4 |  | ✓ |
| 433 | 2 | 16 | 314 | 5 |  | ✓ |
| 433 | 2 | 19 | 324 | 1 | ✓ |  |
| 435 | 1 | ADULT | 334 | 2 | ✓ |  |
| 440 | 2 | ADULT | 328 | 2 | ✓ |  |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 573 | 1 | ADULT | 349 | 2 | ✓ | |
| 578 | 2 | ADULT | 301 | 4 | ✓ | |
| 580 | 2 | ADULT | 328 | 2 | ✓ | |
| 733 | 2 | 9 | 294 | 5 | | ✓ |
| 733 | 2 | 10 | 306 | 10 | ✓ | ✓ |
| 815 | 1 | 7 | 289 | 9 | | ✓ |
| 815 | 1 | 8 | 284 | 7 | | ✓ |
| 815 | 1 | 9 | 325 | 7 | | ✓ |
| 815 | 1 | 10 | 320 | 12 | ✓ | ✓ |
| 815 | 1 | 11 | 323 | 7 | | ✓ |
| 815 | 1 | 13 | 311 | 7 | ✓ | ✓ |
| 923 | 2 | 8 | 301 | 3 | | ✓ |
| 923 | 2 | 9 | 298 | 6 | | ✓ |
| 923 | 2 | 10 | 312 | 8 | ✓ | ✓ |
| 923 | 2 | 11 | 315 | 6 | | ✓ |
| 923 | 2 | 12 | 316 | 6 | ✓ | ✓ |
| 970 | 3 | 5 | 277 | 6 | ✓ | ✓ |
| 970 | 3 | 7 | 304 | 7 | ✓ | ✓ |
| 970 | 3 | 9 | 297 | 6 | | ✓ |
| 970 | 3 | 10 | 292 | 7 | | ✓ |
| 970 | 3 | 11 | 293 | 4 | | ✓ |
| 972 | 1 | 7 | 299 | 9 | | ✓ |
| 972 | 1 | 8 | 307 | 7 | ✓ | ✓ |
| 972 | 1 | 9 | 315 | 6 | | ✓ |
| 972 | 1 | 10 | 316 | 6 | | ✓ |
| 972 | 1 | 11 | 333 | 7 | ✓ | ✓ |
| 973 | 2 | 7 | 265 | 4 | | ✓ |
| 973 | 2 | 8 | 287 | 10 | | ✓ |
| 973 | 2 | 9 | 288 | 8 | | ✓ |
| 973 | 2 | 10 | 292 | 6 | | ✓ |
| 973 | 2 | 11 | 306 | 7 | | ✓ |
| 973 | 2 | 12 | 302 | 7 | ✓ | ✓ |
| 980 | 3 | 4 | 264 | 2 | | ✓ |
| 980 | 3 | 5 | 279 | 7 | | ✓ |
| 989 | 1 | 4 | 259 | 1 | ✓ | |
| 989 | 1 | 5 | 270 | 6 | | ✓ |
| 989 | 1 | 6 | 270 | 6 | | ✓ |
| 989 | 1 | 8 | 280 | 7 | | ✓ |
| 989 | 1 | 9 | 277 | 1 | ✓ | |
| 989 | 1 | 10 | 301 | 1 | ✓ | |
| 989 | 1 | 11 | 289 | 2 | ✓ | |
| 991 | 2 | 3 | 277 | 6 | ✓ | |
| 991 | 2 | 4 | 266 | 8 | | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 991 | 2 | 5 | 272 | 3 | | ✓ |
| 991 | 2 | 6 | 280 | 9 | ✓ | ✓ |
| 991 | 2 | 7 | 279 | 6 | ✓ | ✓ |
| 991 | 2 | 8 | 302 | 7 | | ✓ |
| 991 | 2 | 9 | 306 | 9 | | ✓ |
| 991 | 2 | 10 | 301 | 14 | ✓ | ✓ |
| 998 | 1 | 2 | 273 | 3 | | ✓ |
| 1000 | 3 | 4 | 270 | 1 | ✓ | |
| 1006 | 2 | 3 | 242 | 4 | | ✓ |
| 1006 | 2 | 5 | 284 | 10 | | ✓ |
| 1006 | 2 | 6 | 292 | 7 | | ✓ |
| 1006 | 2 | 7 | 283 | 4 | ✓ | ✓ |
| 1006 | 2 | 8 | 310 | 8 | ✓ | ✓ |
| 1006 | 2 | 9 | 304 | 7 | | ✓ |
| 1006 | 2 | 10 | 298 | 8 | ✓ | ✓ |
| 1008 | 3 | 3 | 293 | 10 | | ✓ |
| 1011 | 3 | 3 | 296 | 6 | | ✓ |
| 1012 | 3 | 3 | 289 | 8 | ✓ | ✓ |
| 1012 | 3 | 8 | 313 | 4 | | ✓ |
| 1013 | 3 | 4 | 294 | 4 | | ✓ |
| 1014 | 3 | 1 | 255 | 4 | ✓ | ✓ |
| 1014 | 3 | 2 | 261 | 11 | ✓ | ✓ |
| 1015 | 2 | 4 | 300 | 3 | | ✓ |
| 1016 | 2 | 5 | 300 | 6 | | ✓ |
| 1016 | 2 | 6 | 307 | 8 | | ✓ |
| 1016 | 2 | 8 | 307 | 10 | ✓ | ✓ |
| 1016 | 2 | 9 | 312 | 2 | ✓ | |
| 1017 | 3 | 9 mths | 210 | 1 | | ✓ |
| 1017 | 3 | 11 mths | 225 | 2 | | ✓ |
| 1017 | 3 | 12 mths | 252 | 4 | ✓ | ✓ |
| 1017 | 3 | 1 | 238 | 7 | ✓ | ✓ |
| 1018 | 2 | 8 mths | 203 | 2 | | ✓ |
| 1018 | 2 | 10 mths | 234 | 3 | ✓ | ✓ |
| 1018 | 2 | 11 mths | 237 | 3 | ✓ | ✓ |
| 1018 | 2 | 12 mths | 231 | 3 | | ✓ |
| 1018 | 2 | 1 | 230 | 11 | ✓ | ✓ |
| 1018 | 2 | 2 | 268 | 11 | ✓ | ✓ |
| 1018 | 2 | 3 | 251 | 1 | ✓ | |
| 1018 | 2 | 4 | 274 | 6 | | ✓ |
| 1018 | 2 | 5 | 268 | 7 | | ✓ |
| 1018 | 2 | 6 | 284 | 7 | | ✓ |
| 1018 | 2 | 7 | 286 | 14 | ✓ | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1020 | 3 | 11 mths | 227 | 1 | ✓ |  |
| 1020 | 3 | 12 mths | 242 | 2 |  | ✓ |
| 1020 | 3 | 13 mths | 232 | 2 |  | ✓ |
| 1020 | 3 | 1 | 234 | 6 | ✓ | ✓ |
| 1020 | 3 | 2 | 278 | 8 |  | ✓ |
| 1020 | 3 | 3 | 288 | 16 | ✓ | ✓ |
| 1020 | 3 | 4 | 279 | 7 |  | ✓ |
| 1020 | 3 | 5 | 307 | 3 |  | ✓ |
| 1020 | 3 | 6 | 306 | 2 |  | ✓ |
| 1020 | 3 | 7 | 295 | 9 |  | ✓ |
| 1021 | 1 | 2 | 274 | 9 | ✓ | ✓ |
| 1021 | 1 | 3 | 285 | 13 | ✓ | ✓ |
| 1021 | 1 | 5 | 291 | 6 | ✓ | ✓ |
| 1021 | 1 | 6 | 313 | 2 |  | ✓ |
| 1022 | 1 | 1 mth | 167 | 2 |  | ✓ |
| 1022 | 1 | 0 | 167 | 2 |  | ✓ |
| 1022 | 1 | 7 mths | 216 | 2 |  | ✓ |
| 1022 | 1 | 8 mths | 220 | 1 |  | ✓ |
| 1022 | 1 | 10 mths | 222 | 5 |  | ✓ |
| 1022 | 1 | 11 mths | 235 | 2 |  | ✓ |
| 1022 | 1 | 1 | 223 | 11 |  | ✓ |
| 1022 | 1 | 2 | 264 | 10 | ✓ | ✓ |
| 1022 | 1 | 3 | 264 | 7 |  | ✓ |
| 1022 | 1 | 4 | 276 | 8 |  | ✓ |
| 1022 | 1 | 5 | 282 | 10 | ✓ | ✓ |
| 1022 | 1 | 6 | 277 | 6 |  | ✓ |
| 1022 | 1 | 7 | 293 | 8 | ✓ | ✓ |
| 1023 | 2 | 9 mths | 226 | 1 |  | ✓ |
| 1023 | 2 | 10 mths | 227 | 2 |  | ✓ |
| 1023 | 2 | 11 mths | 219 | 6 | ✓ | ✓ |
| 1023 | 2 | 12 mths | 230 | 1 | ✓ |  |
| 1023 | 2 | 1 | 222 | 10 | ✓ | ✓ |
| 1023 | 2 | 2 | 262 | 11 | ✓ | ✓ |
| 1023 | 2 | 3 | 267 | 18 | ✓ | ✓ |
| 1023 | 2 | 4 | 277 | 8 |  | ✓ |
| 1023 | 2 | 5 | 278 | 4 |  | ✓ |
| 1023 | 2 | 6 | 293 | 11 |  | ✓ |
| 1023 | 2 | 7 | 294 | 10 | ✓ | ✓ |
| 1024 | 2 | 11 mths | 241 | 4 |  | ✓ |
| 1024 | 2 | 1 | 241 | 4 |  | ✓ |
| 1024 | 2 | 2 | 281 | 8 | ✓ | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1024 | 2 | 3 | 276 | 6 | ✓ | ✓ |
| 1024 | 2 | 4 | 286 | 1 | ✓ | |
| 1024 | 2 | 6 | 310 | 2 | | ✓ |
| 1025 | 1 | 3 | 246 | 2 | | ✓ |
| 1025 | 1 | 6 | 267 | 2 | ✓ | |
| 1031 | 3 | 4 | 313 | 6 | ✓ | ✓ |
| 1031 | 3 | 5 | 316 | 6 | | ✓ |
| 1068 | 3 | 11 mths | 217 | 3 | | ✓ |
| 1068 | 3 | 1 | 217 | 3 | | ✓ |
| 1068 | 3 | 2 | 257 | 8 | ✓ | ✓ |
| 1068 | 3 | 5 | 284 | 10 | ✓ | ✓ |
| 1071 | 3 | 11 mths | 255 | 6 | ✓ | ✓ |
| 1071 | 3 | 13 mths | 250 | 6 | ✓ | ✓ |
| 1071 | 3 | 1 | 253 | 12 | ✓ | ✓ |
| 1072 | 3 | 12 mths | 252 | 5 | | ✓ |
| 1072 | 3 | 14 mths | 260 | 1 | ✓ | |
| 1072 | 3 | 1 | 254 | 6 | ✓ | ✓ |
| 1072 | 3 | 2 | 277 | 4 | ✓ | ✓ |
| 1072 | 3 | 3 | 272 | 7 | | ✓ |
| 1077 | 1 | 11 mths | 244 | 5 | | ✓ |
| 1077 | 1 | 12 mths | 245 | 6 | ✓ | ✓ |
| 1077 | 1 | 13 mths | 255 | 6 | ✓ | ✓ |
| 1077 | 1 | 1 | 248 | 17 | ✓ | ✓ |
| 1077 | 1 | 2 | 269 | 11 | ✓ | ✓ |
| 1077 | 1 | 3 | 284 | 10 | ✓ | ✓ |
| 1077 | 1 | 4 | 292 | 8 | ✓ | ✓ |
| 1077 | 1 | 5 | 309 | 7 | ✓ | ✓ |
| 1078 | 3 | 12 mths | 226 | 3 | | ✓ |
| 1078 | 3 | 1 | 226 | 3 | | ✓ |
| 1078 | 3 | 2 | 226 | 8 | ✓ | ✓ |
| 1079 | 1 | 1 | 235 | 3 | | ✓ |
| 1079 | 1 | 2 | 280 | 10 | ✓ | ✓ |
| 1079 | 1 | 3 | 297 | 1 | ✓ | |
| 1080 | 3 | 2 | 275 | 4 | ✓ | ✓ |
| 1080 | 3 | 3 | 273 | 4 | | ✓ |
| 1081 | 3 | 1 mth | 174 | 1 | ✓ | |
| 1081 | 3 | 0 | 174 | 1 | ✓ | |
| 1081 | 3 | 10 mths | 213 | 1 | ✓ | |
| 1081 | 3 | 1 | 213 | 1 | ✓ | |
| 1081 | 3 | 2 | 238 | 2 | | ✓ |
| 1082 | 3 | 10 mths | 211 | 5 | | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1082 | 3 | 1 | 211 | 5 | | ✓ |
| 1084 | 2 | 11 mths | 225 | 4 | ✓ | ✓ |
| 1084 | 2 | 1 | 225 | 4 | ✓ | ✓ |
| 1085 | 1 | 9 mths | 230 | 3 | | ✓ |
| 1085 | 1 | 1 | 230 | 3 | | ✓ |
| 1085 | 1 | 2 | 253 | 8 | ✓ | ✓ |
| 1085 | 1 | 3 | 260 | 8 | ✓ | ✓ |
| 1086 | 2 | < 1 mth | 163 | 1 | ✓ | |
| 1086 | 2 | 2 mths | 171 | 3 | | ✓ |
| 1086 | 2 | 0 | 168 | 4 | ✓ | ✓ |
| 1086 | 2 | 10 mths | 241 | 2 | ✓ | |
| 1086 | 2 | 11 mths | 246 | 3 | ✓ | ✓ |
| 1086 | 2 | 1 | 244 | 5 | ✓ | ✓ |
| 1086 | 2 | 2 | 255 | 6 | ✓ | ✓ |
| 1086 | 2 | 3 | 249 | 7 | | ✓ |
| 1086 | 2 | 5 | 270 | 14 | ✓ | ✓ |
| 1087 | 3 | < 1 mth | 160 | 2 | ✓ | ✓ |
| 1087 | 3 | 2 mths | 192 | 3 | | ✓ |
| 1087 | 3 | 0 | 176 | 5 | ✓ | ✓ |
| 1087 | 3 | 13 mths | 242 | 9 | ✓ | ✓ |
| 1087 | 3 | 1 | 242 | 9 | ✓ | ✓ |
| 1087 | 3 | 3 | 298 | 5 | | ✓ |
| 1101 | 2 | 12 mths | 214 | 3 | | ✓ |
| 1101 | 2 | 13 mths | 217 | 3 | ✓ | |
| 1101 | 2 | 14 mths | 223 | 4 | | ✓ |
| 1101 | 2 | 1 | 219 | 10 | ✓ | ✓ |
| 1101 | 2 | 2 | 241 | 1 | ✓ | |
| 1101 | 2 | 5 | 281 | 2 | ✓ | |
| 1106 | 3 | < 1 mth | 163 | 6 | | ✓ |
| 1106 | 3 | 1 mth | 173 | 9 | ✓ | ✓ |
| 1106 | 3 | 0 | 169 | 15 | ✓ | ✓ |
| 1106 | 3 | 12 mths | 241 | 6 | ✓ | ✓ |
| 1106 | 3 | 1 | 241 | 6 | ✓ | ✓ |
| 1106 | 3 | 2 | 254 | 7 | ✓ | ✓ |
| 1106 | 3 | 3 | 276 | 10 | ✓ | ✓ |
| 1106 | 3 | 4 | 285 | 5 | ✓ | ✓ |
| 1109 | 2 | < 1 mth | 181 | 4 | ✓ | ✓ |
| 1109 | 2 | 2 mths | 196 | 3 | ✓ | ✓ |
| 1109 | 2 | 0 | 188 | 7 | ✓ | ✓ |
| 1109 | 2 | 12 mths | 262 | 2 | | ✓ |
| 1109 | 2 | 14 mths | 256 | 6 | ✓ | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1109 | 2 | 1 | 257 | 8 | ✓ | ✓ |
| 1109 | 2 | 2 | 258 | 11 | ✓ | ✓ |
| 1109 | 2 | 4 | 276 | 6 |  | ✓ |
| 1110 | 2 | < 1 mth | 169 | 1 | ✓ |  |
| 1110 | 2 | 2 mths | 170 | 2 |  | ✓ |
| 1110 | 2 | 0 | 169 | 3 | ✓ | ✓ |
| 1110 | 2 | 11 mths | 219 | 6 | ✓ | ✓ |
| 1110 | 2 | 12 mths | 235 | 4 |  | ✓ |
| 1110 | 2 | 13 mths | 252 | 1 |  | ✓ |
| 1110 | 2 | 14 mths | 263 | 2 | ✓ |  |
| 1110 | 2 | 1 | 238 | 13 | ✓ | ✓ |
| 1110 | 2 | 2 | 260 | 12 | ✓ | ✓ |
| 1110 | 2 | 3 | 261 | 8 |  | ✓ |
| 1110 | 2 | 4 | 264 | 6 | ✓ | ✓ |
| 1111 | 3 | 1 mth | 173 | 3 |  | ✓ |
| 1111 | 3 | 0 | 173 | 3 |  | ✓ |
| 1113 | 1 | 1 mth | 183 | 3 | ✓ | ✓ |
| 1113 | 1 | 0 | 183 | 3 | ✓ | ✓ |
| 1113 | 1 | 10 mths | 227 | 4 |  | ✓ |
| 1113 | 1 | 11 mths | 230 | 4 |  | ✓ |
| 1113 | 1 | 13 mths | 235 | 3 |  | ✓ |
| 1113 | 1 | 1 | 231 | 11 |  | ✓ |
| 1113 | 1 | 2 | 250 | 7 | ✓ | ✓ |
| 1113 | 1 | 3 | 267 | 11 | ✓ | ✓ |
| 1124 | 3 | 1 | 214 | 1 | ✓ |  |
| 1125 | 3 | 0 | 187 | 2 |  | ✓ |
| 1125 | 3 | 1 | 236 | 8 | ✓ | ✓ |
| 1125 | 3 | 2 | 270 | 2 |  | ✓ |
| 1126 | 2 | 1 mth | 165 | 2 | ✓ |  |
| 1126 | 2 | 2 mths | 174 | 3 |  | ✓ |
| 1126 | 2 | 0 | 170 | 5 | ✓ | ✓ |
| 1126 | 2 | 10 mths | 239 | 6 | ✓ | ✓ |
| 1126 | 2 | 12 mths | 232 | 4 |  | ✓ |
| 1126 | 2 | 1 | 237 | 10 | ✓ | ✓ |
| 1126 | 2 | 2 | 272 | 10 | ✓ | ✓ |
| 1126 | 2 | 3 | 282 | 14 | ✓ | ✓ |
| 1127 | 3 | < 1 mth | 149 | 5 |  | ✓ |
| 1127 | 3 | 1 mth | 177 | 2 | ✓ |  |
| 1127 | 3 | 0 | 158 | 7 | ✓ | ✓ |
| 1128 | 2 | 10 mths | 214 | 7 | ✓ | ✓ |
| 1128 | 2 | 11 mths | 226 | 9 |  | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1128 | 2 | 13 mths | 242 | 6 | ✓ | ✓ |
| 1128 | 2 | 1 | 228 | 22 | ✓ | ✓ |
| 1128 | 2 | 2 | 260 | 15 | ✓ | ✓ |
| 1128 | 2 | 3 | 273 | 7 | ✓ | ✓ |
| 1129 | 1 | 1 mth | 150 | 1 |  | ✓ |
| 1129 | 1 | 0 | 150 | 3 |  | ✓ |
| 1129 | 1 | 10 mths | 227 | 3 | ✓ | ✓ |
| 1129 | 1 | 11 mths | 228 | 12 |  | ✓ |
| 1129 | 1 | 12 mths | 241 | 1 | ✓ |  |
| 1129 | 1 | 1 | 229 | 16 | ✓ | ✓ |
| 1129 | 1 | 2 | 272 | 7 | ✓ | ✓ |
| 1129 | 1 | 3 | 284 | 13 | ✓ | ✓ |
| 1130 | 2 | 9 mths | 215 | 2 | ✓ |  |
| 1130 | 2 | 10 mths | 230 | 6 | ✓ | ✓ |
| 1130 | 2 | 12 mths | 235 | 7 |  | ✓ |
| 1130 | 2 | 1 | 228 | 15 | ✓ | ✓ |
| 1130 | 2 | 2 | 261 | 11 | ✓ | ✓ |
| 1130 | 2 | 3 | 273 | 15 | ✓ | ✓ |
| 1132 | 1 | 1 | 242 | 7 |  | ✓ |
| 1132 | 1 | 2 | 274 | 4 | ✓ | ✓ |
| 1132 | 1 | 3 | 290 | 8 |  | ✓ |
| 1134 | 3 | 9 mths | 223 | 3 |  | ✓ |
| 1134 | 3 | 10 mths | 228 | 10 | ✓ | ✓ |
| 1134 | 3 | 1 | 226 | 13 | ✓ | ✓ |
| 1134 | 3 | 2 | 252 | 6 | ✓ | ✓ |
| 1135 | 3 | 1 | 236 | 9 | ✓ | ✓ |
| 1135 | 3 | 2 | 270 | 2 |  | ✓ |
| 1135 | 3 | 3 | 280 | 6 |  | ✓ |
| 1137 | 1 | 0 | 165 | 12 | ✓ | ✓ |
| 1137 | 1 | 2 | 265 | 2 |  | ✓ |
| 1138 | 3 | 0 | 159 | 7 |  | ✓ |
| 1140 | 3 | 2 mths | 185 | 3 | ✓ | ✓ |
| 1140 | 3 | 0 | 185 | 3 | ✓ | ✓ |
| 1140 | 3 | 10 mths | 238 | 6 |  | ✓ |
| 1140 | 3 | 11 mths | 228 | 9 |  | ✓ |
| 1140 | 3 | 1 | 232 | 15 |  | ✓ |
| 1141 | 1 | 10 mths | 195 | 3 |  | ✓ |
| 1141 | 1 | 11 mths | 206 | 2 | ✓ | ✓ |
| 1141 | 1 | 12 mths | 205 | 9 | ✓ | ✓ |
| 1141 | 1 | 1 | 203 | 14 | ✓ | ✓ |
| 1141 | 1 | 2 | 233 | 10 |  | ✓ |
| 1142 | 3 | 1 mth | 152 | 7 | ✓ | ✓ |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1142 | 3 | 0 | 152 | 7 | ✓ | ✓ |
| 1143 | 2 | 0 | 176 | 1 | ✓ |  |
| 1143 | 2 | < 1 mth | 176 | 1 | ✓ |  |
| 1143 | 2 | 10 mths | 225 | 10 | ✓ | ✓ |
| 1143 | 2 | 13 mths | 236 | 5 |  | ✓ |
| 1143 | 2 | 1 | 230 | 16 | ✓ | ✓ |
| 1143 | 2 | 2 | 280 | 12 | ✓ | ✓ |
| 1144 | 3 | 2 mths | 180 | 2 | ✓ | ✓ |
| 1144 | 3 | 0 | 180 | 2 | ✓ | ✓ |
| 1144 | 3 | 11 mths | 234 | 4 |  | ✓ |
| 1144 | 3 | 13 mths | 245 | 3 | ✓ | ✓ |
| 1144 | 3 | 1 | 238 | 7 | ✓ | ✓ |
| 1144 | 3 | 2 | 267 | 5 | ✓ | ✓ |
| 1146 | 3 | 2 mths | 181 | 5 |  | ✓ |
| 1146 | 3 | 0 | 181 | 5 |  | ✓ |
| 1147 | 3 | < 1 mth | 167 | 5 |  | ✓ |
| 1147 | 3 | 0 | 167 | 5 |  | ✓ |
| 1160 | 3 | 1 mth | 170 | 4 | ✓ | ✓ |
| 1160 | 3 | 0 | 170 | 4 | ✓ | ✓ |
| 1160 | 3 | 10 mths | 224 | 9 |  | ✓ |
| 1160 | 3 | 11 mths | 217 | 5 |  | ✓ |
| 1160 | 3 | 12 mths | 223 | 5 | ✓ | ✓ |
| 1160 | 3 | 13 mths | 230 | 9 | ✓ | ✓ |
| 1160 | 3 | 1 | 225 | 28 | ✓ | ✓ |
| 1161 | 3 | 2 mths | 181 | 2 |  | ✓ |
| 1161 | 3 | 0 | 181 | 2 |  | ✓ |
| 1162 | 1 | 1 mth | 163 | 8 | ✓ | ✓ |
| 1162 | 1 | 2 mths | 170 | 4 |  | ✓ |
| 1162 | 1 | 0 | 164 | 12 | ✓ | ✓ |
| 1163 | 3 | < 1 mth | 159 | 1 | ✓ |  |
| 1163 | 3 | 1 mth | 162 | 6 | ✓ | ✓ |
| 1163 | 3 | 2 mths | 173 | 2 |  | ✓ |
| 1163 | 3 | 0 | 163 | 9 | ✓ | ✓ |
| 1165 | 3 | 1 mth | 168 | 2 |  | ✓ |
| 1165 | 3 | 0 | 168 | 2 |  | ✓ |
| 1165 | 3 | 13 mths | 237 | 4 |  | ✓ |
| 1165 | 3 | 1 | 237 | 4 |  | ✓ |
| 1166 | 3 | 1 mth | 168 | 5 | ✓ | ✓ |
| 1166 | 3 | 0 | 168 | 5 | ✓ | ✓ |
| 1167 | 3 | 1 mth | 178 | 1 | ✓ |  |
| 1167 | 3 | 0 | 178 | 1 | ✓ |  |

| ID | Sex | Age | Length (cm) | Number of Photos | Lasers + BH-DF | DF + BH-DF |
|---|---|---|---|---|---|---|
| 1167 | 3 | 13 mths | 248 | 2 | ✓ | |
| 1167 | 3 | 1 | 248 | 2 | ✓ | |
| 1168 | 3 | 2 mths | 182 | 1 | ✓ | |
| 1168 | 3 | 0 | 182 | 1 | ✓ | |
| 1168 | 3 | 9 mths | 237 | 3 | | ✓ |
| 1168 | 3 | 1 | 237 | 3 | | ✓ |
| 1169 | 3 | < 1 mth | 128 | 1 | ✓ | |
| 1169 | 3 | 0 | 128 | 1 | ✓ | |
| 1178 | 3 | 1 | 233 | 7 | ✓ | ✓ |
| 1179 | 3 | 1 | 236 | 1 | ✓ | |
| 1180 | 3 | 1 mth | 179 | 10 | ✓ | ✓ |
| 1180 | 3 | 2 mths | 183 | 2 | ✓ | ✓ |
| 1180 | 3 | 3 mths | 207 | 5 | | ✓ |
| 1180 | 3 | 0 | 187 | 17 | ✓ | ✓ |
| 1181 | 3 | 1 mth | 171 | 2 | ✓ | |
| 1181 | 3 | 0 | 171 | 2 | ✓ | |
| 1182 | 2 | < 1 mth | 139 | 1 | ✓ | |
| 1182 | 2 | 1 mth | 164 | 2 | | ✓ |
| 1182 | 2 | 0 | 152 | 3 | ✓ | ✓ |
| 1183 | 3 | < 1 mth | 171 | 8 | ✓ | ✓ |
| 1183 | 3 | 0 | 171 | 8 | ✓ | ✓ |
| 1184 | 3 | 1 mth | 161 | 3 | | ✓ |
| 1184 | 3 | 0 | 161 | 3 | | ✓ |
| 1185 | 3 | 0 | 178 | 10 | ✓ | ✓ |
| 1187 | 1 | < 1 mth | 133 | 4 | ✓ | ✓ |
| 1187 | 1 | 0 | 133 | 4 | ✓ | ✓ |

# CHAPTER 5

## SOCIAL DYNAMICS OF A BOTTLENOSE DOLPHIN POPULATION DURING RANGE EXPANSION

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### ABSTRACT

Sociality is an adaptive trait providing a means for individuals to increase fitness by interacting with others. Social structure emerges from these interactions and as empirical studies have now shown, this will change depending on the ecological landscape. Recent changes in the spatial ecology of a bottlenose dolphin population provided a natural experiment to assess changes in social structure during a range expansion. We compared data over two decades from individuals occupying a common space to investigate temporal changes in social structure. More recent data from across the population's range were used to investigate spatial variability in social dynamics. We utilised association analyses with the half weight index; lagged association rates to determine the temporal pattern and stability of the associations; and social network analyses to identify the presence and structure of social groups and determine if the observed association patterns were a result of social behaviour. The social dynamics of this population appears to have changed over two decades with an increase in fission-fusion, with stronger and more associations and a difference in the temporal pattern of associations. These changes were concurrent with a range expansion, with individuals rather than social groups expanding their range. Following the range expansion, results suggested some differences in social structure at the extremes of the population's range, with individuals in the southern part of the range showing a less differentiated social structure and denser network structure, with stronger and more associations and greater gregariousness. Notably, several of these temporal changes in the second decade and spatial differences in the southern part of the range are comparable. Although the drivers of these differences remain unclear, whatever caused the range expansion the social structure of this population has changed both temporally and spatially.

## INTRODUCTION

Social interactions are known to be dynamic and adaptive and can change spatially and temporally in response to environmental conditions (e.g. prey availability, climate, habitat, range use, disturbance) (Ansmann *et al.* 2012, Henzi *et al.* 2009, Pinter-Wollman *et al.* 2014, Wiszniewski *et al.* 2009), demography (e.g. age, sex, reproductive status) (Aureli *et al.* 2008, Elliser and Herzing 2013, Lusseau 2007, Pinter-Wollman *et al.* 2014, Wiszniewski *et al.* 2009) and previous social experiences (Barrett *et al.* 2012, Pinter-Wollman *et al.* 2014). Within a population these dynamic social interactions shape the population's social structure and social network (Barrett *et al.* 2012), which in turn can affect many ecological processes (e.g. population stability, dispersal, information and disease transmission) (Kurvers *et al.* 2014). Sociality also influences fitness (Wilson 1975) and therefore ultimately has population level effects. Fission-fusion dynamics are a key feature to explain social dynamics and structure (Aureli *et al.* 2008). Socioecological studies have shown that marked variation in fission-fusion dynamics can be observed within species (Lusseau *et al.* 2003) and within populations across environmental variation (Henzi *et al.* 2009).

Social systems can be influenced by spatial dynamics (Cantor *et al.* 2012) with changes in animals' spatial ecology potentially altering social interactions, associates and structure as they range across different habitats (Clutton-Brock 1989, Pinter-Wollman *et al.* 2014). Equally, social systems may underlie individual movements and ranging patterns (Fearnbach *et al.* 2013, Pays *et al.* 2012). Socioecological models include differences in resource distribution, predation pressure and infanticide risk to explain the diversity of social systems (Patzelt *et al.* 2014). However, this diversity may also result from stochasticity in spatial processes during range expansions (Patzelt *et al.* 2014). For example, a historical range expansion in ants (*Petalomyrmex phylax*) was thought to be responsible for variation in social structure in different populations and geographic areas (Dalecky *et al.* 2007). Many species are now experiencing rapid changes in spatial ecology caused by climate change (Lenoir and Svenning 2015).

Following range expansion, we may expect differences in the social dynamics of individuals in the original and expanded range. Phillips *et al.* (2010) suggested that founder and establishment biases (i.e. resulting from individuals in the new range not being a random sample of the original population), range advance and standard evolutionary processes (e.g. increases in dispersal and reproductive rate) all result in ecological differences between the new and original ranges. For example, lower density at the edge of the range expansion could result in an increase in population growth rate (Phillips *et al.* 2010). Observed social differences may also be the result of variability in habitat or prey in the newly colonised areas compared to the original range, or demographic differences amongst those individuals that expanded their range (Aureli *et al.* 2008, Pinter-Wollman *et al.* 2014).

In wide ranging social species, long range movements may be made either by social groups moving together or by individuals moving alone. When density declined in Ethiopian wolves (*Canis simensis*), packs remained cohesive and expanded their ranges to re-colonise breeding territories (Marino *et al.* 2013). In addition, genetics have shown that single dominant bottlenose dolphin (*Tursiops truncatus*) matrilines were found at different locations around the western North Atlantic suggesting founding events from different groups splitting from the larger offshore population (Hoelzel 1998, Natoli *et al.* 2004). Well-connected individuals appear to be better at finding food or other resources in novel environments (Kurvers *et al.* 2014), indicating that individuals within social groups could have an advantage during range expansions into novel habitats. In contrast, in sea otters (*Enhydra lutris nereis*) range expansion was believed to require individual pioneers and, as such, colonisation of new areas was thought to be constrained by their sociality (Lafferty and Tinker 2014).

The bottlenose dolphin is broadly distributed and wide ranging with a fission-fusion social system (Connor *et al.* 2000). Studies from across the species' global range have demonstrated how social structure can vary markedly between populations in different habitats (Gowans *et al.* 2007, Lusseau *et al.* 2003, Parsons *et al.* 2003, Wiszniewski *et al.* 2009) and within single populations in response to local changes in ecological conditions (Ansmann *et al.* 2012). Previous studies of the coastal population inhabiting temperate waters off north-east Scotland showed that, despite overlap in spatial use, there was limited interaction between members of two social units (Lusseau *et al.* 2006). Parallel and subsequent studies of ranging patterns over the last two decades have shown that this population expanded its range along the east coast of Scotland (Cheney *et al.* 2013, Wilson *et al.* 2004). In this paper we use this natural experiment to determine whether the range expansion influenced the social dynamics of this population. We first assessed temporal changes in social structure over 23 years, during a period of range expansion, within the northern part of the population's range. We then used a more recent four year dataset from both the northern and southern parts of the population's range to investigate spatial variability in social structuring after the range expansion.

## METHODS

### Study Population and Photo-identification Data

The study was carried out on the resident population of *c*. 195 bottlenose dolphins that occurs along the east coast of Scotland (Cheney *et al.* 2013). Temporal changes in social structure during a range expansion were investigated using data from boat-based photo-identification surveys that were carried out annually between 1990 and 2012 in the Moray Firth, within the northern part of the population's range (Figure 1). All data were collected using standardised photo-identification survey procedures (for full details see Cheney *et al.* 2014, Wilson *et al.* 1997). Dolphin schools were defined as all animals within 100 m engaged in similar activities and if travelling heading in the same direction (Wells *et al.* 1987). We compared the social analysis described below for data from 1990 to 2000 (first decade) and 2001 to 2012 (second decade). In addition, as less data was available for the first decade, we also sub-sampled the data in the second decade where analyses were carried out on odd and even numbered trips separately. This provided similar sample sizes for both decades (see appendix Table A2a). Spatial variation in social structure following the range expansion was investigated through comparison of data from surveys between 2009 and 2012 along the east coast, primarily in the northern (or north) and southern (or south) part of the population's range (Figure 1). Surveys in the southern part of the range followed similar protocols to those used in the Moray Firth but the design and number of surveys varied between years and survey areas (Table 1). All photo-identification pictures were graded for photographic quality (Wilson *et al.* 1999) and analyses restricted to the highest quality photographs (Cheney *et al.* 2013). Each image was matched against a catalogue of known individuals from the east coast of Scotland and all matches were confirmed by at least two experienced researchers.

Figure 1. Areas and key locations on the east coast of Scotland with lines indicating the extent of northern and southern extremes of the population's range.

**Social Analysis**

Data were restricted to the summer (May to September) due to irregular winter sampling, however there was no significant difference in school size between summer (median=6, range 1 to 46) and winter (median = 6, range 1 to 39) (Mann-Whitney U test: W = 207225, $N_1$=1885, $N_2$=218, p = 0.8354). All analyses included distinctive individuals (i.e. those with nicks, unusual fin shapes, deformities, major scratches and white fin-fringes (Wilson *et al.* 1999)) that were seen on at least 5 days. Calves less than 5 years old were excluded as their association was linked to their mothers. Analyses were restricted to those schools where at least 50% of the estimated school was identified in a high quality photograph (Lusseau *et al.* 2006) (76% of the total number of schools observed) (Table 1). All analyses were carried out using the software SOCPROG 2.6 (Whitehead 2009) in Matlab R2015a (The Mathworks Inc. 2015).

Table 1. Data available for social analysis over different time periods and in different survey areas.

| | | | **Schools Encountered** | | **Number of Distinctive Individuals** | |
|---|---|---|---|---|---|---|
| **Area** | **Years** | **Total Trips** | **Total** | **> 50%** | **Total** | **Seen ≥ 5** |
| North | 1990-2000 | 207 | 625 | 404 | 137 | 74 |
| | 2001-2012 | 330 | 1018 | 838 | 139 | 113 |
| East Coast | 2009-2012 | 146 | 614 | 538 | 149 | 136 |
| North | 2009-2012 | 98 | 436 | 392 | 102 | 79* |
| South | 2009-2012 | 45 | 155 | 125 | 85 | 61* |

* 10 distinctive individuals were seen at least 5 times in both of these areas between 2009 and 2012.

Cetacean interactions are difficult to observe and quantify, so individuals were considered associated if they were present in the same school (Whitehead 1997, Whitehead *et al.* 2000, Whitehead and Dufault 1999). Daily sampling periods were chosen to remove any effects of immigration, emigration, birth or death (Whitehead 1999). The association rate for each dyad was calculated using the half weight index (HWI), which minimises the bias due to photo-identification sampling techniques (not all individuals in each school are always identified) and ranges from 0 where two individuals are never seen together to 1 where the two individuals are always seen together (Cairns and Schwager 1987). To determine if associations were significantly different from random, Monte Carlo permutation tests were carried out (Bejder *et al.* 1998, Whitehead *et al.* 2005), both for groups and accounting for differences in gregariousness (an individual's tendency to associate) and movements (Whitehead 2009). The association matrices were randomised until the probability of a difference from random associations stabilised (5000 times) with 1000 flips (individuals are randomly swapped between schools ensuring the number of dolphins, schools, times each individual was seen and school sizes matched the observed data) per permutation. Significantly higher than random standard deviation (SD) of typical group sizes (size experienced by the individual) suggest there are differences in gregariousness, with individuals found in consistently large or small groups

(Whitehead 2009). The presence of long term preferred/avoided associates was indicated by a significantly higher coefficient of variation (CV) for all observed HWIs than for random associations (Whitehead 2008). The social differentiation metric (S) measured how varied the social system was using the likelihood method to estimate the CV of the proportion of time dyads spend together (where S ~ 0 indicates that relationships within the population were homogeneous and > 0.5 indicates a well differentiated society). The correlation coefficient (r) between the actual and calculated association indices determined the power of the analysis (where r = 1 is an excellent representation and 0 is poor) (Whitehead 2008). Shapiro-Wilk normality tests were carried out when required and non-parametric statistics used where appropriate.

The HWI estimates the proportion of time two individuals were together, however other factors, such as different school sizes can cause variation in gregariousness which can result in the HWI overestimating or underestimating the affinity between individuals (Godde *et al.* 2013). For example, highly gregarious individuals may have a high HWI but be associating by chance rather than as a result of social preferences. We calculated the HWIG (the ratio of observed over expected association indices) which represents the strength of a dyadic relationship corrected for gregariousness and only detects association between individuals when affinity was more likely (see Godde *et al.* 2013 for details).

To explore whether this population was divided into clusters (social groups) we used a modularity clustering algorithm (Newman 2006). This method uses a modularity matrix in which the elements are the weight (HWI) between two individuals minus the expected weight if all associations were randomly distributed and where the eigenvector of the dominant eigenvalue provides statistically significant divisions into clusters. These are split iteratively with the most parsimonious division where the modularity coefficient (Q) is maximised (Lusseau *et al.* 2008, Newman 2006, Wiszniewski *et al.* 2010). The advantage of this method is that it allows for the possibility that there is no division and all individuals belong to the same cluster (Q = 0) (Newman 2006), while a modularity >0.3 indicates a useful division of the population (Newman 2004). Association indices are generally high among individuals in the same cluster and low among individuals in different clusters (Whitehead 2009).

Social interactions do not take place in isolation (Croft *et al.* 2005), so to increase understanding of the social dynamics of this bottlenose dolphin population we also investigated the social network structure. We estimated five network centrality measures: strength (a measure of gregariousness or sociability), eigenvector centrality (indicating how well connected individuals were), reach (a measure of indirect connectedness among individuals), clustering coefficient (the proportion of an individual's neighbours that are themselves neighbours) and affinity (the extent to which individuals connect strongly to individuals that also have strong connections) (Whitehead 2008). Individuals must associate non-randomly for a population to be socially structured (Whitehead *et al.* 2005). To investigate whether observed association patterns were a result of social behaviour the weighted social network measures calculated from the data were compared with random networks produced using the Bejder *et al.* (1998) permutation technique using the same individuals, school sizes and number of schools in which each individual was observed (5000 permutations, with 1000 flips).

The temporal pattern and stability of the associations were examined using lagged association rates (LAR), which estimated the probability that if two individuals are associating now, they will still be associated various time lags later. Estimated LARs were compared to null association rates (NAR), the expected value of the LAR if there were no preferred associations. Standard errors were estimated using a jackknife procedure (Whitehead 1995). The standard eight exponential models, based on a combination of three social parameters found in populations with fission-fusion dynamics: 1) rapid dissociations (where some individuals dissociate within one time period); 2) preferred companions (individuals that preferentially associate over time); 3) casual acquaintances (who associate for some time, disassociate and may re-associate) were fitted to the LAR data (Whitehead 1995, 2008). The LAR analyses indicated that our data were over-dispersed and therefore the quasi-Akaike Information Criterion (QAIC) was used to select the most parsimonious model (Burnham and Anderson 2002, Whitehead 2007, Whitehead 2009).

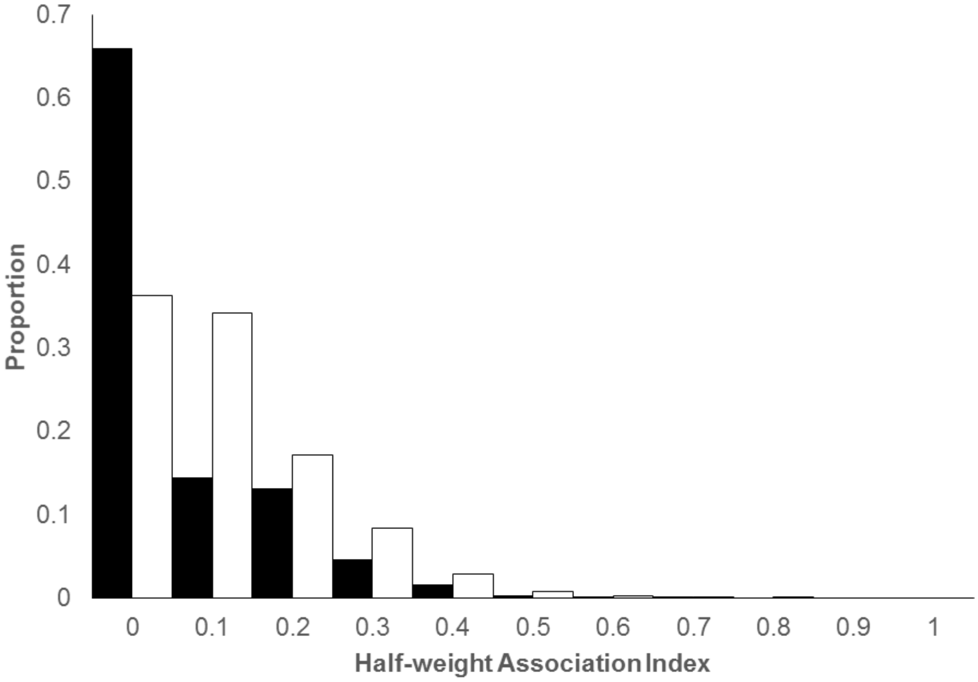
## RESULTS

### Temporal variation in social structure in the northern part of the range

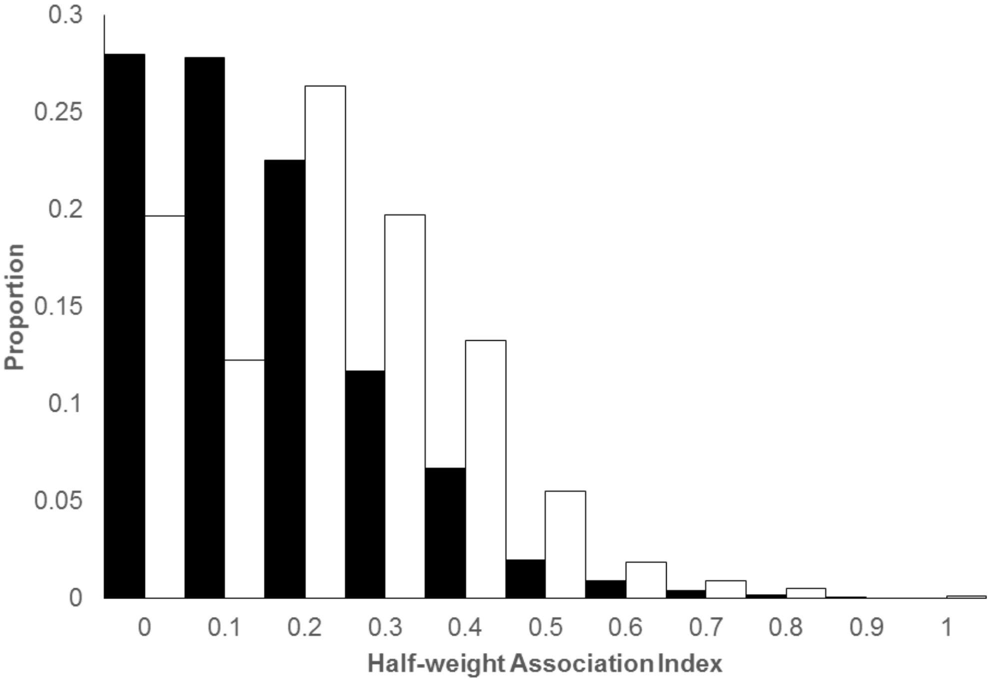
The first and second decades both showed a well differentiated society (Table 2). The mean HWI (Table 2) and the number of associates were higher in the second decade (median = 72, range = 29-105 compared to 23.5, range = 11-45, Mann-Whitney U test: W = 152.5, $N_1$=74, $N_2$=113, p<0.001). The proportion of non-associating pairs (HWI=0) decreased from 66% in the first decade to 36% in the second (Figure 2). There were some preferred/avoided long term associates in both decades where the observed CV of the association indices were higher (1.74 and 1.26) than random values (1.60 and 1.12) (permutation tests, CV p<0.001). There was also a difference in gregariousness among individuals in both decades with the SD of typical group size significantly higher (1.19 and 2.10) than random (1.07 and 1.80) (permutation tests, p<0.01). There was no significant difference in average school size between the two decades (1990-2000: median = 5.5, range = 1 to 40; 2001-2012: median = 6, range = 1 to 45) (Mann-Whitney U test: W = 401106, $N_1$=783, $N_2$=1065, p = 0.161).

Table 2. Number of sampling periods (days) by year and area, mean and mean maximum half weight index (HWI) with standard deviation and social differentiation with correlation coefficient and standard errors from 100 bootstrap replicates.

| Area and Years | Sampling periods | Mean HWI | Mean Max HWI | Social Differentiation (S) | Correlation Coefficient (r) |
|---|---|---|---|---|---|
| **North** | | | | | |
| 1990-2000 | 149 | 0.05 (0.02) | 0.34 (0.10) | 0.897 (0.038) | 0.515 (0.032) |
| 2001-2012 | 282 | 0.08 (0.03) | 0.45 (0.11) | 1.008 (0.016) | 0.801 (0.017) |
| **2009-2012 (All)** | | | | | |
| North | 93 | 0.12 (0.04) | 0.52 (0.13) | 0.823 (0.032) | 0.782 (0.023) |
| South | 39 | 0.19 (0.06) | 0.59 (0.16) | 0.505 (0.067) | 0.625 (0.030) |
| **2009-2012 (10 individuals seen in both areas)** | | | | | |
| North | | 0.11 (0.02) | 0.50 (0.11) | | |
| South | | 0.19 (0.03) | 0.73 (0.23) | | |



a.



b.

Figure 2. Distribution of half-weight association indices between individuals seen in a. the northern part of the population's range from 1990-2000 (black) and 2001-2012 (white) b. northern (black) and southern (white) part of the population's range.

Reach and affinity were higher than the expected value with no individual preferences in both decades, suggesting that individuals were not randomly connected. However, strength and clustering coefficient did not differ from random in the first decade. Gregariousness increased in the second decade with a lower than random clustering coefficient (Table 3). The mean HWIG was the same for both decades (1.04), however the CV was lower in the second decade (1.61 compared to 2.29) which suggests an increase in reach and strength once taking differences in gregariousness into account.

The most parsimonious LAR model suggested that in the first decade there were individuals with preferential associates that remained constant over time, while most individuals disassociated within one day. In contrast, in the second decade there were no preferential associates, but individuals associated and disassociated at time scales of days and years (Figure 3 and Table 3). The LAR stayed above the NAR in the both decades (Figure 3), suggesting there were preferred associates in both decades.

The Newman (2006) modularity technique suggested the population could usefully be divided into four clusters in the first decade, but in the second decade there was no evidence of clusters in the population (Table 4). However, one cluster in the first decade (mainly individuals rarely if ever seen outside the Moray Firth) contained 22 individuals seen over the 23 years of the study, and 21 of these individuals remained highly associated during the second decade. Also, just over half (52%) of the associations were with the same individuals in both decades. Individuals that were seen in the northern part of the range between 1990 and 2000 but were seen more regularly in the south during the second decade came from the other three clusters detected in the first decade. However, a number of other animals from these same clusters continued to be seen regularly in the northern part of the range throughout the study.

Table 3. Models of temporal stability for the northern part of the population's range in the two decades (1990 to 2000 and 2001 to 2012) and the northern and southern extremes of the range in 2009 to 2012. The most parsimonious models with the lowest QAIC are shown. The association rate between individuals, g(d), is a function of the time lag, d, related to the proportion of preferred companions ($P_{cc}$), short-term or casual ($P_{cas}$) and longer term ($P_{perm}$) relationships that last $\tau_{cas}$ days or $\tau_{perm}$ years. The ΔQAIC shows the difference between the QAIC of the most parsimonious model and the next lowest QAIC model (* any model ~2 ΔQAIC (e.g. some support) is shown and for full details of all models and QAIC values see Table A1 in the appendix).

| **Area and Year** | **Model Type and Explanation** | $P_{cas}$ | $\tau_{cas}$ **(days)** | $P_{perm}$ | $\tau_{perm}$ **(years)** | $P_{cc}$ | **ΔQAIC** |
|---|---|---|---|---|---|---|---|
| **North** | | | | | | | |
| 1990-2000 | $g(d) = P_{cc} + P_{cas}e^{-(d/t_{cas})}$ | 0.16 | 390 | - | - | 0.08 | 12.8 |
| 2001-2012 | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.72 | 1.40 | 0.28 | 10.67 | - | 14.6 |
| **2009-2012** | | | | | | | |
| North | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.73 | 1.24 | 0.27 | 5.68 | - | 10.5 |
| South | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.68 | 1.50 | 0.32 | 4.54 | - | 1.9 |
| | $g(d) = P_{cas}e^{-(d/t_{cas})} + P_{perm}e^{-(d/t_{perm})}$ | 1.48 | 1.20 | 0.32 | 4.57 | | * |

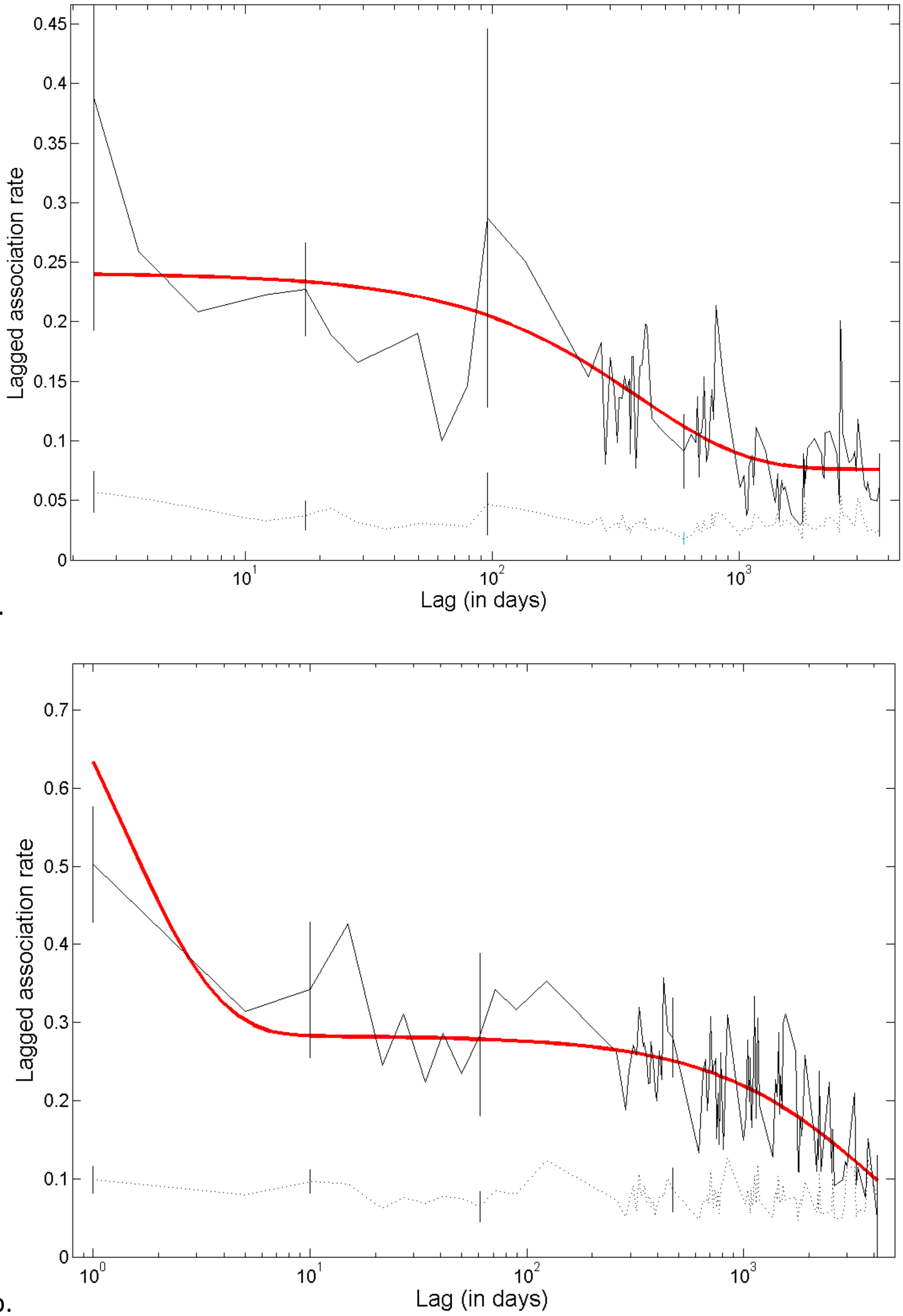


Figure 3. Lagged (solid line) and null (dotted line) association rates for all distinctive individuals (excluding calves) in the northern part of the population's range between May and September a. 1990 to 2000 and b. 2001 to 2012 in schools where at least 50% of the individuals were identified. The thick solid line shows the most parsimonious model (moving average = 400, jackknife error bars every 30 days and x-axis on the log scale).

Table 4. Overall means of network analysis and random networks for distinctive individuals seen more than 5 times using HWI in SOCPROG, with bootstrap standard errors from 1000 replicates, number of network clusters and modularity (Q). Significant differences from the random network using 5000 permutations (1000 flips) are in bold.

| Area / Year | Clusters (Q) | Strength | Eigenvector Centrality | Reach | Clustering Coefficient | Affinity |
|---|---|---|---|---|---|---|
| **North** | | | | | | |
| **1990-2000** | 4 (0.37) | 3.50 (0.29) | **0.10 (0.01)** | **13.92 (2.46)** | **0.16 (0.02)** | **3.90 (0.34)** |
| Random | | 3.50 (1.22) | **0.11 (0.04)** | **13.68 (5.01)** | **0.16 (0.04)** | **3.89 (0.26)** |
| **2001-2012** | 5 (0.28) | **9.00 (0.39)** | **0.09 (0.00)** | **91.60 (8.09)** | **0.19 (0.02)** | **9.96 (0.44)** |
| Random | | **9.00 (3.16)** | **0.09 (0.03)** | **90.91 (35.14)** | **0.22 (0.03)** | **9.94 (0.69)** |
| **2009-2012 (All)** | | | | | | |
| **North** | 5 (0.23) | **9.48 (0.65)** | **0.10 (0.00)** | **101.78 (14.30)** | **0.22 (0.02)** | **10.42 (0.74)** |
| Random | | **9.80 (3.22)** | **0.11 (0.04)** | **106.35 (37.59)** | **0.25 (0.02)** | **10.71 (0.61)** |
| **South** | 4 (0.15) | 11.49 (0.99) | 0.12 (0.00) | 143.16 (24.86) | 0.24 (0.02) | **12.36 (1.10)** |
| Random | | 11.75 (3.29) | 0.12 (0.04) | 148.75 (43.40) | 0.27 (0.02) | **12.60 (0.39)** |
| **2009-2012 (10 individuals seen in both areas)** | | | | | | |
| **North** | | 8.45 | 0.09 | 91.38 | 0.21 | 10.68 |
| **South** | | 11.37 | 0.12 | 142.24 | 0.27 | 12.52 |

**Spatial variation in social structure (2009 to 2012)**

Using the most comprehensive dataset collected across both the northern and southern parts of the range (Figure 1, Table 1) the modularity technique suggested that five clusters were a good division of the population. However, only one of these clusters had a core range (50% contour) that included both the northern and southern parts of the population's range (see appendix). This cluster contained individuals seen mainly in the south. In contrast, animals with core ranges only in the north were spread throughout different clusters. There were also differences in average school sizes between these areas, with smaller schools found in the north (median = 6, range = 1-45) compared to the south (median = 11, range = 1-46) (Mann-Whitney U test: W = 24276.5, $N_1$=436, $N_2$=155, p <0.0001).

Therefore, we investigated the social dynamics of the distinctive individuals seen at least five times during 2009 to 2012 in the northern (79 dolphins) and southern (61 dolphins) parts of the population's range (Table 1). Social analysis suggests that the dyadic interactions in the south tended to be more homogenous than in the north (Table 2). There appeared to be long term preferred/avoided associations amongst animals using both the northern (observed association indices CV = 1.05, random CV = 0.88) and southern parts of their range (observed CV = 0.81, random CV = 0.76) (permutation tests, CV p <0.0001). However, there were differences in gregariousness among individuals in the north with the SD of typical group size significantly higher than random (observed = 2.38, random = 1.82, p<0.0001) but not in the south (SD = 2.47, random SD = 2.23, p>0.05). Also, individuals in the south had a higher mean HWI than those in the north (Table 2 and Figure 2). In the north, dolphins associated with 76% (median = 60, range = 10-72) of individuals seen in this area, slightly lower than in the south where dolphins associated with 85% (median = 52, range = 22-59) of individuals.

All network centrality measures were higher for individuals seen in the south than in the north (Table 4). The mean HWIG was lower in the south (1.028) than the north (1.082) and the CV was much lower in the south (0.936 compared to 2.190). This takes account of the gregariousness in the southern part of the range and is in concordance with an increase in reach and strength in this area. The network measures were all lower than random in both areas, although this was only significant in the northern part of the range (except for affinity) (Table 4).

The most parsimonious LAR model suggested individuals associated and disassociated at time scales of days and year in both areas. In the south there was also some support for a model suggesting some individuals also dissociated within a day, however the mean duration of the daily and yearly associations estimated by the model parameters were similar (Table 3). The modularity technique suggested that there was little evidence for clusters in either area (Table 4).

Only ten distinctive individuals (nine females, one male) were seen at least five times in both the northern and southern parts of the range between 2009 and 2012. Both the average mean and maximum HWI and network centrality measures for these individuals were higher when they were seen in the south (Table 2 and 4).

## DISCUSSION

Social relationships within populations are dynamic and can change temporally and spatially in response to the ecological and social environment (Aureli *et al.* 2008). We explored temporal and spatial variation in the social dynamics of a bottlenose dolphin population concurrent with a range expansion.

### Temporal variation in social structure in the northern part of the range (1990-2012)

There were differences in social structure over the two decade study, despite no difference in average school size. Our results suggest that in the second decade there were stronger and more associations, with an increase in gregariousness and fission-fusion (Table 2, 3 and Figure 3). Lusseau *et al.* (2006) found that the social organisation of this population relies on short-term casual acquaintances and a few longer associations. Although our results from the second decade matched this, this study showed a change over time with individuals with preferential associates in the first decade (Table 3).

There was some consistency in association between individuals. Information on the consistency of social network position over an individual's life is an important but generally unknown feature (Kurvers *et al.* 2014). Long term social bonds can have benefits including increased breeding success and information exchange and decreased aggression and infanticide (Wiszniewski *et al.* 2009). However, there was little evidence in the second decade for the social groups (clusters) seen in the first decade, possibly as a result of more individuals associating and increase in gregariousness.

When range expansion occurs in a population with fission-fusion dynamics we may expect one social group to expand its range. For example, range expansions in carnivore populations were by social groups (Marino *et al.* 2013), while founding events of bottlenose dolphin populations in the coastal western North Atlantic were from individual groups splitting from the larger offshore population (Natoli *et al.* 2004). However, in this study we found that dolphins from different social groups expanded their range. In other social species, initial range expansion has also been by dispersing individuals (Lafferty and Tinker 2014, Nelson and Mech 1999); however in sea otters this was constrained by their social nature (Lafferty and Tinker 2014).

It is possible that these observed differences are a result of more data being available in the second decade. During this period we adapted our survey protocols, from a fixed survey route to flexible surveys and a switch to digital photography, which increased capture probabilities (Cheney *et al.* 2014). However, when the number of surveys was matched between decades by sub-sampling the second decade, the results were very similar including higher mean HWI and no social groups (see appendix Table A2a). Although in general large data sets are required for social analyses the actual amount of data required is complicated by the strength of the social pattern (e.g. a strongly differentiated populations requires fewer average sightings of each dyad) (Whitehead 2008) and this population was highly differentiated in both decades. In addition, for fission fusion social systems results are more robust if sampling frequency is increased rather than increasing the proportion of individuals sampled on each occasion (Farine and Whitehead 2015, Franks *et al.* 2010). However, it remains unclear what effect, if any, this change in survey protocol and resultant increase in capture probabilities may have had on the results of these analyses.

### Spatial variation in social structure (2009 to 2012)

Our study population is highly mobile with individuals ranging along the east coast of Scotland and occasional sightings even further south (Cheney *et al.* 2013). Data from across the entire east coast suggested there were social groups within this population. However, only one of these groups had a core range in the south suggesting this result could be the due to area use rather than a social preference (Lusseau *et al.* 2006). Analyses of dolphins using either the northern or southern part of the range found little evidence of social groups. Using data from mainly the first decade (1990-2002) a previous study found two spatially-defined social units within this population, which was not a result of their spatial distribution (Lusseau *et al.* 2006), possibly further evidence of a change over the two decades. Models of temporal stability were the same in both areas and match results from the previous study (Lusseau *et al.* 2006).

There was spatial variation in some aspects of social structure between individuals that regularly use the north and others that spend most time in the south. In the north individuals change associates regularly, while in the south, individuals have a denser network structure with stronger and more associations and greater gregariousness, which the HWIG results suggest is not the result of the larger school sizes observed there. In chimpanzees demographic variables affected social organisation, with increased cohesiveness and decreased fission-fusion in smaller communities (Lehmann and Boesch 2004). Dolphins in the north also show differences in gregariousness with some individuals seen consistently in large or small groups, which is not apparent in the south. Although the sample size is small, 10 dolphins (5% of the population) showed stronger associations and higher network measures when they were in the southern part of the range than when they were in the north. This may indicate social flexibility, where individuals change their social tactics as a result of changes in the environment (Schradin 2013).

### Changes and differences in social dynamics

The change in social structure over the past two decades was concurrent with a range expansion (Wilson *et al.* 2004), however whether it is the cause, consequence or coincidental to this is uncertain. The less connected social network in the first decade may have resulted in increased fission and dispersal, resulting in the range expansion (Phillips *et al.* 2010). Alternatively, changes in social structure could be the result of the range expansion, caused by the potential increase in this bottlenose dolphin population over the past two decades (Cheney *et al.* 2014, Wilson *et al.* 2004). Population increases can result in changes to social cohesion (Wittemyer *et al.* 2005). Unrelated to the range expansion, both natural and anthropogenic variation over this two decade study could have influenced social structure (Ansmann *et al.* 2012, Elliser and Herzing 2013).

Differences in social structure were also found in dolphins observed in the original and expanded range. Predictions suggest that well-connected individuals with a greater number of social interactions have an advantage in novel habitats as they are better at finding new resources (Kurvers *et al.* 2014). Aplin *et al.* (2012) found that songbirds that were more socially connected did benefit from a higher probability of finding new foraging areas. This may explain the increased gregariousness and more connected social structure in individuals that expanded their range to the south.

Alternatively, both the range expansion and the observed differences in social structure could be the result of habitat quality. The stable number of dolphins using the northern part of the range, in combination with the increasing population abundance (Cheney *et al.* 2014), may indicate that the original northern range is at carrying capacity, forcing the increasing population to expand to the south. Also, within the original range individuals could have changed their social behaviour in response to short-term changes in their environment (Schradin 2013). For example, the increase in the number and strength of associations in the north would be required to increase information exchange and reciprocal cooperative behaviour, if prey resources became more temporally and spatially variable (Lusseau *et al.* 2003, Wiszniewski *et al.* 2009). In addition, habitat differences at the extremes of the range could explain the spatial differences in social structure. Connor *et al.* (2017) found spatial variation in alliance behaviour and suggested this may be due to differences in habitat attributes along a spatial axis such as openness, predation risk and resource variation. For example, increasing prey resources can reduce grouping costs and increase cooperative foraging benefits (Connor *et al.* 2017), which could explain the larger group sizes, increased gregariousness and social connections in the south. Dolphins in this population have previously been found in larger schools when more prey was available (Lusseau *et al.* 2004). Also, southern resident killer whales had larger school sizes with a more interconnected social network when salmon abundance was high, as a result of decreased time spent searching for prey increasing the opportunity for social interactions (Foster *et al.* 2012). Information on habitat quality and prey availability across the range of this population should be a priority. Additionally, demographic factors, such as kinship (Wiszniewski *et al.* 2010), sex and age (Lusseau and

Newman 2004), and mating strategies (Gowans *et al.* 2007, Lusseau 2003) have been found to be important in the social structure of other dolphin populations. Further work is required to determine if these factors vary between these areas.

Notably, several of the temporal changes and spatial differences in social structure are comparable, with more and stronger associations, increasing gregariousness and higher network centrality measures in the second decade and in the southern part of the range. However, it remains unclear exactly what is driving both these changes and differences in social dynamics.

## ACKNOWLEDGEMENTS

We thank all the colleagues who have helped collect data over this 23 year study and Isla Graham for her constructive comments. The BES, ASAB, Greenpeace Environmental Trust, Scottish Natural Heritage, Scottish Government, Whale and Dolphin Conservation, Talisman Energy (UK) Ltd., Department of Energy and Climate Change, Chevron, Natural Environment Research Council and the Universities of Aberdeen and St Andrews all provided funding for photo-identification surveys. Survey work was conducted under Scottish Natural Heritage Animal Scientific Licences.

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## APPENDIX

Additional supporting information.

Kernel analysis methods to estimate social group range.

Figure A1. Kernel density analysis of the 5 social groups identified in the SOCPROG analysis on the east coast of Scotland between 2009 and 2012.

Figure A2. Lagged association rates for individuals seen in the northern and southern part of the population's range between 2009 and 2012.

Figure A3. Modularity clustering technique Q profile for the northern part of the range (1990-2000).

Table A1. Comparison of the QAIC values for the models of temporal stability.

Table A2. Social structure results for the east coast of Scotland (2009-2012) and subsampled northern range (2001-2012).

Table A3. Models of temporal stability where at least 75% of estimated school were identified.

## Kernel analysis methods to estimate social group range.

Association patterns based on the amount of time that animals spend together can be influenced by individual ranging patterns as well as genuine social affiliations (Lusseau *et al.* 2006). Therefore we investigated area use and spatial overlap of social groups using the kernel density function in the Spatial Analyst extension of software ArcGIS 10.0. The first encounter location each day for each social group (identified using the modularity clustering technique, see results) seen on the east coast of Scotland between 2009 and 2012 was used. A mask was set to exclude all landmasses from the analysis. The output cell size was set to 500 m and the search radius to 5000 m. To identify areas of high use we used the geospatial modelling environment extension (Beyer 2012) to calculate isopleths for the 50% (core) range and 95% range.

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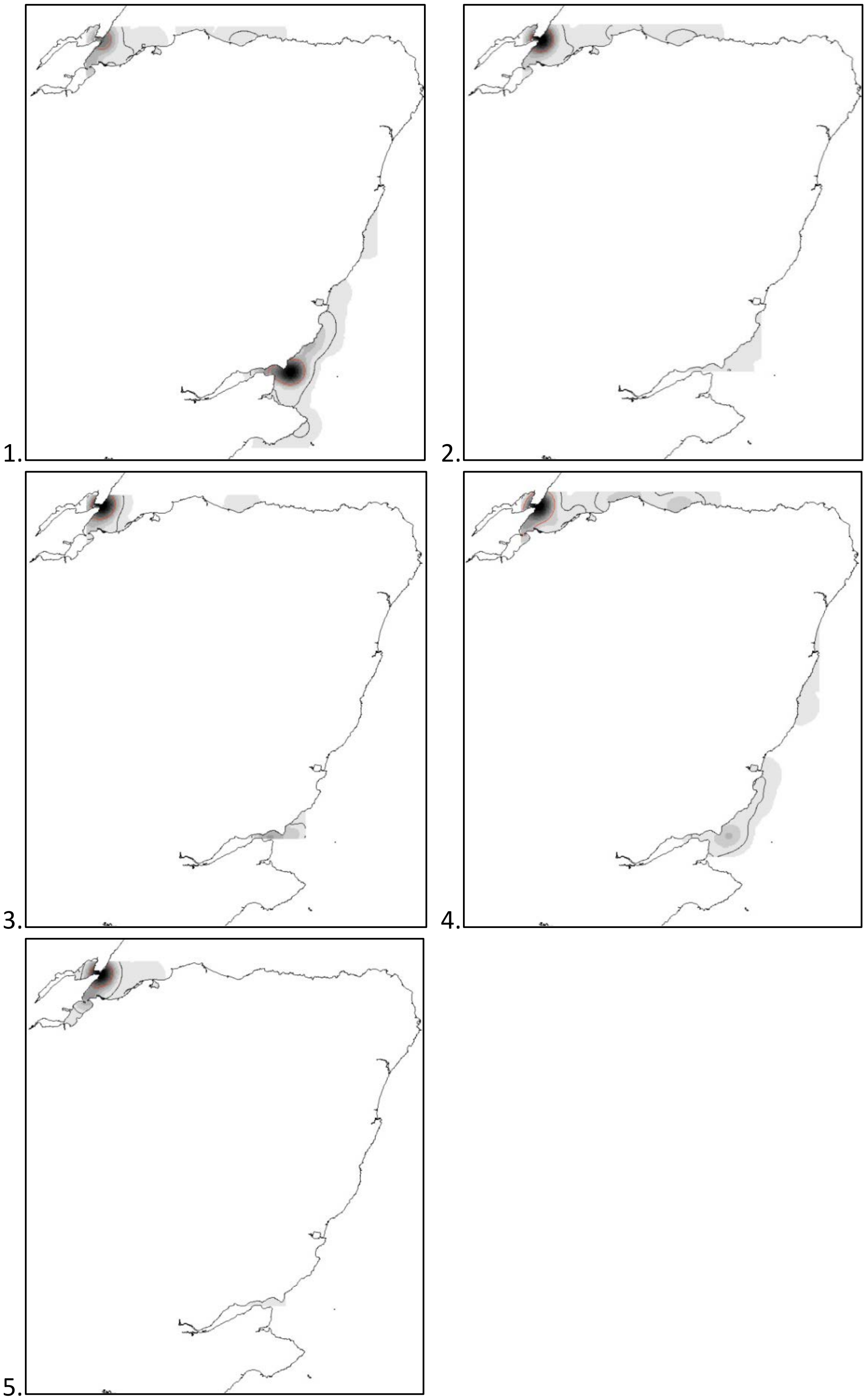
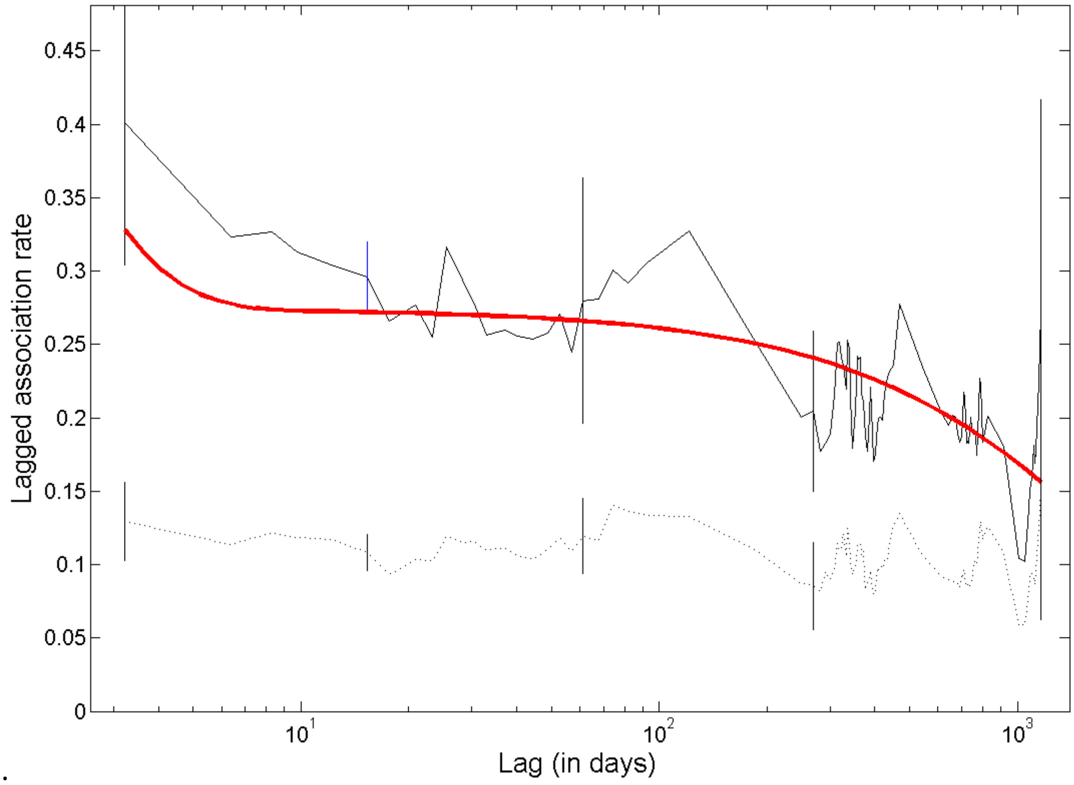
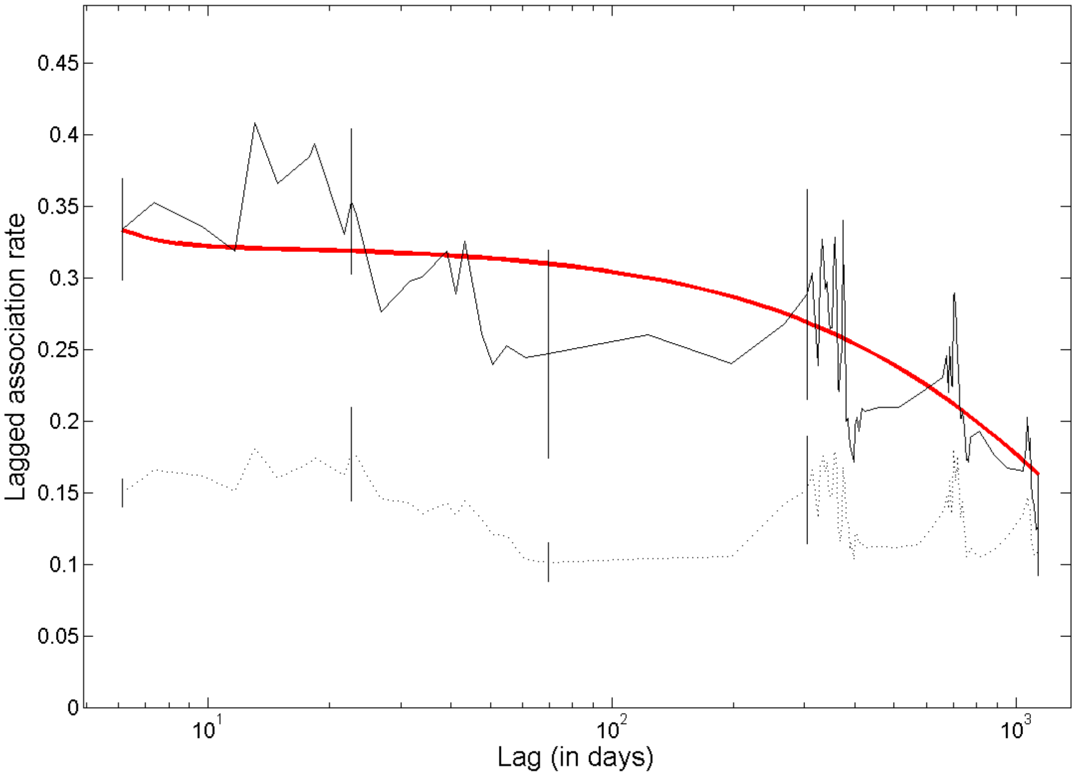


Figure A1. Kernel density analysis of the 5 social groups identified in the SOCPROG analysis on the east coast of Scotland between 2009 and 2012, the darker the greyscale the higher the density, the 50% contour is in red surrounding the core range and 95% contour in black surrounding the home range.



a.



b.

Figure A2. Lagged (solid line) and null (dotted line) association rates for all distinctive individuals (adults and juveniles) between May and September 2009 and 2012 in the a. northern and b. southern part of the range in encounters where at least 50% of the individuals were identified. The thick red line shows the most parsimonious model (moving average = 5000 and 2000, and jackknife error bars every 30 days).

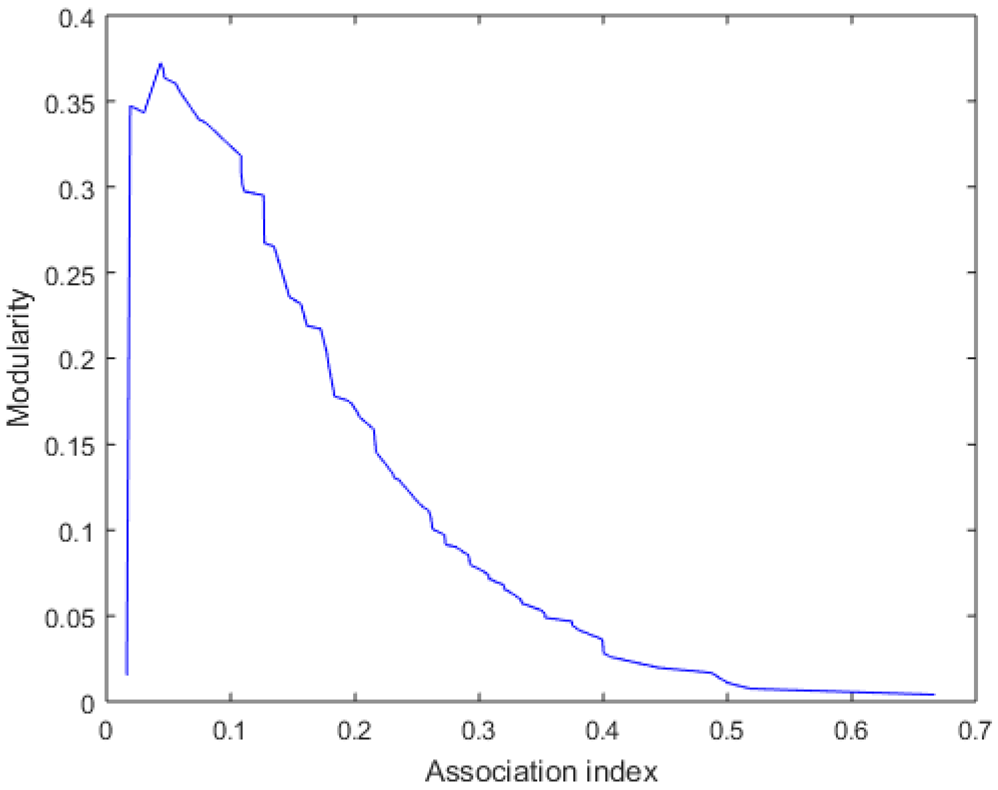


Figure A3. Modularity clustering technique Q profile for the northern part of the range from 1990-2000.

Table A1. Comparison of the QAIC values for the models of temporal stability for the northern part of the population's range in the two decades (1990 to 2000 and 2001 to 2012) and the northern and southern extremes of the range in 2009 to 2012. The association rate between individuals, g(*d*), is a function of the time lag, *d*, related to the proportion of preferred companions ($P_{cc}$), short-term or casual ($P_{cas}$) and longer term ($P_{perm}$) relationships that last $\tau_{cas}$ days or $\tau_{perm}$ years. The most parsimonious models are in bold and ΔQAIC shows the difference between QAIC and that of the best model. ΔQAIC <2 shows substantial support for the model; 4-7 = considerably less support; >10 = essentially no support.

| **MODEL TYPE and EXPLANATION** | **North 1990-2000** | | **North 2001-2012** | | **North 2009-2012** | | **South 2009-2012** | |
|---|---|---|---|---|---|---|---|---|
| | **QAIC** | **ΔQAIC** | **QAIC** | **ΔQAIC** | **QAIC** | **ΔQAIC** | **QAIC** | **ΔQAIC** |
| $g(d) = 1$ | 186642.7 | 182657.9 | 2582324.9 | 2490229.5 | 536794.6 | 516878.0 | 202503.4 | 194333.0 |
| $g(d) = P_{cc}$ | 4104.0 | 119.2 | 93544.0 | 1448.6 | 20116.5 | 199.9 | 8270.8 | 100.4 |
| $g(d) = e^{-(d/t_{cas})}$ | 7766.9 | 3782.1 | 143821.8 | 51726.4 | 32212.0 | 12295.4 | 12804.4 | 4634.0 |
| $g(d) = P_{cas}e^{-(d/t_{cas})}$ | 4025.4 | 40.6 | 92163.8 | 68.4 | 19958.8 | 42.2 | 8173.0 | 2.6 |
| $g(d) = P_{cc} + (1 - P_{cas})e^{-(d/t_{cas})}$ | 4048.5 | 63.7 | 93351.8 | 1256.4 | 20039.6 | 123.0 | 8250.2 | 79.8 |
| $g(d) = P_{cc} + P_{cas}e^{-(d/t_{cas})}$ | **3984.8** | **0** | 92145.8 | 50.4 | 19933.5 | 16.9 | 8205.2 | 34.8 |
| $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 4003.2 | 18.4 | **92095.4** | **0** | **19916.6** | **0** | **8170.4** | **0.0** |
| $g(d) = P_{cas}e^{-(d/t_{cas})} + P_{perm}e^{-(d/t_{perm})}$ | 3997.6 | 12.8 | 92110.0 | 14.6 | 19927.1 | 10.5 | 8172.3 | 1.9 |

Table A2. Results of the social structure analysis for randomly sub-sampled data from a. the North from 2001 to 2012 and b. the most comprehensive dataset across the east coast of Scotland from 2009-2012.

a.

| **Social Analyses** | **North (subsampled data 2001-2012)** | **North (2$^{nd}$ subsampled data 2001-2012)** |
|---|---|---|
| Sampling periods (days) | 139 | 144 |
| Number of individuals | 104 | 97 |
| Mean HWI | 0.09 (0.03) | 0.09 (0.03) |
| Mean Max HWI | 0.48 (0.11) | 0.50 (0.11) |
| Social Differentiation | 0.947 (0.023) | 0.914 (0.026) |
| Correlation Coefficient | 0.750 (0.023) | 0.732 (0.023) |
| Model of temporal stability | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$<br>$P_{cas}$=0.69, $\tau_{cas}$=1.45, $P_{perm}$=0.31, $\tau_{perm}$=9.74 | $g(d) = P_{cas}e^{-(d/t_{cas})} + P_{perm}e^{-(d/t_{perm})}$<br>$P_{cas}$=0.09, $\tau_{cas}$=23.15, $P_{perm}$=0.25, $\tau_{perm}$=13.69 |
| Social Units (Q) | 4 (0.287) | 5 (0.284) |
| Strength | 9.49 (0.57) | 8.62 (0.56) |
| Eigenvector Centrality | 0.09 (0.00) | 0.09 (0.00) |
| Reach | 101.77 (12.69) | 81.46 (10.65) |
| Clustering Coefficient | 0.21 (0.02) | 0.22 (0.02) |
| Affinity | 10.53 (0.65) | 9.31 (0.60) |

b.

| Social Analyses | East Coast (2009-2012) |
|---|---|
| Sampling periods (days) | 123 |
| Number of individuals | 136 |
| Mean HWI | 0.08 (0.03) |
| Mean Max HWI | 0.53 (0.14) |
| Social Differentiation | 1.079 (0.018) |
| Correlation Coefficient | 0.716 (0.019) |
| Model of temporal stability | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$<br>$P_{cas}$=0.72, $\tau_{cas}$=1.12, $P_{perm}$=0.28, $\tau_{perm}$=4.62 |
| Social Units (Q) | 5 (0.39) |
| Strength | 10.63 (0.56) |
| Eigenvector Centrality | 0.08 (0.00) |
| Reach | 124.69 (13.43) |
| Clustering Coefficient | 0.21 (0.01) |
| Affinity | 11.47 (0.62) |

Table A3. Models of temporal stability, where at least 75% of the estimated school were identified, for the northern part of the population's range in the two decades (1990 to 2000 and 2001 to 2012) and the northern and southern extremes of the range in 2009 to 2012. The most parsimonious models with the lowest QAIC are shown. The association rate between individuals, g(*d*), is a function of the time lag, *d*, related to the proportion of constant companions ($P_{cc}$), short-term or casual ($P_{cas}$) and longer term ($P_{perm}$) relationships that last $\tau_{cas}$ days or $\tau_{perm}$ years. The ΔQAIC shows the difference between the QAIC of the most parsimonious model and the next lowest QAIC model (* any model ~2 ΔQAIC (e.g. some support) is shown). (Note: the best models match those when using 50% of the estimated school, and the values of the parameters in the model are very similar).

| **Area and Year** | **Model Type and Explanation** | **$P_{cas}$** | **$\tau_{cas}$ (days)** | **$P_{perm}$** | **$\tau_{perm}$ (years)** | **$P_{cc}$** | **ΔQAIC** |
|---|---|---|---|---|---|---|---|
| **North** | | | | | | | |
| 1990-2000 | $g(d) = P_{cc} + P_{cas}e^{-(d/t_{cas})}$ | 0.19 | 471 | - | - | 0.07 | 7.9 |
| 2001-2012 | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.70 | 1.43 | 0.30 | 9.98 | - | 19.5 |
| **2009-2012** | | | | | | | |
| North | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.70 | 1.13 | 0.30 | 4.43 | - | 8.3 |
| South | $g(d) = P_{cas}e^{-(d/t_{cas})}$ | 0.32 | 1985 | - | - | - | 2.1 |
| | $g(d) = P_{cas}e^{-(d/t_{cas})} + (1 - P_{cas})e^{-(d/t_{perm})}$ | 0.68 | 1.48 | 0.31 | 5.53 | - | * |

# CHAPTER 6

## INCREASING TRENDS IN FECUNDITY AND CALF SURVIVAL OF BOTTLENOSE DOLPHINS IN A MARINE PROTECTED AREA

# CHAPTER 6

## INCREASING TRENDS IN FECUNDITY AND CALF SURVIVAL OF BOTTLENOSE DOLPHINS IN A MARINE PROTECTED AREA [4]

### ABSTRACT

Environmental and anthropogenic changes can have direct impacts on the demography and hence dynamics of animal populations. Accurately estimating temporal variation in demographic rates and assessing their contribution to population abundance are fundamental objectives of many ecological studies and vital for conservation and management. Here we use a 16-year time series from bottlenose dolphins on the east coast of Scotland to investigate changes in fecundity and calf survival since the population's core-habitat was designated a protected area. To account for potential variation in detection and the issues of misclassification (i.e. uncertainty in breeding status), we used an open robust design multistate model with state uncertainty and seasonal effects. The top model highlighted an increase in the proportion of females with new-born calves (unconditional reproductive rate) from 0.16 in 2001 to 0.28 in 2016. There was also evidence of increasing trends in calf survival. First year calf survival (the probability of transitioning from a female with a new-born calf in one year to an older calf the next year) increased from 0.78 to 0.93. Although second year calf survival (transition probability from a female with a one year old calf to a two year old calf) remained lower, it also showed an increase from 0.32 to 0.55. Our results also indicated that there may be some evidence for a cost of reproduction, as females with new-born calves did have a slightly higher mortality than those with older calves. However, further work is required to confirm this. This study suggests there is a positive trend in reproduction and survival which may be contributing to the increasing population.

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[4] This chapter is in preparation as: Cheney, B., Thompson, P.M. & Cordes, L.S. (In prep) Increasing trends in fecundity and calf survival of bottlenose dolphins in a marine protected area. Biological Conservation.

## INTRODUCTION

Environmental and anthropogenic changes can have direct impacts on the demography and hence dynamics of animal populations (Frederiksen *et al.* 2014, Sæther *et al.* 2013). As such, accurately estimating temporal variation in these demographic rates and assessing their contribution to population abundance are fundamental objectives of many ecological studies and vital for conservation and management (Clutton-Brock and Sheldon 2010, Coulson *et al.* 2001). The established principal for long-lived species is that population dynamics are most sensitive to variations in adult female survival (Eberhardt 2002, Gaillard *et al.* 1998). Reproductive costs in females may increase mortality, reduce offspring survival, and result in trade-offs between current and future reproduction (Balme *et al.* 2017, Clutton-Brock *et al.* 1983, Hamel *et al.* 2009). However, those costs may be too small to be detectable, or there may even be a positive relationship between higher female fecundity and survival as a result of individual heterogeneity (Hamel *et al.* 2009). As a result, monitoring adult survival may provide limited insights into population responses to environmental variation (Gaillard *et al.* 1998), whereas reproduction and juvenile survival may show clearer variation in relation to environmental change (Gaillard *et al.* 1998) and limiting resources (Eberhardt 2002). Consequently, understanding trends in reproduction and juvenile survival may provide a more sensitive method to detect impacts of anthropogenic or environmental change before these significantly affect population status.

Understanding the demographic drivers of population change can be particularly challenging for wide-ranging inconspicuous species. For cetacean populations, recent studies of demographic rates have been underpinned by long-term individual-based photo-identification studies (e.g. Clapham *et al.* 2003, Currey *et al.* 2009b, Matkin *et al.* 2014). Fecundity or reproductive rate has been estimated in a number of different ways from using the proportion of identifiable reproductive females with new-born (Craig and Herman 2000, Tezanos-Pinto *et al.* 2015) or older calves (Kogi *et al.* 2004, Wells and Scott 1990), the inverse of the inter-birth interval (Matkin *et al.* 2014), modelling inter-birth intervals based on the probability of birth conditional on previous reproductive histories (Arso Civil *et al.* 2017, Barlow and Clapham 1997, Clapham *et al.* 2003) or simply reporting the mean inter-birth interval (Glockner-Ferrari and Ferrari 1990, Henderson *et al.* 2014, Mann *et al.* 2000). Calf survival to different ages has also been estimated by estimating apparent survival rates with capture-recapture models (Currey *et al.* 2009b).

However, there are key issues with these approaches. Firstly, they do not account for imperfect detections, which are particularly important for inconspicuous and wide-ranging species such as cetaceans. Not all individuals will be observed on all occasions (i.e. they may be missed, or not in the survey area) and breeders can be misclassified as non-breeders if young are not detected (i.e. they die before the female is next observed or may not be sighted with the females). In a number of different species early mortality can be highest during the first month following birth (e.g. Clutton-Brock *et al.* 1991, Henderson *et al.* 2014, Laurenson 1994, Stuart-Smith *et al.* 1997). Even in an area with exceptionally high sighting probabilities, where all or nearly all adults are seen on every trip, some births were missed (Henderson *et al.* 2014). This can result in biased demographic rates (Kendall *et al.* 2003), underestimating fecundity or reproductive rate as well as overestimating inter-birth interval and survival of young (Henderson *et al.* 2014, Mann *et al.* 2000, Urian *et al.* 1996, Wells and Scott 1990). Secondly, some of these approaches (e.g. inter-birth interval) cannot provide robust information on inter-annual variation or temporal trends as they require a long time series of data to estimate a single value.

Here we use a 16-year time series from bottlenose dolphins to investigate changes in fecundity and calf survival since the population’s core-habitat was designated a protected area. To account for potential variation in detection and the issues of misclassification, we use an open robust design multistate model with state uncertainty (Cordes and Thompson 2014, Kendall *et al.* 2003). However, as females in this population can give birth throughout the study period we apply this model with an extension that accounts for seasonal effects. This model allows both arrivals and departures during secondary occasions and change in female state. Previous studies suggest that this population is increasing (Cheney *et al.* 2014) but has stable adult survival (Arso Civil 2014). Therefore, we aimed to determine whether there was evidence that changes in fecundity or calf survival were contributing to this increase in population abundance.

## METHODS

### Study site and data collection

This study used data on bottlenose dolphins utilising the Moray Firth Special Area of Conservation (SAC) (92/43/EEC) on the east coast of Scotland. This population has been studied intensively since 1989 as part of a long-term individual-based demographic study, principally using photo-identification (Cheney *et al.* 2014, Wilson *et al.* 1999, Wilson *et al.* 1997). The population size was estimated at 195 (95% highest posterior density interval 162-253) in 2006 (Cheney *et al.* 2013) and is at least stable and potentially increasing (Cheney *et al.* 2014).

Sightings of females and calves (new-born to 2 years old) were available from between 19 and 39 annual photo-identification surveys carried out within the SAC from May to September 2001 to 2016 (total of 416 surveys). This period was chosen because a change in survey protocol in 2001 led to an increase in re-sightings rates (Cheney et al. 2014). This meant that the majority of calves could be associated with known females (e.g. seen with the calf on at least two occasions and/or in echelon position, consistently surfacing alongside the females' dorsal fin with no other adjacent females). The year of birth of calves was estimated using the presence and clarity of foetal folds (vertical creases down their sides from their position in the womb, which fade over time), skin colour and relative size (Grellier *et al.* 2003). Sightings of females were included once they had been observed with a calf and were therefore known to be reproductively mature. Only the best quality pictures were used in the analyses and identifications were confirmed by two experienced researchers (Cheney *et al.* 2013, Wilson *et al.* 1999).

### Estimating fecundity and calf survival

Fecundity and calf survival were estimated using an open robust design multistate model with state uncertainty and seasonal effects. The open robust design multistate model with state uncertainty (Kendall *et al.* 2003) accounts for misclassification or uncertainty in breeding status (e.g. the female is classified as a non-breeder when she is a breeder as she is observed, but her calf is not) (Kendall *et al.* 2003). This model applies the robust design approach (Pollock 1982) to use information from multiple sightings of females (with or without a calf) within a year to estimate the probability that a calf is detected if it is present. This detection probability is then used to adjust breeding probabilities (for full details of the state uncertainty model see Kendall *et al.* 2003). This new model with seasonal effects also incorporates two new parameters, which allow a change in female state (i.e. arrival or departure of a calf) during secondary occasions. The first is alpha ($\alpha$), the probability that the attribute (in this case the calf) used to assign the state has arrived. This provides a measure of the probability that the calf has been born. The second is *c*, the probability that the attribute allowing the state to be determined still exists, i.e. the probability that the calf is weaned.

In this study females could be assigned to one of three states: females with new-born calves (A), females with older (1 or 2 year old) calves (C), and non-breeders (N). However, N was never observed with certainty as a calf may not be detected, and females without a calf cannot unambiguously be classified as non-breeders (Kendall *et al.* 2003). Therefore, the model also included an uncertain state or unobservable event (u), which was assigned to females when they were not observed with a calf (i.e. a mixture of non-breeders and breeders where the calf was hidden or obscured, not photographed, missing or already dead). Sightings histories for each female were summarised into weeks (i.e. secondary capture occasions) within each year (i.e. primary occasion).

The model parameters of interest were estimates of the proportion of females within the study area that have a new-born calf ($\omega^A$, the unconditional reproductive rate) and the transition probability from a non-breeder in year *T* to female with a new-born calf in year *T* + 1 ($\psi^{NA}$, conditional reproductive rate). The transition probability of a female with a new-born calf in year *T* to an older calf in year *T* + 1 ($\psi^{AC}$) equates to first year calf survival (new-born to 1 year old). Finally, the probability that a female with an older calf (1 year old) in year *T* still had an older calf (2 year old) in year *T* + 1 ($\psi^{CC}$) provides a proxy for second year calf survival (1 to 2 years old) (Figure 1). The model also provides the apparent annual survival of females (S) in each state and their calving probability ($\alpha$) (for full details of other available model parameters see Cordes and Thompson 2014, Kendall *et al.* 2003, Kendall *et al.* 2004).

Following Taylor *et al.* (2008) we a priori identified a limited number of models consistent with bottlenose dolphin biology while being careful not to over-parameterize models (for example we did not explore annual or weekly variation). We fit parameters with a state effect (s), linear or quadratic time trend across primary occasions (T or $T^2$), linear or quadratic time trend across secondary occasions (t or $t^2$) or no variation between states and/or across time (.). For female survival (S), models with and without a state effect were included to explore potential costs of reproduction. In addition this parameter was modelled without annual variability, as female survival was previously found to be stable within this population (Arso Civil 2014). However, to confirm this, a linear trend was added to the best fitting model. We were specifically interested in temporal trends and therefore explored variation in transition probabilities ($\psi$) between states and the proportion of the population in each state each year ($\omega$). Models were therefore constructed with a state effect and a linear time trend across primary occasions for these parameters. To determine if linear trends varied for different states, an interaction between state and time trend (s*T) was included in some models. In addition, to determine if there was a linear time trend in transition probabilities and reproductive rates, the best model was run no variation across time for both $\psi$ and $\omega$. We expected no temporal variability in the probability that a female was released in a specific state ($\pi$), so considered models with no time variation but with and without a state effect. All models contained no state effect for capture probabilities ($p$). We expected this parameter to be independent of female state as our survey area is not a particular nursery ground (i.e. newborn calves have been observed throughout the range of this population (Grellier 2000) and our field protocols aim to photograph all the individuals in a group. However, we did include a quadratic time trend across secondary occasions to capture a seasonal pattern in recapture probabilities over the summer. For the probability of correctly classifying the state of a female ($\delta$), we considered models with a state effect and with no time trend. Female state may be misclassified but there is unlikely to be a trend throughout secondary occasions. However, a quadratic time trend across secondary occasions was added to the best fitting model for confirmation. Again, as the survey area is not a particular nursery area, we suspect there would be no state effect for the probability of entry to the study area (pent: *e*) or probability of departure from study area (d), and models were built without a state effect. As there is an apparent summer increase in dolphins in our study area (Wilson *et al.* 1997), linear time trends across secondary occasions were included for these parameters. In this bottlenose dolphin population new-born calves were observed from May to February (Grellier 2000), with a peak in late summer (Grellier 2000, supporting information Figure S1). Therefore, all the models included a quadratic time trend for $\alpha^A$ across secondary occasions. Finally, all the models had a constant *c* as additional states for older weaned calves (i.e. calf is no longer seen in infant/echelon position with a marked decrease in mother-calf association (Mann *et al.* 2000)) were not included to avoid over-parameterising the model. Additionally, there is a lack of synchrony in time of weaning in dolphins, as bottlenose dolphin calves can be weaned at 2 to 9 years old (Grellier *et al.* 2003, Henderson *et al.* 2014, this study, Mann *et al.* 2000), which limits the use of this parameter.

For the misclassification probability, we presumed that all calves were correctly assigned to their mothers, and therefore a non-breeder could not be wrongly identified as a breeder ($\delta^N$ = 0). We also assumed that a female could not give birth in two consecutive years ($\psi^{AA}$ = 0), as that has never been reported in temperate bottlenose dolphins (Grellier 2000, Henderson *et al.* 2014). Finally, a female could not transition from a non-breeder directly to having an older calf ($\psi^{NC}$ = 0).

Analyses were carried out in R (R Core Team 2016) within the package RMark (Laake 2013) to construct models in MARK (White and Burnham 1999). Model selection was conducted using Akaike's Information Criterion (AIC) (Akaike 1998), adjusted for small sample size (AICc), and AICc weights (Burnham and Anderson 2002). Beta-estimates (β) and 95% confidence intervals (CI) were used to assess effect sizes (i.e. significant when the 95% CI do not overlap with zero).

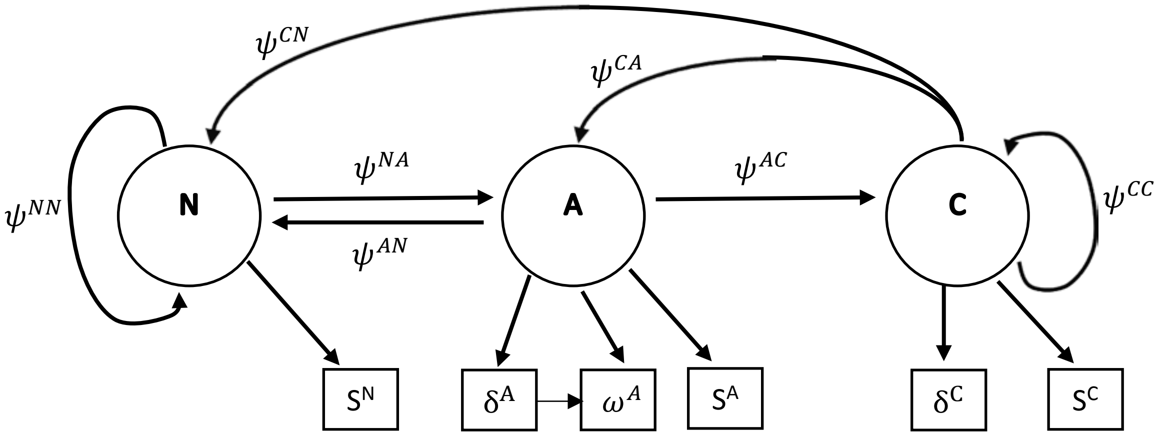

Figure 1. Graphical representation of the open robust design multistate model with state uncertainty and seasonal effects linking each state (N=non-breeder, A = female with newborn calf, C=female with older calf, 1 or 2 years old) by its transition probability ($\psi$) and showing the key parameters estimated ($\delta$ = probability of correctly classifying the state of a female, S = survival and $\omega^A$ = unconditional reproductive rate) and use of $\delta$ to estimate detection and misclassification probabilities and adjust breeding probabilities.

## RESULTS

During the study period, 59 reproductively mature females were sighted (annual mean = 23, SD = 10) and were seen on between one and 17 trips each year (annual mean = 5, SD = 3). These females were known to produce a total of 112 calves (annual mean = 7, SD = 3) across the study period. Of these, 64 calves were seen in their year of birth (annual mean = 4, SD = 4). A minimum of zero and maximum of five calves (mean = 2, SD = 1) were born to each reproductive female over this time period. Thirteen females were seen every year since birth and had their first known calf from 6 to 14 years old (median = 9). In eight cases, a calf was thought to have died in its first year (based upon repeated sightings of females in the following year without a calf). In all eight of these cases, these females were seen with a new calf two years later. A two-year inter-birth interval was also seen with two females whose previous calves (n=3) survived.

The analysis revealed two models that were within 0.3 AICc scores and accounted for 50% of the AICc weight (Table 1). Both specified a state effect on survival and included variation in transition probabilities and the proportion of females occupying different states over time and between states. The only difference between the two top models was that the first model (lowest AICc) suggested a state effect on the probability that a female was released in a specific state ($\pi$). However, the beta estimates suggested this was not estimable ($\pi^C$: SE = 0.00), therefore we chose to present the results from the second model, which was also the simpler with fewer parameters (Table 1).

Table 1. Model selection results for the open robust design multistate models with state uncertainty and seasonal effects estimating reproductive rates and calf survival of bottlenose dolphins in the SAC between 2001 and 2016. The best fitting model is in bold.

| Model | K | ΔAICc | AICc weight |
|---|---|---|---|
| $S(s,.), \psi(s,T), \pi(s,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 26 | 0.00 | 0.258 |
| **$S(s,.), \psi(s,T), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$** | **25** | **0.23** | **0.230** |
| $S(.,.), \psi(s,T), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 23 | 1.21 | 0.141 |
| $S(s,T), \psi(s,T), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 26 | 1.32 | 0.133 |
| $S(s,.), \psi(s,T), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,t^2), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 27 | 1.63 | 0.114 |
| $S(s,.), \psi(s,T), \pi(.,.), \omega(s*T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 24 | 2.19 | 0.086 |
| $S(s,.), \psi(s,.), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 24 | 5.25 | 0.019 |
| $S(s,.), \psi(s*T), \pi(.,.), \omega(s,T), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 27 | 6.50 | 0.010 |
| $S(s,.), \psi(s,T), \pi(.,.), \omega(s,.), p(.,t^2), \delta(s,.), e(.,t), d(.,t), \alpha(A,t^2), c(.,.)$ | 24 | 6.76 | 0.009 |

This model suggested there was an increase (β = 0.11, 95% CI: 0.04-0.18) in the proportion of females with new-born calves (unconditional reproductive rate) from 0.16 (95% CI: 0.11-0.24) in 2001 to 0.28 (95% CI 0.22-0.36) in 2016 (Figure 2). There was also an increasing trend (β = 0.09, 95% CI: 0.02-0.17) in each of the transition probabilities. The probability of transitioning from a female with a new-born calf in year t to an older calf in year t+1 (first year survival) increased over the study period from 0.78 (95% CI 0.53-0.92) in 2001 to 0.93 (95% CI 0.82-0.98) in 2016 (Figure 3a). Although second year survival (transition probability from a female with an one year old calf in year t to a two year old calf in year t+1) remained lower, it also showed an increase from 0.32 (95% CI: 0.19-0.48) to 0.55 (95%CI: 0.44-0.65) (Figure 3b). In addition, the transition probability from non-breeder to female with a new-born calf (conditional reproductive rate) also increased (Figure 4). Models without annual trends in either reproductive rate or transition probability had less support (Table 1) providing further evidence of increasing trends in these demographic rates.

There was no significant difference in apparent annual survival of females that were non-breeders (0.98, 95% CI 0.90-0.996) or females with new-born (0.87, 95% CI 0.77-0.94) or older calves (0.96, 95% CI 0.89-0.99) (Appendix Table A1). However, the model with the lowest AICc suggested there was a significant difference between survival of females with new-born and older calves (β = 2.09, 95% CI: 0.13-4.05) (Appendix Table A2 and Figure A3). This was the only difference in the results of the two top models.

As expected the chosen model suggested a peak in calving during July and August (Figure 4). Additional model results and all associated beta estimates can be found in supplementary information (Figure A2 see Table A1).

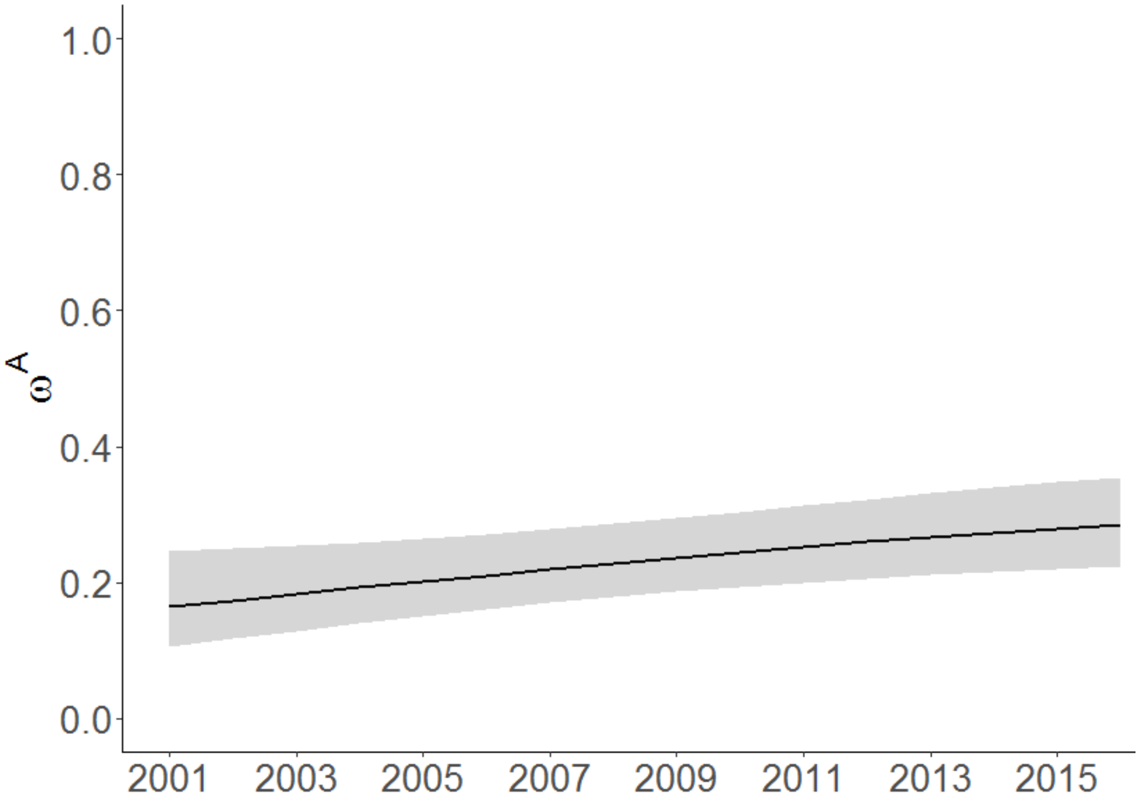

Figure 2. Proportion of females with new-born calves ($\omega^A$, the unconditional reproductive rate) from 2001 to 2016 (with 95% confidence intervals).

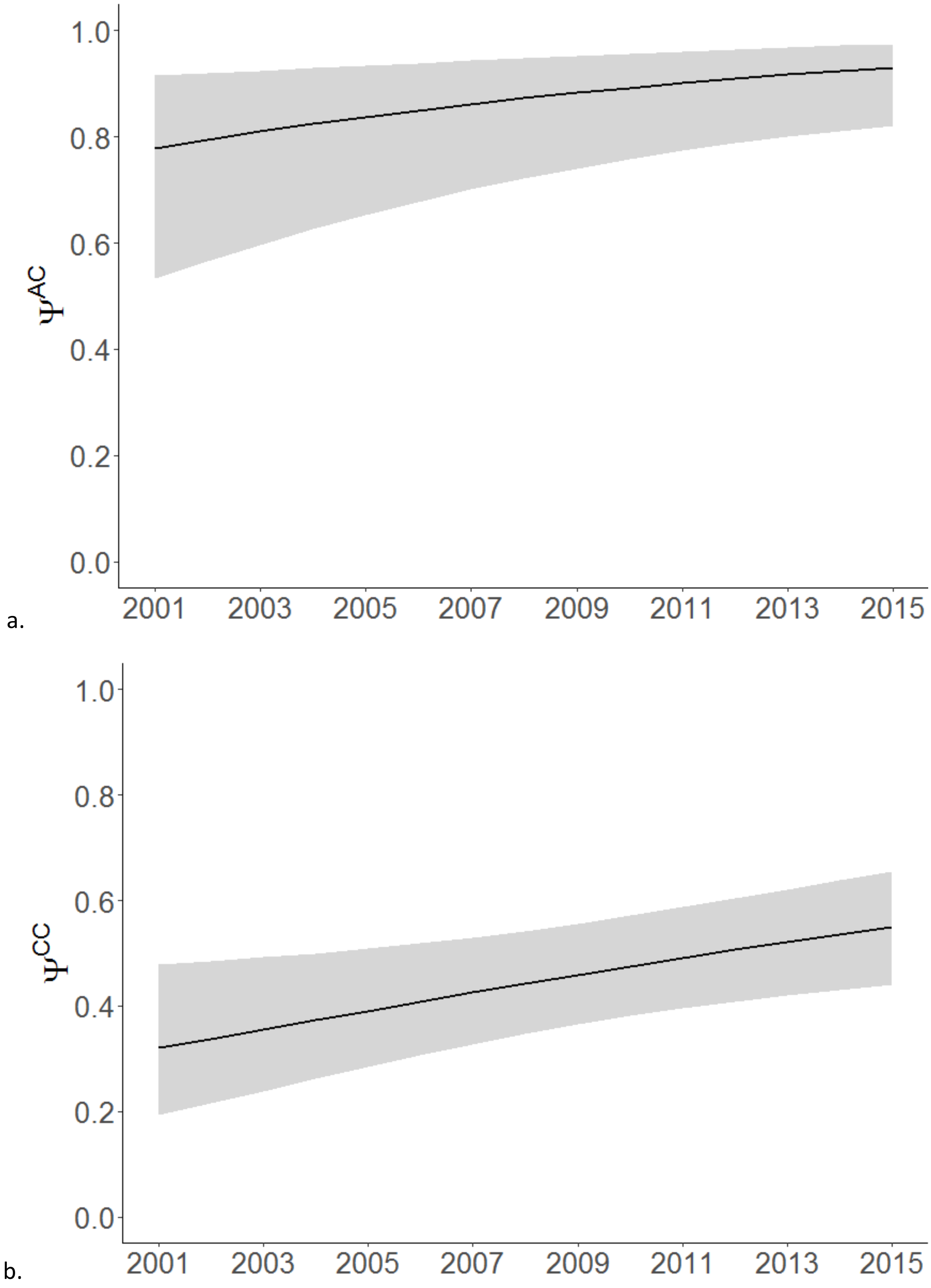

Figure 3. Transition probability from a. a female with a new-born calf in one year to a one year old calf in the subsequent year ($\psi^{AC}$, first year survival) and b. a female with a one year old calf in one year to female with a two year old calf in the subsequent year ($\psi^{CC}$, second year survival) (with 95% confidence intervals).

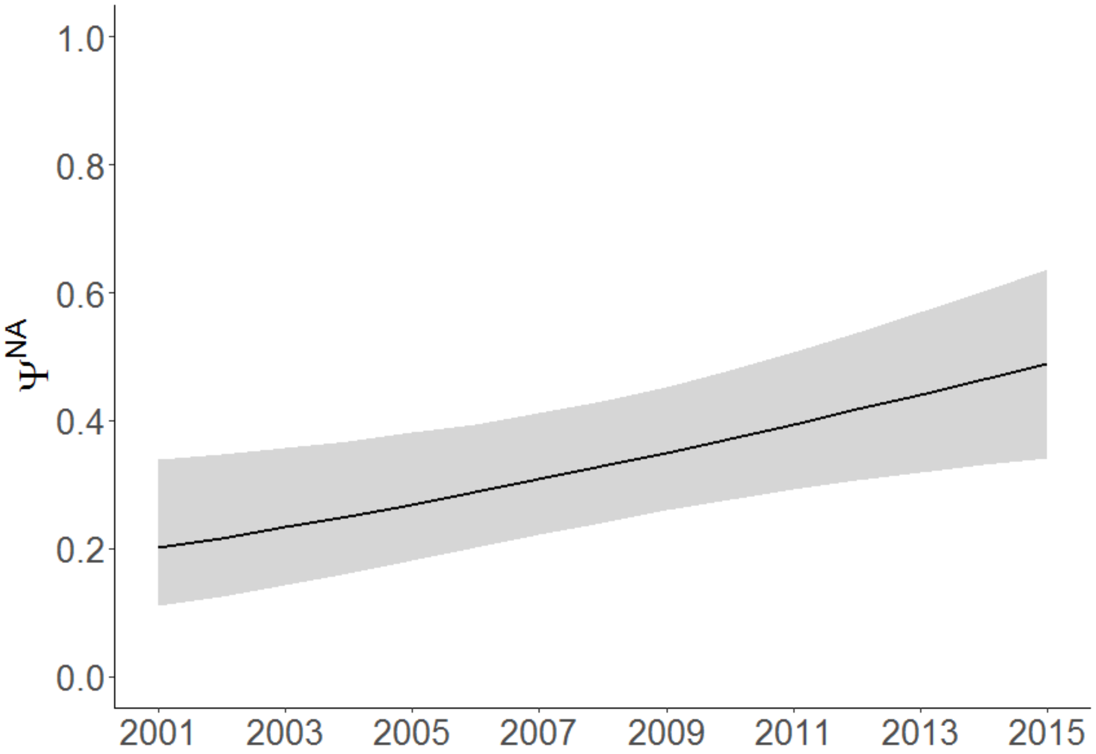

Figure 4. Transition probability from a non-breeder to a female with a new-born calf (conditional reproductive rate, $\psi^{NA}$) (with 95% confidence intervals).

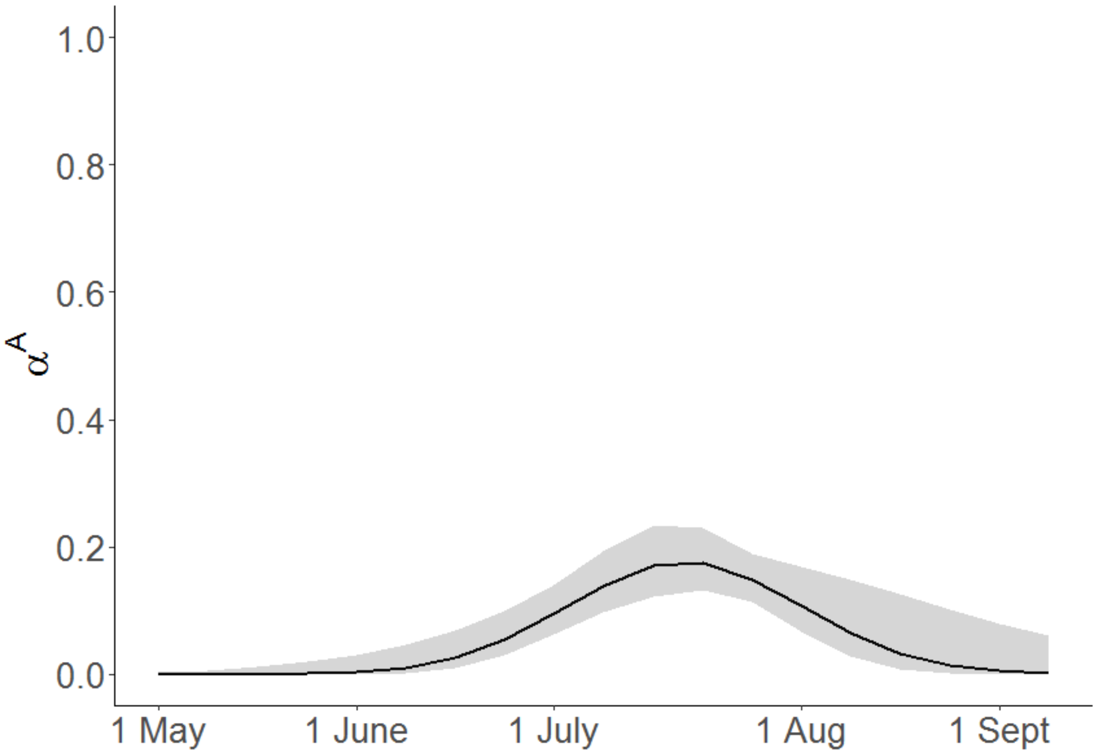

Figure 5. The probability that the attribute (i.e. calf) used to assign the state has arrived ($\alpha$), i.e. the calf has been born. Showing secondary capture occasions (i.e. weeks) from May to September (with 95% confidence intervals).

## DISCUSSION

Fecundity and early survival have impacts on population dynamics but can be difficult to accurately estimate in highly mobile species where every birth cannot be recorded, and where births are asynchronous. We used a novel mark-recapture model that accounts for misclassification of female reproductive state and allows change of female state within the study period to estimate annual reproductive rates and first and second year calf survival. This provides the first estimates of trends in reproductive rate and calf survival for a cetacean population using a protected area.

Results suggest the unconditional reproductive rate in this bottlenose dolphin population has increased over the 16 years of this study. Comparisons with reproductive rates in other bottlenose dolphin populations are difficult as methods vary and do not account for imperfect detection of calves. This may be why, although estimates from early in the time period fall within those reported in other populations (0.14 to 0.27; Kogi *et al.* 2004, Tezanos-Pinto *et al.* 2015, Wells and Scott 1990) our current estimate is higher. As expected, the average reproductive rate in this study (0.23, SE= 0.01) is higher than if estimated using the most common method, the proportion of reproductive females with new-born calves, using data from this study (mean = 0.14, SE = 0.03) or data from another part of the population's range (mean = 0.16, SE = 0.04, Robinson *et al.* (2017)). However, it is similar to an estimate modelled from the inter-birth interval for the entire east coast of Scotland population (0.22, 95% CI 0.22-0.25) (Arso Civil *et al.* 2017). Whilst the approach used by Arso Civil et al. (2017) was able to take account of individual and temporal heterogeneity in re-sightings, neither of these approaches can be used to explore temporal variation in reproductive rates. The novel method that we use here overcomes this constraint, and should provide an important tool assessing trends in reproductive rates. We encourage others to try this method, allowing direct comparisons between populations. This novel technique also accounts for the seasonal nature of births in this population of bottlenose dolphins, with the modelled predictions of a peak in births in July and August similar to findings in a previous study using a different method (Grellier 2000).

Accurately estimating early calf survival from photographic sightings of calves can be difficult because calves may have low sightings probability or die before being observed. Furthermore, young individuals tend to have fewer marks for identification, and may be difficult to follow given that they can become independent at different ages. Here, we used transition probabilities for females in different reproductive states as a proxy for early calf survival. These results suggest that both first and second year survival have increased over the study period, although survival of older calves remains lower. Other studies of trends in calf survival in this species are rare. Currey *et al.* (2009a) found a decline in first year calf survival over two time periods in another temperate bottlenose dolphin population, a result of cold freshwater inflow from a hydroelectric station and a key factor in that population's decline. Although, first year survival estimates in the early phase of our study fell within the reported range for other *Tursiops* spp. populations (0.70 to 0.86, Fruet *et al.* (2015), Kogi *et al.* (2004), Mann *et al.* (2000), Steiner and Bossley (2008), Wells and Scott (1990)) estimates from more recent years were higher. Our 2016 first year survival estimate (0.93, 95% CI 0.82-0.97) is close to a previously estimated apparent adult survival estimate (0.946, SE=0.005, Arso Civil (2014)) for this population. Again comparisons are difficult but this may be, at least in part, due to the lack of shark predation which can be one of the mortality risks for young calves in other areas (Fearnbach *et al.* 2012, Mann and Barnett 1999, Wells 1991). Although second year survival also increased throughout study, it remained substantially lower than first year survival and also lower than previous estimates of second year survival from Australian waters (0.82, Mann *et al.* (2000)). Although this could be a result of the increased probability of missing sightings of older calves as they spend less time with their mothers (Grellier *et al.* 2003), our model choice should have accounted for this. Our latest second year survival estimate (0.55, 95% CI 0.44-0.65) is similar to the survival rate for older, weaned calves in other areas (0.54, Connor *et al.* 2000, Steiner and Bossley 2008). Steiner and Bossley (2008) suggested this higher mortality was a result of anthropogenic activities in the area (e.g. boat strikes and entanglement), however, there has been no evidence of this reported in our study area. Reduction in provisioning by the female as calves get older could result in a decrease in condition and increase in mortality compared to new-born calves. Lactation is thought to last for 18 months to 2 years and solids have been found in the stomachs of calves from ~6 months old (Cockcroft and Ross 1990). End of lactation is known to vary within and between populations (Connor *et al.* 2000) but is not known in this population.

Understanding the demographic causes of changes in population status can provide valuable information for conservation and management (Currey *et al.* 2009b). There is empirical evidence both that our study population has been increasing (Cheney *et al.* 2014) and that adult survival has remained stable (Arso Civil 2014). This study suggests that population growth may be the consequence of an increase in reproduction and first and second year calf survival. Previous modelling exercises have also suggested that high reproductive rates and increased juvenile survival drove recent increases in Steller sea lions (*Eumetopias jubatus*) in Alaska (Maniscalco *et al.* 2015), and that reproduction was key vital rate affecting contrasting population trajectories in two tropical bottlenose dolphin populations (Manlik *et al.* 2016). Evaluation of the contribution of the recent conservation management to these positive trends now requires a better understanding of the key intrinsic and/or extrinsic drivers that have influenced reproduction and calf survival in this population. Fecundity can vary with age (Clutton-Brock and Sheldon 2010) and increasing reproduction may be the result of an increase in the number of prime breeding age females. However, it can also vary with food availability (Brough *et al.* 2016, Mann *et al.* 2000, Ward *et al.* 2009). Data on changes in female age structure are not currently available for our study population, although ongoing work using photogrammetry (Cheney *et al.* In review) may shed light on this question in future. Similarly, understanding of trends in food availability is constrained by limited information on diet in this population and on the availability of suitably fine-scale data on variation in abundance of potential prey. Investigating first and second year calf body condition could help identify the factors driving the increase in early survival. Photogrammetric evidence from this study population suggests that calves that survived their first winter were significantly longer than those that died (Cheney *et al.* In review). This has also been shown in another population where poor calf condition was the main cause of mortality (Mann and Watson-Capps 2005). In another population bottlenose dolphin calf mortality was affected by timing of calving (Brough *et al.* 2016, Henderson *et al.* 2014) and female heterogeneity, with females showing consistent differences in survival of their calves (Henderson *et al.* 2014). These could be a proxies for calf condition. There is evidence of mortality as a result of intraspecific aggression in this population with five of eight calves stranded in the early 1990s killed by conspecifics (Patterson *et al.* 1998). This was identified as infanticide as the calves were thought to be in their first year of life, due to their length (Patterson *et al.* 1998). This potentially explains the lower first year survival at the start of this study but is unlikely to be the cause of the low second year survival. Although there have been no recent reports of infanticide in this population this may be due to the small number of reported bottlenose dolphin strandings (SRUC 2017) rather than a change in this behaviour.

Our results also indicated that there may be some evidence for a cost of reproduction for bottlenose dolphin females in this population, but further work is required to confirm this. Females with new-born calves did have a slightly higher mortality than those with older calves. However, whether this was significant was dependant on the choice between two top models which were very similar. This uncertainty may largely be due to the limited amount of data available. However, heterogeneity in individual female quality can also result in variability in the cost of reproduction, with no reproductive costs for some individuals or in some cases higher survival for breeders (Hamel *et al.* 2009). In addition, reproductive costs are affected by both extrinsic and intrinsic factors (Clutton-Brock *et al.* 1983), which can interact (Boyd *et al.* 1995) and complicate interpretation.

Marine protected areas (MPAs) have been established worldwide to protect marine mammals (Hoyt 2011), although there is limited evidence on their effectiveness as management and conservation tools for this group (see Gormley *et al.* 2012 for an exception). This study suggests there is a positive trend in reproduction and survival in bottlenose dolphins using the Moray Firth SAC. Whether this is a consequence or coincidental to the establishment of the SAC is unknown.

## ACKNOWLEDGEMENTS

We thank all the colleagues and fieldwork assistants who have helped collect data. The BES, ASAB, Greenpeace Environmental Trust, Scottish Natural Heritage, Scottish Government, Whale and Dolphin Conservation, Talisman Energy (UK) Ltd., Department of Energy and Climate Change, Chevron, Natural Environment Research Council, Beatrice Offshore Windfarm Ltd., Moray Offshore Renewables Ltd., Marine Scotland, The Crown Estate and Highlands and Islands Enterprise and the University of Aberdeen all provided funding for annual photo-identification surveys in the Moray Firth. Survey work was conducted under Scottish Natural Heritage Animal Scientific Licences.

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## APPENDIX

Additional supporting information for the published paper.

Table A1. Beta estimates to assess effect sizes from the best fitting model.

Table A2. Beta estimates to assess effect sizes from the lowest AICc model.

Figure A1. Seasonal changes in the timing of first sightings of females with neonates and the number of surveys.

Figure A2. Additional results from the best fitting model.

Figure A3. Results from the lowest AICc model.

Table A1. Beta estimates to assess effect sizes from the best fitting open robust design multistate model with state uncertainty and seasonality ($S(s,.)$, $\psi(s,T)$, $\pi(.,.)$, $\omega(s,T)$, $p(.,t^2)$, $\delta(s,.)$, $e(.,t)$, d(.,t), $\alpha$(A,t$^2$), $c(.,.)$).

| Parameter | Estimate | Standard Error | Lower Confidence Interval | Upper Confidence Interval |
|---|---|---|---|---|
| S:(Intercept) | 1.9787485 | 0.3968469 | 1.2009286 | 2.7565684 |
| S:stratumC | 1.8702147 | 0.9732294 | -0.0373149 | 3.7777443 |
| S:stratumN | 1.2093010 | 0.7539234 | -0.2683888 | 2.6869909 |
| Psi:Time | 0.0952297 | 0.0365711 | 0.0235503 | 0.1669090 |
| Psi:stratumC:tostratumA | -1.6118133 | 0.4462427 | -2.4864490 | -0.7371775 |
| Psi:stratumN:tostratumA | -1.3810308 | 0.3633328 | -2.0931631 | -0.6688985 |
| Psi:stratumA:tostratumC | 1.2567008 | 0.5714552 | 0.1366486 | 2.3767530 |
| Psi:stratumC:tostratumC | -0.5706642 | 0.3959615 | -1.3467486 | 0.2054203 |
| pi:(Intercept) | 38.3383480 | 0.0000000 | 38.3383480 | 38.3383480 |
| Omega:(Intercept) | -1.1736174 | 0.3689554 | -1.8967700 | -0.4504647 |
| Omega:stratumC | 0.6203760 | 0.1551754 | 0.3162323 | 0.9245197 |
| Omega:Time | 0.1072542 | 0.0368062 | 0.0351140 | 0.1793944 |
| p:(Intercept) | 0.1080194 | 0.1314513 | -0.1496252 | 0.3656640 |
| p:Time | -0.1782940 | 0.0320695 | -0.2411503 | -0.1154378 |
| p:I(Time^2) | 0.0091871 | 0.0018190 | 0.0056219 | 0.0127523 |
| Delta:(Intercept) | 0.9135894 | 0.2317021 | 0.4594533 | 1.3677254 |
| Delta:stratum | 1.6277615 | 0.2841064 | 1.0709130 | 2.1846099 |
| pent:(Intercept) | -0.7960786 | 0.1342179 | -1.0591456 | -0.5330116 |
| pent:Time | -0.2187439 | 0.0221562 | -0.2621700 | -0.1753177 |
| d:(Intercept) | -6.9470141 | 0.7037412 | -8.3263468 | -5.5676814 |
| d:Time | 0.3266308 | 0.0573833 | 0.2141596 | 0.4391020 |
| alpha:(Intercept) | 15.3197240 | 485.0930400 | -935.4626600 | 966.1021000 |
| alpha:A:Time | 1.8638345 | 0.6274251 | 0.6340812 | 3.0935877 |
| alpha:A:I(Time^2) | -0.0872796 | 0.0311053 | -0.1482459 | -0.0263132 |
| c:(Intercept) | -7.2512932 | 0.9995006 | -9.2103145 | -5.2922719 |

Table A2. Beta estimates to assess effect sizes from the lowest AICc open robust design multistate model with state uncertainty and seasonality ($S(s,.)$, $\psi(s,T)$, $\pi(s,.)$, $\omega(s,T)$, $p(.,t^2)$, $\delta(s,.)$, $e(.,t)$, d(.,t), $\alpha(\mathrm{A},\mathrm{t}^2)$, $c(.,.)$).

| **Parameter** | **Estimate** | **Standard Error** | **Lower Confidence Interval** | **Upper Confidence Interval** |
|---|---|---|---|---|
| S:(Intercept) | 1.9280338 | 0.3756862 | 1.1916888 | 2.6643788 |
| S:stratumC | 2.0909423 | 1.0016086 | 0.1277893 | 4.0540952 |
| S:stratumN | 1.2630301 | 0.7435160 | -0.1942613 | 2.7203216 |
| Psi:Time | 0.0961188 | 0.0366565 | 0.0242721 | 0.1679656 |
| Psi:stratumC:tostratumA | -1.6244524 | 0.4481690 | -2.5028636 | -0.7460412 |
| Psi:stratumN:tostratumA | -1.3820527 | 0.3641337 | -2.0957548 | -0.6683506 |
| Psi:stratumA:tostratumC | 1.2597948 | 0.5699132 | 0.1427649 | 2.3768248 |
| Psi:stratumC:tostratumC | -0.5915601 | 0.3973685 | -1.3704024 | 0.1872822 |
| pi:(Intercept) | 38.5157680 | 0.0000000 | 38.5157680 | 38.5157680 |
| pi:stratumC | -43.3396360 | 0.0000000 | -43.3396360 | -43.3396360 |
| Omega:(Intercept) | -1.1734839 | 0.3689755 | -1.8966758 | -0.4502920 |
| Omega:stratumC | 0.6202913 | 0.1551815 | 0.3161356 | 0.9244470 |
| Omega:Time | 0.1072618 | 0.0368103 | 0.0351137 | 0.1794099 |
| p:(Intercept) | 0.1090890 | 0.1314775 | -0.1486068 | 0.3667849 |
| p:Time | -0.1787629 | 0.0320768 | -0.2416335 | -0.1158922 |
| p:I(Time^2) | 0.0092212 | 0.0018194 | 0.0056551 | 0.0127873 |
| Delta:(Intercept) | 0.9114563 | 0.2316483 | 0.4574255 | 1.3654870 |
| Delta:stratumC | 1.6303577 | 0.2840285 | 1.0736617 | 2.1870537 |
| pent:(Intercept) | -0.7928528 | 0.1342744 | -1.0560307 | -0.5296749 |
| pent:Time | -0.2186889 | 0.0221538 | -0.2621104 | -0.1752673 |
| d:(Intercept) | -6.9502934 | 0.7033549 | -8.3288691 | -5.5717177 |
| d:Time | 0.3270526 | 0.0573221 | 0.2147013 | 0.4394039 |
| alpha:(Intercept) | 15.44563605 | 34.3013200 | -1031.7850000 | 1062.6762000 |
| alpha:A:Time | 1.8645089 | 0.6276757 | 0.6342645 | 3.0947532 |
| alpha:A:I(Time^2) | -0.0873223 | 0.0311202 | -0.1483180 | -0.0263267 |
| c:(Intercept) | -7.2517309 | 0.9995946 | -9.2109363 | -5.2925255 |

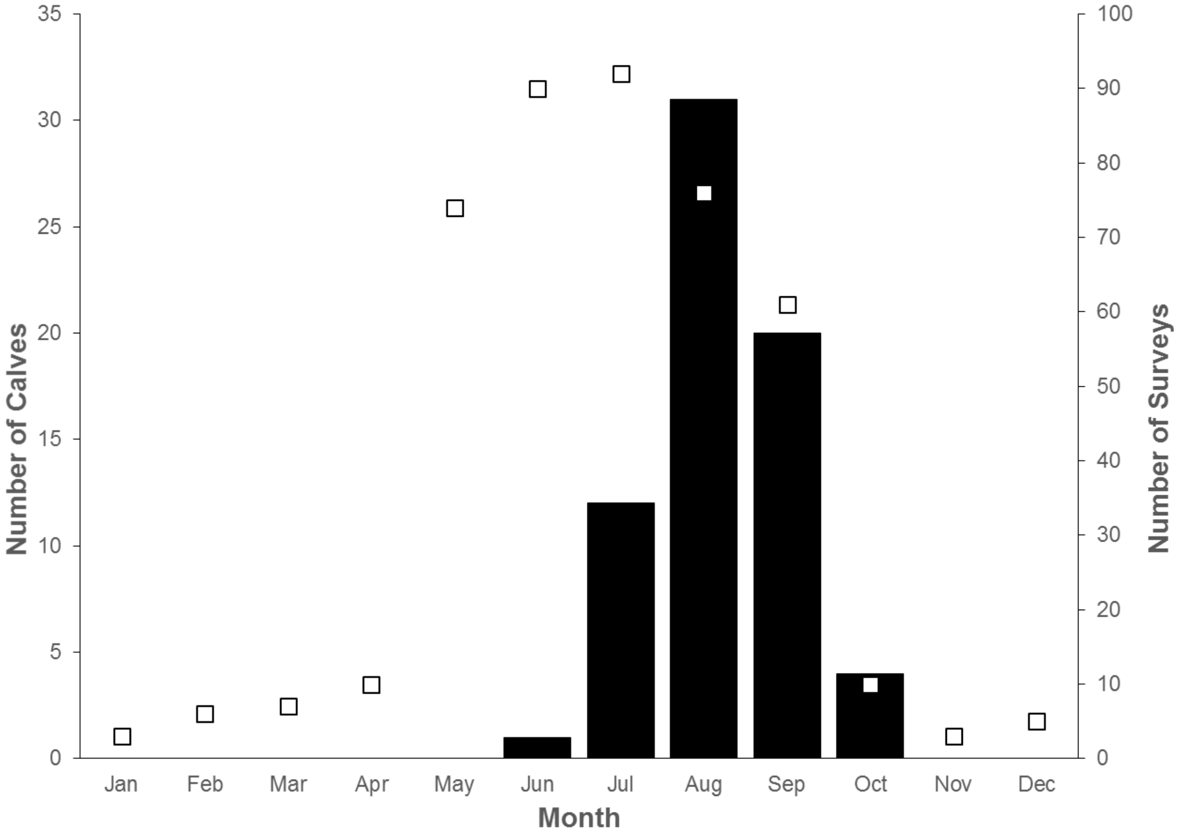

Figure A1. Seasonal changes in the timing of first sightings of females with neonates in the SAC from 2001 to 2015 (black bars), and the number of surveys carried out each month (white squares).

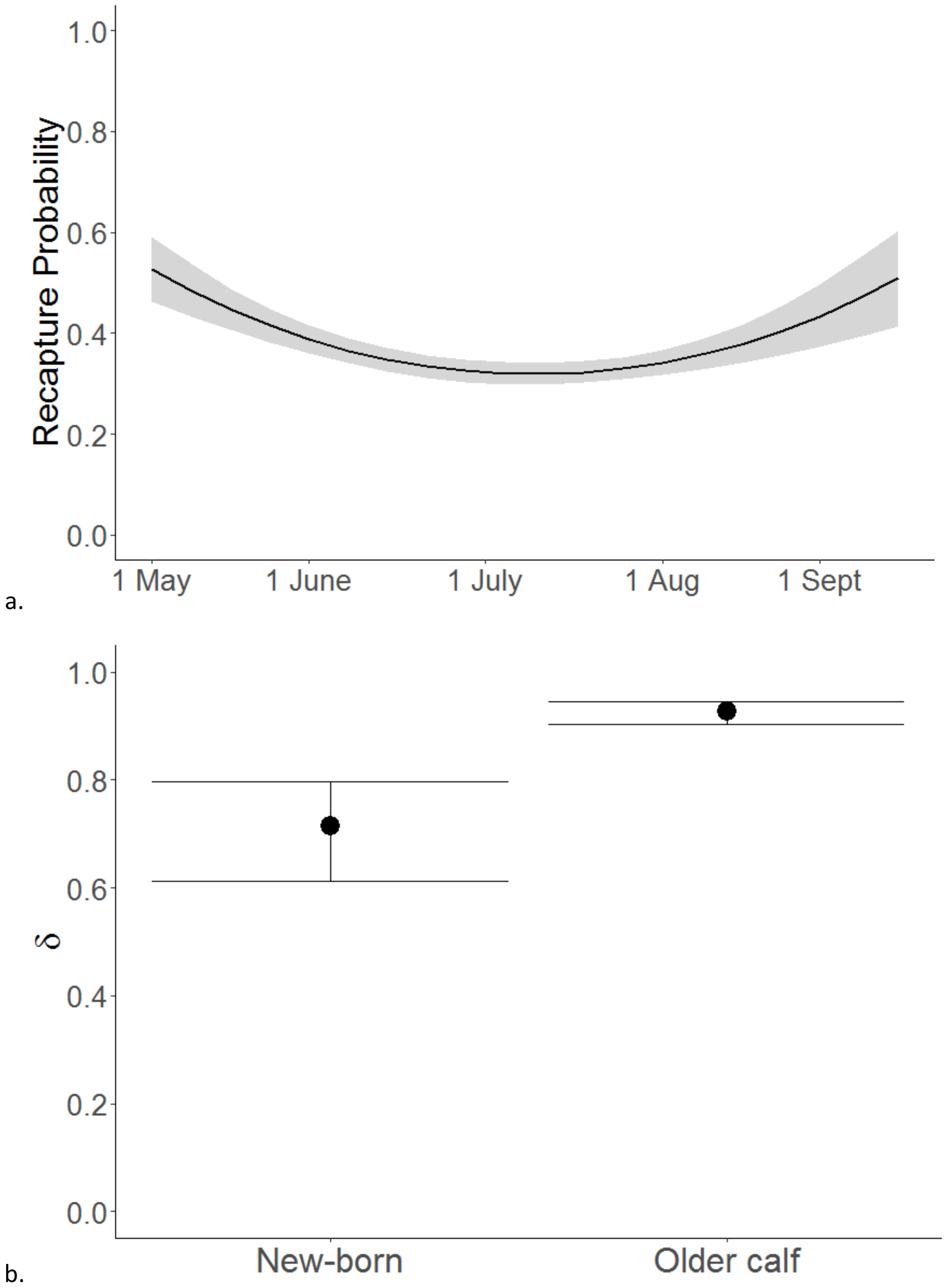

Figure A2. Additional results from the best fitting open robust design multistate model with state uncertainty and seasonality ($S(s,.)$, $\psi(s,T)$, $\pi(.,.)$, $\omega(s,T)$, $p(.,t^2)$, $\delta(s,.)$, $e(.,t)$, $\mathrm{d}(.,\mathrm{t})$, $\alpha(\mathrm{A},\mathrm{t}^2)$, $c(.,.)$ including a. recapture probability for females with new-born calves ($\mathrm{p}^A$) and b. the probability that a calf was observed given that a female was with a new-born ($\delta^{\mathrm{A}}$) or older calf (1 or 2 years old, $\delta^{\mathrm{C}}$) during the summer (all with 95% confidence interval).

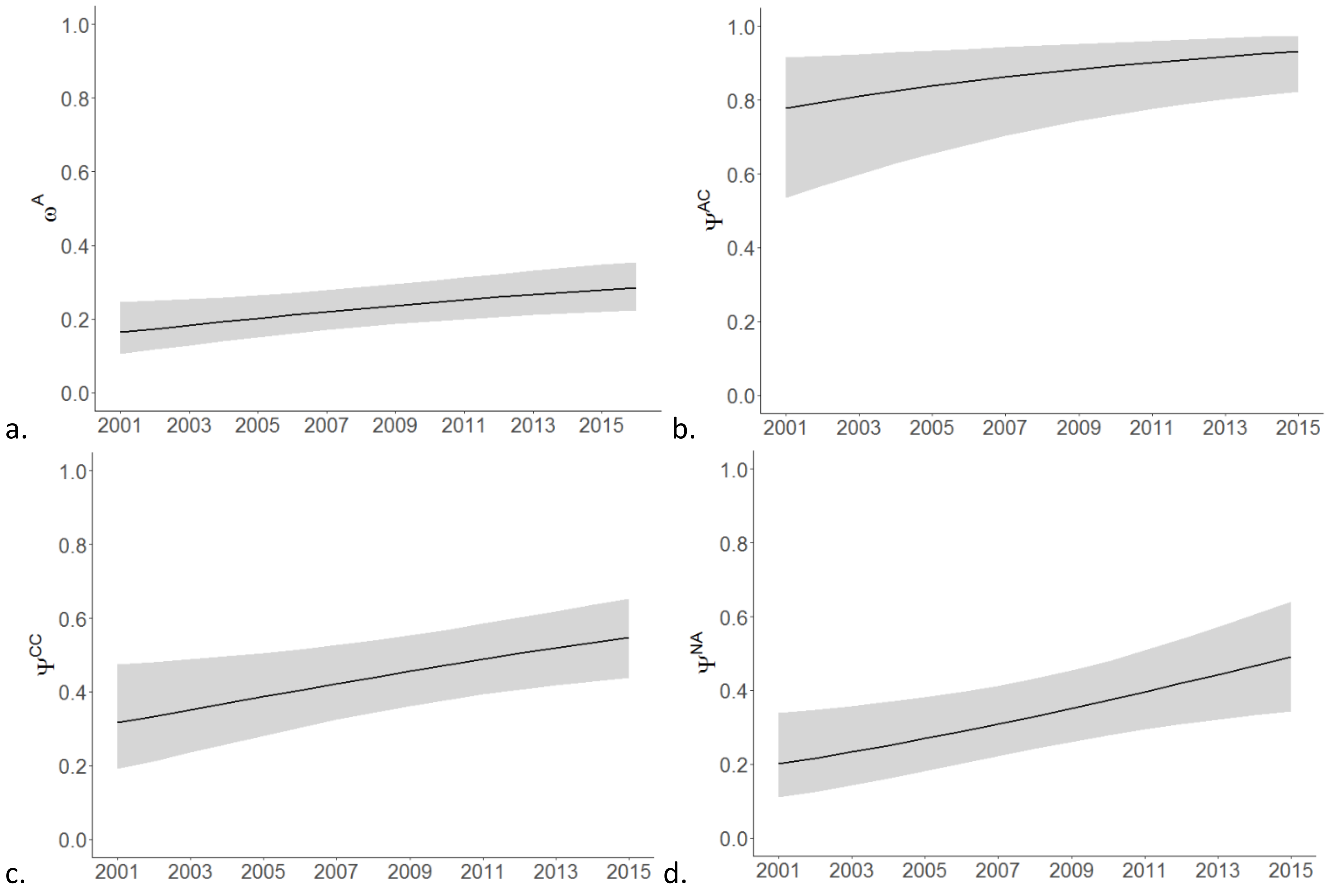

Figure A3. Results from the lowest AICc open robust design multistate model with state uncertainty and seasonality (($S(s,.)$, $\psi(s,T)$, $\pi(s,.)$, $\omega(s,T)$, $p(.,t^2)$, $\delta(s,.)$, $e(.,t)$, d(.,t), $\alpha$(A,$t^2$), $c(.,.)$) including a. proportion of females with new-born calves ($\omega^A$, the unconditional reproductive rate), b. transition probability from a female with a new-born calf in one year to a one year old calf in the subsequent year ($\psi^{AC}$, second year survival), c. transition probability from a female with a 1 year old calf in one year to female with a two year old calf in the subsequent year ($\psi^{CC}$, second year survival), d. transition probability from a non-breeder to a female with a new-born calf (conditional reproductive rate, $\psi^{NA}$) (continued below).

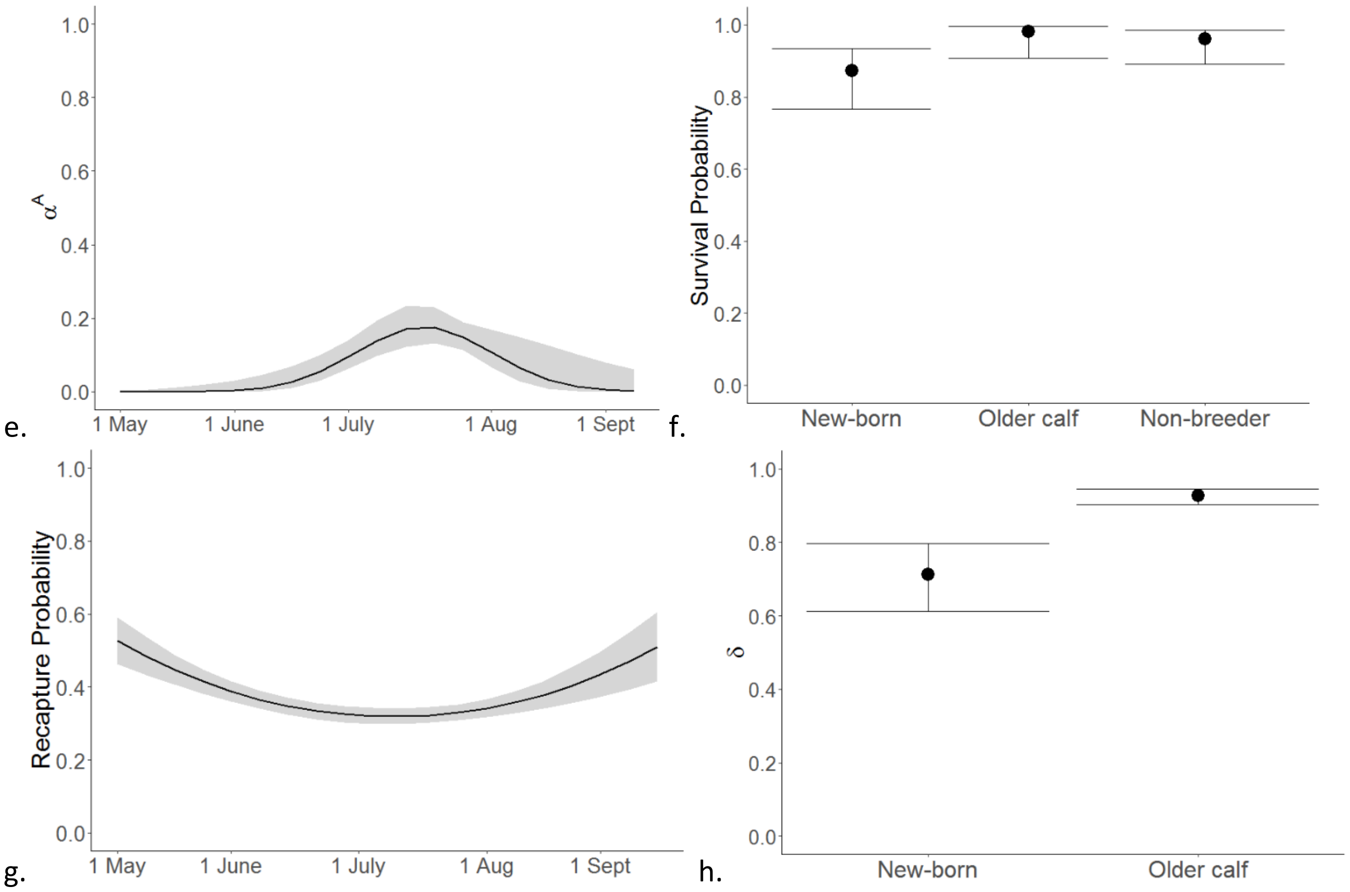

Figure A3 (cont.) e. the probability that the attribute (i.e. calf) used to assign the state has arrived ($\alpha$), i.e. the calf has been born, f. survival probabilities (S) for females with new-born or older calves and non-breeding females, g. recapture probability for females with new-born calves ($p^A$) and h. the probability that a calf was observed given that a female was with a new-born ($\delta^A$) or older calf (1 or 2 years old, $\delta^C$) during the summer (all with 95% confidence interval).

# CHAPTER 7

## GENERAL DISCUSSION

ID#9 with calf ID#11 in 1989

ID#11 with calf ID#1024 in 2007

ID#1024 with calf ID#1200 in 2015

# CHAPTER 7

## GENERAL DISCUSSION

With limited resources for conservation action it is important to evaluate the value and contribution of this long-term individual based photo-identification (photo-ID) study. Within this key questions should be identified and prioritised that will either advance knowledge and/or assist with conservation and management. Although these questions can vary for different species in different habitats, some underpin an evaluation of population status and inform conservation goals and initiatives. Successfully identifying individuals (e.g. using photo-ID) during long-term studies can help answer some of these ecological questions including collecting information on distribution, abundance and trends, social structure, demographic parameters and health. Equally with increasing environmental uncertainty and anthropogenic stressors (e.g. renewable energy, coastal developments, etc.) it is vital to have baseline information to determine responses and predict recoveries. Also, data are required to increase our understanding of interactions to ensure balanced decisions are made on potentially conflicting conservation, environmental and development objectives.

Bottlenose dolphins (*Tursiops truncatus*) are long-lived with low reproductive rates and complex social structures (Wells *et al.* 1987), while showing plasticity in their behaviour, biology and ecology (Parsons *et al.* 2006). As such long-term individual based studies are key to investigating the complexities of their population dynamics including answering essential ecological questions. They are also an important part of the marine ecosystem (Bowen 1997, Katona and Whitehead 1988), can be indicator species (Moore 2008), and as they are highly mobile and widely distributed often in coastal areas they can be affected by many anthropogenic activities. They are used as model systems (e.g. New *et al.* 2013) and are often economically important (Hoyt 2011). All making them an interesting and important group to study, especially aspects of their ecology in different populations in different areas.

## INSIGHTS FROM THIS THESIS

My aim for this thesis was to synthesise over two decades of photo-ID data with the intention of exploring the usefulness of long-term individual based data and answering key questions about the ecology and biology of bottlenose dolphins in Scottish waters. To do this I explored novel techniques in the field (Chapter 4), adapted existing (Chapter 2 and 3) and used new analytical methods (Chapter 6). In addition I aimed to fill gaps in our knowledge of this protected population, contribute to conservation and management and provide information on trends in abundance and life history parameters for future environmental impact assessments.

Other studies in a variety of habitats and geographic regions have highlighted the plasticity of bottlenose dolphins (Parsons *et al.* 2006). This plasticity is likely an important factor allowing the species to exploit different habitats (Lusseau *et al.* 2003). This study discussed some of the differences observed in bottlenose dolphins around Scotland. In particular, marked differences in population sizes and ranging patterns both between and within populations (Chapter 2, 3 and 5) and changes in social structure (Chapter 5), potentially as a result of a range expansion, with differences in individuals at the extremes of the population's range. However, this thesis also highlighted differences between dolphins in Scottish waters and in other geographic areas. For example, larger size, lack of sexual dimorphism and similar growth rates between the sexes (Chapter 4), which are possibly adaptations to the colder water temperatures (e.g. Ross and Cockcroft 1990). In addition females in this population show the potential to calve every two years (Chapter 6), which has only been reported in two other dolphin populations (Henderson *et al.* 2014, Wells *et al.* 1987). They also have a higher reproductive rate with higher first than second year calf survival, possibly due to the lack of predation but also a potential factor of the chosen new method (Chapter 6).

Chapter 2 was the first investigation of and provides background on bottlenose dolphins around Scotland. It fills knowledge gaps on the distribution and status of bottlenose dolphins around Scotland, especially on the west coast. It emphasises the value of citizen science for wide ranging species in complex environments where distribution and movement is not fully understood. For the little known populations on the west coast of Scotland citizen science greatly enhanced research effort and contributed additional photographs. For example, during the first year bottlenose dolphins were only sighted on 18% of photo-ID surveys. Following an expansion of the existing HWDT sightings network, this increased to 38%. Members of the public were also encouraged to provide photographs which provided additional sightings of approximately 75% of the estimated population. Citizen science is being increasing used in ecological studies (Sutherland *et al.* 2013) and was invaluable for this project. This chapter also highlighted the value of collaborative projects where species are wide ranging and one research group cannot logistically or financially cover the entire range. However, these both underscored the need for quality assurance to ensure consistency and reliability of data from a variety of sources. For example, all photo-ID pictures were quality controlled (i.e. grading) and matched by one experienced individual with a consistent protocol. This highlighted differences in quality criteria between research groups and corrected both type I (i.e. not matching a photograph to a catalogued individual) and type II (i.e. matching a photograph to the wrong individual) matching errors. However, the variation in effort, temporally and spatially, constrained some of the conclusions that could be drawn. Despite these limitations this study provided crucial data for conservation and management, including abundance estimates, distribution and connectivity/population definition. Finally, it provided the first indication that the population on the east coast of Scotland had increased.

Although the abundance estimate for the east coast of Scotland bottlenose dolphin population was higher than previously estimated (Chapter 2), this could have been due to the survey design in the earlier studies where it was not possible to encompass the entire range of the population or to the differences in mark recapture models used. This was investigated (Chapter 3) using the original mark recapture models to estimate abundance and trends both within the Special Area of Conservation (SAC) and for the entire population, including data from across the home range. This highlighted the advantages of research outside the protected area to fully understand the status of the population using that area. Previous SAC site condition monitoring reports for Scottish Natural Heritage concluded that the population was “unfavourable (recovering)” (Thompson *et al.* 2006). These new results suggested the population was at least stable and potentially increasing, the number of dolphins using the SAC remained stable and the majority of individuals on the east coast of Scotland use the SAC in any one year. As such the conservation status was changed to “Favourable (recovered)” in 2012 (Cheney *et al.* 2012). This in itself provides interesting challenges in terms of conservation priorities. Should research effort and funding be focussed elsewhere if a population is recovered or should the focus be on determining the causal factors and ensuring this continues?

Long-term studies need to push boundaries and open up new areas of research (Clutton-Brock and Sheldon 2010). It is understood that environmental and anthropogenic stressors may initially have effects on species health and monitoring changes in health may allow quicker detection of negative effects. A novel technique was adapted to remotely and accurately collect information on length in free ranging bottlenose dolphins. This was integrated with data from the long-term individual based research on age and sex (Chapter 4). In addition to identifying the morphological differences in this population, discussed previously, (e.g. larger size, no sexual dimorphism, no sex differences in growth), there were fitness consequences to variation in early growth. This provided the first evidence that calves that died over their first winter were significantly shorter. These data provided information on size at age and growth rates for this population at a time when it is increasing. In other species laser photogrammetry has been used to measure length (Deakos 2010, Rohner *et al.* 2011) but in cetaceans this has focussed on measuring dorsal fin size (Durban and Parsons 2006, Rowe and Dawson 2008, Webster *et al.* 2010), estimating epidermal condition (Rowe *et al.* 2010) and sex (Rowe and Dawson 2009). As far as we are aware this is the first study to remotely measure length and investigate growth in individual cetaceans over multiple years. The technique was also validated for the first time using known length but free ranging bottlenose dolphins in Sarasota, Florida. This study demonstrated that this simple to use and relatively inexpensive method can be easily incorporated into routine photo-ID to measure total length of bottlenose dolphins, investigate growth and the consequences of variability in growth. This method has potential for other species that are difficult or impossible to capture.

It is recognised that information on animal movement can inform conservation and management, for example identifying areas to protect, but is often underutilised (Hays *et al.* 2016). One of the key questions in movement ecology is to what extent social interactions influence movements, for example how individuals influence group behaviour (Hays *et al.* 2016). Dolphins in this population have different and variable ranges and movement, some are rarely if ever seen outside the SAC, others travel across the east coast, others spend the majority of their time around the southern extreme of the home range while some change their ranging pattern over annual or decadal scales (Chapter 2). The range expansion in this population (Wilson *et al.* 2004) provided a natural experiment to investigate whether there was a social dimension to this variability (Chapter 5). Social structure can be dynamic with variability found in populations as a result of demographic (Lehmann and Boesch 2004, Lusseau and Newman 2004), natural (Elliser and Herzing 2013) and anthropogenic factors (Ansmann *et al.* 2012). In this study, contrary to expectations, individuals from different social groups, rather than one social group, appear to have been part of the range expansion. In addition there were observed differences in social structure over two decades and the two extremes of the range. Along similar lines Connor *et al.* (2017) found variation in social structure, in the form of male alliance behaviour, along a spatial axis suggesting an ecological influence. Additional research is required to further examine the differences in movement patterns and determine whether this change in social structure is a cause, consequence or coincidental to the range expansion. Also, as prey is likely to be the fundamental driver of movement (Hays *et al.* 2016) information on prey preferences, distribution and abundance as well as seasonal and annual variability throughout the range of this population is required. Continued investigation into movement of individuals and associated social structure could add to our understanding. However, photo-ID over a large area is logistically and financially challenging. The alternative, tagging, has conservation and practical issues, as obtaining broader scale movement data requires long-term tag attachment, which for smaller cetaceans often requires an invasive attachment method including catching (e.g. Balmer *et al.* 2010, Sveegaard *et al.* 2011).

Chapters 2 and 3 suggested the bottlenose dolphin population on the east coast of Scotland is increasing. However, Whitehead and Gero (2015) found that an apparent increase in abundance in sperm whales (*Physeter macrocephalus*) in the Caribbean was actually the result of immigration and the population suffered high, likely anthropogenic mortality. This demonstrates the value of long-term individual based monitoring and utilising different methods to monitor population dynamics (Whitehead and Gero 2015). In Chapter 6, I used a relatively new method to investigate reproductive rate and early survival in a protected area over 16 years. The reproductive rate for this population has been estimated using the interbirth interval (Arso Civil *et al.* 2017) and from another part of the populations range the proportion of reproductive females with new-born calves (Robinson *et al.* 2017). However, this new method (Chapter 6) accounts for births that are missed and can explore temporal trends in both reproductive rate and calf survival. It was important to estimate calf survival as adult survival was previously estimated to be high and stable (Arso Civil 2014) and therefore was not contributing to the increase in population abundance (Chapter 3). Chapter 6 provided an insight into trends in two demographic rates (reproduction and calf survival) and their contribution to the increasing population abundance, two key questions in ecological research (Clutton-Brock and Sheldon 2010, Sutherland *et al.* 2013). In addition, these results will assist with any future population viability analyses (PVA). PVA can be useful for populations of conservation concern as they can predict population size and risk of extinction (Coulson *et al.* 2001), and explore the consequences of different management options (Thompson *et al.* 2000). However, they require extensive and reliable data on vital rates including temporal changes (Coulson *et al.* 2001). Also, information on life history parameters can assist with predictions of population effects of anthropogenic stressors (Pirotta *et al.* 2015a, Thompson *et al.* 2013) and population recovery (Merrick *et al.* 2009).

Marine protected areas (MPAs) have been established worldwide to protect marine mammals (Hoyt 2011), although there is limited evidence on their effectiveness as management and conservation tools for this group (Gormley *et al.* 2012). Chapters 2, 3 and 6 are rare examples of empirical evidence of a positive trend in population and demographic parameters of a cetacean population using an MPA (see Gormley *et al.* 2012 for another example). Gormley *et al.* (2012) provided the first evidence of an increase in Hector’s dolphin (*Cephalorhynchus hectori*) survival after MPA designation. This thesis shows increasing trends in reproduction and calf survival within an SAC, despite a stable number of dolphins using this area (Chapter 3). However, the population as a whole is likely increasing raising interesting questions about whether dolphins using the SAC are the source of this change. Calving data from outside the SAC could be used with this novel method to investigate. However, both studies highlight the need for long-term data to detect biologically meaningful change (Gormley *et al.* 2012).

## DIRECTIONS FOR FUTURE RESEARCH

Similar to research on species where much of their lives are unobservable, especially cetaceans who spend little time on the surface and visibility underwater is often limited, what is lacking in this thesis are the definitive reasons why. In each chapter I have proposed plausible hypotheses based on research in other populations and species, however, the reasons still remain uncertain. Determining the variability in population dynamics and life history parameters is a good first step, but conservation initiatives and management require information on the drivers of this variability, although clearly this can be difficult.

Therefore, initially it is important to focus on identifying the drivers of the interannual variability in abundance within the SAC (Chapter 3) and the observed trends in demography (Chapter 6). Prey is perhaps the most obvious. The availability of food is one of the most important drivers of animals' ecology. An understanding of prey resources and the predator prey relationship in this area is a key research gap, with uncertainty over diet composition and prey abundance and distribution. Bottlenose dolphins are catholic feeders (Shane *et al.* 1986), but with dietary preferences in different areas (e.g. Bearzi *et al.* 2009, Gannon and Waples 2004). Prey availability, distribution and abundance has been shown to influence many aspects of cetacean ecology including abundance (Bearzi *et al.* 2009), distribution and habitat use (Bailey *et al.* 2013, Hastie *et al.* 2004), movement (Wilson *et al.* 1997), group size (Bearzi *et al.* 2009, Lusseau *et al.* 2004) and fecundity (Ward *et al.* 2009a). Proxies for prey abundance (e.g. seabird breeding success) can be used however results can vary between species (Furness and Camphuysen 1997). Biopsy sampling to identify fatty acids and stable isotopes could provide information on prey preferences in this population and will allow the exploration of diet in different parts of the range (Hooker *et al.* 2001, Krahn *et al.* 2007). Identifying prey types, patches, abundance and temporal and spatial distribution is critical. Techniques such fisheries surveys (both acoustic and sampling) (Korneliussen *et al.* 2008) and using existing available data (e.g. river returns for salmon (Scottish Government 2017)) should be investigated. Recent research using passive acoustic monitoring (PAM) has suggested bottlenose dolphins in this population shift their use of some areas from nocturnal to diurnal at different times of the year, potentially due to diel migration of prey. Again acoustic surveys and sampling has been suggested to investigate this shift. However, the challenges for both are to demonstrate a causal link and to extend these over the longer term to link to the long-term individual based photo-ID study. This work could then be expanded, for example, to investigate individual dolphin's energetic requirements (Noren 2011) or consider the impacts of anthropogenic activity directly on prey (Radford *et al.* 2014). Both would contribute to identifying potential impacts and develop conservation and management initiatives.

Marine renewable developments are a growing industry due to increasing concerns over climate change and the requirement for renewable energy (Miller *et al.* 2013). However, there are potential conflicts between the environmental benefits of these renewable developments and the conservation and management of the marine environment, including marine mammals. Data on the potential and actual impacts of developments are required to inform decision making and ensure developments are not unnecessarily constrained or declined due to poorly understood ecological impacts (Miller *et al.* 2013, Thompson *et al.* 2013). The Appropriate Assessment (AA) for the windfarm currently being built in the Moray Firth concluded "…there are no long-term effects from underwater noise disturbance on the bottlenose dolphin population of the Moray Firth SAC. As such the developments will not adversely affect site integrity of the Moray Firth SAC" (Marine Scotland 2014a). However, there is a requirement, both for the consent condition (Marine Scotland 2014b) and long-term conservation goals, to determine if this holds true or whether there are far field disturbances due to construction, operation and/or decommissioning that will affect this population. For example, determining if the primary impacts, pile-driving noise affecting dolphins' distribution or causing them to leave the SAC, mentioned in the AA occur (Marine Scotland 2014a). A Marine Mammal Monitoring Plan (MMMP) has been developed to carry out photo-ID pre, during and post construction to provide comparisons of vital rates, abundance and proportion of the population using the SAC. These data have also been combined with passive acoustic monitoring studies to compare area use during this period. An additional two windfarms are currently planned in the Moray Firth (Marine Scotland 2017) which may require similar monitoring, providing the opportunity to investigate potential cumulative effects of different developments and extend research objectives using the results from the initial MMMP.

The population of dolphins on the east coast of Scotland is small (Chapter 2) and faces challenges from a range of other anthropogenic activities including proposed ship-to-ship oil transfer, boat traffic and harbour extensions. Focus should be on the key research gaps to assess and manage these potential impacts. This thesis has focused on investigating trends in population abundance, survival and fecundity (Chapter 2, 3 and 6). Chapter 4 recognises that it can take time to recognise biologically significant changes in these population processes, while growth and body condition can indicate health and fitness and therefore provide information on short term responses to environmental and anthropogenic stressors, potentially before they have impacts on population processes. Continuing laser photogrammetry is an easy step as this fits in seamlessly to the existing photo-ID research. This will allow the study of growth in relation to the much lower second year survival (Chapter 6) and ideally comparisons of growth over time and under different ecological, environmental and anthropogenic conditions. To investigate body condition we have recently introduced a pole-cam technique (GoPro camera with gimbal attached to a 10m extending pole) and trialled the use of unmanned aerial systems (UAS) to take aerial photographs. The aim it to combine with our photo-ID data on identity, age and sex to investigate the width of individuals, monitor changes over time and potentially identify pregnant females, providing essential information on individual health. Previously, aerial photographs have been use to investigate energetic costs of reproduction (Christiansen *et al.* 2016), growth and body condition (Durban *et al.* 2015, Durban *et al.* 2016) and behaviour (Nowacek *et al.* 2016). To date these studies have looked at cross-sectional samples within a population (e.g. Christiansen *et al.* 2016, Durban *et al.* 2016). Non-invasive repeat measurements will allow exploration of changes within as well as between individuals, and can potentially allow investigation of the drivers of variability in body condition. Links could then be made between natural variability and anthropogenic disturbance to individual-level impacts and from there to population-level consequences (Nowacek *et al.* 2016). For example, Schick *et al.* (2013) linked variation in body condition to survival in North Atlantic right whales and the effects of anthropogenic stressors. Additional information on health could come from biopsy sampling to investigate pollutant loads in different individuals, age groups and sexes (Herman *et al.* 2005, Krahn *et al.* 2007, Ross *et al.* 2000).

Overall, long-term individual based data are fundamental for understanding how vital rates change in response to disturbance, both environmental and anthropogenic. For example, information on received noise levels from pile-driving could be related to changes in vital rates estimated from photo-ID using frameworks such as PCoD (population consequences of disturbance) (Pirotta *et al.* 2015a, Thompson *et al.* 2013). The PCoD framework aims to link health and body condition and exposure levels to vital rates and from there to population level effects (New *et al.* 2013). This will allow the impacts of coastal developments to be assessed, inform future developments and potentially allow consideration of the cumulative effects of developments throughout the range. However, it is important to include individual heterogeneity as individuals can be exposed to different levels of impacts and can contribute differently to demography and population dynamics (Pirotta *et al.* 2015a). Specifically, research should focus on investigating individual heterogeneity including movement and area use to determine exposure to different disturbances; individual condition and fitness (e.g. body condition and growth using photogrammetry (discussed above)); female heterogeneity (e.g. female reproductive success) and age-specific survival and reproduction.

Detailed information on long-range movements can be difficult to collect with photo-ID data unless surveys are extensive, extremely regular and with collaborators. Tagging small cetaceans has issues, discussed previously. Development in PAM technology could allow signature whistle identification to monitor movements of individual dolphins over longer ranges (Luke Rendell, personal communication). Combining this acoustic localisation with photo-ID may then allow the matching of signature whistles to known individuals.

Understanding females' reproductive success is important as it impacts population dynamics and can be affected by a number of intrinsic (e.g. age, previous reproduction, body mass, offspring sex, inbreeding) and extrinsic (e.g. environmental conditions) factors (Festa-Bianchet *et al.* 2017). Also, individuals can show persistent individual differences (Moyes *et al.* 2011). With nearly three decades of photo-ID data we can explore reproductive success in different ways. For example, how female heterogeneity affects calf survival and growth, the effect of female age (e.g. Ward *et al.* 2009b), reproductive output and lifetime success, senescence (e.g. Ward *et al.* 2009b), successful pregnancies using biopsy sampling (e.g. Krützen *et al.* 2004, Mansour *et al.* 2002) and consequences of length of maternal care (e.g. Balme *et al.* 2017). Male reproductive success (paternity) could also be explored using biopsy sampling, although a large proportion of both adults and calves would need to be sampled (Festa-Bianchet *et al.* 2017). The method in chapter 6 has potential to be developed to further investigate age-specific survival and in theory age-specific reproduction.

The observed range expansion (Wilson *et al.* 2004, Chapter 5) in this population may be continuing, with an increase in reports around Northumberland. To understand the causes and consequences of this range expansion it is important to know whether differences and variability in ranging and movement patterns have benefits or costs to the individual. Evidence suggests there may be more calves and juveniles in the expanded range as the proportion of nicked animals in the south is consistently lower and dolphins tend to gain nicks as they age. It is important to know a population's age structure as it can have important effects on population dynamics (Coulson *et al.* 2001), including survival and reproduction (Festa-Bianchet *et al.* 2017). Laser photogrammetry could provide evidence of a difference in age structure in individuals that have expanded their range outside the SAC, by estimating the age class or size structure of individuals. If true this could suggest differential survival or fecundity in different parts of the range. Using data from the wider population and comparing with results from the SAC (Chapter 6) will indicate whether the reproductive rate or calf survival is different in the south. If not this may suggest that younger animals are dispersing from the SAC. It would then be vital to investigate the drivers. For example, the St Kilda Soay sheep (*Ovis aries*) population is divided into three subunits with differences in survival, recruitment and dispersal, likely due to variation in grazing quality (Coulson *et al.* 1999). Without dispersal the population trajectories of these groups would diverge (Coulson *et al.* 1999). Any evidence of a similar situation in this bottlenose dolphin population has implications for conservation and management.

Comparative studies comparing populations under different ecological conditions can result in important discoveries about ecology and biology (e.g. Wilson *et al.* 1999). Additional research on bottlenose dolphins in Scotland could compare the population dynamics and demographic parameters of west and east coast populations which have different population sizes, distributions and environments (Chapter 2), but are subject to similar anthropogenic pressures. Additionally, using the same statistical method in different populations would help with comparisons and determining the drivers of any differences. For example, using the method in Chapter 6 to investigate fecundity and early survival in different bottlenose dolphin populations worldwide could highlight if our second year survival is low and whether the causal factors are vital to investigate. Finally, comparing and contrasting with other marine mammal species in the same or similar environment but where certain aspects of their ecology may be easier to study could provide insights, especially when subject to the same anthropogenic pressures. For example, the University of Aberdeen's long-term individual based study on harbour seals in the Moray Firth has extensive information on female reproductive success, foraging areas using GPS tag data, and health and fitness is being investigated using blood and blubber samples as well as photogrammetry (Cordes and Thompson 2014, Graham *et al.* 2016). Comparisons of variability in population dynamics and demographics in these two populations should be informative.

Continued monitoring of the SAC is, at present, a legislative requirement (European Union 1992). The existing proposal for this is to utilise photo-ID to estimate abundance and use of the SAC, and status of the population (Thompson *et al.* 2004). In addition photo-ID from the wider population across the range is essential to determine if trends in abundance within the protected area can be attributed to changes in use of an area or reflect the status of the population (Chapter 3). However, this photo-ID research also provides key information on dolphins within this population that underpins additional research. For example, providing data on the individuals seen and number of animals using areas when monitoring responses to piling (Graham *et al.* 2017); information on abundance, females and their calves to predict the effects of coastal developments and boats on individuals and the population (New *et al.* 2013, Pirotta *et al.* 2015a), and data on where and when individual dolphins were observed to determine individual exposure to boat traffic (Pirotta *et al.* 2015b).

## WIDER IMPLICATIONS OF THIS THESIS

This study exploits over two decades of individual based data to answer fundamental questions about the ecology of bottlenose dolphins to inform conservation and management. The first two chapters fulfilled the requirements of existing contracts with the Scottish Government and SNH. However, they also provided the first broad scale picture of the ecology of bottlenose dolphins in Scottish waters and resulted in an ongoing research project on the west coast of Scotland for this protected species. In addition, they provided baseline data for statutory bodies (e.g. Marine Scotland and SNH) to support their regulatory responsibilities and conduct AAs for new developments. The results from Chapter 3 led to a new approach to estimate abundance for statutory reporting on the condition of the Moray Firth SAC and a change to the SAC designation. Recommendations were also made for MPA monitoring of wide ranging species in other areas, specifically extending research outside the protected area to fully understand population status.

The new methods and techniques developed in this thesis are also relevant in other areas and/or for other species, especially long-lived wide-ranging species that cannot be captured. Chapter 3 investigated how changes to survey protocols may have influenced estimates of trends in abundance, a potential issue for any long-term individual based study. Also highlighted was the issue of accurately and precisely estimating the proportion of well-marked animals (theta). This is a poorly discussed issue but important for any mark recapture study where not all individuals are identifiable through time. Investigating variations in theta showed that accurate estimates are critical to any assessment of trends.

Data on survival, fecundity and condition (Chapters 4 and 6) addressed conservation and management questions for this population. However, these results could be applied in models such as PCoD and PVA (discussed previously) to address similar questions in comparable populations where less data are available. For example, King *et al.* (2015) used an estimate of calf survival for harbour porpoises in the north-west Atlantic in a PCoD model for the north sea, where data were unavailable. Chapter 4 also showed, for the first time, that this laser photogrammetry method can be used to accurately and repeatedly measure morphometrics in a longitudinal study of wild animals. This method is suitable for other marine or terrestrial species where captures are impractical, allowing the assessment of temporal variation in individual condition, potentially a more sensitive indicator of population change. Investigating trends in fecundity and early survival is fundamental for conservation and management but difficult to accurately estimate in cryptic species. Chapter 6 utilises a new method that is appropriate for any species where reproductive states are uncertain (e.g. births are missed). This new method can also be used to investigate costs of reproduction, a key component of adult female survival.

In addition, Chapter 5 discusses how sociality can impact ecology and therefore have population level effects. As such the importance of considering the influence of extrinsic factors (e.g. range expansion) on social dynamics was highlighted. This could be relevant in other areas as increasing range shifts are expected in many species as a result of climate change (Lenoir and Svenning 2015).

Finally, the information on abundance and demographics from this population should be invaluable in comparative studies of cetacean populations with differing demographic trends to understand the drivers of these differences and mitigate environmental and anthropogenic effects.

## CONCLUSION

Individual based cetacean studies have come a long way from the early 70's where nicks were cut into the dorsal fins of killer whales to validate the photo-ID technique (Ford *et al.* 2000). Hopefully, the merit of this thesis is that it highlights the contribution of a long-term study, including answering some key ecological questions and identifying how new techniques can be combined with and enhance existing research. In addition, the methods and techniques are relevant to other studies, especially long-lived wide-ranging species that cannot be captured. I trust this work has increased our understanding of bottlenose dolphins in general, around Scotland and provided new insights into the well-studied population on the east coast. This thesis is a rare example of empirical evidence of a positive trend in reproduction and survival in a cetacean population using an MPA (see Gormley *et al.* 2012 for another example). However, further work is required to determine whether this a consequence or coincidental to the establishment of the SAC. Finally, in the future this study should help link individual based ecology (e.g. individual heterogeneity in condition, reproductive success, movement, habitat use and genetics) to population dynamics and effectively predict the effects of environmental and anthropogenic disturbance, further informing conservation and management.

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