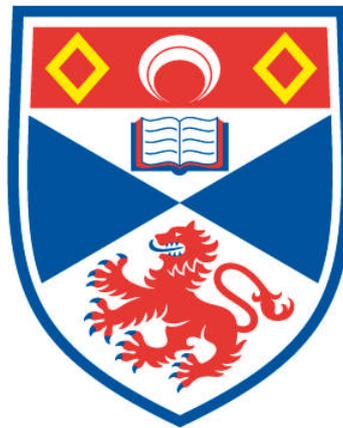


**POPULATION ECOLOGY OF BOTTLENOSE DOLPHINS  
(*TURSIOPS TRUNCATUS*) OFF THE EAST COAST OF  
SCOTLAND**

**Mònica Arso Civil**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews**



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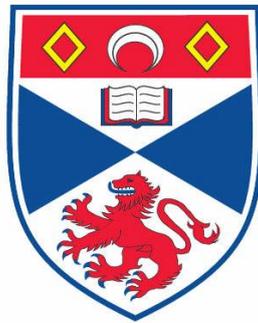
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Population Ecology of Bottlenose Dolphins  
(*Tursiops truncatus*) off the East Coast of Scotland

Mònica Arso Civil



This thesis is submitted in partial fulfilment for the degree of PhD

at the

University of St Andrews

September 2014



Bottlenose dolphins in St Andrews Bay, September 2012 – *photograph by Mònica Arso*

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# Acknowledgements

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First of all I would like to thank my supervisor Professor Phil Hammond for his constant support and guidance during the last four years. Thanks for always being available for a chat or piece of advice on fieldwork, analysis or writing parts of this thesis, and for showing me how important is to take a step back and look at the big picture. Your positivism, practicality and dedication have made the bumpy bits of this PhD road very smooth, and I am very much looking forward to collaborations in the future!

Very special thanks go to Diane and Charlotte, who I first met in the Bahamas in 2006. I could not have imagined back then how that one dinner anchored in Sandy Point waters would start off my way to finishing a PhD. Thanks so much for your friendship, for welcoming me into your lovely home, and for mentoring and encouraging me all these years.

One of the best parts of moving to St Andrews has been spending time with my Scottish/Bahamian family. I cannot thank enough Linds&Gordon and Nic&Jules (and Ellie&Nat&Ollie) for helping me from the very first moment to settle into my new life in Scotland, and welcoming me into your homes so many times I've lost count. Thanks for your friendship and endless good times shared over the years, you've always made me feel at home. To Luke, Claudia, Dylan and Nico, thanks for opening the doors to your house on those many short and long visits, I loved the Sunday morning pancakes!

This project could not have been possible without the collaboration of many people from different organizations that have helped to collect photo-identification data over the last 25 years. I would like to especially thank Valentina Islas and Nicola Quick for providing with detailed data from their PhD projects. Funding for annual surveys over the years in the Moray Firth was provided by 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 (NERC) and the University of Aberdeen. St Andrews Bay surveys have been funded by a Royal Society University Research Fellowship to V.M. Janik, 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.

This work was supported by a Spanish scholarship from “la Caixa” for postgraduate studies in the UK, by the Fundació Universitària Agustí Pedro i Pons (Convocatòria 2010), and by the Department of Energy and Climate Change (UK). The survey work conducted in 2012 and 2013 between Aberdeen and the Firth of Forth was funded by the Department of Energy and Climate Change (DECC) as part of the UK DECC’s offshore energy Strategic Environmental Assessment programme. Surveys were conducted under Scottish Natural Heritage Animal Scientific Licence no.13292 and no.13855.

I’d like to thank a number of data sources: the Proudman Oceanographical Laboratory for providing tidal data (POLPRED and POLTIPS), with thanks to Dr Bernie McConnell and Clint Blight for processing and analysis of the POLPRED data, EDINA ([www.edina.ac.uk](http://www.edina.ac.uk)) for providing depth, slope and aspect data, and the EDINA Geology Digimap / British Geological Survey service for providing sediment data.

The fieldwork in St Andrews Bay would not have been possible without the incredible and priceless help of Julian Dale. Thanks so much for providing with such spoiled fieldwork experience, I cannot thank you enough. And Nic, thanks for all the tips and guidance on collecting data, and thanks for sharing a lot of those days in the water. A big thank you to all the additional people that volunteered their time to help me find dolphins: Caya, Marina, Nadya, Lucía, Sanna, Caro, Mia, Evelyn&Andy, Hanna, Luke, Mafalda, Barbara, Jo, Lindsay, Becci, Ryan&Amy, Stuart, Claire, and Marjo. And a huge thank you to Barbara Cheney, the queen of the dolphin database, thanks so much for solving all my questions so efficiently always, and for all the tips on fieldwork, grading pictures and IDs of the beasts.

It has been great to be part of the SMRU community these last years, who have provided with input and support in many occasions. I want to especially thank Clint Blight for his help on many Manifold and R related issues and for providing bits of code that made my life much much easier, Mike Lonergan for his statistical advice, and Stuart Reid for his technical support. I would also like to thank Mark Bravington for his comments and statistical guidance in the analysis of Chapter 4, and Enrico Pirotta for his valuable help on the use of GEEs. To ‘Phil’s group’, thanks so much for making this experience a much more enjoyable

one: Lindsay, Marina, Sanna, Salomé, Nadya, Claire, Diane, Erin, and Aaron. Not to forget the floorball sessions, the Hot Sox team and the Tuesday's evenings S&B.

Thanks to my family for their unconditional support and love not only during this PhD, but in all my adventures in the past and the ones still to come: pares, David, Ire, Violeta, Abril i tita Marta, moltes, moltes, moltes gràcies... Finally, special thanks to Stuart for putting up with me on this last part of the PhD, supporting and encouraging me every day, and reminding me of what is important in life. Very much looking forward to our future adventures together.

# Abstract

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The population of bottlenose dolphins off the east coast of Scotland has been studied since the late 1980s, initially focused on the inner Moray Firth, where a Special Area of Conservation (SAC) was designated under the EU Habitats Directive. The population has since expanded its distributional range and currently ranges from the Moray Firth to the Firth of Forth. The main aims of this thesis were: (1) to estimate population parameters for this population using a 25 year individual recognition dataset, and (2) to increase knowledge of the distribution and abundance of dolphins in areas outside the SAC, especially to investigate areas of high use in St Andrews Bay. Apparent survival rate for adults and sub-adult dolphins was estimated at 0.946 (SE=0.005) accounting for temporary emigration caused by the population's range expansion. Sex-specific survival was estimated for males (0.951, SE=0.013) and females (0.956, SE=0.011) using multistate models to minimize bias caused by individuals of unknown sex. Using a newly developed approach, fecundity rate was estimated at 0.222 (95% CI=0.218-0.253) from an expected mean inter-birth interval of 4.49 yrs (95% CI=3.94-4.93). Total population size was estimated as ~200 individuals, after accounting for temporary emigration and for heterogeneity in capture probabilities. In St Andrews Bay, an area used regularly in summer by approximately half the estimated population, habitat use modelling identified the entrance to the Firth of Tay and waters around Montrose as high use areas for dolphins, whose presence was influenced by tidal current speed and direction. The results suggest that the conservation and management plan for this small and isolated population of bottlenose dolphins should be reviewed to adapt it to current knowledge, especially regarding the uncertainty around the potential impacts of offshore renewable energy developments off the east coast of Scotland.

# Chapter 1

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## General introduction

### 1.1. Science to inform conservation of marine mammal populations

Current conservation efforts towards marine mammal populations focus on minimizing the impact of human activities that threaten them (*e.g.* incidental mortalities in fisheries, prey depletion, habitat degradation or diseases) (Whitehead *et al.*, 2000, Reeves and Reijnders, 2002). Various aspects of marine mammal life history make them especially vulnerable to such threats. Like other large mammals, marine mammals are long-lived species with high infant mortality and low adult mortality rates, following an age-related mortality pattern typical of mammals (Caughley, 1966). Marine mammals generally exhibit low reproductive rates, typically not maturing for several years and producing few offspring during their lifetimes. This low reproductive potential limits the ability of populations to recover from reduced numbers and increases their vulnerability to extinction (Merrick *et al.*, 2009).

The ability of different populations of marine mammals to recover will be affected not only by differences in their life history parameters, but also by differences in the proximity to and the extent of anthropogenic activities that threaten them (Merrick *et al.*, 2009). Cetacean populations inhabiting coastal, estuarine and riverine waters are exposed to numerous and simultaneous anthropogenic impacts (*e.g.* chemical and noise pollution, degradation or loss of the habitat, depletion of local resources by fisheries, increased boat traffic; Reeves and Reijnders, 2002) because of the proximity and often overlap between their habitats and human activities. Cetacean populations in coastal areas also tend to be small, which makes them inherently at a higher risk of extinction than larger populations (Pimm *et al.*, 1988, Purvis *et al.*, 2000). Because small populations are more affected than larger ones by demographic, spatial, and environmental stochasticity, they are thus more vulnerable to anthropogenic threats (Townsend *et al.*, 2003, Begon *et al.*, 2006). Direct mortality such as by-catch in fishing gear can have a major impact on small isolated populations (Read, 2008). Populations of coastal cetaceans tend to have small and restricted distributional ranges and may have very limited or no connectivity with other populations, making them especially vulnerable from a conservation perspective (*e.g.* D'agrosa *et al.*, 2000, Reeves *et al.*, 2009,

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Gonzalvo *et al.*, 2013). In small fragmented populations, restricted gene flow compromises genetic diversity and ultimately long-term survival, as it is the case of the endemic Hector's and Maui's dolphin populations around New Zealand (Hamner *et al.*, 2012).

Fishing effort at a global scale increased rapidly in the second half of the 20<sup>th</sup> century (FAO, 2014) and represents one of the greatest threats to marine mammals, both due to direct and indirect interactions, especially in populations that overlap substantially with fisheries activities (Read, 2008), *e.g.* in coastal small cetacean populations. By-catch is the incidental catch of non-targeted species, and affects almost all marine mammal species (Whitehead *et al.*, 2000) either by direct interaction with fisheries gear or with marine debris of derelict fishing gear (*e.g.* lines, hooks, nets). Gill-nets and pelagic trawls are used extensively in many parts of the world, and can result in very large numbers of by-caught marine mammals including porpoises, pelagic and coastal dolphins, dugongs, or seals (*e.g.* Vinther and Larsen, 2004, Read *et al.*, 2006, Northridge, 2009, Slooten and Dawson, 2010). In some cases the unsustainable by-catch from local fisheries is the primary source of a population or species decline, the most clear examples being the recently extinct baiji in the Yangtze River (Turvey *et al.*, 2007), and the very likely upcoming extinction in the near future of the vaquita in the Gulf of Mexico (D'agrosa *et al.*, 2000, CIRVA, 2014). In other cases, such as for North Atlantic right whales, by-catch remains as the one of the main causes of mortality despite the conservation efforts (Knowlton *et al.*, 2012). Commercial fisheries also have an indirect effect on marine mammal populations due to the overexploitation of many targeted species (Myers and Worm, 2003) that are also consumed by marine mammals (Pauly *et al.*, 1998, DeMaster *et al.*, 2001, Northridge, 2009). For example, reduced availability of prey caused by overfishing has been identified as one of the factors that may have contributed to the decline of short-beaked common dolphins in the Mediterranean Sea (Bearzi *et al.*, 2003).

Collisions with vessels can severely injure or kill marine mammals and the increase in the occurrence of these events with the increase in marine traffic has become an important conservation concern at a global scale for some species (Kraus *et al.*, 2005, Van Waerebeek *et al.*, 2007, Douglas *et al.*, 2008, Carrillo and Ritter, 2010). The increase in the number of fast boats in coastal areas intensively used by human populations represents added threats to small and already endangered populations of cetaceans (*e.g.* Jefferson, 2000, Stone and Yoshinaga, 2000, Krebs and Rahadi, 2004).

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The rapidly expanding industry of whale-watching and dolphin-based tourism (Hoyt, 2009b) in response to increased demand has not come without impacts to the targeted cetacean populations, mainly in coastal waters. Short-term impacts of such activities have been observed in many species of whales and dolphins, and include behavioural changes reflecting signs of avoidance, *e.g.* with prolonged dives, increased swimming speed, and change in the movement pattern (*e.g.* Nowacek *et al.*, 2001, Williams *et al.*, 2002b, Constantine *et al.*, 2004, Christiansen *et al.*, 2010). Cumulative short-term effects are likely to affect behavioural budgets of individuals, which may have long-term effects on populations. Although demonstrating a long-term population impact is very difficult, this has been suggested for some cetacean populations (Bejder *et al.*, 2006, Lusseau and Bejder, 2007, Stockin *et al.*, 2008).

Marine mammal populations are also exposed to the indirect threat of habitat loss or degradation. This is of particular concern in riverine species, which are dependent on abundant freshwater flow and thus face the threat of water abstraction due to construction of dams (*e.g.* the Ganges River dolphin and the Irrawaddy dolphin; Smith *et al.*, 2009). Habitat degradation also occurs in the forms of chemical and noise pollution. High levels of persistent organochlorines may be present in cetacean species (*e.g.* Minh *et al.*, 1999, Ross *et al.*, 2000, Aguilar *et al.*, 2002). These chemical pollutants have been linked to impaired reproductive performance and immunosuppression in pinnipeds (*e.g.* De Swart *et al.*, 1996, Ylitalo *et al.*, 2005) and belugas (De Guise *et al.*, 1995). However, the effects of these contaminants on cetaceans are generally still poorly understood (Wells *et al.*, 2005, Hall *et al.*, 2006). On the other hand, increasing levels of underwater sound from various sources has raised concerns about the short-term and long-term impacts of noise on cetaceans (Tyack, 2008). Anthropogenic activities such as dredging, piling and seismic explorations can displace individuals (*e.g.* Richardson *et al.*, 1990, Richardson *et al.*, 1999, Carstensen *et al.*, 2006, Bailey *et al.*, 2010, Dähne *et al.*, 2013, Pirotta *et al.*, 2013), although the consequences of those behavioural changes at the population level remain poorly understood (*e.g.* Teilmann and Carstensen, 2012, New *et al.*, 2013).

Climate change is likely to indirectly affect marine mammal populations at large spatial scales, mainly through changes in physical habitat and predator-prey dynamics (Moore, 2009). The long-term trend of global warming will particularly affect species depending

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directly on sea ice or on related ecosystems, but will also potentially affect many other species due to the changes in ocean productivity, food web dynamics or shifts in species distributions (Simmonds and Isaac, 2007, Moore and Huntington, 2008, Hoegh-Guldberg and Bruno, 2010, Forcada *et al.*, 2012).

Scientific research plays an essential role in the conservation and management of marine mammal populations. Detecting a problem (*e.g.* a decline in abundance or an increase in the number of by-caught animals) is the first step towards the conservation of a population; this is generally followed by an assessment of the conservation status of the population as well as investigating the causes of the concern (Read, 2010). In this process, detailed information on population parameters such as survival, fecundity and abundance are needed. In cetaceans, information on fecundity and survival rates is known only for a relatively small number of populations, primarily due to the difficulty in obtaining the long-term longitudinal data needed to estimate these parameters. When available, long-term longitudinal data can be used to investigate changes or trends on population parameters, and inform on the potential causes of changes in the abundance of animals. Reliable data on life history parameters is essential to understand what may be limiting a population's recovery (*e.g.* reproduction, recruitment to the adult population or low adult survival) (Merrick *et al.*, 2009). For example, in the declining bottlenose dolphin population in Doubtful Sound (New Zealand), a decline in first year survival and 1-3 year calf survival has been linked to a reduced recruitment, and ultimately identified as a key factor in the observed decline in abundance (Currey *et al.*, 2009, Currey *et al.*, 2011). In the case of the dramatic decline in the population of Steller sea lions in western Alaska between 1970s and 2000, decreased survival, especially of juveniles, and low fecundity were identified as the key change in vital rates linked to the decline in abundance (Holmes and York, 2003, Pendleton *et al.*, 2006).

As well as helping determine causes of population decline, information on life history parameters can be used to evaluate the extinction risk of populations, ranking them according to a pre-established classification framework, the most widely accepted of which at the global level is the Red List of Threatened Species, maintained by the International Union for Conservation of Nature (IUCN, 2014). A common tool used to predict the future status of a population is to quantify the probability of extinction by using population viability analysis (PVA) (Boyce, 1992, Caswell, 2001). PVAs use stochastic simulation models that estimate

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the viability of small populations under different scenarios, based on life history parameters from the populations. PVAs are used to investigate which populations are at a bigger risk, to understand which life stages are most sensitive to different threats, and to model the effect of implementing conservation measures (*e.g.* Fujiwara and Caswell, 2001, Burkhart and Slooten, 2003, Runge *et al.*, 2004).

The designation of marine protected areas (MPAs) is a widely advocated approach in conservation, intended to protect vulnerable species and ecosystems, preserve biodiversity or re-establish ecosystems (Pauly *et al.*, 2002, Hooker and Gerber, 2004). MPAs have been designated for the protection of marine mammal populations (see table of examples in Hoyt, 2009a and Hooker and Gerber, 2004). An essential piece in the success of MPAs are management plans and their implementation, based on a pre-established list of objectives to achieve for the long-term conservation of the population of interest. The implementation of the management plan is often the most difficult and challenging part to achieve; without this, MPAs risk becoming ‘paper MPAs’ (Reeves *et al.*, 2003, Notarbartolo-Di-Sciara *et al.*, 2008, Hoyt, 2009a).

The definition of MPA boundaries for marine mammals initially focused on the protection of breeding areas; however, it was soon obvious that it was equally important to protect other critical areas for a particular population, which made studies of habitat use a useful tool for the designation of MPAs (Hooker and Gerber, 2004, Evans *et al.*, 2008). MPAs are typically defined by fixed boundaries, which pose a series of challenges for many species. Marine mammals are highly mobile species that may range over very extensive areas between feeding and breeding grounds, may show considerable movements within their distributional range, or change their distribution seasonally (Reeves, 2000). Not surprisingly, the effectiveness of the boundaries of MPAs may be questioned as new information on habitat use and ranging movements appears (*e.g.* Wilson *et al.*, 2004, Slooten and Dawson, 2010).

The work presented in this thesis focuses on one particular population of small cetaceans for which long-term individual longitudinal data are available, aiming to fill in some of the gaps of its biology and ecology, and make this information available for conservation. The focus is the bottlenose dolphin population inhabiting the coastal waters off the east coast of Scotland, for which photo-identification studies started in the late 1980s, resulting in 25 years of

individual longitudinal data that are used in this study to estimate population parameters (see section 1.6. ).

## **1.2. General characteristics of bottlenose dolphins**

### **1.2.1. Distribution and ranging behaviour**

The bottlenose dolphin (*Tursiops spp*) (Montagu, 1821) is one of the most studied and best known species among all cetaceans. It is distributed worldwide in temperate and tropical waters and is found in coastal, estuarine, shelf and offshore areas (Wells and Scott, 2009). The wide variation in size, coloration and morphological characteristics within the species has led to the designation of several nominal species of *Tursiops* in the past. Currently, two species within the genus are defined: the common bottlenose dolphin (*T. truncatus*) and the Indo-Pacific bottlenose dolphin (*T. aduncus*), which differ genetically and morphologically (Wang *et al.*, 1999, Wang *et al.*, 2000).

Bottlenose dolphins (*T.truncatus*) inhabit a wide variety of habitats including estuarine systems, bays, lagoons, and shallow coastal waters, but are also found around oceanic islands, over the continental shelf, and in offshore waters (*e.g.* Scott *et al.*, 1990, Shane, 1990, Ballance, 1992, Simões-Lopes and Fabian, 1999, Klatsky *et al.*, 2007, Baird *et al.*, 2009, Silva *et al.*, 2009b). Within *T. truncatus*, an inshore and an offshore ecotype have been described, which differentiate in their morphology, haematological and cranial morphometry features, genetics, ecology and association patterns (Duffield *et al.*, 1983, Hersh and Duffield, 1990, Rossbach and Herzing, 1999, Segura *et al.*, 2006, Perrin *et al.*, 2011).

Bottlenose dolphins show a wide variety of ranging and movement patterns, which vary between and within populations. Movement patterns in different populations include seasonal migrations, year round site fidelity, long-term residency, and mid to long-distance movements (Wells *et al.*, 1999, Wells and Scott, 2009, Bearzi *et al.*, 2010, Robinson *et al.*, 2012). In populations showing long-term year-round residency, individuals within the population may show different ranging patterns in distance and frequency of movements (Scott *et al.*, 1990), or show a stratified distribution within the home range (Wilson *et al.*, 1997a, Ingram and Rogan, 2002).

### **1.2.2. Diet and foraging behaviour**

Bottlenose dolphins are described as catholic feeders, exploiting a great variety of food resources in the different geographical areas, likely in response to local availability of prey resources. Diet composition varies between and within populations, as well as between age classes and sex, and may vary seasonally (*e.g.* Blanco *et al.*, 2001, Santos *et al.*, 2007). In some areas, diet is composed only or mostly of fish (Kenney *et al.*, 1997, Barros and Wells, 1998, Blanco *et al.*, 2001), and can include benthic species associated with seagrass or very shallow water habitats, as well as demersal species. Soniferous fish are an important component in the diet in many locations, which suggests that bottlenose dolphins use passive listening to locate prey (Barros and Wells, 1998, Gannon and Waples, 2004). A part from fish, other prey species in the diet of bottlenose dolphins include cephalopods (squid and octopus), crustaceans, and small rays and sharks (Mead and Potter, 1990, Blanco *et al.*, 2001).

Bottlenose dolphins are well known for the diversity of feeding behaviours and strategies they display in different populations or among different individuals within a population. They may forage individually or cooperatively, to target individual solitary prey or fish in schools (Connor *et al.*, 2000). Their feeding strategies may target specific prey or particular habitats including: following trawlers to take discarded fish (Leatherwood, 1975, Corkeron *et al.*, 1990, Broadhurst, 1998), cooperating with local fishermen (Pryor and Lindbergh, 1990, Simões-Lopes *et al.*, 1998, Daura -Jorge *et al.*, 2013), feeding around fish farms (López, 2006), benthic-feeding involving digging into the substrate with their rostrum (Rossbach and Herzing, 1997), feeding against strong currents or at certain stages of the tide (Shane, 1990, Fury and Harrison, 2011), herding and catching fish against physiographic features (Shane, 1990), stranding themselves on mudbanks or beaches after herding fish against those (Sargeant *et al.*, 2005, Duffy-Echevarria *et al.*, 2008), and ‘whacking’ fish onto the air with their flukes (Wells *et al.*, 1987, Shane, 1990), among others.

### **1.2.3. Life history**

Bottlenose dolphins are long-lived mammals. As of 2013, the oldest male recorded in Sarasota Bay was 50 years old, and the oldest female was 62 years old (Wells, 2014). Females typically reach sexual and physical maturity at 5 to 13 years of age, while males

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typically reach it later, at 9 to 14 years of age (Wells and Scott, 2009). Female reproductive lifespan is prolonged, with females of the Sarasota Bay resident population still producing calves at the age of 48 years old. Paternity tests from that same area showed that males have sired calves at 13 to 40 years of age (Wells, 2014).

Although births are reported at all times of the year, a seasonal pattern with a distinctive peak during some months of the year is described in many populations (*e.g.* Scott *et al.*, 1990, Grellier, 2000, Mann *et al.*, 2000, Thayer *et al.*, 2003). Gestation in bottlenose dolphins lasts 12 months (Schroeder, 1990), after which females give birth to a single offspring that remains associated with the mother for an extended period of time, typically between 3 and 6 years, but up to 10 years on occasions (Wells *et al.*, 1987, Mann *et al.*, 2000, Grellier *et al.*, 2003). The duration of the lactation period and dependency on the mother can vary considerably among individuals though (Connor *et al.*, 2000). Observed inter-birth intervals vary among individual mothers. In Sarasota, the minimum inter-birth interval is two years, although 3 to 6 year intervals are most common (Wells *et al.*, 1987). Mortality rates in the first year of life are high, *e.g.* 19% in Sarasota and 29% in Shark Bay (Wells and Scott, 1990, Mann *et al.*, 2000), especially for calves from primiparous females (Wells, 2014).

### **1.3. Legal framework**

Bottlenose dolphins are listed as ‘Least Concern’ by the International Union for Conservation of Nature (IUCN) (Hammond *et al.*, 2012) and are protected by a number of national and international legislative agreements and directives. At the global level, bottlenose dolphins are listed under Appendix II of the Convention on International Trade in Endangered Species (CITES). They are also included in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), also known as the Bonn Convention (1983), under which they are also included in the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS).

At the European level, bottlenose dolphins are listed under Appendix II of the Bern convention which prohibits all forms of deliberate capture, keeping or killing, deliberate damage or destruction to important breeding and resting sites and any form of deliberate

disturbance or trade in this species. They are considered species of ‘Community interest’ in need of strict protection being listed under Annex IV of the EU Habitats Directive (formally known as the Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora). The Habitats Directive was translated into Scottish law through the Conservation (Natural Habitats, &c.) Regulations 1994, under which it is an offence to deliberately or recklessly capture, injure, kill or disturb individuals of all cetacean species, considered European Protected Species (EPS). Bottlenose dolphins are also listed under Annex II of the EU Habitats Directive, requiring the designation of Special Areas of Conservation (SACs). SACs are chosen to make a significant contribution to species or habitat conservation and, together with Special Protection Areas (SPAs) for birds, form the Natura 2000 network of European protected sites. SPAs are designated for species of birds classified as rare or vulnerable (as listed in the Annex I of the EU Habitats Directive) or regularly occurring migratory species. The UK has two SACs designated specifically for bottlenose dolphins, one is the Moray Firth SAC in Scotland and the other is the Cardigan Bay SAC in Wales.

Within the UK, bottlenose dolphins are also protected by the Wildlife and Countryside Act (1981), the Countryside and Rights of Way (CRoW) Act (2000), the Marine and Coastal Access Act (2009), and are listed as priority species in the UK Post-2010 Biodiversity Framework. In Scotland, bottlenose dolphins are also protected by the Nature Conservation (Scotland) Act (2004) and the Marine (Scotland) Act (2010).

### **1.4. Bottlenose dolphins off the east coast of Scotland**

The first records of the presence of bottlenose dolphins in Scotland are from stranded animals in the late 1800s. More regular records exist from 1929, kept by the Natural History Museum of London, in which reported strandings are mostly from the Moray Firth and the Hebrides, the majority from the 1990s and 2000s (Thompson *et al.*, 2011). Data collated between 1979 and 1997 for the JNCC cetacean atlas show a large number of sightings in the north-east of Scotland, especially around the Moray Firth (Reid *et al.*, 2003). Data collected by the Sea Watch Foundation between 1966 and 2007 include sightings along the east coast of Scotland, from the Moray Firth to the Firth of Forth (Cheney *et al.*, 2013).

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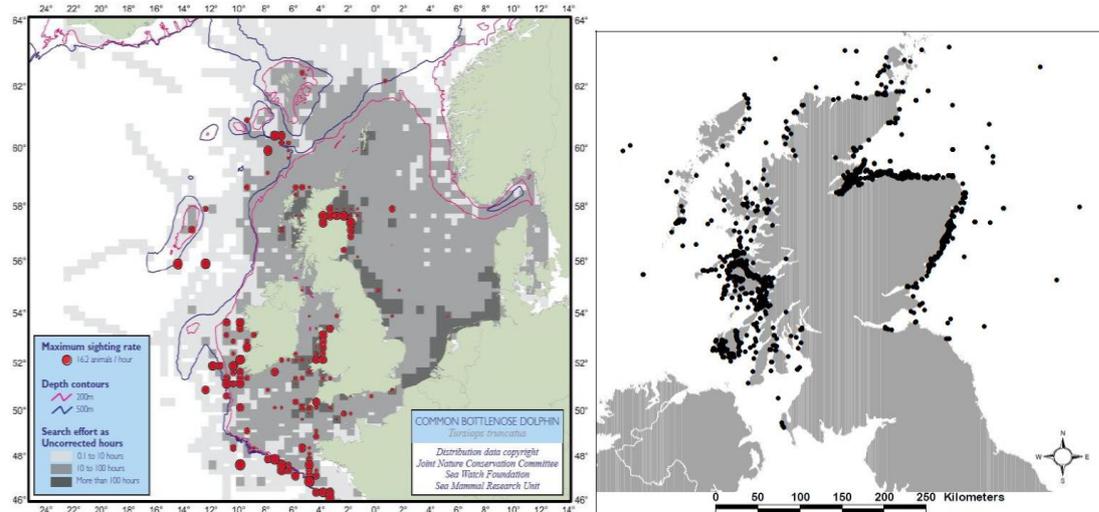


Figure 1.1. Bottlenose dolphin distribution on the NW Europe from the JNCC Cetacean Atlas (extracted from Reid *et al.*, 2003) and sightings of bottlenose dolphins around Scotland from 1966 to 2007 recorded by the Sea Watch Foundation and the Hebridean Whale and Dolphin Trust (extracted from Thompson *et al.*, 2011).

### 1.4.1. Designation of the Moray Firth SAC

To meet the UK's commitments to the EU Habitats Directive and the ASCOBANS, a candidate Special Area of Conservation (cSAC) for the inner Moray Firth was put forward in 1996 to protect the only known 'resident' population of bottlenose dolphins in the North Sea. The information that was used to determine the boundaries of the Moray Firth cSAC was based on sighting data collected during wide-scale seabird surveys in the 1980s in the Moray Firth (Mudge *et al.*, 1984) and from dedicated photo-identification boat surveys conducted between 1989 and 1991 mainly in the inner Moray Firth (*i.e.* where the SAC is located), but also along the southern coasts of the outer Moray Firth and the Aberdeenshire coasts (Curran *et al.*, 1996). The analysis of the data collected during those initial surveys suggested that the inner Moray Firth was the main area of occurrence of this population, although individuals were also occasionally sighted in other surveyed areas (Curran *et al.*, 1996, Wilson *et al.*, 1997a). The proposed area for the cSAC covered the inner Moray Firth and was delimited by a line drawn from Helmsdale on the northern coast to Lossiemouth on the south coast (Figure 1.2). A first minimum estimate of population size of 62 animals was obtained in 1991, based on counts from a coordinated shore-based survey (Hammond and Thompson, 1991). Later on, based on photo-identification data collected during boat surveys in 1990 to 1993 in the

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inner Moray Firth, the population size was estimated at  $129 \pm 15$  SE individuals (Wilson *et al.*, 1999b).

A population viability analysis (PVA) was developed for this population in 1999 to provide information for management options. The model used population parameters from the literature and also the few available from the study population (adult and calf mortality rates and crude birth rate) based on 8 years of data (Sanders-Reed *et al.*, 1999). The model predicted an apparent annual decline of 5.67% (SD=1.01%) and a median number of 45 (95% CI = 33-64) years to quasi-extinction. These results highlighted the need of a precautionary approach in the management of this population (Thompson *et al.*, 2000).

### **1.4.2. Range expansion**

Sightings of bottlenose dolphins outside the inner Moray Firth went from being occasional in the late 1980s and early 1990s to being frequently reported during the 1990s. Sightings along the coast in the southern outer Moray Firth became more frequent from 1991 onwards (Lewis and Evans, 1993) and during the 2000s (Robinson *et al.*, 2007, Culloch and Robinson, 2008). Further south, along the Aberdeenshire coast, sightings of bottlenose dolphins were also reported more frequently from the mid 1990s (Weir and Stockin, 2001, Stockin *et al.*, 2006, Anderwald and Evans, 2010). A similar situation occurred in St Andrews Bay, where sightings started to increase from the mid 1990s (Wilson *et al.*, 2004, Anderwald and Evans, 2010). The known distributional range of this population now extends from the Moray Firth to the Firth of Forth (Figure 1.2). Wilson *et al.* (2004) concluded that this apparent change in the population's distributional range was the consequence of a range expansion rather than a range-shift or influx of new individuals from other populations. The authors also highlighted that the degree of protection offered by the designated SAC may be reduced.

### **1.4.3. Population structure and abundance**

The closest known populations of bottlenose dolphins are located on the west coast of Scotland. In the Outer Hebrides, a small population of dolphins is consistently sighted using the Sound of Barra (Grellier and Wilson, 2003, Cheney *et al.*, 2013), and another larger community occurs throughout the Inner Hebrides and mainland coast (Cheney *et al.*, 2013). Individuals within the study population (*i.e.* off the east coast of Scotland between the inner

Moray Firth and the Firth of Forth) are known to be highly mobile and range throughout the population's range. However, results from comparative photo-ID studies indicate a lack of movement of individuals between the east and the west coasts (Cheney *et al.*, 2013). The results of genetic analysis show low levels of genetic diversity within the population, and indicate that the study population is demographically isolated from others in the west coast and elsewhere around Britain (Parsons *et al.*, 2002, Islas-Villanueva, 2009, Thompson *et al.*, 2011). All these studies suggest that the study population should be considered as a separate unit for management purposes (Cheney *et al.*, 2013).

Estimates of abundance of bottlenose dolphins using the Moray Firth SAC are available since 1990 (Cheney *et al.*, 2012), most recently as part of the monitoring programme designed for the SAC. The most recent available estimate of abundance of animals using the SAC is of 114 individuals (95% CI = 96-135) in 2010 (Cheney *et al.*, 2014). Knowledge of the abundance of animals in other areas of the distributional range is more limited. Abundance estimates for the southern outer Moray Firth range between 61 and 108 individuals based on data collected between 2001 to 2004 (Culloch and Robinson, 2008). Weir *et al.* (2008) provide a minimum number of 62 individuals seen in the Aberdeenshire on an annual basis between 1999 and 2008. For St Andrews Bay, only one unpublished estimate of abundance is available based on data from 2003 and 2004, between 81 and 142 dolphins (Quick, 2006). The most recent and precise estimate of total population size for the currently known distributional range is at 195 individuals (95% CI = 162-253), based on data from 2006 (Cheney *et al.*, 2013).

## **1.5. Study area**

### **1.5.1. General characteristics**

Data used in this thesis were collected in an area covering the coastal waters between the inner Moray Firth (current SAC) and the Firth of Forth, as shown in Figure 1.2. Data from different time periods between 1989 and 2013 covered different areas within the overall study area, and the extension of each dataset in terms of study area coverage is specified as appropriate in each chapter.

## General introduction

The east coast of Scotland is mainly characterised by long straight stretches of coastline with little shelter from the North Sea except for bays and estuaries, of which the major ones are the Moray Firth, the Firth of Tay and the Firth of Forth (Baxter *et al.*, 2008). Sediments around Scotland are generally sandy or gravelly, with muddy sediments occurring mainly near shore (*e.g.* in estuaries) (Baxter *et al.*, 2008). The non-tidal circulation of waters in the North Sea is mainly anti-clockwise, but it is strongly affected by the winds and density-driven coastal currents. Tidal range is generally between 4 and 5 meters, and generates tidal currents that are strong and intensified in local areas with particular topographic characteristics (Baxter *et al.*, 2011).

Apart from the Moray Firth SAC, the area between the Moray Firth and the Firth of Forth also includes an SAC for harbour seals in the Firth of Tay and Eden Estuary and another one for grey seals around the Isle of May. Several Special Protection Areas (SPAs) with a marine component exist along the coast, including those in the Firth of Tay and Eden Estuary (Figure 1.2).

### **1.5.2. Marine renewable energy developments**

The development of marine offshore renewable energy generation is an industry in expansion in Scotland, which has raised environmental concerns including potential impacts on marine mammal populations (Madsen *et al.*, 2006, Bailey *et al.*, 2010, Thompson *et al.*, 2013).

Scotland's aim to meet the EU 2020 target of 20% of energy consumption to be from renewable sources is planned to be achieved partially through developments in offshore wind, wave and tidal energy. In the east of Scotland, there are currently plans for two offshore wind farms in the Scottish Territorial waters off the Firths of Forth and Tay (Inch Cape and Nearth na Gaoithe), as well as an offshore site off the Firth of Forth as part the third round of site allocations for offshore wind developments launched by the Crown Estate (UK) in 2008 (Round 3) (Figure 1.2). The Inch Cape offshore wind farm site is located in the outer Firth of Tay region 15-22 km to the east of the Angus coastline, covers an area of 150km<sup>2</sup>, and it is anticipated that it will consist of up to 213 turbines (SeaEnergy Renewables Limited, 2010). The Nearth na Gaoithe offshore wind farm site is located approximately 15.5 km east of Fife Ness, covering an area of 105 km<sup>2</sup> and will include an estimated number of wind turbines between 73 and 90 (Mainstream Renewable Power, 2014). The Round 3 offshore wind farm

## General introduction

zone is located approximately 25 km east of Fife and covers an area of 2,852 km<sup>2</sup> in the outer Firth of Forth (SeaGreen Wind Energy, 2011b).

Further north, in Aberdeen Bay, there are plans for an offshore deployment centre with 11 turbines currently planned (EOWDC), 2.4 km from the shore line and covering 7 km<sup>2</sup> (Vattenfall and Aberdeen Renewable Energy Group, 2012). In offshore waters about 20-30 km from Peterhead, the Buchan Deep site will comprise five floating turbines (Statoil Wind Ltd, 2013). In the outer Moray Firth there are three proposed wind farms as part of the Moray Firth Offshore Renewables Ltd project (MORL, 2012) and adjacent to these there is a construction project for the Beatrice Offshore wind farm (Figure 1.2).

## General introduction

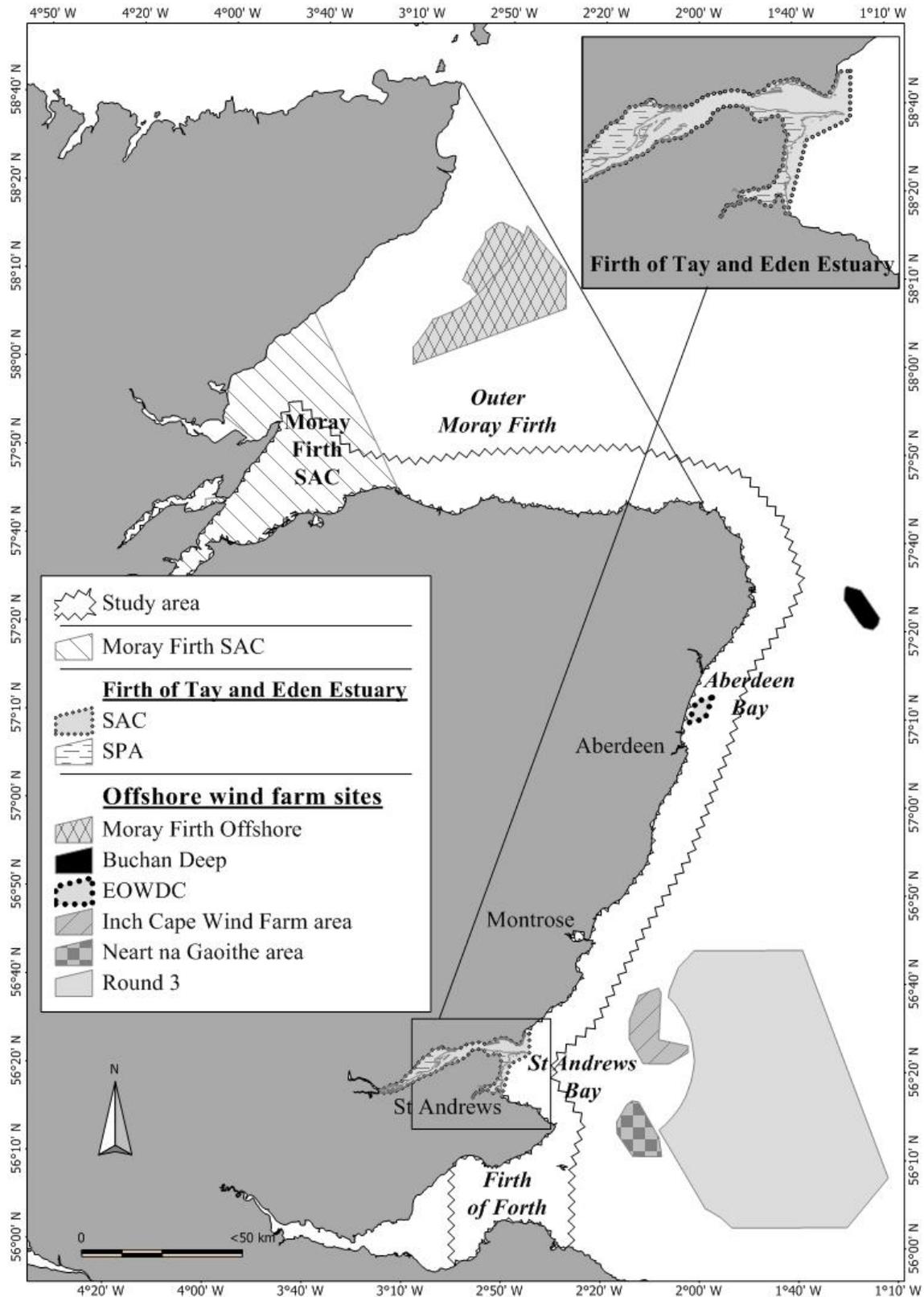


Figure 1.2. Map of the east coast of Scotland with locations for the Moray Firth SAC for bottlenose dolphins, SAC for harbour seals and SPA for birds in the Firth of Tay and Eden Estuary, and offshore wind farm development sites. The overall study area is represented by the zig-zag area.

## 1.6. Thesis overview

Data used in this thesis include 25 years of individual recognition data collected as part of a collaborative project on the ecology of bottlenose dolphins off the east coast of Scotland, coordinated by the University of Aberdeen and the University of St Andrews. This long-term individual photo-identification dataset is used to estimate key population parameters for the study population. Most of the studies on this population have focused on the Moray Firth SAC, but much less is known about other areas of the distributional range. This thesis also aims to fill in that gap by providing information on the distribution, habitat use and abundance of animals in areas outside the SAC.

In the first data chapter (Chapter 2), I fit capture-recapture models to the photo-identification data for the period 1989 to 2013 to estimate apparent survival probability for adult and sub-adult bottlenose dolphins. To minimize the potential bias in the apparent survival estimates caused by changes in the population's range during the study period, I use an analytical approach that could account for so-called temporary emigration (Kendall *et al.*, 1997) (*i.e.* individuals are available for sampling on some occasions but not on others). In Chapter 2, I also estimate sex-specific survival probabilities using the available information about the sex of the individuals. I choose an analytical approach to minimize the bias caused by individuals of unknown sex.

In Chapter 3, I use the same approach used in Chapter 2 to obtain annual estimates of total population size from 1990 to 2013. I investigate the bias in abundance caused by two sources of unequal probability of capture by fitting models that can account for individual heterogeneity and for temporary emigration. Additionally, I estimate the abundance of animals using St Andrews Bay for the period 2009-2013 and using Aberdeenshire for the years 2012-2013. I compare these results with the estimates of total population, and discuss the conservation and management implications for the Moray Firth SAC.

In Chapter 4, I develop a new analytical approach to estimate fecundity rate from inter-birth intervals. I use the individual reproductive histories from females in the study population collected between 1989 and 2012 to develop and test the approach. Additionally, I use simulated datasets to validate the approach and investigate the most common data-driven biases related to the estimation of inter-birth intervals in cetaceans.

## General introduction

In Chapter 5, I use the data I collected during dedicated surveys in 2012-2013 first to describe the distribution and occurrence of bottlenose dolphins between Aberdeen and the Firth of Forth. Then I use a modelling approach to investigate the dolphins' use of St Andrews Bay and the entrance to the Firth of Tay in relation to a range of environmental variables, and to predict areas of high use.

The final discussion in Chapter 6 brings together the results from Chapters 2 to 5 into a wider ecological and conservation context. Discussion of the population's current conservation and management is informed by the new findings on the abundance of dolphins and high use areas outside the designated SAC, within a framework of the marine renewable energy development plans in Scotland. The results on the estimated population parameters are summarized and incorporated into future research plans for the study population.

## Chapter 2

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### Survival estimation using robust design and multistate models

#### 2.1. Introduction

Identifying whether populations are increasing or declining and understanding what are the drivers behind fluctuations in their numbers are important questions in population ecology (Begon *et al.*, 2006). Information on survival, abundance and recruitment rate are of interest in both theoretical and applied ecology, as they help to understand population dynamics in an ecological and conservation context (*e.g.* Gaillard *et al.*, 1993, Galimberti *et al.*, 2001, Beissinger and McCullough, 2002, Williams *et al.*, 2002a).

Patterns in the variation of survival rates are important indicators in population dynamics from a management and conservation point of view (*e.g.* Kraus *et al.*, 2005, Altwegg *et al.*, 2008). Reliable estimates of survival probabilities are required in stock and population assessments (*e.g.* Doak *et al.*, 1994, Anders *et al.*, 1997, Best *et al.*, 2001), and are one of the key parameters to determine the long-term viability of populations (White *et al.*, 2002). In mammals, survival estimates tend to follow an age-related pattern typically characterized by an initial high juvenile mortality, followed by a period of relatively low mortality, and ending with a rapidly increasing mortality in the oldest age-classes (Caughley, 1966), and males tend to have higher mortality rates than females (*e.g.* Trivers, 1972). These variations in age- and sex-specific survival rates modulate the population dynamics in different ways, with adult survival generally having a greater effect on population trends than juvenile survival (Fowler, 1987).

Differentiated mortality rates between sexes in mammals has been mainly attributed to sexual selection costs (*e.g.* Trivers, 1972, Promislow, 1992). The same pattern has been observed in marine mammal species including southern elephant seals (Pistorius *et al.*, 1999), harbour seals (Hastings *et al.*, 2012), killer whales (Olesiuk *et al.*, 1990), and sperm whales (Ralls *et al.*, 1980). Sex-specific mortality in marine mammals has been attributed to the costs of male selection in polygynous mating systems (*e.g.* Ralls *et al.*,

1980), to social structure and sex differences in ranging patterns (*e.g.* Stolen and Barlow, 2003), and to sex differences in the accumulation of toxic burdens with age (*e.g.* Weisbrod *et al.*, 2001, Schwacke *et al.*, 2002) that could affect the development of diseases (Van-Bressem *et al.*, 2009).

Long-term individual-based studies are an effective tool to estimate population parameters including the probability of survival, especially in discrete populations in which individuals can be repeatedly captured over time (Clutton-Brock and Sheldon, 2010). Such studies are of particular interest in long-lived species, for which the ability to detect changes in demographic parameters requires years or decades of data. Capture-recapture techniques, based on individual-based studies, have been extensively used in ecology, especially to estimate survival probabilities and abundance of animals (Hammond, 2010). Based on this method, individuals are captured, marked and released, and then recaptured in subsequent sampling occasions. The resulting individual capture histories are used to estimate the population parameters of interest. Capture-recapture methods have been widely applied to estimate survival and other population parameters in birds (*e.g.* Weimerskirch *et al.*, 1997, Seamans *et al.*, 2002), reptiles (*e.g.* Kazmaier *et al.*, 2001, Casale *et al.*, 2007), terrestrial mammals (*e.g.* Gaillard *et al.*, 1998, Karanth *et al.*, 2006, Ozgul *et al.*, 2006), and marine mammals (*e.g.* Langtimm *et al.*, 2004, Bradford *et al.*, 2006, Cordes and Thompson, 2013).

Capture-recapture models rely on a number of assumptions about the captured individuals and about the probability of capture (summarized in Hammond, 1986, Hammond, 2010). These are:

1. Marks are unique, cannot be lost and are correctly recorded;
2. Marking does not affect the catchability of the animal (behaviour or survival);
3. Marked and unmarked animals mix completely between sampling occasions;
4. All animals have the same probability of being captured at any sampling occasion, whether marked or not.

Assumptions 2, 3, and 4 relate to the basic capture-recapture models, violations of which can be accommodated in more complex models.

Capture-recapture models are either closed or open population models. Closed population models (Otis *et al.*, 1978) assume a constant population with no additions or permanent deletions for the duration of the study period, and are used to estimate abundance of animals (Schwarz and Seber, 1999). Estimating survival probabilities requires open population models that do not assume a static population. The Cormack-Jolly-Seber (CJS) open population model was first developed to estimate survival probabilities using capture-recapture data (Cormack, 1964, Jolly, 1965, Seber, 1965). Since then, generalizations and special cases have been developed from the original model (summarized in Lebreton *et al.*, 1992) and have been used in different species of birds, reptiles, terrestrial and marine mammals (*e.g.* Gaillard *et al.*, 1993, Jorgenson *et al.*, 1997, Weimerskirch *et al.*, 1997, Zeh *et al.*, 2002, Pistorius *et al.*, 2004, Casale *et al.*, 2007). Estimated survival probabilities from the CJS model refer to ‘apparent’ survival because they are the probability of an animal being alive (‘true’ survival probability) conditional on being available for capture in the sample area. Animals that emigrate from the study area and are not available for recapture appear to have died because the model cannot distinguish permanent loss (*i.e.* death) from permanent emigration (Pledger *et al.*, 2003).

Conventional open population models implicitly assume that any emigration from the study population is permanent (Kendall *et al.*, 1997), but this assumption is difficult to meet in many capture-recapture studies. For example, individuals may transit through an area while migrating, in which case they are captured once but may then never be available for capture after first release (Pradel *et al.*, 1997), negatively biasing estimates of survival probability. Also, individuals may range over wide areas, beyond the limits of the sampled area, in which case individuals are available for sampling on some occasions but not on others (Kendall *et al.*, 1997). This so-called temporary emigration can be random in which all animals have the same probability of being outside the study area at any sampling occasion, regardless of whether or not they were inside or outside on the previous occasion. When temporary emigration is random, open-population models produce unbiased estimates of survival (Kendall *et al.*, 1997). However, when the probability of temporary emigration depends on whether or not the animal was available in the study area during the previous sampling occasion (*i.e.* the pattern is

Markovian), conventional open-population models can produce negatively biased estimates of survival (Kendall *et al.*, 1997).

Methods have been developed to account for transience and temporary emigration in capture-recapture models and produce unbiased survival estimates. The robust design (RD) (Pollock, 1982, Kendall *et al.*, 1995, Kendall *et al.*, 1997) combines both open and closed population models with estimators that incorporate temporary emigration. This approach divides the data into primary sampling occasions (periods), each of which is divided into a series of secondary sampling occasions (Figure 2.1).

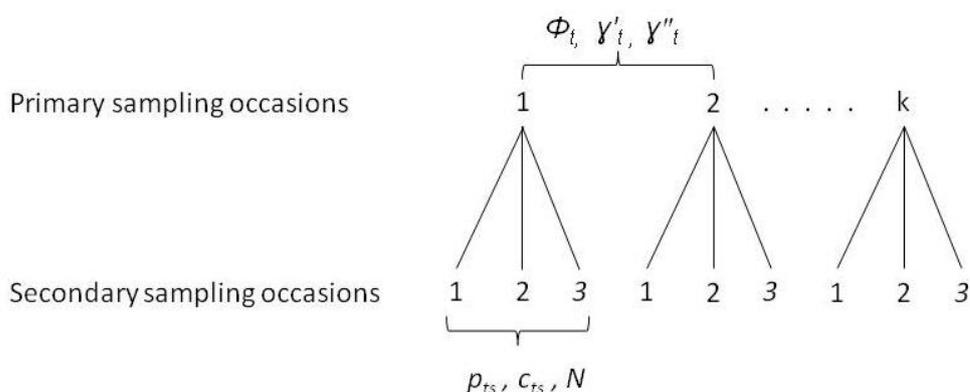


Figure 2.1. Structure of the robust design model. Each primary sampling occasion is divided into multiple secondary sampling occasions. Survival ( $\Phi_t$ ) and temporary emigration rates ( $\gamma'_t$  and  $\gamma''_t$ ) are estimated between primary sampling occasions ( $t$ ); capture ( $p_{ts}$ ) and recapture ( $c_{ts}$ ) probabilities, and abundance ( $N$ ) are estimated using data from secondary sampling occasions ( $s$ ).

The time between primary occasions should be long enough to allow for changes in the population; these data are used by open population models to estimate apparent survival and temporary emigration probabilities. The time between secondary sampling occasions should be long enough to allow for mixing of animals but short enough so that within a primary period the population is effectively closed; closed population models use these data to derive estimates of capture probability and population size. RD models tend to produce estimates that are generally more precise and less biased by temporary emigration (Kendall *et al.*, 1997).

In cetacean populations, capture-recapture studies are normally based on the ability to recognize individuals from natural markings (Hammond *et al.*, 1990), although some

studies have also used genetic sampling techniques to generate capture-recapture data (*e.g.* Palsbøll *et al.*, 1997, Miller *et al.*, 2005). Natural markings used to recognize individuals in cetaceans typically include nicks and notches in the dorsal fin (*e.g.* bottlenose dolphins; Read *et al.*, 2003), markings and pigmentation in the fluke tail (*e.g.* humpback whales; Katona and Whitehead, 1981), callosity patterns on the rostrum (*e.g.* right whales; Payne *et al.*, 1981), pigmentation in the flanks (*e.g.* blue whales; Sears *et al.*, 1990), and pigmentation of the saddle patch (*e.g.* killer whales; Olesiuk *et al.*, 1990). Different individuals within a population will have different markings (*e.g.* one or many nicks in the trailing edge of the dorsal fin), but each individual should contain enough information in the markings to ensure that each marked animal is unique (Hammond, 2010). Based on this method, marked individuals are ‘captured’ when they are first photographed and ‘recaptured’ when photographs are taken on subsequent sampling occasions. Robust design models have been increasingly applied to capture-recapture data from cetacean populations to estimate survival probabilities and rates of temporary emigration (*e.g.* Bradford *et al.*, 2006, Silva *et al.*, 2009a, Speakman *et al.*, 2010, Nicholson *et al.*, 2012, Smith *et al.*, 2013).

Methods to determine the sex of individuals in cetacean species include visual observation of the genital area, biopsy sampling or repeated observations of a potential female with a young calf. These methods typically require sighting individuals repeatedly to correctly ascertain the sex; generally sex can only be determined for a subset of animals. This means that the individuals that survive and are re-sighted for a greater number of years have a greater opportunity to be sexed. Un-sexed individuals will typically be sighted fewer times. Therefore, the probability of survival of sexed individuals tends to be positively biased simply because they are sighted more regularly than un-sexed animals (Nichols *et al.*, 2004). For example, Ramp *et al.* (2006) identified potential biases in the combined survival estimate for male and female blue whales because sexed whales were sighted more regularly and for longer periods than un-sexed whales. The same potential biases were recognized for the sex-specific survival estimates of humpback whales in the Gulf of St Lawrence (Ramp *et al.*, 2010).

Several approaches have been developed to minimize bias in sex-specific survival estimates from capture-recapture data in which sex is unknown for many individuals

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(Nichols *et al.*, 2004, Pradel *et al.*, 2008). The “*ad hoc* approach” (*e.g.* Nichols *et al.*, 2004, Cordes and Thompson, 2013) uses sightings of individuals only after sex has been determined and produces unbiased results but with the cost that the precision of estimates is reduced because data are discarded. Another approach is to use multistate models (MS) (*e.g.* Hestbeck *et al.*, 1991, Brownie *et al.*, 1993), with an unknown state, which can account for uncertainty in sex assignment and produce unbiased results. However, survival estimates for un-sexed individuals may exhibit some bias as this group tends to include younger animals on average from both sexes exhibiting heterogeneous survival (Nichols *et al.*, 2004).

The bottlenose dolphin is one of many species of small cetaceans that can be individually recognized based on natural markings (Würsig and Jefferson, 1990). These markings include temporary marks such as tooth rakes and other scratches, and permanent marks such as nicks and notches on the trailing edge of the dorsal fin, particular fin shapes or deformities, or white fringes, which can all be tracked throughout the dolphin’s life time (Wilson *et al.*, 1999b). Capture-recapture methods have been commonly applied to estimate survival probabilities in bottlenose dolphin populations (*e.g.* Read *et al.*, 2003, Currey *et al.*, 2009, Speakman *et al.*, 2010). Available estimates of survival probability in bottlenose dolphins are generally high, as expected in a long-lived species (Table 2.1).

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Table 2.1. Summary of survival estimates and sex-specific survival estimates for bottlenose dolphins (*T. truncatus*, *T. aduncus*, and *T. sps*) based on capture-recapture methods.

Species	Population	Survival	Female survival	Male survival	Source
<i>T. truncatus</i>	East Scotland	0.942±0.015	-	-	Sanders-Reed <i>et al.</i> (1999)
<i>T. truncatus</i>	East Scotland	0.93±0.029	-	-	Corkrey <i>et al.</i> (2008)
<i>T. truncatus</i>	Sado Estuary	0.95±0.015 to 0.99±0.008	-	-	Gaspar (2003)
<i>T. truncatus</i>	NE Adriatic Sea	0.914±0.032	0.842±0.081 to 0.989±0.002	0.902±0.019 <sup>1</sup>	Fortuna (2006)
<i>T. truncatus</i>	Doubtful Sound	0.937; 95% CI=0.917-0.953	95%CI=0.919-0.974	95% CI=0.911-0.966	Currey <i>et al.</i> (2009)
<i>T. truncatus</i>	Azores	0.97±0.029	-	-	Silva <i>et al.</i> (2009a)
<i>T. truncatus</i>	Sarasota	0.96±0.008	-	-	Wells and Scott (1990)
<i>T. truncatus</i>	Southern Brazil	0.917; 95% CI=0.876-0.961	-	-	Daura -Jorge <i>et al.</i> (2013)
<i>T. truncatus</i>	Charleston, SC	0.951±0.035	-	-	Speakman <i>et al.</i> (2010)
<i>T. species</i>	Shark Bay	0.95±0.02	-	-	Nicholson <i>et al.</i> (2012)
<i>T. aduncus</i>	Bunbury	0.95±0.02	-	-	Smith <i>et al.</i> (2013)
<i>T. aduncus</i>	Bangladesh	0.958±0.035 <sup>2</sup> ; 0.976±0.022 <sup>3</sup>	-	-	Mansur <i>et al.</i> (2012)

<sup>1</sup> Male and unknown sex survival

<sup>2</sup> Adult and juvenile survival

<sup>3</sup> Adult survival

The population of bottlenose dolphins off the east coast of Scotland has been studied since 1989 as part of a collaborative project between the Lighthouse Field Station at the University of Aberdeen and the Sea Mammal Research Unit at the University of St Andrews. To date, 25 years of photo-identification data have been collected on the individual dolphins of this population. Motivated by the designation of the Moray Firth as a candidate Special Area of Conservation (cSAC) under the Annex II of the EU Habitats Directive (92/43/EEC), earlier population modelling based on data collected during the 1990s predicted a population decline (Sanders-Reed *et al.*, 1999). A few years later, another study maintained the likelihood of a decline but with weak evidence (Corkrey *et al.*, 2008). Studies following the submission to the European Commission of the Moray Firth as a candidate SAC showed that many of the individuals using the SAC ranged well beyond its limits. Dolphins originally sighted in the inner Moray Firth were increasingly seen in the outer Moray Firth, the Aberdeenshire coast and St Andrews Bay (Wilson *et al.*, 2004, Stockin *et al.*, 2006, Culloch and Robinson, 2008), leading to the conclusion of a population range expansion. Currently, the known distributional range for this population extends from the Moray Firth south to the Firth of Forth (Cheney *et al.*, 2013). This population's range expansion may have resulted in temporary emigration from the Moray Firth, which might have been confounded with the predicted decline of this population (Corkrey *et al.*, 2008).

The analysis for this chapter uses photo-identification data collected over a period of 25 years in an area that extends from the Moray Firth to the Firth of Forth. The extensive dataset encompasses changes in the population's range and in sampling effort through the study period. To investigate whether changes in the population's range affected previous survival estimates, robust design models accounting for temporary emigration were applied to photo-identification data regardless of the individual's sex or age to estimate apparent survival and temporary emigration probabilities. Multistate (MS) models were then applied to the same dataset with added information about the sex of the individuals in order to estimate sex-specific apparent survival probabilities.

## **2.2. Methods**

### **2.2.1. Study area and survey effort**

Between 1989 and 2013, the University of Aberdeen and the University of St Andrews conducted annual boat-based surveys off the NE coast of Scotland as part of a collaborative project to collect photo-identification data on bottlenose dolphins. Survey methodologies from this collaborative project are described in detail in Wilson (1995) and Wilson et al., (1997a, 2004). Survey methodologies for the data collected in 2003-04 and 2006-07 in St Andrews Bay as part of two separate PhD projects from the University of St Andrews are described in Quick (2006) and Islas-Villanueva (2009), respectively. The survey methodologies implemented in St Andrews Bay in 2012 and 2013 for this study are detailed in Chapter 5.

Sampling effort (*i.e.* the number of boat-based surveys) varied over the years as well as among the different areas within the known distributional range of the population. Because of this, the overall distributional range was divided into different areas for summarising effort and encounters with bottlenose dolphins. These areas were the Moray Firth SAC, the Outer Moray Firth, the Grampian coast, St Andrews Bay and the Tay, and the Firth of Forth (Figure 2.2).

Most surveys occurred during the summer months from May to September; in some but not all years, surveys were also conducted during the winter months, especially in the first half of the study period. To maintain consistency in survey effort over the time series, the sampling interval from May through September was selected for this analysis. A summary of the annual survey effort and number of encounters with bottlenose dolphins during the summer months from 1989 to 2013 is shown in Figure 2.3.

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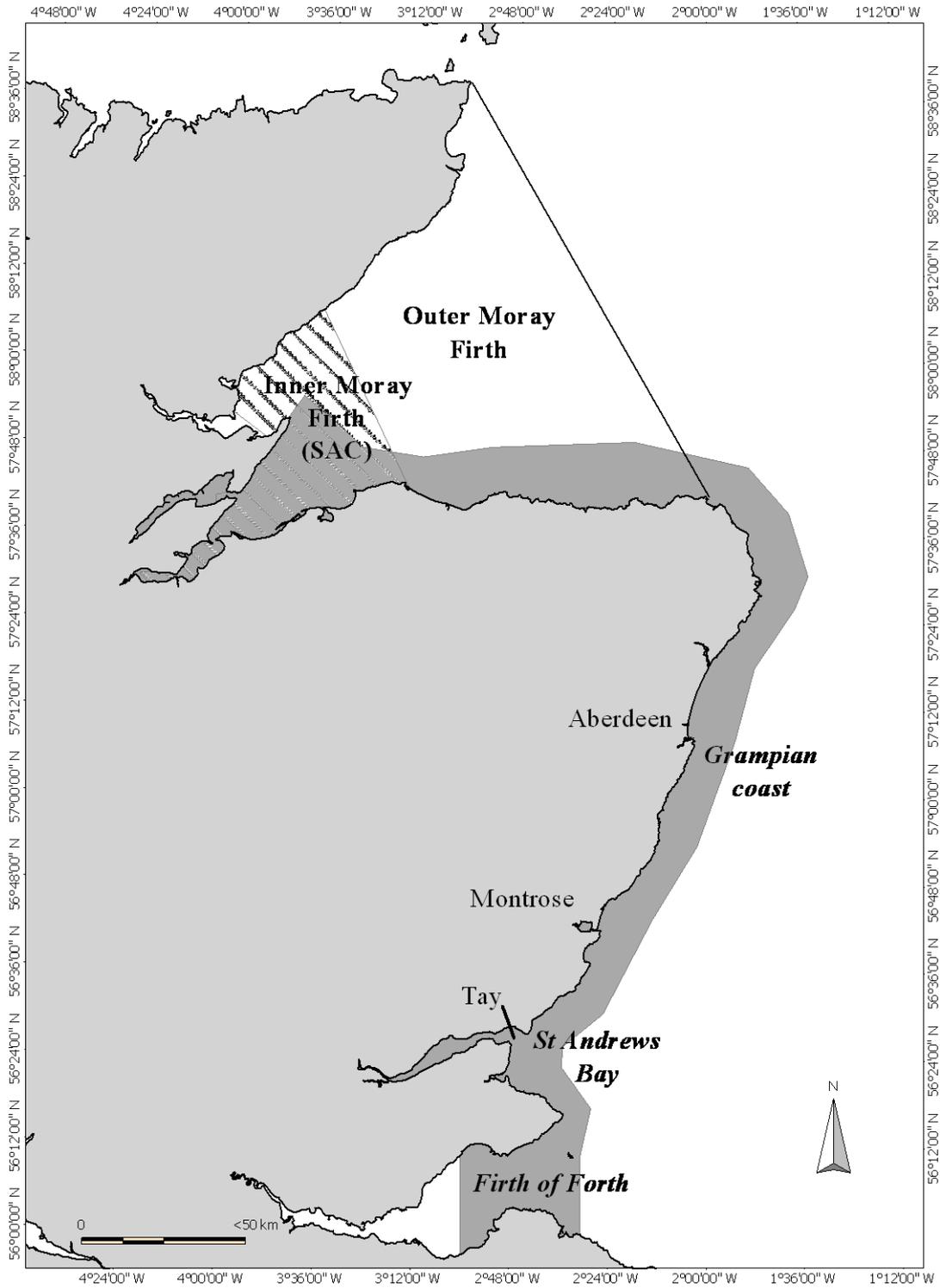


Figure 2.2. Map of NE Scotland showing the study area (shading), which includes the inner Moray Firth, the Outer Moray Firth, the Grampian coast, St Andrews Bay and the Tay, and the Firth of Forth.

## Chapter 2: Survival rates

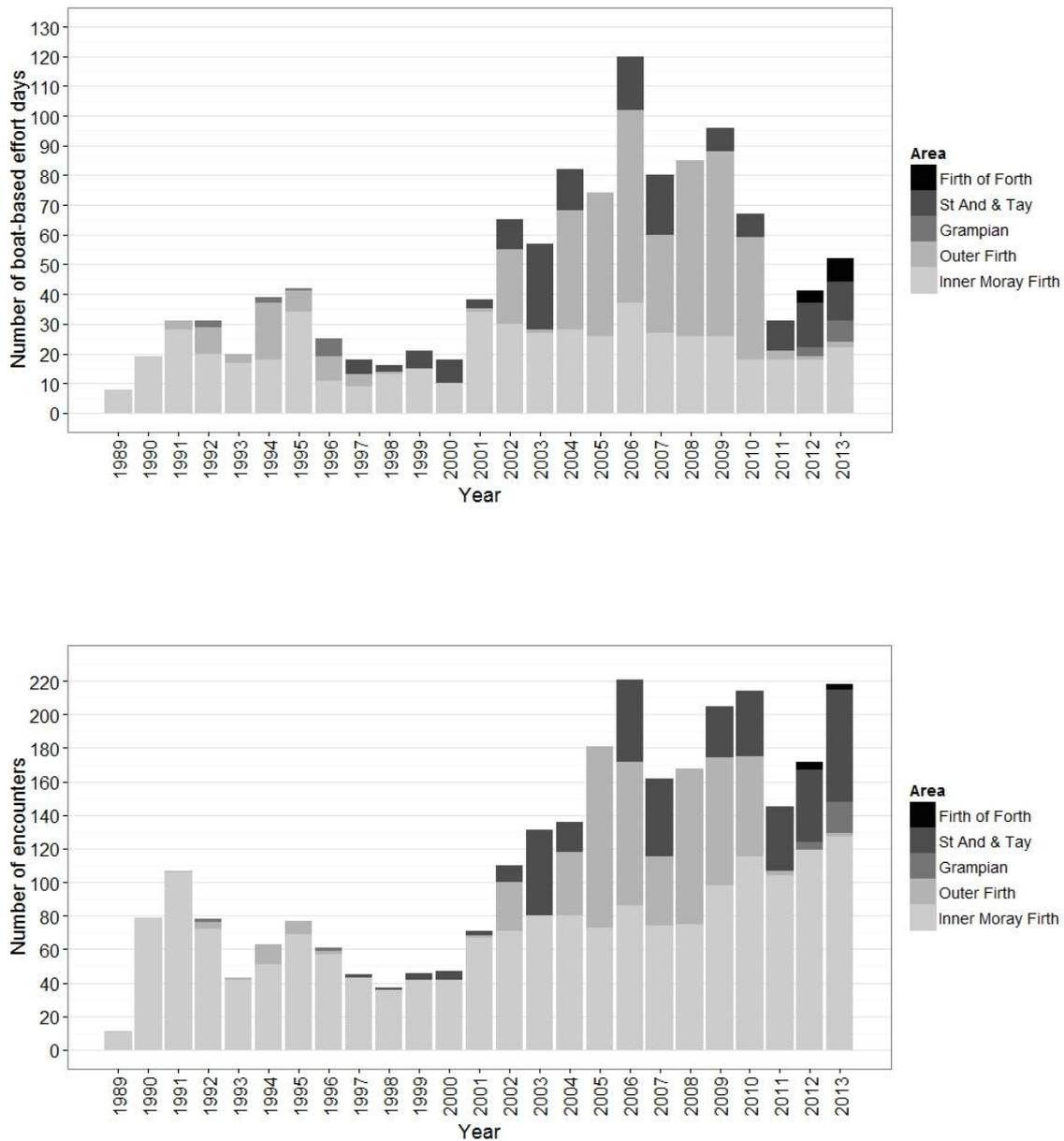


Figure 2.3. Number of boat-based effort days (top) and number of bottlenose dolphin encounters (bottom) from 1989 to 2013. Numbers refer to data collected in the summer months (May-September) in each area of interest, and combines all sources of data used for this analysis. Areas include the Inner Moray Firth, the Outer Moray Firth, the Grampian coast, St Andrews Bay and the Tay, and the Firth of Forth.

As reflected in Figure 2.3, surveys were conducted consistently every year in the inner Moray Firth between 1989 and 2013. Sampling effort started to expand outside the Inner Moray Firth in 1992 with a few trips to the Outer Moray Firth and Grampian coast, and then gradually extended south, to include St Andrews Bay, the Tay, and the

Firth of Forth. In St Andrews Bay and the Tay, effort started in 1997, but increased markedly during the two PhD projects in 2003-04 (Quick, 2006) and 2006-07 (Islas-Villanueva, 2009). After a gap year in 2008 in which no trips were conducted during the summer months, photo-identification effort resumed in 2009 and continued annually until 2013. Survey effort was focused solely in St Andrews Bay and the Tay from 2009 to 2011 but extended from Aberdeen to the Firth of Forth, including St Andrews Bay and the Tay, in 2012 and 2013, as part of this study.

### **2.2.2. Photo-identification data collection and processing**

Although a variety of boat platforms and multiple field technicians and skippers have been involved in running the surveys over the years, photo-identification data have been collected following similar and standardised protocols over time. In general, boat-based surveys were carried out in small boats when weather conditions were favourable (sea conditions of Beaufort 0 to 3). If weather conditions changed during a trip, data collection was aborted until weather improved or the trip was abandoned. For the duration of the trip, the boat's position was logged at regular time intervals using a GPS unit. When a group of dolphins was sighted, it was approached slowly and the boat was positioned parallel to the group's track in order to collect the photo-identification data. Time and location were logged at the start and end of the encounter with the group. The time spent with each group varied, but was kept to the minimum needed to obtain all the necessary data. Information on the trip and on each encounter was logged into "Daily Trip Record" and "Encounter" forms (see Appendices 1a and 1b).

Photographs were taken with film cameras from 1989 to 2000 and with digital cameras from 2001 to 2013. During the encounters with bottlenose dolphin groups, the aim was to photograph as many individuals in the group as possible, regardless of the number of natural marks on their dorsal fin, and from both sides if lighting and time allowed. The photo-identification data collected from 2003-04 and 2006-07 in St Andrews Bay were for two PhD projects in which the collection of photo-identification data was not the primary objective but was part of other data collection. Quick (2006) collected photo-identification data during individual focal follows, meaning that the boat's track was determined by the focal animal. Instead of attempting to photograph every animal in a

group from both sides, only photographs of the focal follow animal and its close associates were taken. Photographs were also collected during opportunistic encounters between focal follows. Islas-Villanueva (2009) did follow the protocols established within the collaborative project and attempted to photograph all individuals in a group and from both sides. After all photographs were taken biopsy sampling from targeted individuals occurred. Despite differences in how photo-identification data were collected, all the photographs taken during both these projects were processed following the same protocol used in the long-term collaborative project, as described below.

Until 2000, all photographs taken within the collaborative project were attempted to be matched to an existing catalogue of bottlenose dolphins in the study area, regardless of their photographic quality. Since 2001, only photographs that had previously been graded as high quality pictures were used for the identification of individual dolphins, because low-quality photographs were excluded from most analyses. All photographs of the dorsal fins taken during boat-based trips were graded for photographic quality according to criteria adapted from Wilson et al. (1999b) (see Appendix 1c). Based on this, photographs in which the dorsal fin was large enough, in focus, parallel to the camera and not covered by water or splashes were graded as high quality photographs (*i.e.* grades 3.1, 3.2, 3.3 – see Appendix 1c). Each high quality photograph was then matched to the catalogue of individually recognizable bottlenose dolphins maintained since 1989 by the University of Aberdeen Lighthouse Field Station. Both the photographic quality grading and the matching of the individual dolphins were confirmed by at least three different experienced researchers at the end of each field season.

### **2.2.3. Estimating survival and temporary emigration using the robust design**

Robust design (RD) models (Pollock, 1982, Kendall *et al.*, 1995, Kendall *et al.*, 1997) were used to estimate apparent survival and temporary emigration probabilities based on the 25 years of capture-recapture data (1989-2013). Only marked individuals (*i.e.* those with individually recognisable long-lasting nicks on the trailing edge of the dorsal fin) from high quality photographs were included in the analysis to avoid misidentification of individuals.

## Chapter 2: Survival rates

Each annual field season (May to September) was treated as a primary sampling occasion within which the population was assumed to be closed. Each primary sampling occasion was subsequently divided into multiple secondary sampling occasions by grouping together all sightings of bottlenose dolphins within each month. Table 2.2 shows a summary of the annual survey effort dates and number of months sampled. Capture histories consisting of 1s and 0s were constructed for all marked individuals, to define whether or not an individual was captured (*i.e.* photographed with quality grade 3.1, 3.2 or 3.3, see Appendix 1c) within a sampling period (*i.e.* each month).

Table 2.2. Summary of annual survey effort from 1989 to 2013 between May and September, including information on the number of marked and newly marked dolphins captured annually, and the number of secondary occasions (*i.e.* months) in each year (continues in the next page).

<b>Year</b>	<b>Sampling period</b>	<b>Secondary occasions</b>	<b>Marked individuals</b>	<b>Newly marked</b>
1989	02 Jul - 02 Sep	3	42	42
1990	03 May - 14 Aug	4	47	13
1991	17 May - 12 Sep	5	37	6
1992	14 May - 24 Sep	5	51	6
1993	02 May - 23 Sep	5	36	5
1994	02 Jun - 24 Sep	4	36	2
1995	12 May - 20 Sep	5	47	6
1996	07 May - 05 Sep	5	39	5
1997	24 May - 24 Sep	5	26	2
1998	18 May - 22 Sep	5	28	2
1999	01 May - 22 Sep	5	34	6
2000	01 May - 19 Sep	5	34	5
2001	01 May - 17 Sep	5	72	20

Year	Sampling period	Secondary occasions	Marked individuals	Newly marked
2002	01 May - 09 Sep	5	65	8
2003	01 May - 28 Sep	5	74	10
2004	02 May - 11 Sep	5	87	7
2005	03 May - 17 Sep	5	54	1
2006	04 May - 25 Sep	5	84	8
2007	02 May - 28 Sep	5	82	5
2008	06 May - 26 Sep	5	41	1
2009	02 May - 30 Sep	5	89	13
2010	05 May - 21 Sep	5	92	6
2011	03 May - 29 Sep	5	89	3
2012	02 May – 27 Sep	5	103	10
2013	02 May – 27 Sep	5	103	8

The model assumptions under the RD are a combination of the assumptions for closed and open population models, and can be summarised as: (1) all animals are uniquely marked and marks are not lost or missed; (2) capture probabilities are equal for all individuals (marked and unmarked) at any sampling occasion (except if heterogeneity in capture probabilities is accounted for in the secondary occasions); (3) the population is demographically closed within any primary sampling occasion and any changes occur between primary sampling occasions; (4) all animals have the same probability of survival from one sampling occasion to another, regardless of their availability for capture.

The following parameters were estimated under the RD models:

$\phi_t$  = the probability that a dolphin survives from primary period  $t$  to primary period  $t+1$ ;

$p_{ts}$  = the probability of any individual dolphin being captured in secondary sample  $s$  of primary period  $t$ , given that it is alive and available during period  $t$ ;

$\bar{\gamma}_t, \gamma_t$  = the probability that a dolphin is unavailable for capture during primary period  $t$ , given that the animal was available or unavailable, respectively, for capture during primary period  $t-1$  and survives to period  $t$ . Under the no emigration model,  $\bar{\gamma}_t$

$= \hat{\gamma}_t = 0$ ; under the random emigration model,  $\hat{\gamma}_t = \hat{\gamma}_t$ ; and under the Markovian emigration model,  $\hat{\gamma}_t \neq \hat{\gamma}_t$ .

To provide identifiability of the gamma parameters ( $\hat{\gamma}_t, \hat{\gamma}_t$ ) for the Markovian emigration model when the parameters are time specific, the last two  $\hat{\gamma}_t$  and  $\hat{\gamma}_t$  need to be constrained to be equal to  $\hat{\gamma}_{t-1}$  and  $\hat{\gamma}_{t-1}$  respectively because otherwise they are confounded with  $\phi_{t-1}$  (Kendall *et al.*, 1997).

Closed population models allowing for capture probability to vary by time, behavioural response or individual heterogeneity are available to use within the RD framework to estimate capture probability ( $p_{ts}$ ) during secondary sampling occasions. Behavioural response models were not fitted to the data because photo-identification is not expected to cause any trap-dependency in the captured individuals. Thus, recapture probability ( $c$ ) was set to equal capture probability ( $p$ ) for all models. Individual heterogeneity was modelled using the Pledger (2000) mixture models, in which the population is assumed to comprise a mixture of individuals with different probability of capture. A mixture parameter  $\pi$  was included in models with no emigration and with temporary emigration to define two mixtures in the probabilities of capture.

A model with no emigration ( $\hat{\gamma}_t = \hat{\gamma}_t = 0$ ) was initially fitted to investigate time-dependence effects in the probability of capture between primary periods  $t$  and within primary periods  $txs$ , and of heterogeneity in capture probabilities ( $\pi$ ; Pledger 2000). Then, the presence of temporary emigration was investigated using models with random and Markovian emigration (Kendall *et al.*, 1997), and allowing survival probability to be constant ( $\cdot$ ) or to vary between primary periods ( $t$ ). A RD model accounting for both sources of unequal capture probability (*i.e.* temporary emigration and heterogeneity of capture probabilities) was also fitted.

#### **2.2.4. Determining the sex of individuals**

The sex of animals was determined based on a combination of the following methods: (1) photographs of the genital area, (2) molecular analysis of biopsy samples taken in 2006 and 2007 (see Islas-Villanueva, 2009 for details on biopsy sampling and molecular analysis), (3) repeated observations of an adult dolphin in the company of a newborn or

young calf, and (4) from a quantitative analysis of mother-calf association patterns developed by Grellier *et al.* (2003) for this population.

### 2.2.5. Estimating sex-specific survival using the multistate model

Multistate (MS) models (Hestbeck *et al.*, 1991, Brownie *et al.*, 1993) were used to estimate the sex-specific probability of apparent survival. For this analysis, each year in the dataset was treated as a sampling occasion, pooling together all sightings of individuals made during the same year. Individuals were classified as male (M), female (F), and unknown sex (U) if sex had not been determined. An individual was recorded as unknown (U) every year in which it was sighted until the sex was determined (M or F), and then remained in that state for all following re-sightings. As in the RD models, the non-sighting of an individual in a year was recorded with a “0”.

The following parameters were estimated under the MS models:

$\phi_{ij}$  = the probability that a dolphin survives from year  $t$  to the following year  $t+1$  in state  $j$  (*i.e.* the sex of the animal M, F, or U);

$p_{ij}$  = the probability that any individual dolphin is resighted in year  $t$  in state  $j$ ;

$\psi_{ijk}$  = the probability that an individual moves from state  $j$  to state  $k$  between year  $t$  and year  $t+1$ . Individuals were only allowed to transition from U to M ( $\psi^{UM}$ ) and from U to F ( $\psi^{UF}$ ), fixing all other transitions to zero. Additionally, transitions  $\psi^{UM}$  and  $\psi^{UF}$  were also fixed to zero when no males or females were sexed in a year. The multinomial logit link function was used for transition probabilities.

An initial set of candidate models was created to investigate the effects on survival, recapture and transition probabilities of no variation ( $\cdot$ ), time-dependence ( $t$ ), and state ( $sex = U, M, F$ ). Based on the results from the RD models (see below), capture probability was allowed to vary between years in all models. Models with constant transition probabilities over time were not considered because the number of animals sexed varied markedly across years; in some years no individuals were sexed whereas in the years when biopsy samples were taken large numbers of individuals could be sexed. To test sex-specific differences in survival and recapture probabilities, models with

$M=F \neq U$ ,  $M=U \neq F$ ,  $F=U \neq M$  in the probability of survival and in the probability of recapture were also included.

Additionally, for comparison, a CJS model with an “*ad hoc* approach” (Nichols *et al.*, 2004) was used to estimate sex-specific survival. For this model, only sexed males and females were included in the analysis and capture histories started after the time at which sex was unambiguously ascertained (*i.e.* all sightings from individuals occurring before their sex was determined (‘U’) were rewritten as non-sightings ‘0’).

### **2.2.6. GOF test, model selection and model parameter averaging**

There is no goodness-of-fit (GOF) test available in MARK (White and Burnham, 1999) for RD models and thus a variance inflation factor could not be estimated to adjust the models for over-dispersion. For MS models there is a GOF test available, which can be implemented in program U-CARE (Choquet *et al.*, 2009), and the variance inflation factor ( $\hat{c}$ ) can be calculated. If the variance inflation factor indicates over-dispersion of the data (*i.e.*  $\hat{c} > 1$ ), the  $\hat{c}$  value can be used to compute QAIC (quasi-AIC) to inflate the estimated sampling variances and thus adjust the standard errors of the estimated parameters. However, the GOF test reported a good fit with a variance inflation factor of 1.107 (Chi-square=101.86, df=92), and thus no adjustment to the AICc and standard errors was necessary.

Consequently, model selection was based on the Akaike Information Criterion (AIC) (Akaike, 1973) adjusted for small samples (AIC<sub>c</sub>) (Burnham and Anderson, 2002), and the model with the lowest AIC<sub>c</sub> was selected as the best fitting model. Model averaging was used to average parameter estimates and respective SEs based on the AICc weights to account for model uncertainty (Burnham and Anderson, 2002), as appropriate.

Model structures and parameters were specified for all RD and MS models using the package RMark (Laake, 2013) in R (R Core Team, 2014). RMark works as a “front page” to program MARK (White and Burnham, 1999) that runs all the specified models.

### 2.2.7. Validity of model assumptions

The assumption of equal probability of capture among individuals is generally the most difficult to meet in mark-recapture studies with cetacean populations; failure to account for heterogeneity in capture probabilities can produce severe bias in population estimates (Pollock *et al.*, 1990, Hammond, 2010), although the effect on survival probability may be small (Carothers, 1973). Differences in capture probabilities can be caused by responses to capture (*i.e.* the boat), differences in age, sex, or behaviour, social structure, individual ranging preferences, and temporary emigration. Photo-identification does not involve physical interaction with the animals and thus behavioural responses from the marking were not expected in this study as in other studies of this kind (*e.g.* Wilson *et al.*, 1999b, Read *et al.*, 2003, Nicholson *et al.*, 2012). All individuals encountered in a group were attempted to be photographed, regardless of their behaviour and level of marking to minimise sources of heterogeneity due to individual differences. The only exception to this may be the photo-identification data collected in St Andrews Bay in 2003-04 by Quick (2006), because the individuals photographed were determined by the animals involved in the focal follow.

Because the sampling effort varied in the number survey days and in the extent of the area sampled, not all individuals might have been available for sampling during each sampling occasion (Figure 2.3). The expansion on the population's distributional range (Wilson *et al.*, 2004) meant that some individuals were spending more time outside the surveyed area, increasing the proportion of animals not being available for sampling, especially in the years in which sampling was only occurring in the Moray Firth. This lack of overlap between sampling effort and individuals' ranging preferences could have introduced heterogeneity in capture probabilities, and is discussed in detail in section 2.4. and in Chapter 3. The increase in sampling effort to other areas including St Andrews Bay and the Tay in the later years is expected to have reduced issues with unequal capture probabilities among individuals. To investigate the assumption of equal probability of capture, models accounting for heterogeneity in capture probabilities and temporary emigration were used.

Another assumption of mark-recapture analysis is that marks should be permanent and recognizable across time (Hammond, 1986). Nicks and notches on the trailing edge of the dorsal fin of bottlenose dolphins are permanent (Wilson *et al.*, 1999b), but natural marks may change with time as new marks are added to existing ones. The uninterrupted photo-identification effort over the years should minimize the probability of losing track of individuals as new marks are added. Also, using high quality pictures from well marked individuals minimizes the probability of mis-identifying an individual (Stevick *et al.*, 2001).

The population was assumed to be closed over secondary sampling occasions within each primary sampling period. However, each primary sampling period lasted between 3 and 5 months, depending on the year, so there was likely a violation of the assumption of population closure; this point is expanded in the Discussion. The RD also assumes that survival probability is not affected by the availability of capture of the individuals, *i.e.* the temporary emigration and immigration in the population. Although this assumption cannot be verified, there are no indications that animals are exposed to different sources of mortality within and outside the study area, and thus the effect of temporary emigration on survival probability is assumed to be negligible.

### **2.3. Results**

#### **2.3.1. Robust design models**

Photo-identification data selection resulted in the capture histories of 200 marked individuals that could be used for this analysis, based on high quality pictures taken during 254 field trips. The first data collected in St Andrews Bay were from 1998, because earlier photographs did not meet the quality criteria to be included in the analysis. The number of marked individuals identified per year varied, ranging between 26 and 103 individuals (Figure 2.4). The capture frequencies varied among individuals, with 1 individual sighted every single year, and 37 (18%) sighted in only one year (Figure 2.5).

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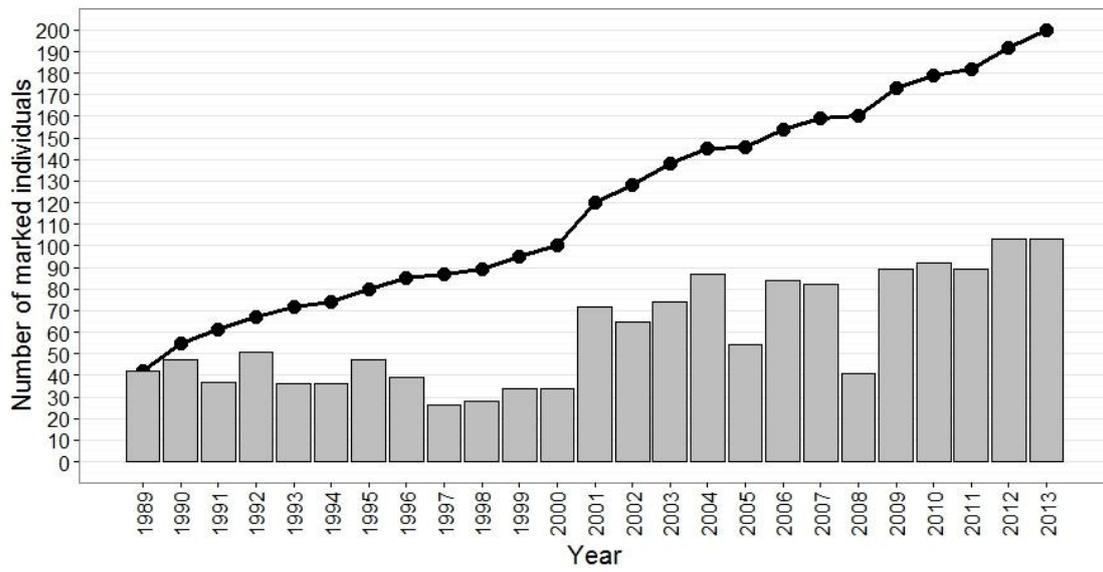


Figure 2.4. Number of marked individuals identified by year and cumulative number of marked individuals.

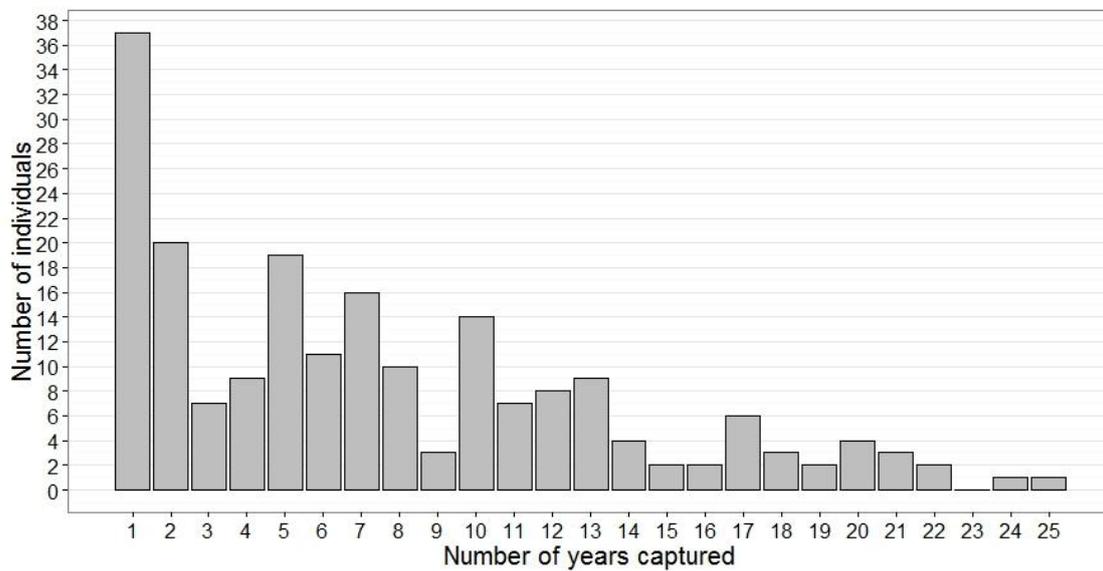


Figure 2.5. Distribution of capture frequencies of marked individuals

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The best fitting model from the initial modelling of no-movement models had a constant probability of survival, heterogeneity in capture probabilities and a different capture probability for each sampling occasion (Model 1, Table 2.3). This model received more support than models that either did not account for heterogeneity in capture probabilities or in which capture probabilities only varied annually but not within year. Based on this model, the probability of apparent survival was estimated at 0.946 (SE =0.005, 95% CI = 0.934 – 0.955).

Table 2.3. Model selection diagnostics for the RD models with no temporary emigration. For all models  $p(x) = c(x) = \text{no behaviour effect}$ . Effects of heterogeneity ( $\pi$ ), and time were tested on modelling the probability of capture ( $p$ ); (.)=constant; (t) = varies between years; (txs) = varies between and within years.

Model #	Model	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weights	Model likelihood	No. par	Residual deviance
1	$\phi$ (.) $g''=g'=0$ $p(\text{txs})$ $\pi(t)$	911.7285	0	1	1	293	7792.131
2	$\phi$ (.) $g''=g'=0$ $p(\text{txs})$	1265.305	353.5763	0	0	147	8477.022
3	$\phi$ (t) $g''=g'=0$ $p(\text{txs})$	1287.344	375.615	0	0	170	8448.731
4	$\phi$ (.) $g''=g'=0$ $p(t)$ $\pi(t)$	1937.873	1026.144	0	0	93	9265.173
5	$\phi$ (t) $g''=g'=0$ $p(t)$ $\pi(t)$	1978.974	1067.245	0	0	101	9289.374
6	$\phi$ (.) $g''=g'=0$ $p(t)$ $\pi(.)$	2065.913	1154.185	0	0	77	9426.782
7	$\phi$ (t) $g''=g'=0$ $p(t)$ $\pi(.)$	2088.74	1177.011	0	0	100	9401.257
8	$\phi$ (.) $g''=g'=0$ $p(t)$	2330.704	1418.975	0	0	51	9745.480
9	$\phi$ (t) $g''=g'=0$ $p(t)$	2349.638	1437.91	0	0	74	9716.768
10	$\phi$ (.) $g''=g'=0$ $p(.)$	3265.888	2354.159	0	0	27	10729.730
11	$\phi$ (t) $g''=g'=0$ $p(.)$	3277.26	2365.532	0	0	50	10694.090

On the second modelling round, constant and time-specific random and Markovian emigration models were fitted to the data, with constant or time-specific survival, and allowing capture probability to vary with each sampling occasion. The values of the final and penultimate  $\gamma''$  and  $\gamma'$  in time-specific models were constrained to be equal in models to allow the identifiability of the parameters (Kendall et al. 1997). The best supported model in the second round had constant survival, time-specific random

emigration and a different capture probability for each capture occasion (Model 1, Table 2.4). Based on this model, the probability of apparent survival was 0.946 (SE=0.005, 95% CI 0.934 to 0.955). The probability of emigrating temporarily from the study area and remaining an emigrant ranged between 0.000 (SE=0.004) and 0.516 (SE=0.055) (Figure 2.6). Capture probabilities varied greatly between and within years; from the best fitting model, annual mean capture probability varied from 0.162 to 0.683 (Figure 2.7). From the same candidate set, the model with constant survival and no movement (Model 10, Table 2.4) estimated a probability of apparent survival of 0.945 (SE = 0.005, 95% CI = 0.933-0.954).

Models accounting for both individual heterogeneity and temporary emigration were also fitted (not shown) although they had issues with over parameterization (discussed later). The best of these models had constant survival, Markovian temporary emigration, two mixtures and a different capture probability for each capture occasion. The estimated apparent survival probability based on this model was 0.946 (SE = 0.005, 95% CI = 0.935-0.956).

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Table 2.4. Model selection diagnostics for RD models to estimate survival ( $\phi$ ), capture ( $p$ ), and emigration ( $\gamma$ ) probabilities. For all models  $p(x) = c(x) =$  no behaviour effect. Models are ordered by Akaike Information Criterion (AICc).  $\Delta$ AICc: difference in the AICc of any given model from that of the minimum AICc model; (.)=constant; (txs)=time-specific;  $\gamma_{\cdot} = \gamma_{\cdot} = 0 =$  no emigration model;  $\gamma_{(x)} = \gamma_{(x)} =$  Markovian emigration model;  $\gamma_{(x)} = \gamma_{(x)} =$  Random emigration model.

Model #	Model	Emigration	AICc	Delta AICc	AICc weights	Model likelihood	No. par	Residual deviance
1	$\phi (\cdot) g''(t)=g'(t) p(\text{txs})$	Random	928.4159	0	0.95666	1	170	8089.8032
2	$\phi (t) g''(t) g'(t) p(\text{txs})$	Markovian	934.6048	6.1889	0.04334	0.0453	215	7995.5511
3	$\phi (t) g''(t)=g'(t) p(\text{txs})$	Random	955.9829	27.567	0	0	193	8066.3638
4	$\phi (t) g''(t) g'(\cdot) p(\text{txs})$	Markovian	975.5968	47.1809	0	0	194	8083.7444
5	$\phi (\cdot) g''(t) g'(t) p(\text{txs})$	Markovian	1006.0128	77.5969	0	0	192	8118.6255
6	$\phi (t) g''(\cdot)=g'(\cdot) p(\text{txs})$	Random	1018.8342	90.4183	0	0	171	8178.0179
7	$\phi (t) g''(\cdot) g'(t) p(\text{txs})$	Markovian	1050.2041	121.7882	0	0	193	8160.5849
8	$\phi (\cdot) g''(\cdot) g'(\cdot) p(\text{txs})$	Markovian	1075.6604	147.2445	0	0	149	8283.0277
9	$\phi (\cdot) g''(\cdot)=g'(\cdot) p(\text{txs})$	Random	1081.7202	153.3043	0	0	148	8291.2631
10	$\phi (t) g''(\cdot) g'(\cdot) p(\text{txs})$	Markovian	1090.5186	162.1027	0	0	172	8247.4976
11	$\phi (\cdot) g''(\cdot) g'(t) p(\text{txs})$	Markovian	1143.4633	215.0474	0	0	170	8304.8506
12	$\phi (\cdot) g''(t) g'(\cdot) p(\text{txs})$	Markovian	1236.6741	308.2582	0	0	171	8395.858
13	$\phi (\cdot) g''=g'=0 p(\text{txs})$	No emig	1265.3048	336.8889	0	0	147	8477.0220
14	$\phi (t) g''=g'=0 p(\text{txs})$	No emig	1287.3435	358.9276	0	0	170	8448.7309

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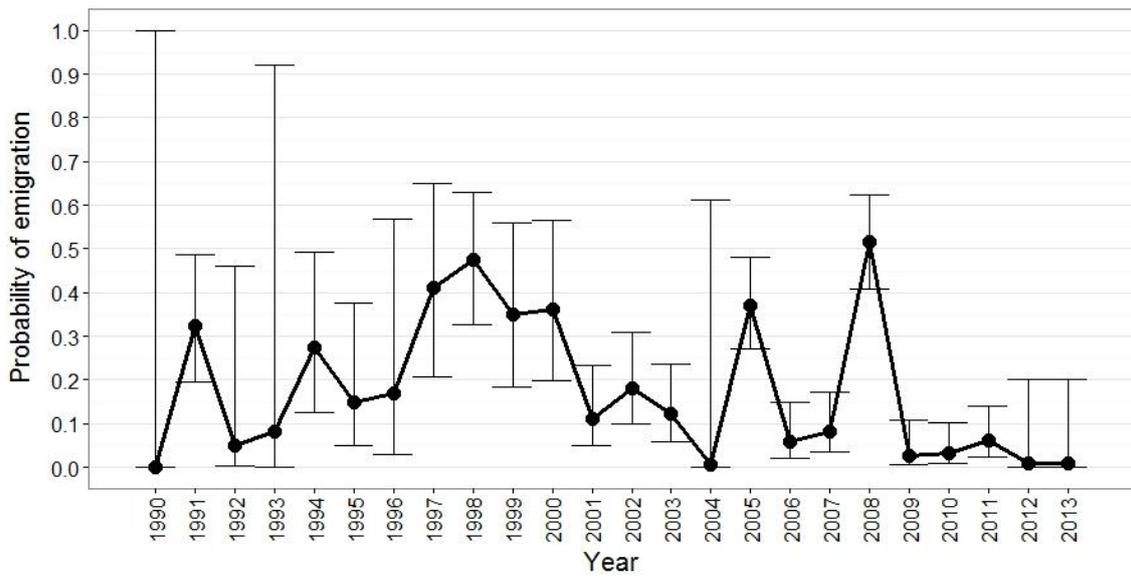


Figure 2.6. Estimates of probability of emigration from the most supported model (with 95% CI).

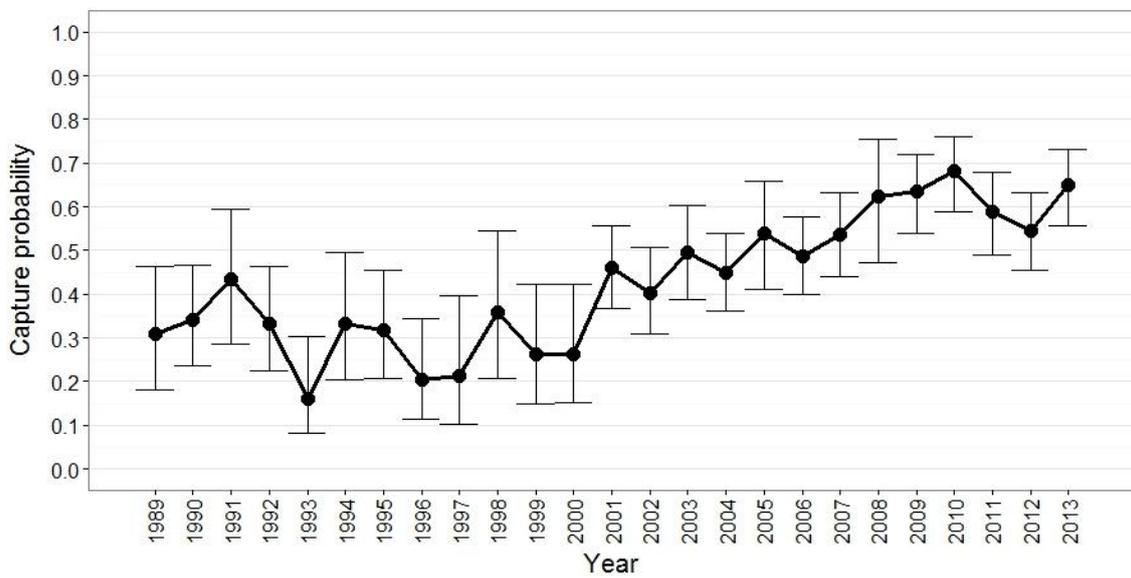


Figure 2.7. Within year mean estimated probability of capture from the best RD model (with 95% CI)

### 2.3.2. Multistate and “*ad hoc*” models

Sex was determined for 59 females and 41 males, representing 50% of the total 200 individuals; 100 individuals remained as unknown sex.

The five best models of the candidate set fell within a  $\Delta\text{AICc}$  of 3 (Table 2.5, Models 1 to 5), indicating that they all had considerable support from the data. To account for model uncertainty, parameter averaging was used to estimate the following sex-specific survival probabilities: 0.956 (SE=0.011; 95% CI=0.928-0.973) for females, 0.951 (SE=0.013; 95% CI=0.918-0.971) for males and 0.939 (SE=0.007; 95% CI=0.922-0.952) for unsexed individuals. These estimates were slightly lower but consistent with the model averaged estimates of survival from the “*ad hoc*” CJS most supported models for females (0.966, SE=0.008; 95% CI=0.945-0.979), and males (0.960, SE=0.013; 95% CI=0.924-0.979). Model-averaged estimates of recapture probabilities for each year were usually high, ranging from 0.395 to 0.988 (Figure 2.8)

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Table 2.5. Model selection diagnostics for the multistate models used to estimate survival ( $\phi$ ), capture ( $p$ ), and transition ( $\psi$ ) probabilities. Only the first 20 models are shown here, see full list in Appendix 2. Models are ordered by AICc. Delta AICc: difference in the AICc of any given model from that of the minimum AICc model; (.) = constant; (T) = time-specific; (sex) = state-specific (M, F, and U); (U=M≠F; M=F≠U; M=F≠U).

Model #	Model	AICc	Delta AICc	AICc weights	Model likelihood	No. par	Residual deviance
1	$\phi$ (F=M≠U)p(F=U≠M, T) $\psi$ (., T)	13710.17	0	0.36877	1	42	12939.04
2	$\phi$ (M=U≠F)p(F=U≠M, T) $\psi$ (., T)	13711.12	0.956	0.22864	0.62	42	12940.00
3	$\phi$ (.) p(F=U≠M, T) $\psi$ (., T)	13711.65	1.4782	0.1761	0.4775	41	12942.65
4	$\phi$ (sex) p(F=U≠M, T) $\psi$ (., T)	13712.23	2.067	0.13119	0.3558	43	12938.98
5	$\phi$ (F=U≠M) p(F=U≠M, T) $\psi$ (., T)	13713.26	3.093	0.07854	0.213	42	12942.13
6	$\phi$ (F=M≠U)p(F=U≠M, T) $\psi$ (sex, T)	13718.85	8.6807	0.00481	0.013	49	12932.74
7	$\phi$ (M=U≠F)p(F=U≠M, T) $\psi$ (sex, T)	13719.81	9.6387	0.00298	0.0081	49	12933.70
8	$\phi$ (.) p(F=U≠M, T) $\psi$ (sex, T)	13720.36	10.1896	0.00226	0.0061	48	12936.40
9	$\phi$ (sex) p(F=U≠M, T) $\psi$ (sex, T)	13720.93	10.766	0.00169	0.0046	50	12932.68
10	$\phi$ (F=U≠M) p(F=U≠M, T) $\psi$ (sex, T)	13721.99	11.8247	0.001	0.0027	49	12935.89
11	$\phi$ (F=M≠U) p(sex, T) $\psi$ (., T)	13722.63	12.4617	0.00073	0.002	60	12912.67
12	$\phi$ (M=U≠F,.) p(.,T) $\psi$ (., T)	13722.85	12.681	0.00065	0.0018	39	12958.09
13	$\phi$ (M=U≠F) p(sex, T) $\psi$ (., T)	13723.57	13.3997	0.00045	0.0012	60	12913.61
14	$\phi$ (F=M≠U) p(.,T) $\psi$ (., T)	13723.57	13.406	0.00045	0.0012	39	12958.82
15	$\phi$ (.)p(.,T) $\psi$ (., T)	13724.01	13.8447	0.00036	0.001	38	12961.37
16	$\phi$ (.) p(sex, T) $\psi$ (., T)	13724.12	13.9508	0.00034	0.0009	59	12916.34
17	$\phi$ (sex) p(sex, T) $\psi$ (., T)	13724.75	14.5789	0.00025	0.0007	61	12912.60
18	$\phi$ (sex) p(.,T) $\psi$ (., T)	13724.88	14.7075	0.00024	0.0007	40	12958.00
19	$\phi$ (F=U≠M) p(sex, T) $\psi$ (., T)	13725.8	15.6307	0.00015	0.0004	60	12915.84
20	$\phi$ (F=U≠M)p(.,T) $\psi$ (., T)	13726.13	15.959	0.00013	0.0004	39	12961.37

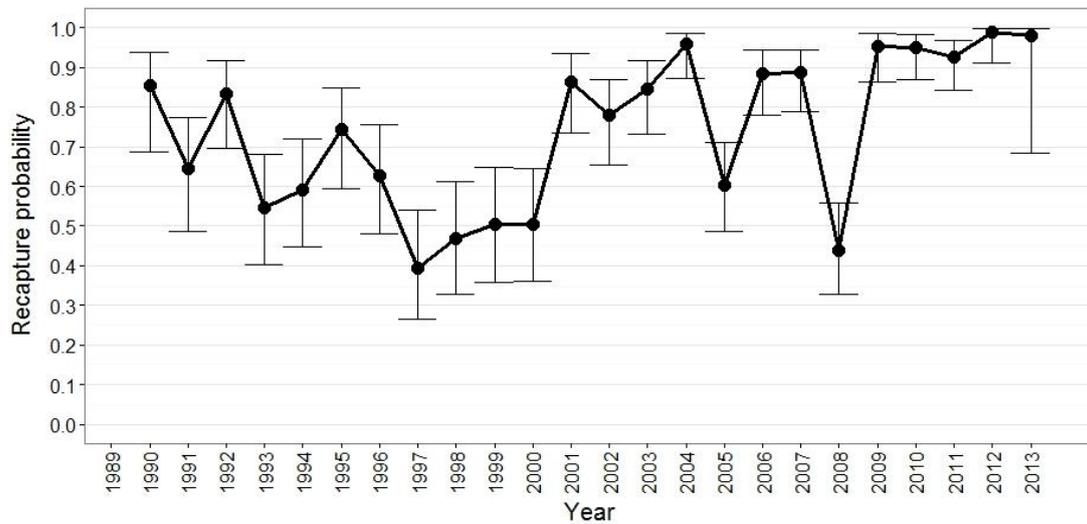


Figure 2.8. Annual model-averaged probability of recapture from the MS models (with 95% CI).

## 2.4. Discussion

### 2.4.1. Probability of capture

Restricting capture probabilities to be constant or vary only between but not within years did not receive any support based on the first round of no-movement models. This is not surprising taking into account the variations in weather conditions, sampling effort, and individual ranging preferences, which were expected to result in varying capture probabilities. The smaller sample sizes during the first years of the study period are likely to explain some of the fluctuations in capture probabilities between and within years (Figure 2.7 and Figure 2.8). Also, the combination of the expansion in the population's range during the second half of the 1990s (Wilson *et al.*, 2004) and the fact that sampling effort outside the inner Moray Firth was minimal during this same time period probably had a strong influence on capture probabilities. As shown in Figure 2.8, recapture probabilities between years from the MS models show a decrease in the mid 1990s when part of the population was likely to have spent more time outside the surveyed area and may not have been available for sampling. Then, as effort gradually expanded outside the Moray Firth during in the late 1990s and into the second half of the study period, more animals were available for sampling, and capture probabilities increased, showing much less variation except for 2005 and 2008. The

gap in effort in St Andrews Bay and Tayside in 2005 and 2008 (Figure 2.3) is clearly reflected in the substantial decrease in recapture probability in those years (Figure 2.8); individuals that were primarily distributed outside the Moray Firth that were captured in 2004 and 2007 were not available for recapture in 2005 and 2008, respectively.

Even though the assumption of population closure within each primary sampling period (among secondary sampling occasions) was likely violated because primary periods extended between 3 and 5 months, the bias in probability of capture is likely to be small because the robust design model results suggested that movement in and out of the study area between years was completely random.

### **2.4.2. Accounting for unequal catchability**

Dealing with unequal probability of capture among individuals was addressed in two ways in this analysis. First, heterogeneity of capture probabilities within each year was accounted for by using a mixture model (Pledger, 2000) within a robust design framework but no temporary emigration. Second, unequal probability of capture among individuals between years from temporary emigration was accounted for within the RD models. In both cases, most support was given to models that accounted for individual heterogeneity or for temporary emigration, most likely because they were able to account for unequal capture probabilities among individuals caused by a combination of individual heterogeneity in capture probabilities, individual ranging preferences and sampling variability, as mentioned above.

A model accounting for both heterogeneity of capture probabilities and temporary emigration is generally difficult to apply to capture-recapture data from cetacean populations due to data limitations for such data-demanding models and the risk of over parameterization (*e.g.* Silva *et al.*, 2009a, Nicholson *et al.*, 2012, Daura -Jorge *et al.*, 2013). In this analysis, there were sufficient data to fit the model, which received more support than a model only accounting for individual heterogeneity. However, the resulting model contained 338 different parameters compared to 170 parameters from the best fitting model accounting for temporary emigration, and to 293 parameters from the best fitting model accounting for individual heterogeneity. Additionally, some parameters of probability of emigration/immigration ( $\gamma_t^{\leftarrow}$ ,  $\gamma_t^{\rightarrow}$ ), mixture parameters ( $\pi$ ), and probabilities of capture ( $p$ ) were not estimated by the model.

This more complex model was thus considered less robust and not used to estimate the probability of apparent survival.

Unequal probability of capture produces negatively-biased population size estimates and, in most cases, estimates of apparent survival probability, but the latter are much less affected (Carothers, 1973). Also, the bias in survival estimates is minimized when average capture probabilities are high (Pollock *et al.*, 1990), which is the case in this analysis, with average between year recapture probability ranging from 0.395 to 0.988 (Figure 2.8). When temporary emigration occurs, estimates of survival from open-population models remain unbiased when temporary emigration is completely random (Kendall *et al.*, 1997), as in this analysis. When temporary emigration is Markovian, survival estimates can be more biased, either negatively or positively, mainly depending on the relation between  $\hat{\gamma}_t$  and  $\hat{\gamma}_t$  (Kendall *et al.*, 1997).

The results showed that the estimates of apparent survival from models accounting for either heterogeneity in capture probabilities or temporary emigration, and both or neither of these were all very similar (0.946 SE=0.005; 0.946 SE=0.005; 0.946, SE=0.005; and 0.945, SE=0.005; respectively). Thus, the potential bias caused by temporary emigration and heterogeneity in capture probabilities was minimal. Despite this, the use of a robust design framework is still generally a good option because it leads to efficient estimation of survival and generally more precise estimates, even in the absence of temporary emigration (Kendall and Nichols, 1995).

### 2.4.3. Temporary emigration rates

As previously mentioned, the failure of sampling effort to respond to the expansion of the distributional range of the population in the late 1990s (Wilson *et al.*, 2004) may have generated a problem of temporary emigration. A decrease in the probability of emigration over the years might then be expected as sampling effort gradually expanded outside the Moray Firth and fewer individuals were left outside the sampled area. The estimated probabilities of emigration varied during the study period but there was a pattern (Figure 2.6). The probabilities of emigration increased from the start of the period until the late 1990s, when the trend shifted and probabilities of emigration decreased until the early 2000s. The increasing trend in the probabilities of emigration from the start of the study until the late

1990s may indicate that the range expansion actually started earlier than previously believed (Wilson *et al.*, 2004). From 2004 onwards, the probabilities of emigration were very small, except for the outlier years 2005 and 2008. In those years, the lack of data collection trips in St Andrews Bay and the Firth of Tay is reflected in the high values of the probability of temporary emigration in both 2005 and 2008 (Figure 2.6).

The estimated probabilities of temporary emigration (0.000 SE=0.004 to 0.516 (SE=0.055) were lower than those obtained in the Azores (0.421±0.124 SE to 0.760±0.057 SE; Silva *et al.*, 2009a) and in the eastern gulf of Shark Bay (0.33 to 0.66; Nicholson *et al.*, 2012). In the Azores, only a small proportion of the individuals seen are resident, and the rest include temporary emigrants and transients (Silva *et al.*, 2009a), whereas in Shark Bay the study area was unlikely to include the entire individual range of animals with home ranges extending outside its limits (Nicholson *et al.*, 2012). Long-distance movements of bottlenose dolphins have been reported between eastern Scotland and Ireland (Robinson *et al.*, 2012). However, these individuals were only seen over a period of weeks in the outer Moray Firth, and were never observed associated with individuals included in the long-term photo-identification dataset of the Scottish east coast population. For the study population, the results seem to indicate that there is now little temporary emigration from the sampled areas, reflecting a population with a high degree of residency and no indication of transient individuals (Cheney *et al.*, 2013).

#### **2.4.4. Probability of survival**

The best estimate of the probability of annual apparent survival from this study was 0.946 (SE=0.005). This estimate is a negatively biased estimate of true survival if permanent emigration occurs (Kendall *et al.*, 1997). For this analysis, estimates of apparent survival probability were practically the same in the models with no emigration (0.945 SE=0.005), which is consistent with the results showing generally low levels of temporary emigration.

The estimated annual survival is at the lower end of the range reported for other populations of bottlenose dolphins. It is comparable to estimates reported for the Sado Estuary (0.95 (SE=0.015) to 0.99 (SE=0.008); Gaspar, 2003), Shark Bay and Bunbury (0.95 (SE=0.02); Nicholson *et al.* 2012, Smith *et al.*, 2013), Charleston (0.951 (SE=0.035); Speakman *et al.*, 2010) and Doubtful Sound (0.937 95% CI : 0.917-0.953; Currey *et al.*, 2009), higher than

estimates reported in the NE Adriatic sea (0.914 (SE=0.032); Fortuna, 2006) and southern Brazil (0.917 95% CI=0.876-0.961; Daura -Jorge *et al.*, 2013) but slightly lower than estimates from Sarasota Bay (0.96 (SE=0.008); Wells and Scott, 1990), the Azores (0.97 (SE=0.029); Silva *et al.*, 2009a), and Bangladesh (0.976 (SE=0.022); Mansur *et al.*, 2012). The estimates from these last three locations may be higher because those studies only included adults, whereas our study included both adults and sub-adults, which tend to have higher mortality rates than adults in mammals (Caughley, 1966).

The survival estimate for the study population is similar to that previously reported for this population by Sanders-Reed *et al.* (1999) (0.942, SE=0.015) but slightly higher than that reported by Corkrey *et al.* (2008) (0.93, SE=0.029). Demographic modelling based on these previously reported estimates of survival showed that a decline was more probable than an increase for this population (Sanders-Reed *et al.*, 1999, Corkrey *et al.*, 2008). However, none of these studies included photo-identification data from outside the Moray Firth, because there were either none or too few at the time, and thus there was the concern that the predicted likely decline was confounded with temporary emigration (Corkrey *et al.*, 2008) due to the population's range expansion (Wilson *et al.*, 2004). The analysis presented here is based on a larger dataset compared to earlier studies, and encompasses the changes in the population's range but also the subsequent changes in sampling effort. Also, temporary emigration in the data was able to be modelled using the RD, and thus minimize potential bias in the estimates of survival probability. Based on the estimates of survival from this analysis, the mortality rate for this population is estimated to be of 5.4%, lower than that reported based on 1990-1997 data (5.81%; Sanders-Reed *et al.*, 1999), and that from Corkrey *et al.* (2008) (7%) based on data from 1990 to 2002.

### **2.4.5. Sex-specific survival**

The use of multi-state (MS) models provided an analytical approach to estimate sex-specific survival for a wild population of bottlenose dolphins and overcome issues related to methods of assigning the sex. These results add valuable information to the very limited available information on sex-specific survival rates for bottlenose dolphins.

MS models implicitly assume that any emigration from the study population during the study period is permanent (Kendall *et al.*, 1997) and thus cannot account for temporary emigration.

However, the results from the RD models seem to indicate that there is little temporary emigration in the data and thus little bias is expected to affect the survival probabilities from the MS models. These models can account for sex-uncertainty when sex cannot be easily determined for all ages and sampling occasions, but implicitly assume that when sex is assessed, it is done without error (Nichols *et al.*, 2004). Care was taken to avoid mistakes in sex assessment in all methods used in this study. Biopsy samples were only taken after a target individual with distinct marks was chosen and good quality photographs of its dorsal fin were taken (Islas-Villanueva, 2009). Photographs of the genital area were only assigned to an identified individual when certain of its identification. Sexing of females based on the association with a calf was only confirmed after sighting a female repeatedly with a newborn or young calf.

The MS models estimate a model-averaged probability of apparent survival of 0.956 (SE=0.011) for females, 0.951 (SE=0.013) for males and 0.939 (SE=0.007) for un-sexed individuals. This last group reflects a mixture of individuals from both sexes, which are likely to be on average younger because of the methods used to determine the sex of the individuals. Because younger individuals tend to have relatively lower survival rates in mammals (Caughley, 1966), they are likely to have caused a negative bias to the estimate of all-aged survival for the un-sexed individuals. For this population then, the survival probabilities translate into mortality rates of 4.4% in females and 4.9% in males.

Available sex-specific survival estimates for bottlenose dolphins in other populations are scarce and some are based on stranded animals but they all suggest lower survival (higher mortality) rates for males (Scott and Chivers, 1990, Scott *et al.*, 1990, Fernandez and Hohn, 1998, Stolen and Barlow, 2003, Fortuna, 2006, Currey *et al.*, 2009). These differences in survival between sexes are also reported in other long-lived marine mammal species including sperm whales (Ralls *et al.*, 1980), killer whales (Olesiuk *et al.*, 1990), California sea lions (Hernández-Camacho *et al.*, 2008), humpback whales (Ramp *et al.*, 2010) and harbour seals (Hastings *et al.*, 2012). However, there was weak statistical evidence for a difference in the apparent probability of survival for females and males based on model selection in both the MS and the “*ad hoc*” CJS models. In both modelling approaches, models with sex-specific survival or with a common survival for both sexes fell within a difference of 3 AICc units, receiving similar support. However, even a slight difference in the mortality

rate between males and females may be important for a population viability analysis requiring sex-specific life history parameters.

The higher mortality rate of males in marine mammals has been attributed to various factors with differentiated effects on both sexes, including costs of sexual selection, gender differences in ranging patterns, and differences in toxic burdens (*e.g.* Ralls *et al.*, 1980, Weisbrod *et al.*, 2001, Stolen and Barlow, 2003). For the current study, there is a lack of data to investigate all these different potential causes in the population study, which limits the interpretation of the ecological or evolutionary drivers behind those differences, but some interpretation can be made. For example, male bottlenose dolphins in the study population show a significantly higher percentage of body scarring and dorsal fin nicks compared to females (Marley *et al.*, 2013), which has been related to intra-sexual male competition for females in other populations (*e.g.* Scott *et al.*, 2005, Rowe and Dawson, 2009). If intra- male competition occurs in the study population, it may represent added costs for males that may compromise their fitness and hence survival.

On the other hand, the study population shows individual differences in ranging behaviour and a high degree of mobility within its distributional range (Cheney *et al.*, 2013). Sex differences in dispersal are common in mammal species to increase access to resources and mates, and to avoid inbreeding (Greenwood, 1980); in other populations of bottlenose dolphins males have been shown to disperse more than females (*e.g.* Scott *et al.*, 1990, Möller and Beheregaray, 2004). At this time there is no detailed information on differences in the individual movements of males and females from the study population but, if males happened to move across wider areas or move more often across their distributional range compared to females, as seen in other studies, it could increase their costs and potentially affect their survival.

The occurrence of epidermal lesions, well documented for this bottlenose dolphin population (Thompson and Hammond, 1992, Wilson *et al.*, 1997b), has been linked to signs of disease in which anthropogenic contaminants might play a contributory role. The exact role of contaminants in the survival of marine mammals is still unclear (Ross, 2002), and no link has been found between the prevalence or severity of skin lesions and the presence of contaminants in tissue samples (Wilson *et al.*, 1999a). Epidermal lesions appear to be a long-term feature of this population that do not seem to compromise the survival of individuals as

they are present in all age classes (Wilson *et al.*, 2000), and the severity of epidermal lesions in this population is actually greater in females than males (Wilson *et al.*, 1997b).

## **2.5. Conclusions**

The probability of apparent survival for the bottlenose dolphins off the east coast of Scotland estimated by RD models (0.946, SE=0.005) is comparable to other populations of bottlenose dolphins, and similar to the survival rates previously estimated for this population. The estimates of temporary emigration are consistent with a population with a high degree of residency and generally no transient individuals. The results also highlight the importance of using a modelling approach that can account for temporary emigration in years in which sampling effort may not provide adequate coverage of the distributional range of the population.

The sex-specific survival estimates add valuable information to the limited data available for wild populations of bottlenose dolphins. Even though there was weak evidence for a difference in survival between sexes, the difference in mortality rate may be important to a population viability analysis requiring sex-specific life history parameters. Even though the MS modelling approach could not account for temporary emigration, little bias in survival probabilities is expected due to temporary emigration based on the results from the RD models.

## Chapter 3

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### Abundance of bottlenose dolphins off the east coast of Scotland with a focus on St Andrews Bay and Aberdeenshire

#### 3.1. Introduction

Population size is a key component needed to understand the environmental, anthropogenic and other factors that may influence population dynamics (Williams *et al.*, 2002a), and to form the basis of conservation and management actions (Evans and Hammond, 2004). Information on the size of a population is the first step to evaluate and determine its conservation status (*e.g.* Barlow *et al.*, 1997, Reisinger *et al.*, 2011), while information on changes or trends in abundance is needed to understand whether a population is increasing or declining (*e.g.* Stevick *et al.*, 2003, Fruet *et al.*, 2011), or shifting its distributional range seasonally or permanently (*e.g.* Nicholson *et al.*, 2012, Tezanos-Pinto *et al.*, 2013). This information can then be used to determine whether or not conservation measures need to be implemented (*e.g.* Beasley *et al.*, 2013), and to understand the effectiveness of existing management actions (*e.g.* Gerrodette *et al.*, 2011). Because cetacean populations cannot be censused, their abundance has to be estimated; the accuracy and precision of estimates will influence the ability to determine trends (Taylor and Gerrodette, 1993) in time for effective conservation needs to be identified and management measures to be implemented (Taylor *et al.*, 2007).

A number of methods have been used to estimate animal abundance in cetacean populations (Hammond, 2010) including: extrapolation of animal counts (*e.g.* Rugh *et al.*, 2005, Noad *et al.*, 2006); line transect sampling (Buckland *et al.*, 2001, *e.g.* Hammond *et al.*, 2013, Branch 2011) and mark-recapture analysis of individually identified animals (*e.g.* Verborgh *et al.*, 2009, Cantor *et al.*, 2012). The latter methods have mostly been used for bottlenose dolphin populations (*e.g.* Wilson *et al.*, 1999b, Read *et al.*, 2003, Silva *et al.*, 2009a, Smith *et al.*, 2013) because individuals possess permanent markings on their dorsal fins that allow them to be identified photographically over long time periods, as detailed in Chapter 2.

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Animal abundance can be estimated using open or closed population mark-recapture models, which differ primarily in the assumption of whether or not the population is assumed to be closed to births, deaths and permanent immigration/emigration (Jolly, 1965, Seber, 1965, Otis *et al.*, 1978, Hammond, 2010). Assumptions common to both model types relate to the individual recognition data: all animals are uniquely identifiable, no marks are lost, all marked animals are accurately recognized and recorded. Assumptions relating to the probability of capturing animals vary depending on the complexity of the models used.

An important assumption of simple conventional mark-recapture models is that all animals have the same probability of being captured at any one sampling occasion. This is very difficult to meet in cetacean populations (Hammond, 1986, Hammond, 1990). Sex, age or individual differences are likely to result in some animals having more chance of being captured than others. For example, individuals may have different ranges or differ in their preferences within similar ranges so that they are differentially available for capture within the sampled area. Differences in behaviour can also affect the probability of capturing individuals in different sampling occasions. For example, animals may react differently to the boat, with some being attracted to it to bow ride while others might swim away from it. Different age classes might surface within different ranges of the boat, potentially affecting the quality of the photographs of the individuals farther away from the boat (*e.g.* mothers with newborn calves might be more evasive and keep a greater distance from the boat). On occasions, differences in the probability of capture among individuals are caused by a combination of limited sampling effort and individual ranging preferences. Sample areas do not tend to cover the entire distributional range of the study population, and marine mammals typically have individual preferences for particular areas. As a result, animals spending more time in the sample area will have more chances to be captured (*e.g.* Hammond, 1990). All these factors are likely to violate the assumption of homogeneity of capture probabilities among the different individuals in the population, commonly known as heterogeneity of capture probabilities (Chao, 1987).

The bias in the abundance estimates can be severe when heterogeneity of capture probabilities is not accounted for (Pollock *et al.*, 1990, Hammond, 2010). If some

animals are recaptured more times than expected over the study period time, the average probability of capture will be overestimated and as a consequence abundance will be underestimated. The violation of this assumption can be minimized by having a good sampling design that maximises the probability of capturing individuals (Evans and Hammond, 2004). This may be achieved for example by increasing the photo-identification effort or by adapting the survey design to maximise the probability of encountering animals. Even then, it is important to investigate the presence of heterogeneity in capture probabilities in the data and account for it in the mark-recapture models when possible. Open-population models do not have the ability to account for heterogeneity of capture probabilities, but robust estimators that have been developed within closed population models to account for it, by modelling both temporal and individual unequal catchability (*e.g.* Otis *et al.*, 1978, Pledger, 2000).

When animals are available for sampling in some occasions but not in others it is known as temporary emigration. This may occur when the sampled area only represents a fraction of the population's distributional range and individuals in the population have different ranging preferences. In this case, some individuals might be completely outside the sampled area on one or more occasions and thus will not be available for capture. This will lead to fewer recaptures than expected, underestimating the probability of capture, and consequently overestimating abundance. Closed population models do not allow for either permanent or temporary emigration and immigration to occur (Otis *et al.*, 1978), and when temporary emigration is present in the data, and is not accounted for, it will positively bias the estimates of abundance (Seber, 1982, Kendall and Nichols, 1995, Kendall, 1999). This is a common issue in cetacean studies, and present in many bottlenose dolphin population studies (*e.g.* Silva *et al.*, 2009a, Nicholson *et al.*, 2012, Smith *et al.*, 2013).

Robust design models (Pollock, 1982, Kendall *et al.*, 1995, Kendall *et al.*, 1997) offer the advantage of combining characteristics from both closed and open population models. These models allow temporary emigration probabilities to be estimated separately so that this type of movement is not confounded with capture probability (Kendall *et al.*, 1997); these models have increasingly been used to estimate abundance in cetacean populations (*e.g.* Cantor *et al.*, 2012, Nicholson *et al.*, 2012, Daura -Jorge *et*

*al.*, 2013, Smith *et al.*, 2013). In the robust design, the time between primary sampling periods is used to estimate the probability of animals temporarily emigrating from the study area so that the estimates of probability of capture and abundance tend to be less biased by heterogeneity in capture probabilities (Kendall and Nichols, 1995, Kendall *et al.*, 1997). The mark-recapture models used to estimate the apparent survival probability for the study population in Chapter 2 indicated presence of heterogeneity of capture probabilities in the no movement models, and of random temporary emigration in the models allowing for it. These two sources of unequal catchability will bias the estimates of abundance if the model does not account for them, but will do it with opposite directions, causing a negative and positive bias, respectively.

The study of the Scottish east coast bottlenose dolphin population initially focused only on the area of the inner Moray Firth. Based on the information collected in the late 1980s and early 1990s, that area was identified as the core area used by this population, leading to the designation of the Moray Firth Special Area of Conservation (SAC). However, it was already known that bottlenose dolphins were using other areas outside the SAC, such as the southern parts of the outer Moray Firth, the coastal waters of Aberdeenshire and St Andrews Bay (Wilson *et al.*, 2004). In the area of St Andrews Bay, starting in the 1990s anecdotal reports increased in frequency over the years (Weir and Stockin, 2001, Wilson *et al.*, 2004) until photo-identification effort started in 1997. The photo-identification data collected in St Andrews Bay since then shows that this area, located at the southern end of the population's range, is frequently used by at least part of the population, and that individuals frequently move between the different areas of the distributional range (*i.e.* between the Moray Firth, the Grampian coast and Fife) (Thompson *et al.*, 2011). Bottlenose dolphins are also commonly found in Aberdeenshire waters, where studies have described their distribution in coastal waters (Stockin *et al.*, 2006, Weir *et al.*, 2008) with a focus around Aberdeen harbour (Sini *et al.*, 2005, Pirotta *et al.*, 2013). Aberdeen harbour is the main logistical support centre for the oil and gas industry in the North Sea and an important port for fisheries, transport and tourist industries (Aberdeen Harbour Board, 2013). This results in intense boat traffic in and out of the harbour every year, which is likely to increase in the future given the importance of this port (Aberdeen Harbour Board, 2013). In addition to oil and gas activities, large scale offshore wind farms are being considered in sites off the

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Firth of Tay and Forth (SeaGreen Wind Energy, 2011a), and an offshore deployment centre to test offshore wind technology will be developed in Aberdeen Bay (Vattenfall and Aberdeen Renewable Energy Group, 2012). All these activities have the potential to impact the bottlenose dolphins using those areas of interest (*e.g.* Pirotta *et al.*, 2013)

Estimates of abundance of bottlenose dolphins using the Moray Firth SAC are available since 1990 (Cheney *et al.*, 2012), most recently as part of the monitoring programme designed for the Special Area of Conservation. Total population abundance estimates have also been published for different study periods and based on a variety of conventional and Bayesian analytical approaches (Wilson *et al.*, 1999b, Durban *et al.*, 2005, Corkrey *et al.*, 2008, Cheney *et al.*, 2013). However, only one unpublished estimate of abundance is available for the area of St Andrews Bay, based on both conventional and Bayesian methods of analysis applied to photo-identification data collected in 2003 and 2004 (Quick, 2006). Combining the results from both methods, the best estimates were included in a conservative 95% confidence range of 81 to 142 dolphins. Weir *et al.* (2008) provide a minimum number of individuals seen in the Aberdeenshire on an annual basis based on photo-identification data, but no abundance estimate is available so far for that area.

The analysis in this Chapter uses the same analytical approach applied in Chapter 2 to estimate the apparent survival rate. Robust design mark-recapture models were used to provide annual estimates of total population abundance using the area between the Moray Firth SAC and the Firth of Forth (the whole known population range), based on the long-term photo-identification dataset (1990 to 2013). Analysis using these models investigated the bias in abundance (direction and extent) caused by individual heterogeneity of capture probabilities and by temporary emigration. The abundance of animals using St Andrews Bay was estimated based on a subset of the data (2009 to 2013) for which consistent photo-identification effort occurred in that area. Using the same capture-recapture models used to estimate total abundance allowed for comparisons between the local abundance in St Andrews Bay and the total population abundance. Based on photo-identification data collected in 2012 and 2013, closed population models were used to estimate the abundance of bottlenose dolphins using the area between Aberdeen and Stonehaven.

## 3.2. Methods

### 3.2.1. Study areas and datasets

Three areas of interest were defined for this analysis: (1) an overall study area extending from the Moray Firth SAC south to the Firth of Forth, which covers the current known distributional range for this population, (2) a subarea between Aberdeen and Stonehaven to include the waters of Aberdeenshire in the Grampian coast, and (3) another subarea extending from Montrose south to Fife Ness, at the entrance to the Firth of Forth, including St Andrews Bay and the entrance to the Firth of Tay (Figure 3.1).

To estimate the total population abundance of bottlenose dolphins along the east coast of Scotland (overall area), photo-identification data collected in the time period 1990 to 2013 were used; this is the same dataset used in Chapter 2 to estimate the probability of apparent survival for the population. The first year of existing data (1989) was excluded from this analysis because information on the proportion of marked animals for each trip was not available (*i.e.* information needed to inflate the annual estimates of marked animals from the capture-recapture models to estimates of total number of animals – see below). Locations of the groups of bottlenose dolphins encountered from 1990 to 2013 that were included in the analysis are plotted in Figure 3.2.

To estimate the number of animals using St Andrews Bay, a subset of data were selected from the main dataset to include all photo-identification data collected during encounters with bottlenose dolphins in the area between Montrose and Fife Ness between 2009 and 2013 (Figure 3.3). Even though photo-identification occurred in St Andrews Bay before 2009 (see Figure 2.3 in Chapter 2), only the last 5 years of data were selected because those years had consistent photo-identification effort conducted in St Andrews Bay as well as in the overall study area, allowing for comparisons.

To estimate the number of animals using the Aberdeenshire coast, photo-identification data collected in the summer months of 2012 and 2013 between Aberdeen and Stonehaven were selected (Figure 3.4). Previous photo-identification data collected in this same area in 2008 were used to compare the occurrence of individual dolphins in

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that specific area between the periods 2008 and 2012-13, but were excluded from the abundance estimate.

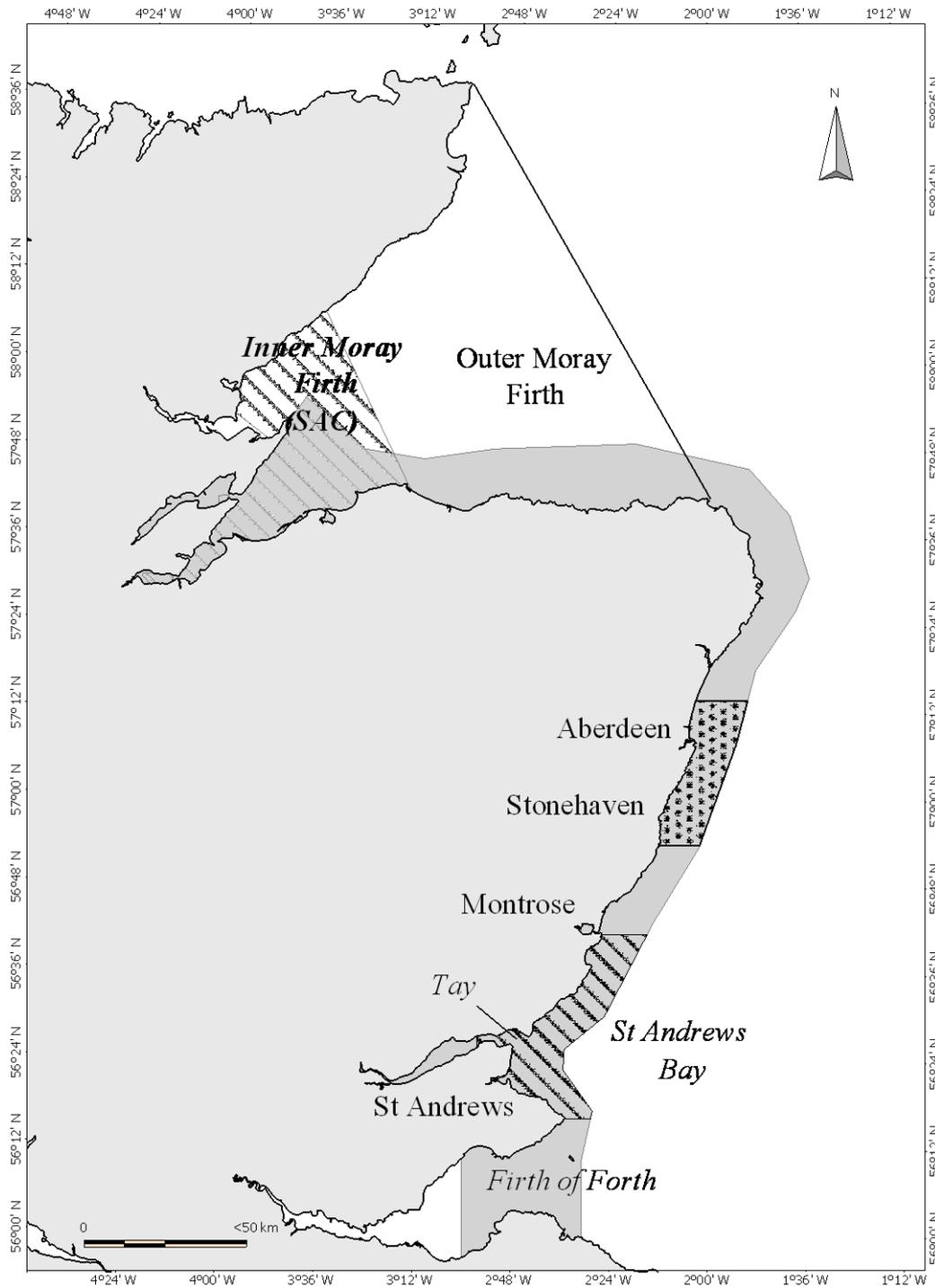


Figure 3.1. Areas of interest used to estimate abundance, including the overall study area from the Moray Firth SAC south to the Firth of Forth (grey), the subarea of Aberdeenshire extending from Aberdeen to Stonehaven (dotted), and the subarea of St Andrews Bay (dashed).

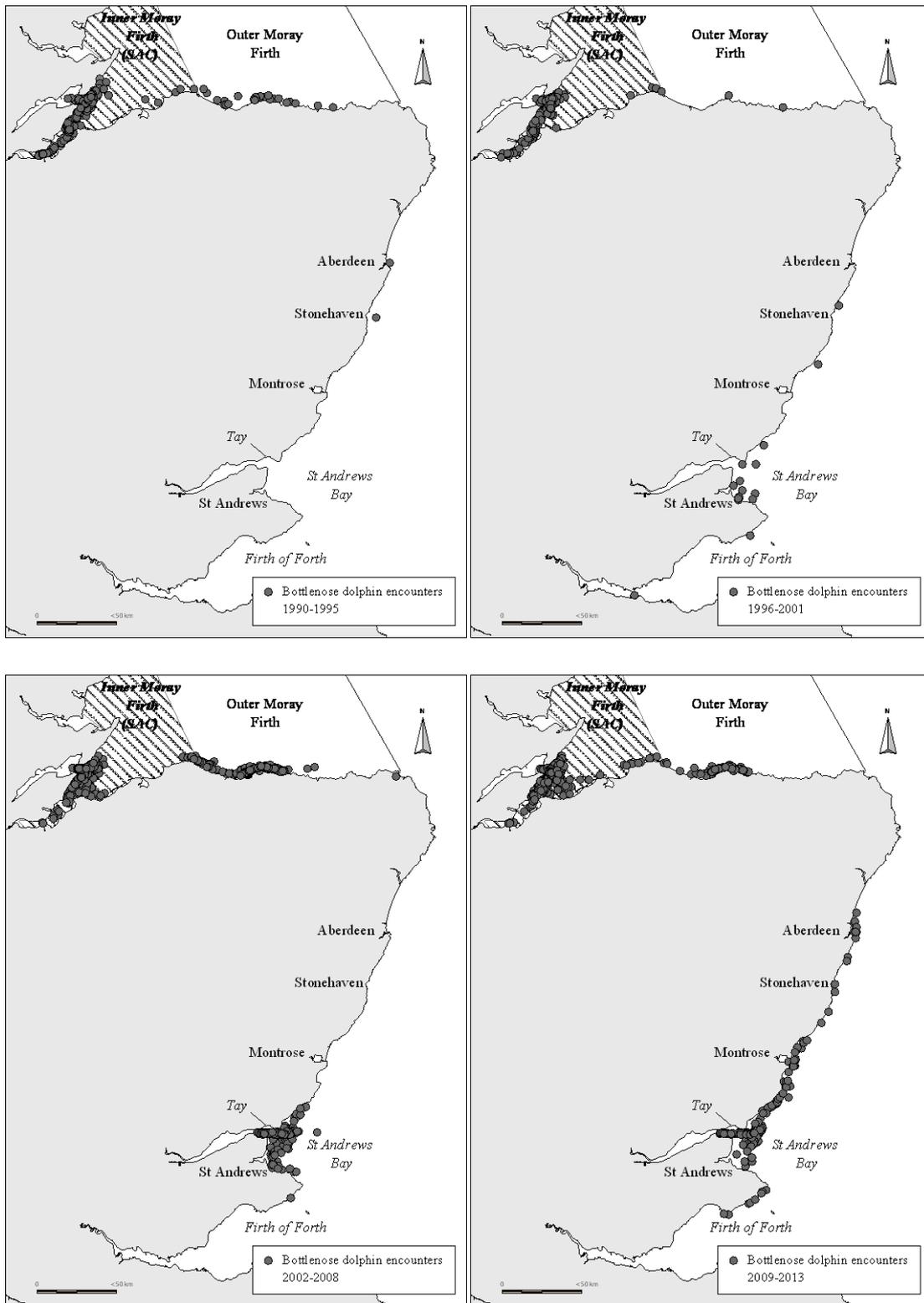


Figure 3.2. Location of bottlenose dolphin groups encountered between May and September in the long-term dataset, for 1990-1995, 1996-2001, 2002-2008, and 2009-2013.

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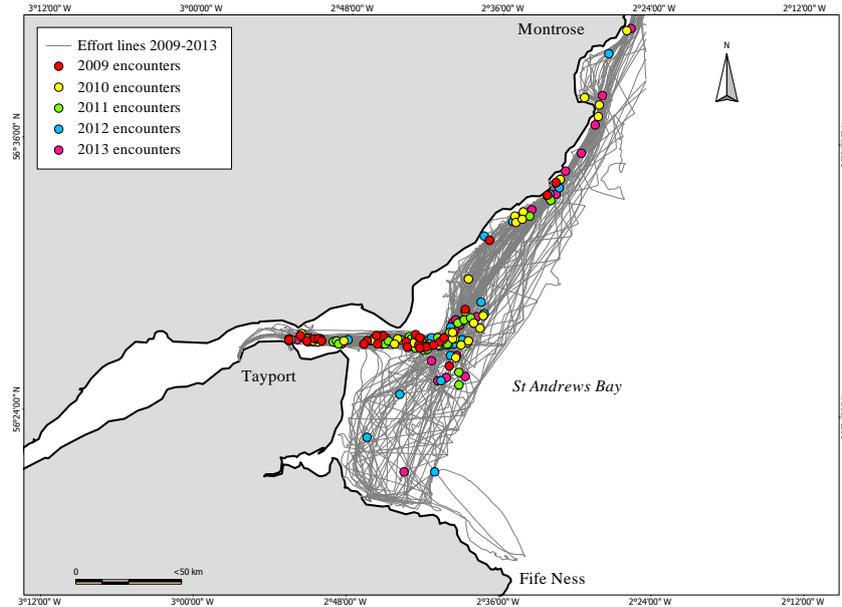


Figure 3.3. Survey effort and location of encounters of bottlenose dolphins for 2009-2013 in the area between Montrose and Fife Ness.

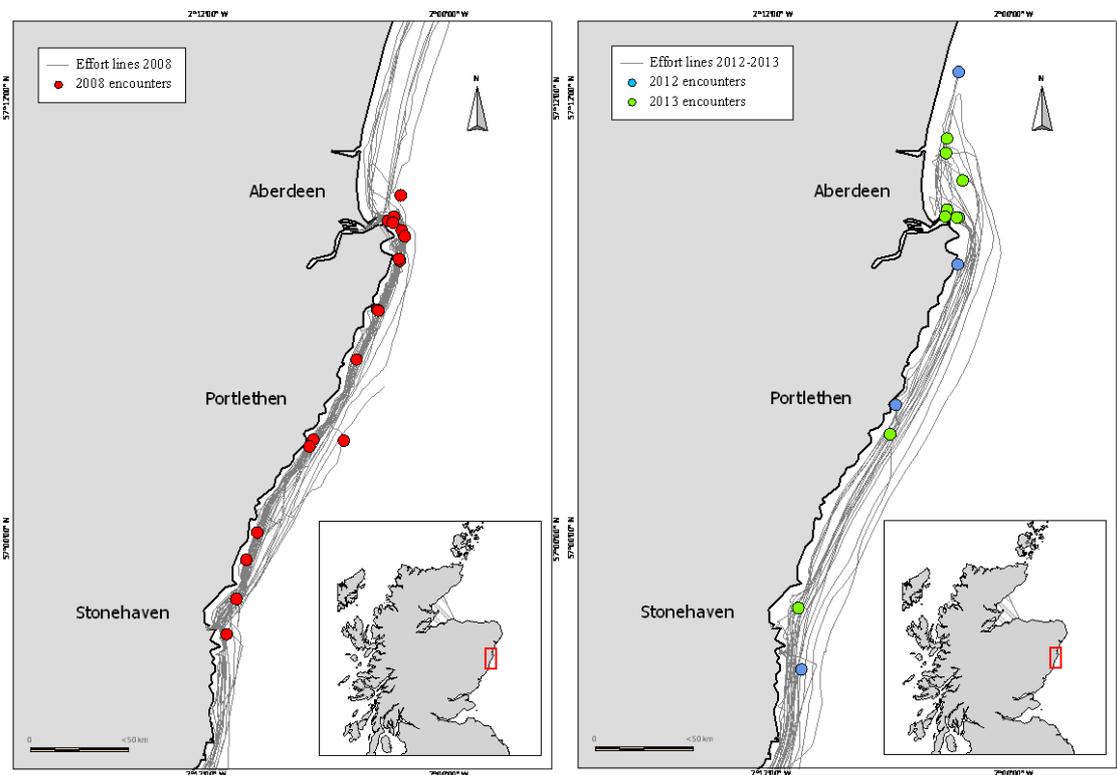


Figure 3.4. Survey effort and location of encounters with bottlenose dolphins for 2008 and 2012-2013 in the area of Aberdeenshire.

### 3.2.2. Mark recapture models

#### 3.2.2.1. *Robust design mark-recapture models*

The abundance of bottlenose dolphins in the overall area and in St Andrews Bay was estimated using robust design (RD) models (Pollock, 1982, Kendall *et al.*, 1995, Kendall *et al.*, 1997). Within the RD, closed population models are applied to the secondary encounter occasions within each primary sampling period to provide an estimate of abundance ( $\hat{N}$ ). In this analysis, as in Chapter 2, each annual field season from May to September was treated as a primary sampling period, which was divided into multiple secondary sampling occasions by pulling together all sightings within each month. As detailed in Chapter 2, all photographs taken during the encounters with bottlenose dolphins were first graded for their photographic quality. All high quality pictures with grades 3.1, 3.2 and 3.3 (see Appendix 1c) were matched to a catalogue of known individual dolphins based on the natural marks on their dorsal fin. Only high quality pictures from marked individuals (*i.e.* with permanent marks such as nicks and notches) were used to construct capture histories, to define whether or not a marked individual was captured within a sampling period and area of interest. The number of secondary sampling occasions within each year and the number of marked individuals included in the analysis for both the overall study area and the subarea of St Andrews Bay are summarized in Table 3.1.

To estimate the abundance of animals using the overall area, a first attempt was made to fit models that could account for both temporary emigration and heterogeneity of capture probabilities. The fitted models had two mixtures (Pledger, 2000) to account for heterogeneity of capture probabilities, allowed capture probabilities to vary between sampling occasions, and had either constant or time varying random or Markovian temporary emigration. However, the resulting models were over-parameterized with each model having between 294 to 338 parameters, and all models failed to estimate a large proportion of the temporary emigration and mixture parameters (not shown). Thus, models accounting for both temporary emigration and heterogeneity of capture probabilities were not considered further. Instead, the abundance of bottlenose dolphins was estimated from the most supported RD model accounting for temporary emigration

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in Chapter 2 (Model  $\phi(\cdot) g''(t)=g'(t) p(txs)$  in Table 2.4 from Chapter 2; see Chapter 2 for definitions of parameters). The effects of not accounting for heterogeneity of capture probabilities or not accounting for temporary emigration were also investigated (see section 3.2.5. ).

The St Andrews Bay area represents only a part of the population's distributional range, and animals are known to move between areas within the range (Cheney *et al.*, 2013). If animals spent time in other parts of the range, such as the Moray Firth, they might not have been available for sampling in St Andrews Bay for some of the years of the period 2009 to 2013. To account for this, a candidate set of models with no emigration, random and Markovian temporary emigration (Kendall *et al.*, 1997) were fitted to the subset of capture histories of individuals encountered in St Andrews from 2009 to 2013. In all models, capture probabilities were allowed to vary between and within primary periods, based on the results from Chapter 2. Annual estimates of abundance of marked animals were derived from the most supported model from the candidate set, using Akaike's Information Criterion adjusted for small sample size (AICc, Burnham and Anderson, 2002) for model selection.

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Table 3.1. Photo-identification survey effort conducted between 1990 and 2013 in the overall study area and between 2009 and 2013 in St Andrews Bay area (also included in the overall effort). Survey effort dates, number of secondary sampling occasions (*i.e.* months), and total and newly marked individuals annually captured in each area are shown.

Year	Overall study area				Effort	2ary occ	Marked inds	New inds
	Effort	2ary occ	Marked inds	New inds				
1990	03 May-14 Aug	4	47	13				
1991	17 May-12 Sep	5	37	6				
1992	14 May-24 Sep	5	51	6				
1993	02 May-23 Sep	5	36	5				
1994	02 Jun-24 Sep	4	36	2				
1995	12 May-20 Sep	5	47	6				
1996	07 May-05 Sep	5	39	5				
1997	24 May-24 Sep	5	26	2				
1998	18 May-22 Sep	5	28	2				
1999	01 May-22 Sep	5	34	6				
2000	01 May-19 Sep	5	34	5				
2001	01 May-17 Sep	5	72	20				
2002	01 May-09 Sep	5	65	8				
2003	01 May-28 Sep	5	74	10				
2004	02 May-11 Sep	5	87	7				
2005	03 May-17 Sep	5	54	1				
2006	04 May-25 Sep	5	84	8				
2007	02 May-28 Sep	5	82	5				
					<b>St Andrews Bay area</b>			
					<b>Effort</b>	<b>2ary occ</b>	<b>Marked inds</b>	<b>New inds</b>
2008	06 May-26 Sep	5	41	1				
2009	02 May-30 Sep	5	89	13	21 Jun-24 Aug	3	43	43
2010	05 May-21 Sep	5	92	6	17 Jun-01 Sep	4	42	9
2011	03 May-29 Sep	5	89	3	10 Jun-31 Aug	3	42	4
2012	02 May-27 Sep	5	103	10	09 May-27 Sep	5	40	6
2013	02 May-27 Sep	5	103	8	07 May-27 Sep	5	39	6

### 3.2.2.2. *Closed population models using CAPTURE*

Only seven trips were conducted in Aberdeenshire between 2012 and 2013, providing too few sampling occasions to use a robust design approach to estimate the abundance of bottlenose dolphins in each year. Instead, a single abundance estimate was produced for both years combined. Each trip was a sampling occasion, resulting in a total of seven sampling occasions that were used to fit a closed population mark-recapture model.

Program CAPTURE (Rexstad and Burnham, 1991), implemented within program MARK (White and Burnham, 1999), was used to determine the most appropriate closed population model to estimate the abundance of marked animals. By combining both years, the assumption of population closure was likely to be violated between the years, although that should only introduce a small bias on the abundance estimate. Closed population models within CAPTURE allow capture probabilities to be constant ( $M_o$ ), to vary by time ( $M_t$ ), or behaviour ( $M_b$ ), to include individual heterogeneity ( $M_h$ ), or be a combination of the basic models ( $M_{th}$ ,  $M_{tb}$ ,  $M_{bh}$ ). The presence of heterogeneity in capture probabilities was further investigated by fitting a closed population model with two mixtures (Pledger, 2000) in program MARK (White and Burnham 1999).

<b>Trip</b>	<b># Encounters</b>	<b>Marked inds</b>	<b>New inds</b>
14 July 2012	1	5	5
08 Aug 2012	1	7	2
20 Sep 2012	1	5	2
09 Jun 2013	2	9	6
25 Jun 2013	3	5	2
09 Jul 2013	2	6	1
18 Jul 2013	2	7	1

Figure 3.5. Number of marked and newly marked individuals captured in each trip in Aberdeenshire in 2012 and 2013.

### 3.2.3. Proportion of marked animals

The estimates of abundance from the mark-recapture models relate to the marked animals (*i.e.* individuals within the population with permanent marks such as nicks and notches), and must be inflated to the total number of animals (*i.e.* marked and unmarked individuals) by dividing by the proportion of marked individuals in the population, usually referred to as theta ( $\theta$ ).

Assuming photo-identification effort was maximised to photograph all animals encountered, regardless of their level of marking, the proportion of marked individuals within each trip was calculated based on high quality photographs taken from the right-hand side (RHS) and the left-hand side (LHS) of the animals. To do so, the number of marked individuals photographed from the RHS and the LHS in each trip was divided by the total number of individuals photographed from each side, respectively. As a result, two values of the proportion of marked individuals were calculated for each trip, one for the RHS and another for the LHS, unless only photographs from one side were taken.

One challenge when calculating theta is to distinguish among multiple unmarked animals. On some occasions individuals with only temporary marks such as scars or rakes could not be matched to the catalogue of individually identified dolphins due to their low number of marks. However, they could still be differentiated from any other individuals encountered in the same trip and photographed from the same side of the body (LHS or RHS), based on a variety of skin temporary markings (*e.g.* scars and tooth rakes, skin lesions, white fringes, nicks, notches). Thus, it was possible to distinguish all the different individuals photographed from each side for each trip.

Once the proportion of marked animals was calculated for each side and trip, a Generalized Linear Model (GLM) with a binomial distribution and a logit link function was used to model the proportion of marked individuals, theta ( $\theta$ ). The proportion of marked individuals for each side and trip was the response variable and year was used as an explanatory variable to investigate the effect of year on theta. Different models were fitted to data from the whole study area, data from St Andrews Bay and data from Aberdeen. Data were tested for dispersion by estimating the dispersion parameter using

a quasi-binomial distribution and Pearson residuals were plotted against fitted values to assess the goodness of fit of the model.

### 3.2.4. Total abundance

To calculate the total abundance of individuals (marked and unmarked) ( $\hat{N}_{\text{total}}$ ), each estimate of annual abundance of marked individuals ( $\hat{N}$ ) from the best RD model was divided by the corresponding annual proportion of marked individuals ( $\theta$ ):

$$\hat{N}_{\text{total}} = \frac{\hat{N}}{\theta}$$

The variance for the total abundance estimate was derived using the delta method:

$$\text{var}(\hat{N}_{\text{total}}) = \hat{N}_{\text{total}}^2 \left( \frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{\text{var}(\hat{\theta})}{\hat{\theta}^2} \right)$$

Log-normal confidence intervals were derived for total abundance estimates following Burnham et al. (1987) recommendation. The lower and upper limits of the 95% confidence interval were calculated as  $N_{\text{total}}/C$  to  $N_{\text{total}}*C$ , where  $N_{\text{total}}$  is the total abundance estimate and  $C$  is calculated as follows:

$$C = \exp \left( 1.96 \sqrt{\ln \left( 1 + CV_{\hat{N}_{\text{total}}}^2 \right)} \right)$$

### 3.2.5. Accounting for unequal probability of capture

To investigate the effect of unequal probability of capture on the estimates of population size, the abundance of marked individuals using the overall study area every year between 1990 and 2013 was estimated using capture-recapture robust design models that could account for either (1) heterogeneity of capture probabilities, (2) temporary emigration, or (3) neither of these. To account for the first source of unequal catchability, a model with no emigration, heterogeneity of capture probabilities ( $\pi$ ; Pledger, 2000), and probability of capture varying between and within primary periods

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was used (model  $\varphi(.) g''=g'=0 p(txs) p_i(t)$  in Table 2.3 from Chapter 2). Definitions of the parameters can be found in Chapter 2. To account for the second source of unequal catchability, the best fitting model accounting for temporary emigration and probability of capture varying between and within primary periods based on the model selection diagnostics from Chapter 2 was used (model  $\varphi(.) g''(t)=g'(t) p(txs)$  in Table 2.4 from Chapter 2). Finally, a null model was used, with probability of capture varying only between and within primary periods (model  $\varphi(.) g''=g'=0 p(txs)$  in Table 2.3 from Chapter 2).

To calculate the magnitude and direction of the bias caused in the estimate of abundance by unequal probability of capture among individuals, the annual abundance estimates from the null model were compared to those from the models either accounting for temporary emigration or for heterogeneity of capture probabilities. Comparisons between estimates of abundance were made based on those from the marked individuals because the proportion of marked individuals is a scalar common to all estimates from different models in a given year.

### 3.3. Results

#### 3.3.1. Total population size

The capture histories of 197 marked individuals were used to estimate annual abundance of marked animals using the overall study area between 1990 and 2013, using the most supported RD model from Chapter 2 (Table 3.2 and Figure 3.6). The estimates for the proportion of marked individuals from the GLM model for the overall study area varied across years from 0.39 (CV=0.10) to 0.63 (CV=0.04). Once scaled up by these, the total number of bottlenose dolphins ( $\hat{N}_{total}$ ) using the study area annually from 1990 to 2013 ranged from the lowest estimate of 66 (95% CI 45-96) individuals in 1997, to the highest estimate of 208 individuals (95% CI 198-219) in 2012 (Table 3.2).

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Table 3.2. Annual estimates of abundance of animals using the overall study area from 1990 to 2013, with associated precision. ‘Marked inds’ = numbers of marked individuals captured;  $\hat{\theta}$  = proportion of marked animals;  $\hat{N}$  = abundance of marked animals;  $\hat{N}_{total}$  = total abundance of animals (continues on next page).

Year	Marked inds	$\hat{\theta}$	CV ( $\hat{\theta}$ )	$\hat{N}$	CV ( $\hat{N}$ )	$\hat{N}_{total}$ (95% CI)	CV ( $\hat{N}_{total}$ )
1990	47	0.51	0.06	55	0.16	107 (89-128)	0.09
1991	37	0.40	0.06	39	0.07	97 (84-113)	0.08
1992	51	0.47	0.06	57	0.05	120 (102-142)	0.08
1993	36	0.50	0.09	59	0.06	118 (78-179)	0.22
1994	36	0.50	0.08	44	0.20	86 (67-112)	0.13
1995	47	0.52	0.06	54	0.10	103 (86-123)	0.09
1996	39	0.39	0.10	54	0.07	140 (99-197)	0.18
1997	26	0.55	0.10	36	0.15	66 (45-96)	0.20
1998	28	0.45	0.09	31	0.17	69 (55-86)	0.12
1999	34	0.60	0.08	42	0.08	70 (54-91)	0.13
2000	34	0.46	0.09	42	0.11	92 (70-120)	0.14
2001	72	0.59	0.03	72	0.11	123 (115-132)	0.03
2002	65	0.62	0.03	67	0.02	109 (100-118)	0.04
2003	74	0.53	0.05	75	0.03	143 (130-158)	0.05
2004	87	0.63	0.04	88	0.02	140 (129-152)	0.04
2005	54	0.53	0.05	54	0.02	101 (91-113)	0.05
2006	84	0.55	0.04	84	0.02	154 (143-165)	0.04
2007	82	0.59	0.03	82	0.01	138 (130-148)	0.03
2008	41	0.57	0.04	41	0.01	72 (67-77)	0.04
2009	89	0.54	0.02	89	0.00	164 (157-171)	0.02
2010	92	0.51	0.02	92	0.00	182 (174-190)	0.02
2011	89	0.52	0.02	89	0.00	170 (162-178)	0.02
2012	103	0.50	0.02	103	0.01	208 (198-219)	0.03
2013	103	0.54	0.02	103	0.01	192 (183-201)	0.02

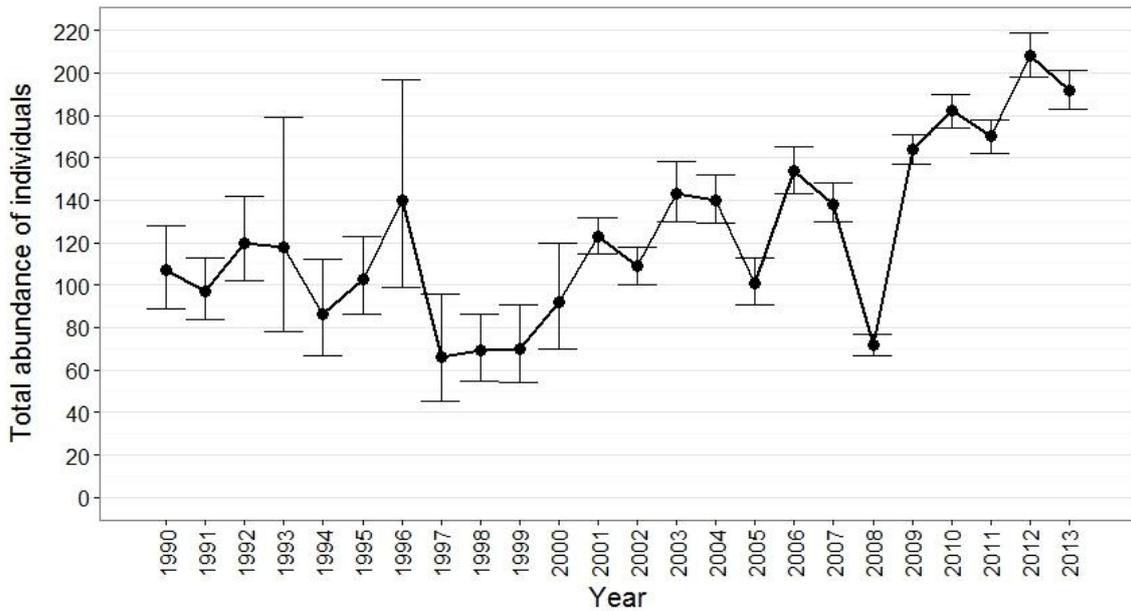


Figure 3.6. Annual estimates of total abundance (with 95% confidence intervals) of bottlenose dolphins using the overall area extending from the Moray Firth to the Firth of Forth for the study period 1990 to 2013.

As seen in (Table 3.2), the estimate of abundance of marked individuals ( $\hat{N}$ ) from 2005 onwards equalled the number of marked animals captured in those years, and the associated coefficient of variation (CV) was less than 0.03. In the years 2008, 2009, 2010 and 2013 the CV was 0.00. This is indicative of high capture probabilities in each sampling occasion within a year so that the probability of not capturing an animal over all sampling occasions is very small. For example, in the years 2008, 2009, 2010 and 2013 the estimated average probability of capture ( $\hat{p}_t$ ) was very high, close to 1 (0.994, 0.997, 0.998, and 0.997 respectively). This is illustrated by the following equation used for the abundance estimator, in which the denominator is the overall annual probability of capture (1 – the probability of not being captured):

$$\hat{N} = \frac{M_{t+1}}{1 - (1 - \hat{p}_1)(1 - \hat{p}_2)(1 - \hat{p}_3)(1 - \hat{p}_4)(1 - \hat{p}_5)}$$

where  $\hat{N}$  = annual abundance of marked animals in a population;  $M_{t+1}$  = the number of marked animals captured in a year;  $\hat{p}_t$  = probability that any individual will be encountered in sampling occasion  $t$ , and this example is for a five sampling occasion capture-recapture study.

### 3.3.2. Abundance of animals in St Andrews Bay area

Photo-identification data from all encounters with bottlenose dolphins in the subarea of St Andrews Bay for the years 2009 to 2013 resulted in capture histories for 68 marked individuals, based on high quality photographs taken during 60 boat-based field trips.

The most supported model from the candidate set was a model with constant survival, constant random emigration and a different capture probability for each sampling occasion (Model 1, Table 3.3). The number of marked individuals identified every year ranged between 39 and 43 individuals, and the proportion of marked individuals from the GLM model fitting ranged between 0.46 (CV=0.05) and 0.52 (CV=0.05) (Table 3.4).

Based on the most supported model the abundance of marked animals using St Andrews Bay ranged between 40 (CV=0.04) individuals in 2013 and 47 (CV=0.06) individuals in 2009. Once scaled up by means of the proportion of marked individuals, annual abundance estimates of animals using the area of St Andrews Bay ranged from 81 (95% CI 74-90) individuals in 2012 to 91 (95% CI 82-100) individuals in 2010 (Table 3.4). Compared to the total population size (*i.e.* abundance of animals using the overall study area from the Moray Firth to the Firth of Forth, Table 3.2), between 39% and 55% of the total population used the area of St Andrews Bay between 2009 and 2013.

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Table 3.3. Model selection to estimate abundance of animals in the area of St Andrews Bay. Models are ordered by their AICc.  $\Delta AICc$ : difference in the AICc compared to the minimum AICc; (.)=constant; (txs)=time-specific;  $\psi_t = \psi_t = 0$  = no emigration model;  $\psi_{(x)} \psi_{(x)}$  = Markovian emigration model;  $\psi_{(x)} = \psi_{(x)}$  = Random emigration model;

#	Model	Emigration	AICc	$\Delta AICc$	AICc Weights	Model Likelihood	# Par	Deviance
1	$\phi(.) \psi''(.) = \psi'(.) p(tx)$	Random	65.0858	0	0.51370	1.0000	27	609.9648
2	$\phi(.) \psi''(.) \psi'(.) p(tx)$	Markovian	67.3215	2.2357	0.16797	0.3270	28	609.9280
3	$\phi(.) \psi''(t) = \psi'(t) p(tx)$	Random	67.8481	2.7623	0.12909	0.2513	29	608.1713
4	$\phi(.) \psi''(.) \psi'(t) p(tx)$	Markovian	68.5749	3.4891	0.08976	0.1747	29	608.8981
6	$\phi(.) \psi''(t) \psi'(.) p(tx)$	Markovian	70.6445	5.5587	0.03189	0.0621	30	608.6736
7	$\phi(t) \psi''(.) = \psi'(.) p(tx)$	Random	70.9199	5.8341	0.02779	0.0541	30	608.9491
8	$\phi(.) \psi''(t) \psi'(t) p(tx)$	Markovian	71.7416	6.6558	0.01843	0.0359	31	607.4657
9	$\phi(t) \psi''(.) \psi'(.) p(tx)$	Markovian	73.208	8.1222	0.00885	0.0172	31	608.9321
10	$\phi(t) \psi''(t) = \psi'(t) p(tx)$	Random	74.157	9.0712	0.00551	0.0107	32	607.5651
11	$\phi(t) \psi''(.) \psi'(t) p(tx)$	Markovian	74.4219	9.3361	0.00482	0.0094	32	607.8300
14	$\phi(t) \psi''(t) \psi'(.) p(tx)$	Markovian	77.0313	11.9455	0.00131	0.0025	33	608.1124
15	$\phi(t) \psi''(t) \psi'(t) p(tx)$	Markovian	77.7948	12.709	0.00089	0.0017	34	606.5377
17	$\phi(.) \psi'' = \psi' = 0 p(tx)$	No emig	100.6054	35.5196	0	0	26	647.7463
18	$\phi(t) \psi'' = \psi' = 0 p(tx)$	No emig	102.5019	37.4161	0	0	29	642.8251

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Table 3.4. Annual estimates of total abundance of animals using the St Andrews Bay area from 2009 to 2013, with associated variance. ‘*Marked inds*’ = numbers of marked individuals captured;  $\theta$  = proportion of marked animals;  $\hat{N}$  = abundance of marked animals;  $\hat{N}_{total}$  = total abundance of animals. ‘% population abundance’ = estimate of abundance in St Andrews Bay as a proportion of estimated total population size (from Table 3.2).

Year	Marked inds	$\hat{\theta}$	CV ( $\hat{\theta}$ )	$\hat{N}$	CV ( $\hat{N}$ )	$N_{total}$ (95% CI)	CV ( $N_{total}$ )	% Population abundance
2009	43	0.52	0.05	47	0.06	90 (77-106)	0.08	55 %
2010	42	0.46	0.05	42	0.00	91 (82-100)	0.05	50 %
2011	42	0.50	0.05	42	0.00	83 (76-91)	0.05	49 %
2012	40	0.49	0.05	40	0.00	81 (74-90)	0.05	39 %
2013	39	0.48	0.06	40	0.04	84 (73-96)	0.07	44 %

### 3.3.3. Occurrence and abundance of animals in Aberdeenshire

In 2008, 56 different individuals (marked and unmarked) were identified from 2518 photographs taken in eleven trips between January and April. In 2012 and 2013, 661 and 656 photographs were taken, allowing the identification of 17 and 27 different individuals in each year. Over the three years, 79 identifiable individual dolphins (*i.e.* animals with enough natural marks to be matched to the existing catalogue of bottlenose dolphins for this population) were encountered in the waters between Stonehaven and Aberdeen. Thirteen of the individuals seen in 2008 were encountered again in the same area in 2012 or 2013, representing greater than 16% of the total number of dolphins encountered across the three years. Three individuals were seen in all three years and eight individuals were seen in both 2012 and 2013.

High quality photographs from 2012 and 2013 were used to investigate whether the individuals identified between Stonehaven and Aberdeen had also been sighted in other areas of the distributional range of the population (Moray Firth SAC or in St Andrews Bay) in those two years (Table 3.5). In 2012, two individuals were sighted between Stonehaven and Aberdeen and nowhere else, ten were also sighted in St Andrews Bay

and five in the Moray Firth SAC. In 2013, three individuals were sighted only between Stonehaven and Aberdeen, while another eight were also sighted further south off Montrose. Eleven individuals were also sighted in St Andrews Bay and another four in the Moray Firth SAC. Only one individual was sighted in all three areas in either year. All individuals identified between Stonehaven and Aberdeen in 2012 and 2013 had been seen in other parts of the distributional range in previous years.

Table 3.5. Re-sighting history of identified dolphins between the different areas in 2012 and 2013. Areas include Stonehaven to Aberdeen, St Andrews Bay, and Moray Firth SAC. \* *Another 8 individuals seen between Stonehaven and Aberdeen were also seen off Montrose.*

Areas sighted	Number of individuals	
	2012	2013
Stonehaven to Aberdeen only	2	3
Stonehaven to Aberdeen & St A Bay	10	11
Stonehaven to Aberdeen & Moray Firth SAC	5	4
All three areas	0	1
Total	17	19 *

### 3.3.4. Abundance of animals in Aberdeenshire

Between 2012 and 2013, 19 well-marked individuals were seen over seven capture occasions (three trips in 2012 and four trips in 2013). The model *Mh* (*Jackknife*) was selected as the most appropriate one for these data based on the goodness of fit tests calculated within program CAPTURE, and estimated an abundance of 31 well-marked individuals (CV=0.21, 95% CI 24 to 51 individuals). The total abundance of animals using the area between Stonehaven and Aberdeen in the years 2012 and 2013 was estimated to be 53 individuals (CV=0.23; 95% CI = 34 to 83 individuals), after inflating the estimate of well-marked individuals by the estimated proportion of well-marked animals of 0.58 (CV=0.09). The mixture model (Pledger, 2000) accounting for heterogeneity using two mixtures implemented in MARK indicated that approximately

25% (mixture proportion = 0.256; SE=0.11) of the individuals using the area between Stonehaven and Aberdeen in 2012 and 2013 had a higher probability of being seen compared to the other 75% of the individuals. This model estimated an abundance of 24 well-marked individuals (CV=0.18, 95% CI = 20 to 41 individuals). The total abundance of animals using the area between Stonehaven and Aberdeen in the years 2012 and 2013 based on this model was estimated to be 40 individuals (CV=0.20; 95% CI = 27 to 60 individuals).

### 3.3.5. Bias caused by unequal probability of capture

Not accounting for temporary emigration caused a positive bias in the abundance estimates of marked animals, with the abundance estimates from the null model (*Null model*:  $\phi(\cdot) \psi'=\psi''=0 p(\text{txs})$ ) being consistently larger than the abundance estimates from the model accounting for temporary emigration (*Emigration model*:  $\phi(\cdot) \psi''(t)=\psi'(t) p(\text{txs})$ ) (Figure 3.7 and Table 3.6). On the contrary, not accounting for heterogeneity in capture probabilities caused a negative bias, with the abundance estimates of marked animals from the null model being consistently smaller than those from the model accounting for heterogeneity of capture probabilities (*Heterogeneity model*:  $\phi(\cdot) p(\text{txs}) \pi(t)$ ).

The extent of bias in the annual estimates of abundance varied across years for both the bias caused by temporary emigration and by heterogeneity in capture probabilities (Table 3.6 and Figure 3.8). Not accounting for temporary emigration produced a larger bias during the 1990s, with a peak in 1997 in which the abundance estimate from the null model was 29% larger compared to the same estimate from the emigration model. From 1998 onwards, the temporary emigration bias decreased each year to reach a minimal 0-1% bias, except in 2005 and 2008, when the estimates of abundance from the null model were overestimated by 10% and 14%, respectively, compared to the results from the emigration model. On the other hand, not accounting for heterogeneity in capture probabilities seemed to have the greatest effect in the years 1997 to 2003, causing a negative bias between 13% and 58%. From 2004 to 2013, the bias was reduced to less than 5%, with the exception again of 2005 and 2008, for which the estimates of abundance were biased by 38% and 48%, respectively.

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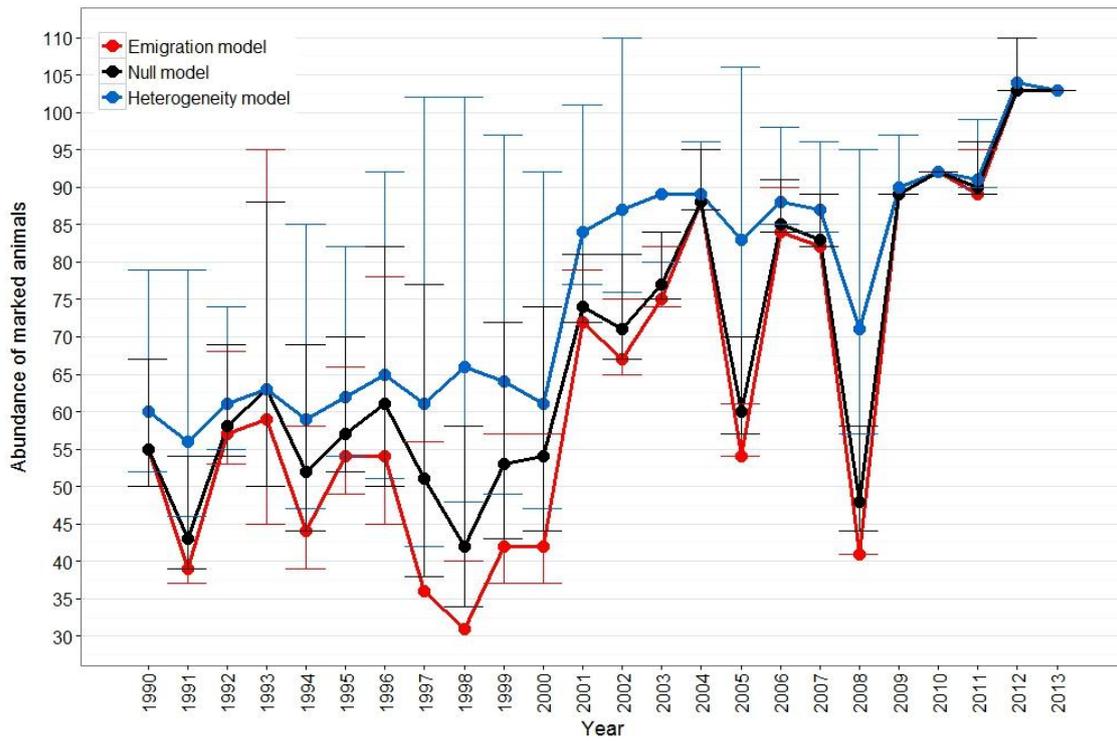


Figure 3.7. Annual abundance estimates of marked animals (95% CI) from 1990 to 2013 estimated using the emigration model (red), the null model (black) and the heterogeneity model (blue).

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Table 3.6. Annual abundance estimates of marked animals from the emigration model, the null model and the heterogeneity model for the years 1990 to 2013; LCI and UCI are the lower and upper 95% CI. The extent and direction (negative or positive) of bias in the abundance of marked animals estimated from the null model are shown when compared to the emigration model (*Emigration bias (%)*, left) and to the heterogeneity model (*Heterogeneity bias (%)*, right) (continued on next page).

Year	Emigration model				Emigration	Null model				Heterogeneity	Heterogeneity model			
	$\hat{N}$	CV	LCI	UCI	bias (%)	$\hat{N}$	CV	LCI	UCI	bias (%)	$\hat{N}$	CV	LCI	UCI
1990	55	0.07	50	67	0.00	55	0.07	50	67	-9.13	60	0.10	52	79
1991	39	0.05	37	46	9.22	43	0.08	39	54	-29.96	56	0.14	46	79
1992	57	0.06	53	68	1.73	58	0.06	54	69	-5.18	61	0.07	55	74
1993	59	0.20	45	95	6.38	63	0.15	50	88	0.00	63	0.15	50	88
1994	44	0.10	39	58	15.43	52	0.12	44	69	-13.50	59	0.15	47	85
1995	54	0.07	49	66	5.24	57	0.08	52	70	-8.74	62	0.11	54	82
1996	54	0.15	45	78	11.57	61	0.13	50	82	-6.61	65	0.15	51	92
1997	36	0.17	29	56	29.44	51	0.18	38	77	-19.63	61	0.23	42	102
1998	31	0.08	29	40	26.48	42	0.14	34	58	-57.79	66	0.20	48	102
1999	42	0.11	37	57	20.92	53	0.13	43	72	-20.92	64	0.18	49	97
2000	42	0.11	37	57	22.34	54	0.14	44	74	-13.03	61	0.18	47	92
2001	72	0.02	72	79	2.71	74	0.02	72	81	-13.55	84	0.07	77	101
2002	67	0.03	65	75	5.63	71	0.04	67	81	-22.54	87	0.09	76	110
2003	75	0.02	74	82	2.60	77	0.03	75	84	-15.59	89	0.08	80	111
2004	88	0.02	87	95	0.00	88	0.02	87	95	-1.13	89	0.02	87	96

Year	Emigration model				Emigration bias (%)	Null model				Heterogeneity bias (%)	Heterogeneity model			
	$\hat{N}$	SE	LCI	UCI		$\hat{N}$	CV	LCI	UCI		$\hat{N}$	CV	LCI	UCI
<b>2005</b>	54	0.02	54	61	9.93	60	0.05	57	70	-38.07	83	0.11	70	106
<b>2006</b>	84	0.01	84	90	1.18	85	0.02	84	91	-3.54	88	0.03	85	98
<b>2007</b>	82	0.01	82	89	1.20	83	0.02	82	89	-4.82	87	0.03	84	96
<b>2008</b>	41	0.00	41	41	14.64	48	0.07	44	58	-48.11	71	0.13	57	95
<b>2009</b>	89	0.00	89	89	0.00	89	0.00	89	89	-1.12	90	0.02	89	97
<b>2010</b>	92	0.00	92	92	0.00	92	0.00	92	92	0.00	92	0.00	92	92
<b>2011</b>	89	0.01	89	95	1.12	90	0.01	89	96	0.00	91	0.02	90	99
<b>2012</b>	103	0.01	103	110	0.00	103	0.01	103	110	-0.97	104	0.01	103	110
<b>2013</b>	103	0.00	103	103	0.00	103	0.00	103	103	0.00	103	0.00	103	103

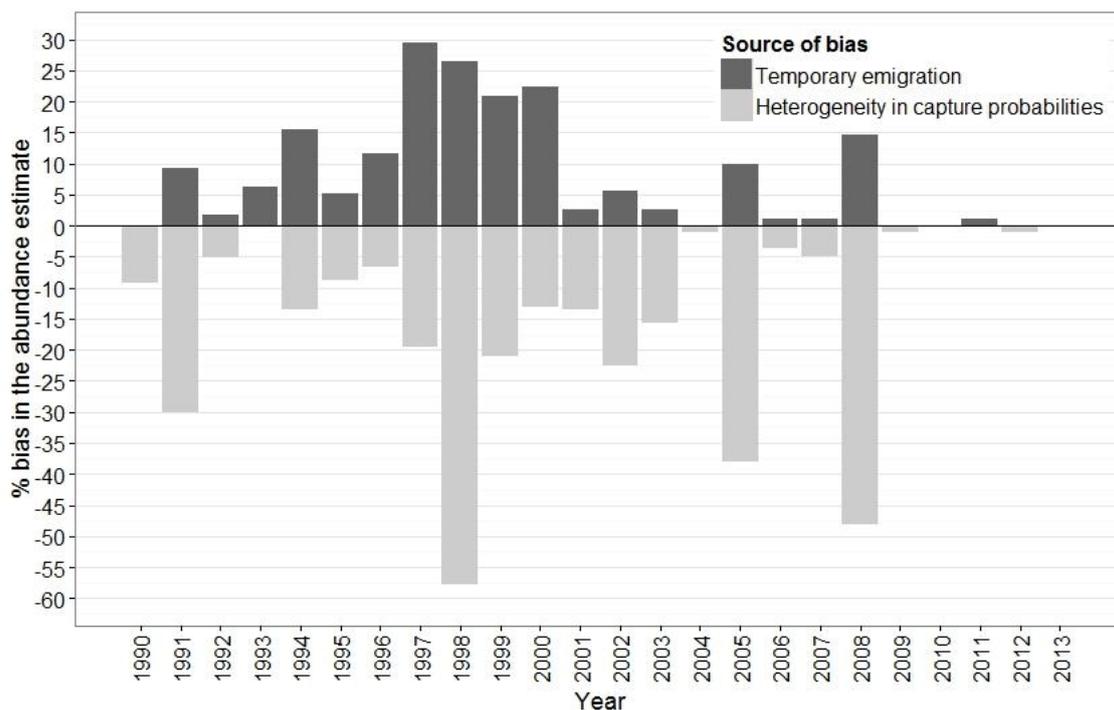


Figure 3.8. Percentage of bias in the abundance of marked animals ( $\hat{N}$ ) estimated from the null model caused by not accounting for either temporary emigration (top half, positive bias) or heterogeneity in capture probabilities (bottom half, negative bias).

### 3.4. Discussion

#### 3.4.1. Abundance estimates: bias from unequal catchability among individuals

Fitting a model that could account for both heterogeneity in capture probabilities and temporary emigration resulted in a model with a very large number of parameters (338), some of which were not estimated (see Chapter 2). When accounting for these sources of unequal catchability separately in Chapter 2, model selection indicated both the presence of heterogeneity of capture probabilities and temporary emigration. The comparisons between the estimates of abundance from the three fitted models reflected the expected biases: heterogeneity in capture probabilities causes a negative bias and the presence of temporary emigrants causes a positive bias (Pollock *et al.*, 1990, Kendall and Nichols, 1995).

The changes in the extent of both biases over the time series are a reflection of the changes in the probability of capturing individuals, which results from a combination of the behaviour of individual animals and variability in sampling effort. The bias caused by temporary emigration increased during the 1990s, coinciding with expansion in the population's range (Wilson *et al.*, 2004). Analysis of the photo-identification data collected between 1990 and 2000 showed that not all individuals were seen equally throughout the expanded distributional range; out of 54 individuals seen throughout those 11 years, 26% were only seen in the inner Moray Firth (*i.e.* the current SAC), 13% were seen in both the inner and outer Moray Firth, and 33% were seen both in the Moray Firth and south along the coast to St Andrews Bay (Wilson *et al.*, 2004). Because the photo-identification effort outside the Moray Firth did not start until the late 1990s, animals that were outside the Moray Firth during the 1990s were effectively temporary emigrants unavailable for capture, causing a positive bias in the abundance estimates from the null model. After 1999, the extent of the bias caused by temporary emigration decreased to generally less than 5%, coinciding with an increase in sampling effort across the population's distributional range.

Photo-identification data from the later years, in which effort was consistent throughout the study area, show that of the total number of marked individuals seen every year, around 30% are seen only around St Andrews Bay in any one year but are not encountered in other areas such as the Moray Firth. For example, from 2009 to 2012, 31, 31, 34 and 28 marked individuals were seen only in St Andrews Bay out of a total 89, 92, 89, and 103 marked animals seen in the entire study area, respectively. Thus, it is no surprise to have two peaks in the bias due to temporary emigration in 2005 and 2008, when no effort occurred in St Andrews Bay and a large proportion of the population had no chance to be captured. The years 2009 to 2013 had the most extensive and consistent photo-identification effort of the whole time-series across the entire population's distributional range. As a result of this high level of sampling effort, issues with temporary emigration completely disappeared, and estimates of abundance were not biased by it as in previous years (Figure 3.8 and Table 3.6).

The bias caused by heterogeneity in capture probabilities did not show such an obvious pattern as that caused by temporary emigration, although it was generally larger than the bias from temporary emigration throughout the study period. The extent of the bias caused by heterogeneity was generally larger in the years 1997 to 2003, which would correspond

approximately to the years between the population's expansion range and the increase in photo-identification effort. Variation in sampling effort over years may not introduce sampling heterogeneity as long as all animals have an approximately equal chance to be captured during each sampling period. However, this is unlikely to be true for those years in the late 1990s and early 2000s, when photo-identification effort outside the Moray Firth was minimal and inconsistent. Only small numbers of bottlenose dolphin groups were encountered outside the Moray Firth in that time period (Figure 3.2). For example, only one to five groups were encountered annually in St Andrews Bay between 1997 and 2001, far less than the average of 46 groups encountered in the Moray Firth for those same years.

Thus, the chances of encountering individuals that may have had a preference for the area of St Andrews Bay in those years were very small compared to the chances of encountering animals with a preference for the Moray Firth. Also, the estimated averaged capture probabilities within each year (*i.e.* secondary occasions) ranged from 0.21 to 0.26 in 1997, 1999 and 2000, compared to, for example, an average capture probability of 0.65 in 2013 (a year with consistent high sampling effort across the study area). Low capture probabilities increase the effects of heterogeneity of capture probabilities (Hammond, 1986); in years with high capture probability, it matters less if some individuals are more difficult to capture because most animals are captured eventually.

In 2003 and 2004, sampling methods used to photograph the animals in St Andrews Bay as part of the PhD project by Quick (2006) may have introduced extra sampling heterogeneity because survey design was driven by focal-follows of particular well-marked individuals instead of randomly photographing as many individuals as possible in all encounters. However, any bias caused by heterogeneity of capture probabilities was only evident in 2003 (16%) from the results (Table 3.6 and Figure 3.8), but not in 2004 (1%). It is likely that even if some sampling heterogeneity was introduced in those years in St Andrews Bay, it was minimized once the capture histories of animals in St Andrews Bay were combined with data from the other areas. Not accounting for heterogeneity of capture probabilities in the null model biased the abundance estimates in 2005 and 2008, by 38% and 48%, respectively. The lack of effort in St Andrews Bay in those two years resulted in those animals with preference for that particular area being out of the sample area in those two sampling occasions, which was likely to have introduced large amounts of sampling heterogeneity.

It is impossible to completely ensure equal probability of capture among individuals in cetacean studies such as this one. A good sampling design should minimize the bias caused by both heterogeneity in capture probabilities and temporary emigration (Evans and Hammond, 2004). In this study, increasing the sampling area in the later years (2009-2013) to cover the whole known population range had the effect of minimizing the bias from heterogeneity of capture probabilities and from temporary emigration to negligible levels between 0% and 1% (Table 3.6 and Figure 3.8). The abundance estimates suffered from opposite bias, with variable extent of the bias from both sources of unequal probability of capture varying among years. However, the results showed that the bias caused by heterogeneity in capture probabilities was generally higher than the bias from temporary emigration and thus suggest that accounting for heterogeneity of capture probabilities may be more important than accounting for temporary emigration to minimize the bias in abundance.

### **3.4.2. Total population size**

The differences in sampling effort over the years were reflected in the annual abundance estimates. For example, the substantial decrease in total abundance in 2005 (101 individuals, 95% CI 91-113) and 2008 (72 individuals, 95% CI 67-77) compared to previous and subsequent years reflects bias caused by unequal probability of capture among the individuals. The model used accounted for temporary emigration, caused by some individuals with preference for areas outside the Moray Firth not being available for capture in those years. However, the lack of sampling effort outside the Moray Firth in those two years introduced large levels of sampling heterogeneity in capture probabilities, which caused a much larger bias in the abundance estimates compared to the bias caused by temporary emigration (Table 3.6). Thus, the model accounting for heterogeneity of capture probabilities is probably a more appropriate one to estimate total population size for those years, with 156 (95% CI: 123-196) and 123 (95% CI: 95-160) individuals respectively.

In 1997 to 2000, total abundance estimates were some of the lowest in the time series (66 to 92 individuals). In those years, very few encounters with bottlenose dolphins occurred outside the Moray Firth despite the already expanded range of the population (Wilson *et al.*, 2004), and the bias due to temporary emigration was the greatest of the whole time series (Table 3.6). However, the negative bias caused by heterogeneity of capture probabilities was

even higher. After 2000, as photo-identification expanded outside the Moray Firth, the estimated abundance increased to similar sizes of earlier estimates from the mid-1990s.

The 120 (95% CI: 102-142) individuals estimated in 1992 and the 154 (95% CI: 143-165) individuals estimated in 2006 are similar to estimates reported in Wilson *et al.* (1999b) (129 animals, 95% CI: 110-174) and in Cheney *et al.* (2013) (195 animals, 95% CI: 162-253) for those two years, respectively. Wilson *et al.* (1999b) used a closed population model allowing for heterogeneity of capture probabilities (Mth, Chao *et al.*, 1992). However, Cheney *et al.* (2013) used a Bayesian state-space capture-recapture approach (Corkrey *et al.*, 2008) which prevents direct comparisons between abundance estimates from these two studies.

The abundance estimates obtained for 2009 to 2013 provide the most accurate indication of the current size of the Scottish east coast bottlenose dolphin population (Table 3.2). In those years, photo-identification effort occurred consistently from the Moray Firth south to the Firth of Forth, an area that represents the known range of the population, maximizing the probability of encountering animals, and thus minimizing the violation of equal catchability among individuals and the effect of temporary emigration. In that time period, the recapture probabilities between years were close to one (ranging from 0.93 to 0.99), and the average probabilities of capture in secondary sampling occasions within each year were also very high, ranging from 0.55 to 0.68. Estimated total population size ranged from 164 (95% CI: 157-171) to 208 (95% CI: 198-219) individuals between 2009 and 2013.

These estimates are remarkably similar to those for other coastal bottlenose dolphin populations, including in Sarasota Bay (160 individuals, Allen, 2014), the resident population in Choctawhatchee Bay, Florida ( $179 \pm 8$  SE, Conn *et al.*, 2011), the population in Kvarnerić, north-eastern Adriatic sea (103 to 165 individuals, Fortuna, 2006), the North Carolina southern population (141 individuals, 95% CI: 112-200, Read *et al.*, 2003), the population in the Shannon estuary, Ireland ( $113 \pm 16$  SE, Ingram, 2000), and the population in Cardigan Bay, Wales (150 individuals in the SAC and 248 individuals in the entire Cardigan Bay in 2007, Pesante *et al.*, 2008).

Because of the changes in the population's range and in the survey effort since the start of the study in 1989, it is not possible to draw firm conclusions about whether the population has increased over time or not. However, an update on earlier modelling work looking at the

viability of the study population (Corkrey *et al.*, 2008) suggests that the population is either stable or increasing (Cheney *et al.*, 2014).

### **3.4.3. Occurrence and abundance of animals off Aberdeenshire**

The results from this analysis suggest that over 25% of the estimated population used the coast of Aberdeenshire in 2012 and 2013 compared to the total population abundance estimates for those years (Table 3.2), and observations made during the encounters around Aberdeen harbour in 2012 and 2013 agree with other studies that have defined that area as a foraging spot for the dolphins (Sini *et al.*, 2005, Stockin *et al.*, 2006). Altogether, these results suggest that the waters of the Aberdeenshire coast are an important area for at least part of the population, as a foraging spot and/or as a transiting area between the most distant extremes of the population's range. Aberdeen harbour is a very active port with intense boat traffic, mostly from the oil and gas offshore industries but also from fisheries, transport and tourism industries. In 2012 and 2013 alone, 8142 and 7834 boats arrived into Aberdeen Harbour, 60-70% of which were large offshore supply vessels (Aberdeen Harbour Board, 2013). It remains unknown whether the intense boat traffic has a negative effect on the bottlenose dolphins in this area because reactions to the boats are highly variable (Sini *et al.*, 2005) but other activities such as dredging in the harbour have been linked to a decreased amount of time spent by the dolphins in it and thus potentially displacing them from a foraging patch (Pirota *et al.*, 2013). The importance of Aberdeenshire in the context of the conservation and management for this population is further discussed in Chapter 6.

### **3.4.4. Abundance of animals in St Andrews Bay**

The most supported model to estimate the abundance of animals using St Andrews Bay was a model that included constant (time independent) random temporary emigration. The support for models incorporating temporary emigration was expected, taking into account that St Andrews Bay represents only a part of the distributional range of this population, and that animals in this population range widely throughout the study area (Cheney *et al.*, 2013). Out of the 68 marked individuals included in the analysis and thus captured in St Andrews Bay at some point between 2009 and 2013, 31 individuals were not seen in St Andrews Bay for one or more years in that time period but were photographed in other areas of the distributional range (*i.e.* the Firth of Forth, the Grampian coast, or the Moray Firth). For example, in 2012,

40 marked individuals were captured in St Andrews Bay, while 18 marked individuals that had been seen in St Andrews in previous years (2009-2011) were captured in other areas in 2012. In the following year (2013), of those 18 individuals, 5 were captured again in St Andrews Bay, 10 were captured in other areas, and 3 were not captured at all.

The abundance estimates for 2009 to 2013 indicated that, on average, 47% of the population used St Andrews Bay every year. This is in accordance with the abundance and usage of St Andrews Bay in the summers of 2003 and 2004 estimated by Quick (2006), when again around half of the population used that area. These results show the importance of St Andrews Bay for this population, and highlight the need to reconsider the conservation and management actions currently implemented for this population, as discussed in the next section and in Chapter 6 together with the results from the usage of St Andrews Bay by the bottlenose dolphins of this population.

### **3.4.5. Conservation and management implications for the Moray Firth SAC**

The Scottish east coast bottlenose dolphin population is the only known resident population of this species in the North Sea, and the highest latitude coastal population of the species. Individuals within the population are known to be highly mobile, ranging from the inner Moray Firth to the Firth of Forth, which are separated by over 300km of coastline (Cheney *et al.*, 2013). Occasional sightings of known individuals from the study population have been reported outside the defined distributional range, for example near Whitley Bay in England (Thompson *et al.*, 2011), but the closest known coastal populations are in the Western Isles (Grellier and Wilson, 2003) and in Cardigan Bay, Wales (Pesante *et al.*, 2008). The Scottish east coast bottlenose dolphin population can thus be considered a largely discrete and isolated population. With an abundance of around 200 animals, this is a small population that may be vulnerable to anthropogenic and natural impacts, (*e.g.* oil and gas activities, renewable offshore energy activities, climate warming), as well as demographic stochasticity.

It is important to understand the spatio-temporal changes that may occur in the distribution and habitat use of a population, and try to incorporate those changes to improve the management and protection measures (Wilson *et al.*, 2004). This has been successfully done in the Azores, in which the initial design of a candidate Marine Protected Area (cMPA) was reviewed and extended after finding that the cMPA did not include core areas of high priority

habitat for the resident population of bottlenose dolphins (Silva *et al.*, 2012). In other cases, MPAs have been proposed on the basis of specific habitat use and activities for the population, such as feeding or resting activities (*e.g.* Notarbartolo-di-Sciara *et al.*, 2009, Ashe *et al.*, 2010). The current knowledge of the study population, based on photo-identification and genetic data, suggests that the Scottish east coast bottlenose dolphin population should be considered as a single unit for management purposes (Cheney *et al.*, 2013). The early data from the late 1980s and start of 1990s defined the boundaries of a cSAC that included the majority of the population's known range at that time (Wilson *et al.*, 1997a). Some years later, Wilson *et al.* (2004) suggested that the SAC might no longer be as effective in protecting this population after showing that it had expanded its range, and acknowledged the difficulties in the design and efficiency of the SAC for this population. Results from the monitoring programme show that the Moray Firth SAC is used by more than half of the population every year (Cheney *et al.*, 2014), but the boundaries of the SAC currently cover only a small proportion of the population's known distributional range. The estimates of abundance in St Andrews Bay from this analysis show this area is also currently used by half of the population, although it lacks protection against any anthropogenic activities in the area that may affect the population. These results question whether the SAC is still affording the protection and management of this population for which it was designed for, and suggest that the conservation and management plan for this population should be reviewed to adapt to the current knowledge (this is discussed further in Chapter 6).

### **3.5. Conclusions**

Heterogeneity of capture probabilities is an inherent issue in cetacean mark-recapture studies, and this study is no exception. Differences in sampling effort over years, combined with a range expansion of the population, introduced unequal probability of capture among individuals, which caused bias in abundance estimates that varied in extent and direction depending on the year. The results show the importance of minimizing these issues with a good sampling design, as well as accounting for it with the appropriate modelling approach. The last few years of the study period provide the most accurate population size for this population because of the extensive sampling effort across the distributional range. A total population of around 200 individuals is comparable to other coastal populations of bottlenose

### Chapter 3: Abundance of animals

dolphins but is still a small, discrete and isolated population that may be vulnerable to anthropogenic impacts.

The area of St Andrews Bay has been used by individuals from this population since the 1990s but very limited information has been available on the actual usage of the area. The current analysis provides the most up to date and accurate abundance estimates for this area, with approximately half of the population using St Andrews Bay on an annual basis.

## Chapter 4

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### A new approach to estimate fecundity rate from inter-birth intervals

#### 4.1. Introduction

Information on life-history parameters is important to understand a species' population dynamics in its ecological context, providing information on how populations adapt to their environment and respond to temporal changes (Yoccoz and Ims, 1999, Baker *et al.*, 2010). Accurate information on life-history parameters is also essential to evaluate a population's status and viability, and consequently provide the best information towards effective conservation and management (*e.g.* Kraus *et al.*, 2001, Runge *et al.*, 2004, Currey *et al.*, 2011). For example, information on life history parameters is needed for population viability analysis, a tool commonly used to assess which populations are most at risk of extinction, using stochastic simulation models to estimate the viability of small populations under different scenarios and to investigate how variation in life history parameters may affect a population's trend (Boyce, 1992, Caswell, 2001). Population viability analyses have been applied to a wide range of species including small and large terrestrial mammals (*e.g.* Armbruster *et al.*, 1999, Lindenmayer and Lacy, 2002), pinnipeds (*e.g.* Galimberti *et al.*, 2001, Winship and Trites, 2006), sirenians (*e.g.* Marmontel *et al.*, 1997) and cetaceans (*e.g.* Thompson *et al.*, 2000, Burkhart and Slooten, 2003, Hashimoto *et al.*, 2013).

The life history of long-lived mammals is characterised by low birth rates and high survival rates. In cetaceans, information on population parameters such as fecundity and survival rates is known only for a relatively small number of populations, primarily due to the difficulty in obtaining long-term longitudinal data needed to estimate these parameters. However, reproductive parameters such as fecundity rate are key to any population viability analysis. Fecundity rate can be defined as the percentage of reproductive females that reproduce annually in a population, and can be calculated as the inverse of the inter-birth interval. The inter-birth interval is defined as the time between successive births, including a gestation period, a lactation period and a resting

period. The gestation period is typically fixed within each species, generally between 10 to 12 months (Perrin *et al.*, 1984), but the lactation and resting period may vary among populations and individuals (Whitehead and Mann, 2000). In cetaceans, birth intervals vary markedly among species, mostly within odontocetes (see summary in Boness *et al.*, 2009), but are normally a minimum of two years except for minke whales and harbour porpoises that typically reproduce annually (Chivers, 2009).

The longest longitudinal studies of cetaceans began in the 1970s for populations of North Atlantic humpback whales (Clapham, 1996), Northeast Pacific killer whales (Olesiuk *et al.*, 1990), southern right whales off Peninsula Valdes (Payne *et al.*, 1990) and Sarasota Bay bottlenose dolphins (Wells and Scott, 1990). Other studies of population dynamics of bottlenose dolphins around the world have often used the Sarasota bottlenose dolphin population as a reference, using life-history parameters estimated from that population in the absence of data for a specific population (*e.g.* Thompson *et al.*, 2000, Fortuna, 2006, Currey *et al.*, 2009).

The approaches commonly used to estimate reproductive parameters based on photo-identification re-sighting data in cetaceans tend to be biased. Estimates of birth intervals tend to be positively biased because births will be missed when animals are not seen every year but negatively biased when the length of the study does not allow the longest birth intervals to be observed (Barlow and Clapham, 1997). There have been some attempts to model birth intervals in cetacean species, but only for right whales (Payne *et al.*, 1990, Cooke *et al.*, 2001) and humpback whales (Barlow, 1990, Barlow and Clapham, 1997); birth intervals have not been modelled for any dolphin species. Despite being one of the most well-known species of cetaceans with long-term data available for several populations, all available information on birth intervals for bottlenose dolphins has been reported as mean birth intervals from observed data (Table 4.1). Consequently, as described by Barlow and Clapham (1997), the birth intervals reported for bottlenose dolphins are likely to be biased as they are generally based on short study periods compared to the life span for this species and reproductive histories based on photo-identification data are likely to have gaps.

The approach developed by Barlow and Clapham (1997) estimates conditional birth-interval probabilities (*i.e.* the probability of giving birth a given number of years after a

previous birth, conditional on the animal not having calved since that birth) by means of maximum likelihood methods; the method was illustrated using individual sighting histories of humpback whales in the Gulf of Maine. Maximum likelihood estimators were used to find the values of birth-interval probabilities that maximise the probability of obtaining the observed 5 year birth histories of individual females following a birth event. The authors set a limit of 5 years for observations because of computational limitations and because the probability of calving after 5 years was very low in Gulf of Maine humpback whales. Monte Carlo simulations were then used to determine the bias and precision of the estimated birth-interval probabilities.

The analytical approach developed here is also based on the probability of a female giving birth, conditional on a previous birth a given number of years ago, from which an expected inter-birth interval can be estimated. The modelling of the birth probabilities is done in the framework of a generalized linear mixed model to account for variability among individuals and years. To develop and test the analytical approach, individual reproductive histories from the Scottish east coast bottlenose dolphin population (Wilson *et al.*, 1999b, Wilson *et al.*, 2004, Cheney *et al.*, 2013) collected over a period of 24 years were used. Simulated datasets mimicking the reproductive and sighting histories of females from the study population were used to validate the analytical method and investigate the most common data-driven biases related to the estimation of inter-birth intervals in cetaceans.

## Chapter 4: Fecundity rate

Table 4.1. Summary of available information on inter-birth intervals and fecundity rates for bottlenose dolphins (*T. truncatus*, *T. aduncus* and *T. sp*) (continues in next page)

Species	Inter-birth Interval (years)	Range (years)	No. of intervals	Fecundity rate	Study (years)	Source
<i>T. truncatus</i>	2 <sup>4</sup> and 3	-	2	-	5	Bearzi <i>et al.</i> (1997)
<i>T. truncatus</i>	3 (SD=1.15)	2 to 5 <sup>5</sup>	7	-	6	Haase and Schneider (2001)
<i>T. truncatus</i>	2.9 (SD=1.19)	2 to 7	49	0.22 (SD=0.089) <sup>6</sup>	12	Thayer (2007)
<i>T. truncatus</i>	3.3	2 to 6	33		12	Feingold and Evans (2013)
<i>T. truncatus</i>		3 to 11	7		16	Gaspar (2003)
<i>T. truncatus</i>	-	-	-	0.171 (SE=0.046) <sup>7</sup>	9	Fortuna (2006)
<i>T. truncatus</i>	3 <sup>8</sup>	-	-	-	-	Cockcroft and Ross (1989)
<i>T. truncatus</i>	2.1 <sup>9</sup> ; 3.5 <sup>10</sup> ; 5.34 <sup>11</sup>	(1.72-2.47) <sup>6</sup> ; (2.93-4.06) <sup>7</sup> ; (4.96-5.73) <sup>8</sup>	10 <sup>6</sup> ; 6 <sup>7</sup> ; 29 <sup>8</sup>	-	17	Henderson <i>et al.</i> (2014)

<sup>4</sup> Previous calf died.

<sup>5</sup> All three of the 2-year intervals and one of the 3-year intervals were from females that lost their calf on the first year.

<sup>6</sup> Fecundity rate = number of calves surviving to one year divided by the number of mature females that year.

<sup>7</sup> Fecundity rate = number of known newborn calves divided by the number of reproductive females that year.

<sup>8</sup> Interval estimated based on the duration of gestation and lactation and data on ovarian scars in stranded animals.

<sup>9</sup> Previous calf died within its first month.

<sup>10</sup> Previous calf died within its first year.

<sup>11</sup> Previous calf survived the first year.

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Species	Inter-birth Interval (years)	Range (years)	No. of intervals	Fecundity rate	Study (years)	Source
<i>T. truncatus</i>	-	-	-	0.144 (SD=0.244) <sup>3</sup>	8	Wells and Scott (1990)
<i>T. truncatus</i>	4.5	3 to 6	-	-	-	Wells <i>et al.</i> (1987)
<i>T. truncatus</i>	2.1 <sup>12</sup> ; 3.5 <sup>13</sup> ; 5.34 <sup>14</sup>	(1.72-2.47) <sup>6</sup> ; (2.93-4.06) <sup>7</sup> ; (4.96-5.73) <sup>8</sup>	10 <sup>6</sup> ; 6 <sup>7</sup> ; 29 <sup>8</sup>	-	17	Henderson <i>et al.</i> (2014)
<i>T. aduncus</i>	3.4 (SD=0.93)	1 to 6 <sup>15</sup>	26	-	8	Kogi <i>et al.</i> (2004)
<i>T. aduncus</i>	3.8 (SD=1.1) <sup>16</sup> ; 1.7 (SD=0.8) <sup>1</sup>	2.9 to 6 <sup>9</sup> ; 1.1 to 2.9 <sup>1</sup>	9 <sup>9</sup> ; 5 <sup>1</sup>	-	17	Steiner and Bossley (2008)
<i>T. species</i>	4.55 ± 1	3 to 6.2	33	-	11	Mann <i>et al.</i> (2000)

<sup>12</sup> Previous calf died within its first month.

<sup>13</sup> Previous calf died within its first year.

<sup>14</sup> Previous calf survived the first year.

<sup>15</sup> Intervals of 1 and 2 years were from females that lost their calf on the first year.

<sup>16</sup> Mean interval when the previous calf was weaned.

## 4.2. Methods

### 4.2.1. Dataset

For this analysis, bottlenose dolphin photo-identification data collected between 1989 and 2012 in the study area extending from the Moray Firth SAC to the Firth of Forth were used. Only data from the long-term collaborative project were included here; data from the PhD projects in 2003-04 (Quick, 2006) and 2006-07 (Islas-Villanueva, 2009) were excluded because addition of those datasets did not contribute any additional information on mother-calf pairs. Instead of limiting the sampling period to the summer months, as in Chapter 2, all available photo-identification data collected during the year were used, therefore maximising the probability of observing calves. Only photographs graded as high quality pictures according to the grading protocol detailed in Chapter 2 were used to construct the females' sighting and reproductive histories.

### 4.2.2. Assigning calves to mothers and determining year of birth

Assigning calves to mothers was based on the reliable presence of a dependent calf during field observations. Mother-calf pairs were confirmed if the potential mother and a calf were repeatedly seen swimming close together in two or more sampling trips. On the few occasions in which mother-calf pairs were observed in only one sampling trip, a mother-calf pair was only confirmed if the young of the year (*i.e.* calf under one year of age) was seen swimming in the characteristic echelon position throughout the encounter, the swimming position in which the young of the year is seen swimming very close to its mother's mid-lateral flank (Noren and Edwards, 2011). In addition, a number of mother-calf pairs observed in this population during 1990 to 1997 were confirmed by Grellier *et al.* (2003) based on a quantitative analysis of mother-calf association patterns developed for this population. That analysis also allowed confirmation that in this population the level of association of a calf with its mother remains consistently high during the first 2 to 3 years of life.

When a calf was first sighted as a young of the year (*i.e.* during the first year of life), the year of birth (YOB) equalled the year in which the calf was first seen. Young of the year were distinguished from older calves by their small size, pale skin, the presence of

prominent foetal folds and foetal lines, a characteristic head-out surfacing and nearly constant contact with the mother. However, in many cases a calf was not seen in its year of birth but as an older calf. When a female was not seen in a given year, but sighted repeatedly in subsequent years with an older calf, the YOB of the calf was determined by its relative size and prominence of foetal lines, which in this population remain visible at least during the first two years of life. Calves' YOB was only extrapolated as far as two years as studies from this and other populations of bottlenose dolphins suggest that a calf is likely to become independent of its mother around its third year (Mann *et al.*, 2000, Grellier *et al.*, 2003).

### 4.2.3. Constructing female calving histories

All the confirmed mother-calf pairs observed between 1989 and 2012 were used to construct individual calving histories for each reproductive female, describing whether a reproductive female had been observed or not each year and the year(s) she had given birth to a calf (Table 4.2). To maximise the number of individual calving histories included in the analysis, all known reproductive females in the population were included, regardless of their level of individual distinctiveness, as long as they had enough natural marks to be identified with confidence. Females with no permanent marks (*i.e.* no nicks or notches) were identified and matched between years based on temporary marks such as tooth rakes, scratches, scars, skin diseases, and white fin-fringes as well as based on unusual fin shapes and deformities. These types of marks are visible in the animals over different durations for this population, from weeks to years (Wilson *et al.* 1999), generally allowing them to be identified between years. To minimize misidentifying an individual, only high-quality photographs were used, and when a female had to be identified solely based on temporary marks, a minimum of three different recognizable marks were required to match the individual between years.

Several problems arise when using photo-identification data to describe individual calving histories: (1) births may be missed when females are not sighted in a year; (2) births may occur outside the sampling season (*e.g.* sampling trips occurred only between May and September in the second half of the study period); (3) a calf may die before the female is encountered for the first time following the birth; (4) a calf born to a female may be wrongly assigned to another female (*i.e.* creating a false positive in that

female's calving history); or (5) a calf born to a female may not be assigned at all (*i.e.* creating a false negative in the mother's calving history). In all these situations there is a risk of biasing the observed inter-birth intervals (IBIs).

Births occurring outside the sampling months could be still detected during the following season if the new calf survived and could then be recorded and correctly assigned to the mother. However, some births may have been missed if a new calf died before it was observed or when the association between a new calf and its mother could not be established.

Females in this population have been shown to be capable of reproducing on a 2-year cycle after the death of a newborn calf (Grellier 2000) but there is no record since the start of the study in 1989 of a female giving birth in two consecutive years under any conditions. Thus, it was assumed that a female could neither give birth in the year immediately after a known birth, nor in the year immediately before a known birth based on a gestation period of 12 months (Schroeder, 1990). Data from the individual calving histories were selected for each reproductive female in order to model the probability of giving birth a given number of years after a previous birth, starting on the YOY of the first calf to each female (highlighted in grey in Table 4.2).

Under the assumptions explained above, females that were not sighted in years pre- and post- a known birth event were assumed to be alive and without a young of the year, as long as the female was also seen alive in subsequent years. For example, female #440 had her first known calf in 2003 and three more calves in 2006, 2009 and 2012. She was sighted every year from 2003 to 2012 except in 2005. In that year, however, she was assumed to be alive and without a young of the year, based on the above assumptions, because she would have been pregnant in 2005 in order to have a calf in 2006. Thus, for female #440 the years 2003 to 2012 were all included to model the probability of birth (Table 4.2).

#### **4.2.4. Modelling the conditional probability of birth**

The conditional probability of birth is defined as the probability that a female will give birth  $t$  years after a previous birth, under the condition that the female survives and has not calved since the previous birth. Individual calving histories of reproductive female

bottlenose dolphins were used to model the conditional probability of birth as a function of the number of years since a female's previous birth (YSPB), regardless of the fate of the newborn calf. The analysis was done in the framework of a generalized linear mixed model (GLMM), which combines a generalized linear model (GLM) to estimate fixed effects and deals with non-normal data by using a link function from the exponential family, and a linear mixed model (LMM) that allows for random effects.

The conditional probability of birth was modelled using a binomial response variable with two possible outcomes: 0 if a female did not give birth in a year; 1 if a female gave birth in a year. The fixed effects initially included were the number of years since a previous birth (*YSPB*), its quadratic form ( $YSPB^2$ ) (to account for possible non-linearity in the relationship), and the number of calves previously born to each female (*borncalves*) (to allow experience to influence birth probability). Individual and temporal variation were modelled by including female identity (*femaleID*) and year (*Year*) as random effects, which avoids over-parameterization by reducing the number of parameters needed to be estimated. However, a model with *Year* as a factor variable was also fitted to investigate any temporal pattern in the probability of giving birth that may be explained by changes in the photo-identification effort over years and thus in the probability of detecting births over the study period. The GLMMs were fitted with a binomial error distribution and the logit link function (Bolker et al. 2009). All models were fitted using the lme4 package (Bates *et al.*, 2012) in R (R Core Team, 2014).

Model selection was based on Akaike Information Criterion (AIC) (Akaike 1973), and the model with the lowest AIC was selected as having the most support from the data. Model coefficients from the best model were then used to back-transform the probabilities of giving birth based on each YSPB included in the data (*i.e.* probability of having a calf after 1,2,...,*t* years since a female had her previous calf). These probabilities were used to estimate the mean inter-birth interval (see next section).

#### 4.2.5. Estimating expected inter-birth interval and fecundity rate

##### 4.2.5.1. *Expected inter-birth interval*

The expected inter-birth interval for the population was estimated in two steps. First, the probabilities of each inter-birth interval (IBI) in the population were estimated:

$$P (IBI = 1) = p_1,$$

$$P (IBI = 2) = (1 - p_1) * p_2,$$

$$P (IBI = 3) = (1 - p_1) * (1 - p_2) * p_3,$$

⋮

$$P (IBI = t) = (1 - p_1) * (1 - p_2) * p_t.$$

where  $P (IBI = 1), P (IBI = 2), \dots, P (IBI = t)$  are the probabilities of an inter-birth interval of 1, 2, ...,  $t$  years in the population; and  $p_1, p_2, \dots, p_t$  are the conditional probabilities of giving birth after 1, 2, ...,  $t$  years since the previous birth occurred (*i.e.* YSPB), back-transformed from the fitted model coefficients. The sum of the probabilities of each inter-birth interval in the population must equal one:

$$\sum_{IBI=1}^t P(IBI = t) = 1$$

Then, the expected inter-birth interval (*exp IBI*) was estimated as the sum of each of the inter-birth interval probabilities multiplied by the number of years in each interval:

$$exp IBI = \sum_{IBI=1}^t [P(IBI = t) * t]$$

To estimate a confidence interval around the expected IBI, a parametric bootstrap based on the fitted model was used. The variance-covariance matrix from the best model was used to obtain a new set of model coefficient values in each bootstrap replicate. Those coefficient values were then used to estimate a new expected IBI based on the formulae

given above. The 2.5% and 97.5% percentiles of 10,000 expected IBIs estimated by the bootstrap procedure defined the estimated 95% confidence interval.

#### **4.2.5.2. Fecundity rate**

The fecundity rate, defined here as the annual probability of a mature female having a calf, was estimated as the reciprocal of the expected inter-birth interval:

$$Fecundity\ rate = \frac{1}{exp\ IBI}$$

The 95% confidence interval around the estimated fecundity rate was estimated from the 2.5% and 97.5% percentiles of the 10,000 fecundity rate estimates from the parametric bootstrap procedure, as described above.

Due to variations in photo-identification effort over the study period, both in the number of sampling trips and in the size of the sampled area between 1989 and 2003, 50% (54 out of 108) of the observed new born calves could not be associated with reproductive females, and thus were excluded from the analysis. On the contrary, from 2004 to 2012 all observed new born calves could be associated with a reproductive female with confidence. To investigate the potential bias produced by failing to assign all calves to their mothers before 2004, the expected inter-birth interval and fecundity rate for the periods 1989 to 2003 and 2004 to 2012 were also estimated separately and compared.

#### **4.2.6. Simulation of female sighting and calving histories**

Simulated data samples that mimicked the dynamics of the reproductive females in the study population were constructed to validate the analytical method and to investigate the effects of various sources of potential bias in estimates of expected IBI and, therefore, fecundity rate. The simulation of data samples was done in two steps: (1) a biological process to generate a population of females and their calving histories; and (2) a sampling process to generate information on the sighting and calving histories of the females, mimicking the photo-identification survey effort conducted during the actual study.

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In the biological process, a matrix was created to store the survival and calving histories of a potential 1000 females that were projected for a time period of fifty years. Females entered the population based on a random process from a recruitment probability of  $(1 - \varphi_F) = 0.04$ , where  $\varphi_F = 0.96$  is the estimated probability of a female surviving from one year to the next that was estimated for the study population (apparent survival - see Chapter 2, section 2.3.2. ). Once in the population, the probability of surviving from one year to the next was generated for each female from a normal distribution with mean 0.96 and standard error 0.01 ( $\varphi_F$ ; apparent female survival). Each female could give birth to her first calf and thus become a reproductive female from a random process based on an observed mean annual fecundity rate of 0.25 (SE=0.03) in the study population. This mean was estimated from observed annual fecundity rates that were calculated annually between 1989 and 2012 by dividing the observed number of calves born to known females in a year by the number of known reproductive females sighted in that year. Females were considered to be reproductively active from their first calf birth. Finally, and conditional on having given birth to a first calf, each reproductive female could give birth in any subsequent year based on the conditional probabilities of having a calf after 1, 2, ...,  $t$  years (YSPB) from the best GLMM model.

A sampling process then was applied to the resulting simulated female calving histories to mimic photo-identification effort from a typical study. Reproductive females and calves might not be seen in a given year due to variation in effort, weather conditions or quality of the photographs taken (*i.e.* only high quality photographs will translate into an animal being captured); all these aspects are reflected in variation in the probability of capture. It was assumed that the probability of sighting a female was independent of her reproductive status and also that if a female was seen in a year in which she gave birth, her newborn calf would be correctly recorded. Annual capture probabilities ( $p_{YEAR}$ , for 1 to 50 years) were randomly generated for each year from a normal distribution with mean 0.74 and standard deviation 0.19, previously estimated for the study population in Chapter 2 using multi-state models. Individual heterogeneity in capture probability was also included in the sampling process to reflect that not all individuals have the same probability of capture in each sampling occasion. To do so, an individual coefficient of heterogeneity ( $Ind_{het}$ ) was randomly created for each simulated female from a normal distribution with a mean of one and standard deviation

equal to 0.1. Then, the resulting probability of capture for each individual female in any given year was calculated as the annual probability of capture multiplied by the individual coefficient of heterogeneity as  $p = (p_{YEAR} * Ind_{het})$ .

All simulations were conducted using software R (R Core Team, 2014).

#### **4.2.7. Using simulated data to validate the approach and to investigate potential biases**

Using the method described above, simulated data samples of female calving histories were generated and used to validate the analytical approach, in order to estimate and understand the expected bias when applied to the study population long-term dataset. To do so, 100 data samples of female sighting and calving histories were simulated. Each simulated data sample was processed in the same way as done previously with the real population data to: (1) select the data for analysis, (2) model the conditional probability of giving birth after 1, 2, ...,  $t$  years using GLMMs, and (3) estimate an expected inter-birth interval and fecundity rate with associated 95% CI using a parametric bootstrap based on the best fitted model. Then, based on the results, an overall mean expected inter-birth interval and fecundity rate were estimated for the 100 simulated data samples and compared to the study population's expected inter-birth interval and fecundity rate (*i.e.* based on the real data).

Simulated data samples were also used to investigate the effects of various sources of potential bias in estimates of expected IBI and, therefore, fecundity rate. These sources of potential bias were: (1) including gaps in the data (*i.e.* including all years of data starting at the year when the first calf is born, even when a female was not seen in a particular year and thus assuming that female was alive and did not give birth to a calf in that particular year); (2) assuming different capture probabilities in the collected photo-identification data; and (3) varying the length of the study.

To investigate the effect of including gaps in the data, 10 data samples were simulated and the sighting and calving histories were selected twice for each simulated dataset. The first time, data were selected following the same criteria applied to the study population (see 4.2.3. ) and thus excluding gaps in the sighting history of each female (*i.e.* years in which a female was not sighted, except the years immediately before or

after a known birth). The second time, data were selected to include all years after the first known birth, regardless of whether or not a female was sighted in subsequent years (*i.e.* including gaps in the data in years in which it was assumed that a female was seen without a new born calf despite not being seen). Each pair of selected data samples from each simulation was used to obtain an expected inter-birth interval and fecundity rate and the results were compared.

To investigate the effect of different capture probabilities on the estimation of expected inter-birth interval and hence fecundity rate, 10 different data samples were again simulated. Each simulated data sample was sampled eleven different times, each with a different probability of capture, ranging from a very low probability of capture of 0.1 to a probability of capture of 0.99 which effectively means capturing all the individuals. To do so, instead of using the study population's annual capture probability ( $p_{YEAR}$ ) as in the other simulations, the capture probability was randomly generated from a normal distribution with a mean that ranged from 0.1 to 0.99. For each mean, a standard deviation was calculated by multiplying the mean by the coefficient of variation from the study population's probability of capture to reflect the same variation. The individual coefficient of heterogeneity ( $Ind_{het}$ ) was generated for each female as for the other simulations. With this, the final probability of capture for each female in any given year was calculated by multiplying the annual probability of capture for that sampling process (0.1 to 0.99) and the individual coefficient of heterogeneity as  $p = (p_{YEAR} * Ind_{het})$ . Final probabilities of capture were bounded between 0 and 1 to avoid generating probabilities bigger than 1 when the annual probability of capture was very large (*e.g.*  $p_{YEAR} = 0.99$ ). Expected inter-birth interval and fecundity rate were estimated for each of the eleven sampled datasets from each simulated data sample, repeated for the ten simulated data samples, and the estimates were compared across simulated datasets with increasing probability of capture.

Finally, to investigate how different study lengths may affect estimation of the inter-birth interval and thus fecundity rate, another set of 10 simulated data samples of fifty years each was created. Each data sample was subsequently subsampled to select the 5, 10, 15, 20, and 25 most recent years. Selecting the most recent years avoided having low numbers of reproductive females at the start of each data series. Expected inter-

birth interval and fecundity rate were estimated and compared for each of the selected study lengths in each of the simulated data samples.

### 4.3. Results

#### 4.3.1. Observed calving histories

Between 1989 and 2012, 213 births of identified calves occurred in the study area, 162 of which (76%) could be assigned to 84 known females. For the other 51 calves (24%), there was insufficient confidence to assign it to a mother because the calf was seen in close proximity to different females. Three females were seen every year since their birth and had their first calf at 13, 6 and 9 years of age (ID numbers #433, 733, and 923, respectively, in Table 4.2). One other female with a known year of birth (ID #11) had her first known calf at the age of 14 years; however she was not seen in 1996 or 1998 when she could potentially have had a calf (Table 1.2).

Following the criteria described in section 4.2.3. calving histories were selected to model the probability of giving birth using GLMMs. The selected data corresponded to the calving histories of 78 females that had calves between 1987 and 2012 (Table 4.2, highlighted in grey) (the other six females had their first calf in 2012, the last year of the study period, and were excluded from the analysis). The selected 78 females each produced between 1 and 6 calves, summing to a total of 155 calves (Table 4.2).

The total number of calves born in any one year varied greatly among years, ranging from 0 to 20 calves, partially caused by changes in sampling effort (*i.e.* years with less effort offer fewer opportunities to detect births) (Figure 4.1 and Table 4.2). From 2004 onwards, all new born calves could be associated to a reproductive female. The annual number of reproductive females alive (*i.e.* those known to have reproduced at least once between 1987 and any given year) also varied, with a maximum of 60 reproductive females captured in 2012 (Figure 4.1 and Table 4.2). The observed inter-birth intervals of females sighted annually between known births ranged between 2 and 9 years (Figure 4.2). There were seven intervals of 2 years. In five cases, the first calf was known to be dead or presumed dead because it was not seen again after the first year; in the other two cases, the first calf was successfully weaned at 2 years of age.

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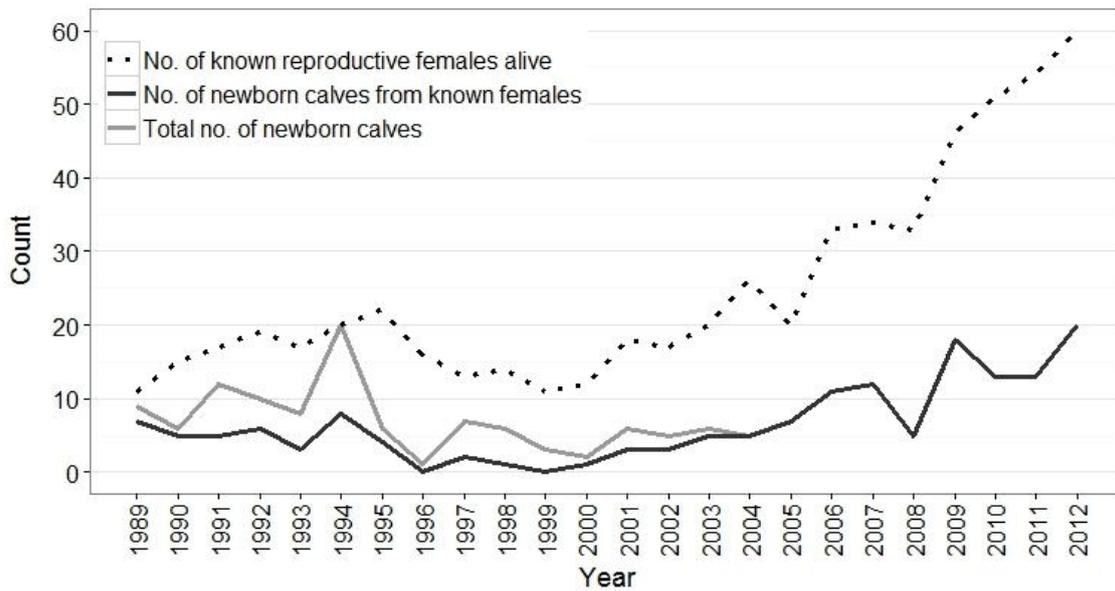


Figure 4.1. Annual counts of newborn calves (from known females and total number) and reproductive females from photo-ID data collected between 1989 and 2012.

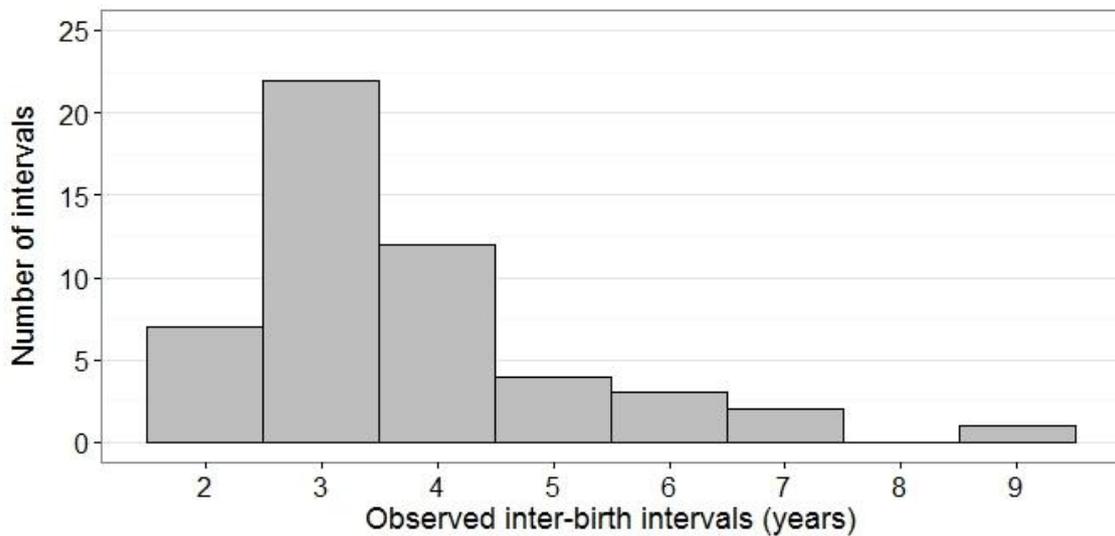


Figure 4.2. Observed inter-birth intervals of females sighted annually between known births from 1989 to 2012.

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Table 4.2. Sighting and calving histories of reproductive females from 1987 to 2012. Data used to model the probability of birth are highlighted in grey. Notations: “0” = not sighted, “1” = sighted, “●” = with newborn calf, “-” = female still to be born or known to be dead. Total number of calves (# C) and reproductive females (# F) by year are shown at the bottom of the table (continues on next two pages). ●<sup>J</sup> Year of birth estimated when photo-ID effort started in 1989 and the calves were seen in association with their mothers.

ID #	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	# C
4			1	●	0	1	1	●	1	1	0	0	0	●	1	1	1	1	0	●	1	1	0	0	0	0	4
9		● <sup>J</sup>	1	1	1	0	0	1	1	1	0	0	0	0	1	0	1	1	0	●	1	0	1	1	1	1	2
11	-	0	1	1	1	1	1	1	1	0	1	0	1	1	1	●	1	1	1	1	●	1	1	●	1	●	4
24			1	1	1	●	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
27		● <sup>J</sup>	1	1	●	1	1	1	1	0	●	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
30			●	1	1	●	1	1	1	0	1	1	1	1	●	1	1	1	0	1	0	0	●	1	1	1	4
31			1	1	1	1	1	1	●	1	1	1	1	1	●	1	1	1	●	1	1	1	1	1	1	●	4
52			1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	●	1	1	1	●	1	●	3
55			1	1	●	1	0	●	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	2
58			1	0	●	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
61			1	1	0	1	0	●	1	0	1	1	1	1	1	1	0	1	0	●	1	1	0	0	0	0	2
64	● <sup>J</sup>		1	1	1	1	●	1	1	1	●	1	1	1	1	1	●	1	1	1	●	1	1	1	1	●	6
68			●	1	0	●	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	●	1	1	3
79			1	1	1	●	0	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1
85	● <sup>J</sup>		0	●	1	●	1	●	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
94			●	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
98			0	1	1	●	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
106			0	●	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
107			0	●	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
116			1	1	1	1	1	1	1	0	0	1	1	0	1	1	1	●	0	1	0	0	1	1	1	1	1
120			●	1	1	1	1	●	1	0	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	2
122			●	1	1	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
165			1	1	1	1	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
191			●	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
192			0	●	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
209			0	0	1	0	1	0	●	1	0	0	0	0	1	1	0	1	1	0	0	1	1	●	0	1	2
213			0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
227			1	0	1	1	0	●	1	1	0	0	0	0	1	1	1	1	0	1	1	0	1	●	1	1	2
237			●	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
240			0	1	1	1	1	1	●	1	1	1	1	1	1	1	1	●	0	0	1	0	●	1	1	●	4
241			0	0	●	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
307			0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	1	1	●	1	1	●	1	1	●	3
323			0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	●	1	1	●	2
344			1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	1	●	1	1	1
391			0	0	0	0	●	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
430			0	0	0	0	0	1	1	0	0	0	0	0	1	●	1	1	1	1	1	●	1	1	1	1	2
433			-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	●	1	1	1	1	0	1

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ID #	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	# C	
449			0	0	0	0	•	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
440			0	0	0	0	0	1	1	1	1	0	0	0	1	1	•	1	0	•	1	1	•	1	1	•	1	4
571			0	0	0	0	0	0	•	1	1	1	1	1	1	0	1	1	•	1	1	0	•	1	1	1	1	3
578			0	0	0	0	0	0	0	1	1	1	1	1	1	1	•	1	1	1	•	1	1	1	•	1	1	3
580			0	0	0	0	0	0	0	1	0	1	1	0	1	1	•	1	1	1	1	1	1	1	•	1	1	2
673			0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	1	1	•	1	1	1	1	1	1
732			0	0	0	0	0	0	0	0	0	•	1	1	1	1	•	1	1	1	•	1	1	1	•	1	1	4
733			-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	•	1	1	•	1	0	0	0	0	0	2
744			0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	•	1	1
745			0	0	0	0	0	0	0	0	0	0	1	0	1	•	1	1	•	1	1	•	1	1	1	1	1	3
773			0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	•	0	1	•	1	1	•	1	•	1	4
788			0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	•	1	1	0	0	0	0	0	1
800			0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	•	1	1	•	1	0	1	2	
805			0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	•	1	1	1	
809			0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	•	1	0	1	1	1	•	1	2	
816			0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	•	1	1	
820			0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	•	1	1	1	•	1	2	
832			0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	•	1	
866			0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	•	1	1	1	1	
872			0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	•	1	0	1	1	1	1	•	2	
880			0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	•	1	1	1	•	1	2	
909			0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	•	1	1	•	1	1	1	2	
913			0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	•	1	1	•	1	1	•	1	1	3	
923			-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	1	1	1	1	1	1	•	1	1	1	
932			0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	•	1	1	•	1	•	1	3	
963			0	0	0	0	0	0	0	0	0	0	0	0	0	•	0	1	1	1	•	1	1	•	1	1	3	
965			0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	•	1	1	0	•	1	1	•	3	
969			0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	•	1	1	1	•	1	2	
985			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	•	1	
1002			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1	•	1	2	
1026			0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	•	1	1	1	1	
1027			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	•	1	1	
1028			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1	1	1	1	
1029			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1	1	•	2	
1030			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	•	1	1	•	1	1	1	1	2	
1043			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	•	1	1	
1054			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	•	0	1	1	1	1	1	
1058			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1	
1060			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	•	1	1	1	
1062			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	•	1	1	•	2	
1064			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1	
1075			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	•	1	1	1	1	
1076			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	•	1	1	
1090			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	•	1	1	1	

ID #	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	# C	
1092			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1
1096			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	•	1	1	1	•	2
1100			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	•	1
# F			11	15	17	19	17	20	22	16	13	14	11	12	18	17	20	26	20	33	34	33	46	51	54	60		
# C	2	2	7	5	5	6	3	8	4	0	2	1	0	1	3	3	5	5	7	11	12	5	18	13	13	20	161	

**4.3.2. Conditional probability of giving birth and expected inter-birth interval for the study population**

**4.3.2.1. Study period 1989-2012**

Based on data selected for the entire study period 1989 to 2012, the most supported model based on the AIC score included the linear and quadratic terms of *YSPB* as fixed effects, and *FemaleID* and *Year* as random effects (Model 2, AIC = 288.0, Table 4.3). The next two models (Models 4 and 6, AIC = 288.4 and 288.9) had effectively the same AIC value and thus were considered to support the data equally well. However, for purposes of estimating the mean IBI and confidence interval, the coefficients estimated from the best model (Model 2) were used.

The model with *Year* as a factor variable received almost as much support as the top three models (Model 9, Table 4.3). The model coefficients for the factorial parameter *Year* did not show a significant trend ( $p$ -value = 0.12), but this model and the top two models with *Year* as random effect suggests that there was significant year to year variability in the probability of giving birth.

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Table 4.3. GLMM candidate model set based on the data period 1989-2012 showing the model parameter specification (rand = random effect; factor = factor variable), residual deviance and AIC ordered from low to high values; b = conditional probability of giving birth; YSPB = Years Since Previous Birth (linear term); YSPB.Q = Years Since Previous Birth (quadratic term); borncalves = number of previous births to each female).

Model#	Model parameter specification	Deviance	AIC
2	b ~YSPB+ YSPB.Q + femaleID (rand) + Year (rand)	278.0	288.0
4	b ~YSPB + YSPB.Q + Year (rand)	280.4	288.4
6	b ~YSPB + YSPB.Q + femaleID (rand)	280.9	288.9
9	b ~YSPB + YSPB.Q + Year (factor) + femaleID (rand)	233.8	289.8
1	b ~YSPB + YSPB.Q + borncalves + femaleID (rand) + Year (rand)	278.0	290.0
3	b ~YSPB + YSPB.Q + borncalves + Year (rand)	280.4	290.4
5	b ~YSPB + YSPB.Q + borncalves + femaleID (rand)	280.6	290.6
7	b ~YSPB + femaleID (rand) + Year (rand)	294.5	302.5
8	b ~YSPB.Q + femaleID (rand) + Year (rand)	317.9	325.9

The probability of giving birth conditional on the number of years since the previous birth (YSPB), based on the best model, increased from 0.005 at YSPB = 1 year to 0.609 at YSPB = 6 years and then decreased to 0.205 at YSPB = 9 years (Figure 4.3 and Table 4.4). Based on these, the probability of each inter-birth interval (IBI) was calculated, with the highest being 0.307 for IBI = 4 years, and the lowest at both extremes of the range of observed IBIs (1 and 9 years), with a probability of 0.05. Together, the probabilities of each IBI summed up to 0.982, which is close to the expected 1 and indicates that the probability of IBIs greater than 9 years was very small. The expected IBI for the study population over the period 1989-2012 was calculated as 4.49 years (95% CI = 3.94 to 4.93 years). The fecundity rate estimated from the expected inter-birth interval was 0.222 (95% CI = 0.218 to 0.253), meaning that, on average, 22% of the mature females produced newborn calves (male and female) annually in this population.

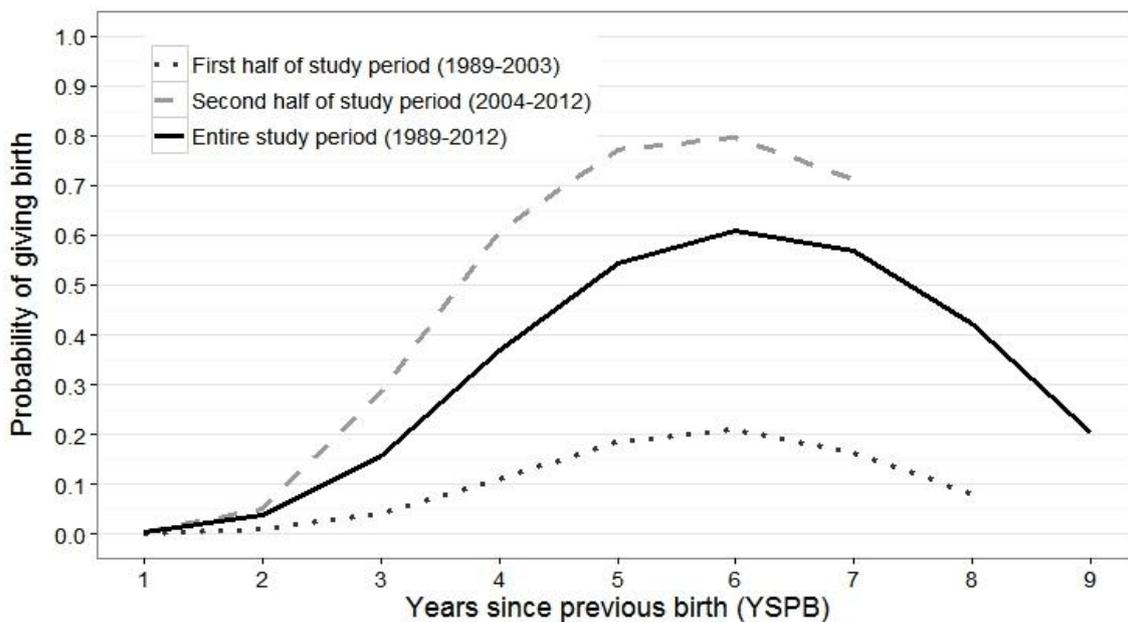


Figure 4.3. Probability of giving birth conditional on the number of years since the previous birth occurred (YSPB) based on the best model output for the entire study period 1989-2012, and for the time periods 1989-2003 and 2004-2012.

Table 4.4. Conditional probability of giving birth after 1, 2 ... t years (YSPB) and estimated probability of each inter-birth interval (IBI) for the periods 1989-2012, 1989-2003, and 2004-2012.

YSPB / IBI (years)	1989-2012		1989-2003		2004-2012	
	Conditional probability of birth	IBI probability	Conditional probability of birth	IBI probability	Conditional probability of birth	IBI probability
1	0.005	0.005	0.001	0.001	0.004	0.004
2	0.036	0.037	0.009	0.009	0.051	0.051
3	0.157	0.151	0.040	0.040	0.283	0.267
4	0.369	0.298	0.109	0.104	0.610	0.413
5	0.543	0.277	0.185	0.157	0.770	0.204
6	0.609	0.142	0.209	0.144	0.796	0.048
7	0.570	0.052	0.162	0.089	0.712	0.10
8	0.421	0.016	0.082	0.037	-	-
9	0.205	0.005	-	-	-	-
Σ	-	0.982	-	0.580	-	0.996

#### 4.3.2.2. Study period 1989-2003

For the period 1989 to 2003, the selected data included 37 females that had 53 calves in total with 16 complete birth intervals observed that ranged between 2 and 6 years. After a birth event, the maximum number of consecutive years in which a female was seen every year without giving birth was 8 years (female #240, Table 4.2). The most supported model for these data was again a model that included the linear and quadratic terms of *YSPB* as fixed effects, and *FemaleID* and *Year* as random effects (Table 4.5).

Table 4.5. GLMM candidate model set based on the data period 1989-2003 showing the model parameter specification (rand = random effect; factor = factor variable), residual deviance and AIC ordered from low to high values; b = conditional probability of giving birth; YSPB = Years Since Previous Birth (linear term); YSPB.Q = Years Since Previous Birth (quadratic term); borncalves = number of previous births to each female).

Model#	Model parameter specification	Deviance	AIC
2	b ~YSPB + YSPB.Q + femaleID (random) + Year (random)	87.9	97.9
4	b ~YSPB + YSPB.Q + Year (random)	90.3	98.3
6	b ~YSPB + YSPB.Q + femaleID (random)	90.4	98.4
3	b ~YSPB + YSPB.Q + borncalves + Year (random)	89.3	99.3
5	b ~YSPB + YSPB.Q + borncalves + femaleID (random)	89.9	99.9
1	b ~YSPB + YSPB.Q + borncalves + femaleID (rand) + Year (rand)	87.6	99.6
7	b ~YSPB + femaleID (random) + Year (random)	92.1	100.1
8	b ~YSPB.Q + femaleID (random) + Year (random)	97.3	105.3
9	b ~YSPB + YSPB.Q + Year (factor) + femaleID (random)	65.2	107.2

The probability of giving birth conditional on the number of years since the previous birth (YSPB) based on the best model was generally much lower than with the data from the entire study period (range 0.001 to 0.209) (Figure 4.3) and the probability of each inter-birth interval ranged between 0.001 for an IBI = 1 year to 0.157 for an IBI = 5 years (Table 4.6). The probabilities of each IBI summed only to 0.580, much lower than the expected value of 1. The expected inter-birth interval for the study population over the period 1989-2003 was 3.12 years (95% CI = 1.11 to 5.81 years). The fecundity

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rate estimated from the expected inter-birth interval was 0.320 (95% CI = 0.172 to 0.901). This means that, on average, 32% of the mature females produced newborn calves (male and female) annually in this population for the time period 1989 to 2003.

The analytical approach was able model the conditional probabilities of birth based on the data from this study period but produced very small probabilities for each of the IBIs that did not sum to one as expected, indicating a failure to allocate much of the probability to the observed inter-birth intervals. Thus, the method provided a poor description of the data for this time period and the results should be used with caution, as discussed below (section 4.4.1.2. ).

The data for 1989-2003 had a large proportion of females with a single birth event (26 out of 37 females, 70% of the females), which was suspected to cause the failure of the approach when applied to this dataset. To investigate this, models were fitted to a subset of the data for 1989-2003 containing only females with two or more birth events (11 females). The most supported model for these data produced higher conditional probabilities of birth, and the probabilities of each IBI summed to 0.935 as expected (Table 4.6). Excluding females with a single birth produced an expected inter-birth interval over the period 1989-2003 of 4.15 years (95% CI = 2.79 to 4.67 years). The fecundity rate estimated from the expected inter-birth interval was 0.241 (95% CI = 0.214 to 0.358). The implications of including a large proportion of females with a single birth for the performance of the analytical method are further discussed in section 4.4.1.2. .

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Table 4.6. Conditional probability of giving birth after 1, 2 ... t years (YSPB) and estimated probability of each inter-birth interval (IBI) for the period 1989-2012 for datasets including all the females ('Original data') or just females with more than one birth event ('Females with >1 birth')

YSPB / IBI (years)	1989-2003 Original data		1989-2003 Females with >1 birth	
	Conditional probability of birth	IBI probability	Conditional probability of birth	IBI probability
1	0.001	0.001	0.017	0.017
2	0.009	0.009	0.050	0.049
3	0.040	0.040	0.136	0.127
4	0.109	0.104	0.306	0.247
5	0.185	0.157	0.541	0.303
6	0.209	0.144	0.749	0.192
7	0.162	0.089	-	-
8	0.082	0.037	-	-
9	-	-	-	-
Σ	-	0.580	-	0.935

### 4.3.2.3. Study period 2004-2012

Between 2004 and 2012, there were 58 females that gave birth to 101 calves generating 43 complete observed birth intervals, with a maximum of 7 years. For this second part of the study period, the most supported model included the linear and quadratic terms of *YSPB* as fixed effects, but only *FemaleID* as a random effect (AIC = 169); a lower AIC score than the following three models (each with AIC=171) (Table 4.7).

The conditional probability of giving birth based on the best model ranged between 0.004 and 0.712 (Figure 4.3) and the probability of each inter-birth interval ranged between 0.004 for IBI = 1 year to 0.413 for IBI = 4 years (Table 4.8). The probabilities of each IBI summed to 0.996, very close to the expected value of 1, indicating that the probability of IBIs greater than 7 years was small. The expected inter-birth interval for the study population over the period 2004-2012 was 3.93 years (95% CI = 3.58 – 4.21 years) and the fecundity rate 0.254 (95% CI = 0.237 to 0.278). This means that, on

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average, 25% of the mature females produced newborn calves (male and female) annually in this population for the time period 2004 to 2012.

Table 4.7. GLMM candidate model set based on the data period 2004-2012 showing the model parameter specification (rand = random effect; factor = factor variable), deviance and AIC ordered from low to high values; b = conditional probability of giving birth; YSPB = Years Since Previous Birth (linear term); YSPB.Q = Years Since Previous Birth (quadratic term); borncalves = number of previous births to each female).

Model#	Model parameter specification	Deviance	AIC
6	b ~YSPB + YSPB.Q + femaleID (random)	161.3	169.3
4	b ~YSPB + YSPB.Q + Year (random)	163.2	171.2
5	b ~YSPB + YSPB.Q + borncalves + femaleID (random)	161.2	171.2
2	b ~YSPB + YSPB.Q + femaleID (random) + Year (random)	161.3	171.3
3	b ~YSPB + YSPB.Q + borncalves + Year (random)	163.1	173.1
1	b ~YSPB + YSPB.Q + borncalves + femaleID (random)+Year(random)	161.2	173.2
7	b ~YSPB + femaleID (random) + Year (random)	169.3	177.3
9	b ~YSPB.Q + femaleID (random) + Year (random)	154.7	180.7
8	b ~YSPB + YSPB.Q + Year (factor) + femaleID (random)	185.8	193.8

The proportion of females with a single birth event in this dataset was much lower (23 females out of 58 females, 40%) than for the 1989-2003 data, but models were also fitted to data excluding females with a single birth as done with the first time period. The most supported model for these data produced slightly higher conditional probabilities of birth, and the probabilities of each IBI summed to 0.999 (Table 4.8). Excluding females with a single birth produced an expected inter-birth interval over the period 1989-2003 of 3.69 years (95% CI = 3.33 to 4.04 years). The annual fecundity rate estimated from the expected inter-birth interval was 0.271 (95% CI = 0.247 to 0.300).

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Table 4.8. Conditional probability of giving birth after 1, 2 ... t years (YSPB) and estimated probability of each inter-birth interval (IBI) for the period 2004-2012 for datasets including all the females ('Original data') or just females with more than one birth event ('Females with > 1 birth')

YSPB / IBI (years)	2004-2012 Original data		2004-2012 Females with > 1 birth	
	Conditional probability of birth	IBI probability	Conditional probability of birth	IBI probability
1	0.004	0.004	0.004	0.004
2	0.051	0.051	0.066	0.066
3	0.283	0.267	0.373	0.347
4	0.610	0.413	0.725	0.423
5	0.770	0.204	0.860	0.138
6	0.796	0.048	0.883	0.020
7	0.712	0.10	0.830	0.002
8	-	-	-	-
9	-	-	-	-
Σ	-	0.996	-	0.999

### 4.3.3. Simulated data samples to validate the approach and investigate potential biases

#### 4.3.3.1. Validation of the analytical approach

Expected inter-birth intervals estimated from the 100 simulated data samples ranged from 4.23 to 4.50 years with an overall mean of 4.37 years. Compared to the study population's expected inter-birth interval of 4.49 years (95% CI = 3.94 to 4.93), the expected inter-birth interval from the simulated data was, on average, 2.8% smaller than from the study population, although all fell within the estimated 95% confidence interval. The fecundity rate of the simulated data samples ranged between 0.222 to 0.236, with an overall mean of 0.229, and thus 2.8% larger than the fecundity rate estimated for the study population (0.222; 95%CI = 0.218 – 0.253).

#### 4.3.3.2. *Effects of including gaps in the data*

Including gaps in the sighting and calving histories during the data selection process consistently resulted in larger estimates of the inter-birth interval (mean expected IBI = 5.95 years), overestimated by 36%, on average, compared to the estimates from data without gaps (mean expected IBI = 4.36 years), and generally with wider associated 95% CI (Figure 4.4). The fecundity rate was underestimated by 26%, on average, when gaps were included in the data selection (mean fecundity rate = 0.168) compared to data without gaps (mean fecundity rate = 0.229).

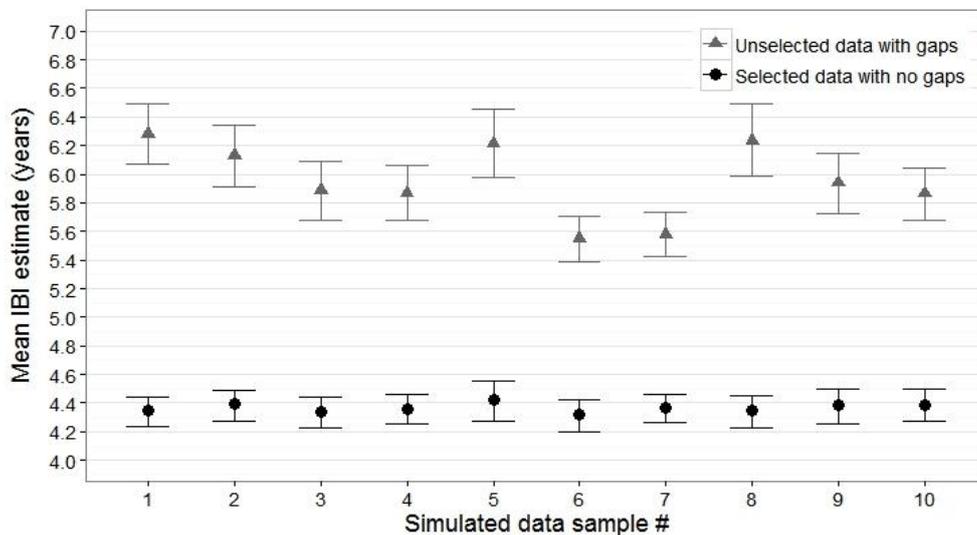


Figure 4.4. Expected inter-birth interval (IBI) estimates (with 95% CI) from ten simulated data samples for calving histories selected with or without gaps in the females' sighting histories.

#### 4.3.3.3. *Effects of different probabilities of capture*

Simulated datasets sampled with a probability of capture of 0.99 resulted in a mean inter-birth interval estimate of 4.44 years, on average, ranging between 4.32 to 4.53 years. The fecundity rate was 0.225 on average (range 0.221 to 0.231). These estimates were taken as a reference to investigate the effect of different probabilities of capture on the resulting expected inter-birth interval estimates and fecundity rates, as summarized in Table 4.9.

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Table 4.9. Expected inter-birth interval (IBI) and fecundity rate estimates averaged for each group of 10 simulated datasets sampled with a probability of capture ranging from 0.1 to 0.9. The bias in the expected IBI and in the fecundity rate is shown as a percentage of the difference from the mean expected IBI and fecundity rate from simulated datasets sampled with a probability of capture of 0.99 (in grey).

<b>Probability of capture</b>	<b>Mean IBI</b>	<b>% bias (mean IBI)</b>	<b>Fecundity rate</b>	<b>% bias (fecundity rate)</b>
0.1	3.38 (2.99 to 4.00)	-23.7 (-9.8 to -32.4)	0.299 (0.250 to 0.333)	32.6 (10.9 to 47.8)
0.2	3.66 (2.87 to 4.00)	-17.4 (-9.8 to -35.3)	0.277 (0.250 to 0.348)	23.0 (10.8 to 54.6)
0.3	3.78 (3.38 to 4.01)	-14.7 (-9.6 to -23.8)	0.265 (0.249 to 0.296)	17.6 (10.6 to 31.2)
0.4	4.01 (3.89 to 4.15)	-9.6 (-6.3 to -12.3)	0.249 (0.241 to 0.257)	10.6 (6.8 to 14.0)
0.5	4.13 (4.02 to 4.30)	-6.8 (-3.0 to -9.4)	0.242 (0.232 to 0.249)	7.3 (3.1 to 10.3)
0.6	4.24 (4.13 to 4.38)	-4.3 (-1.2 to -6.8)	0.236 (0.228 to 0.242)	4.5 (1.2 to 7.3)
0.7	4.34 (4.22 to 4.42)	-2.2 (-1.2 to -6.8)	0.230 (0.226 to 0.237)	2.2 (0.3 to 5.0)
0.8	4.35 (4.21 to 4.48)	-1.9 (1.8 to -5.1)	0.229 (0.223 to 0.238)	2.0 (-1.1 to 5.4)
0.9	4.41 (4.27 to 4.47)	-0.6 (0.7 to -3.7)	0.226 (0.224 to 0.234)	0.6 (-0.8 to 3.9)
0.99	4.44 (4.32 to 4.53)	0.0 (2.1 to -2.5)	0.225 (0.221 to 0.231)	0.0 (-2.0 to 2.6)

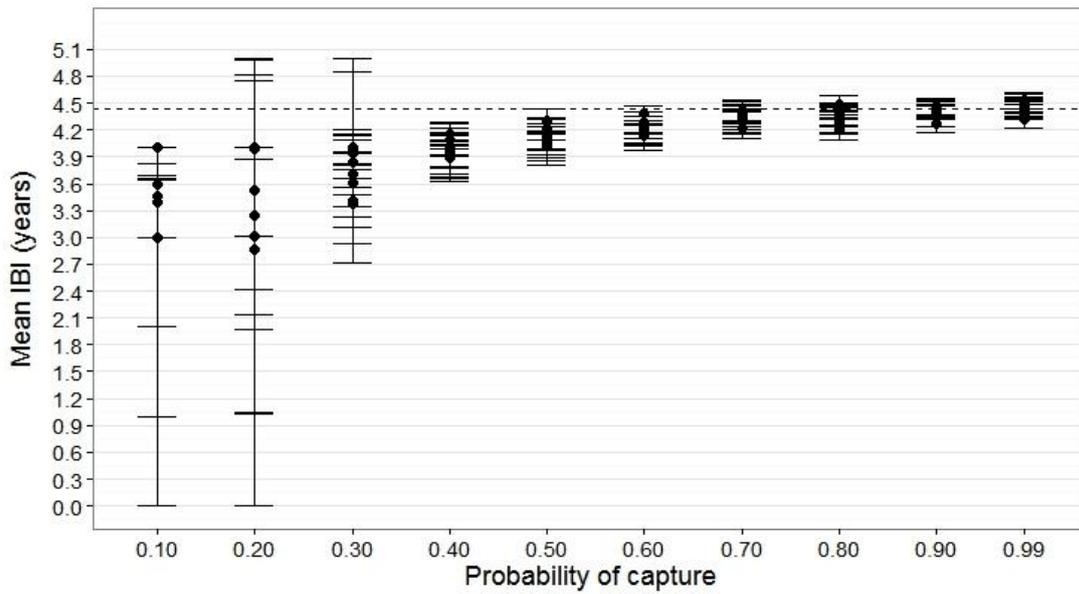


Figure 4.5. Mean expected inter-birth interval (IBI) estimates with 95% CI from simulated datasets sampled using probabilities of capture ranging from 0.1 to 0.99. The dotted line indicates an mean expected IBI of 4.44 years estimated from simulated datasets sampled with a probability of capture equal to 0.99.

Simulated datasets sampled with low capture probabilities (0.1 to 0.3) resulted in greatly underestimated expected inter-birth intervals with very wide 95% confidence intervals (Table 4.9 and Figure 4.5). With these low capture probabilities, the expected inter-birth interval was 3.66 years on average, thus being negatively biased by 18.6% (range 9.6% to 35.3%) compared to the expected inter-birth interval when capture probability equalled 0.99. The mean fecundity rate was 0.280, and thus overestimated by 24.4%, on average, compared to the mean fecundity rate from a probability of capture of 0.99.

With capture probabilities between 0.4 and 0.6, the expected inter-birth interval was still underestimated by 6.2%, on average, (range 1.2% to 12.3%) with an overall average of 4.13 years, compared to the reference true expected IBI for the simulated populations. Similarly, the estimated mean fecundity rate was 0.242 and thus still overestimated by 7.5%, on average. However, for high capture probabilities between 0.7 and 0.9, the

average bias in the expected inter-birth interval and fecundity rate was only -1.6% and 1.6%, respectively.

#### **4.3.3.4.        *Effects of different study lengths***

In general, increasing study length resulted in less biased and more precise estimates of expected inter-birth interval (Table 4.10 and Figure 4.6). Study lengths of 5 years of data from the simulated data samples produced inter-birth interval estimates of 3.95 years, on average, being underestimated by 9.5%, on average, (range 8.4% to 17.5%) compared to using all 50 years of data. Estimated fecundity rate was 0.253, on average, 10.6% positively biased compared to the estimate from all 50 years of data. In all simulated data samples of 5 years, even though the inter-birth interval could be estimated, the coefficients of the fixed effect parameters from the best model were not significant ( $p\text{-value} > 0.05$ ). Also, estimates of the expected inter-birth interval were highly imprecise, with 95% CI ranging between 0 and 4 in all occasions except one, in which it ranged between 1.1 and 3.7 years.

Increasing the number of study years resulted in increased numbers of sightings of reproductive females and observed births, and longer observed intervals. Study lengths of 10 years produced expected inter-birth intervals of 4.28 years, on average, still with wide 95% confidence intervals, and a bias of -9.2% to 4.75% compared to the 50 years of simulated data. The resulting fecundity rate estimates for these 10-year data samples were biased -4.5 to +10.1%. Study lengths of 15 years produced expected inter-birth intervals with narrower confidence intervals. Both inter-birth interval and fecundity rate estimates were biased only from -3 to +3% compared to 50 years of simulated data. Study lengths of 20 and 25 years produced similar results, with inter-birth interval estimates biased between +0.3 and -2.5%. The fecundity rate estimate was 0.23, between -1.2 and +2.6% biased.

## Chapter 4: Fecundity rate

Table 4.10. Expected inter-birth interval (IBI) and fecundity rate estimates averaged for study lengths of 5, 10, 15, 20, 25 and 50 years from simulated datasets. The bias in the expected IBI and fecundity rate is shown as a percentage of the difference from the mean expected IBI and fecundity rate from 50 years of simulated data samples.

<b>Study length (years)</b>	<b>Expected IBI</b>	<b>% bias (exp IBI)</b>	<b>Fecundity rate</b>	<b>% bias (fecundity rate)</b>
5	3.95 (3.60 to 3.99)	-9.5 (-17.5 to -8.4)	0.253 (0.250 to 0.277)	10.6 (9.2 to 21.1)
10	4.28 (3.96 to 4.58)	-1.9 (-9.2 to 4.7)	0.234 (0.218 to 0.252)	2.1 (-4.5 to 10.1)
15	4.36 (4.24 to 4.50)	-0.2 (-3.0 to 3.0)	0.229 (0.222 to 0.236)	0.22 (-2.9 to 3.1)
20	4.35 (4.26 to 4.42)	-0.4 (-2.5 to 1.1)	0.230 (0.226 to 0.235)	0.4 (-1.2 to 2.6)
25	4.34 (4.27 to 4.38)	-0.6 (-2.2 to 0.3)	0.230 (0.228 to 0.234)	0.6 (-0.3 to 2.2)
50	4.37 (4.26 to 4.46)	0.0 (-2.4 to 2.1)	0.229 (0.224 to 0.234)	0.0 (-2.0 to 2.4)

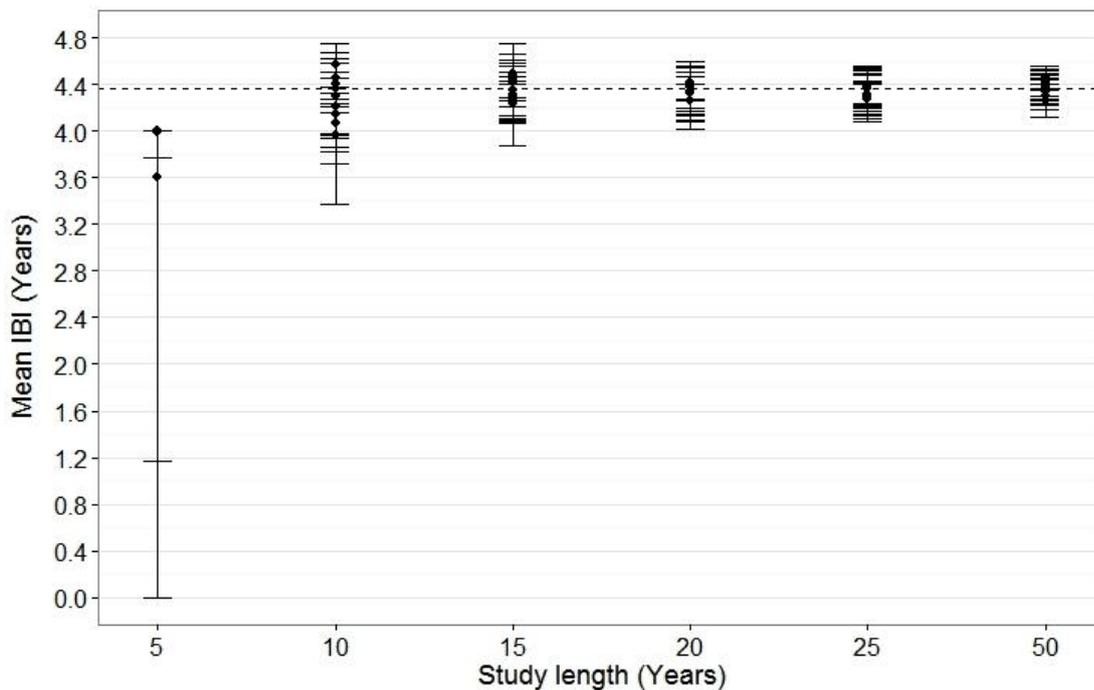


Figure 4.6. Expected inter-birth interval (IBI) estimates with 95% CI from study lengths of 5, 10, 15, 20, 25 and 50 years from simulated datasets. The dotted line indicates a mean expected IBI of 4.44 years estimated with 50 years from simulated data samples.

## 4.4. Discussion

### 4.4.1. Analytical approach and data limitations

#### 4.4.1.1. Analytical approach

The bias in the estimated expected inter-birth interval from the study population was less than 3% compared to the simulated datasets, and the overall expected inter-birth interval from the simulations (4.37 years) fell well within the 95% confidence interval around the mean interval estimated for the study population (3.94 to 4.93 years). These results demonstrate that the analytical approach developed here is unbiased as applied to the study population and, therefore, potentially to other studies of long-lived mammals.

The assumption that a female was unable to give birth in consecutive years is justified by the lack of observations of births in consecutive years in the study population since the photo-ID

effort started in 1989. Inter-birth intervals of around one year are very rare in bottlenose dolphins and have only been reported for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). In Mikura Island, Japan, Kogi *et al.* (2004) report inter-birth intervals of 1 year for two females, and in Adelaide, South Australia, Steiner and Bossley (2008) report an inter-birth interval of 1.08 years for another two females. In all cases, the previous calf had died.

The simulated biological and sampling processes aimed to mimic as far as possible the dynamics of reproductive bottlenose dolphin females from the study population. However, the assumptions that no births would be missed as long as the reproductive female was sighted in the particular year that she gave birth is practically impossible to sustain in any photo-identification study with cetaceans, because females may give birth but the calf may die before the female is sighted again. It is not possible to quantify the number of births that may be missed in the study population, and it was therefore impossible to account for this in the simulations.

### **4.4.1.2. Data limitations**

There are two main data-driven biases that can affect the estimated inter-birth intervals: short study periods that do not allow for the longer inter-birth intervals to be observed and thus cause underestimates in expected inter-birth interval (Barlow and Clapham, 1997); and missing births in the calving histories of individual females causing overestimates in expected inter-birth interval (Baker, 1987).

The data selected for this analysis come from a 24 year photo-identification study, already a much longer study period than most (*e.g.* Mann *et al.*, 2000, Steiner and Bossley, 2008, Henderson *et al.*, 2014). As shown by the simulations, short study periods result in biased and imprecise expected inter-birth interval estimates because longer intervals cannot be observed and the number of observed births and intervals is very small. Even a study period of 24 years still only represents about 50% of the possible life span of a female bottlenose dolphin (*e.g.* the oldest female in Sarasota Bay, Florida, was 63 years old as of 2013; Wells, 2014) and, because reproductive females enter the dataset at different times during the study period, the individual histories generally span short periods. Even with a high probability of capture, as in the study population, there will be gaps in the data, a common issue in cetacean photo-identification studies. Gaps in the data cause the probability of observing longer inter-birth

intervals to be smaller than for shorter intervals. However, results from the simulations with sub-sampled datasets of 25 years produced estimates with a bias of 0.6%, on average, compared to the 50 year study, so the expected inter-birth interval and fecundity rate for the study population should not suffer from the inherent bias defined by Barlow and Clapham (1997).

On the other hand, the detection of births depends on the probability of sighting the mother in association with a newborn calf, which directly depends on the photo-identification effort. In the first half of the study period (from 1989 and 2003), many calves could not be assigned with confidence to reproductive females and most likely births of known reproductive females were missed in that time period. From 2004 to 2012, all observed newborn calves could be assigned to a reproductive female, in part due to the more intense photo-identification effort throughout the distributional range of the population. Even then, births might still have been missed if a calf was born and died before the mother was sighted again. The first time period (1989-2003) had fewer than half the number of observed births and intervals than the second time period (2004-2012), and the resulting estimates for expected inter-birth interval and fecundity rate had extremely wide 95% confidence intervals. The lack of precision in those estimates makes it difficult to compare with the results from the second time period.

Also, the analytical approach failed to allocate much of the probability to the observed inter-birth intervals during the first time period (1989-2003). The inclusion of a large number of females with a single birth event in the data clearly had a major effect on the ability of the approach to perform as expected. Because those females never had a second calf, their probability of giving birth was zero, which drove the conditional probabilities of birth down, resulting in very low conditional probabilities of birth based on the model (Table 4.6). These issues had little effect in the second time period (2003-2012), which had a much lower proportion of females with single births. However, the poor description of the observed data by the modelling approach in the first time period limits the interpretation of the expected inter-birth interval and any comparisons with the results from the second time period or the overall data. The expected inter-birth intervals estimated for the second time period including or excluding those females with single births were very similar (3.69 yrs and 3.93 yrs) and their associated 95% CI overlapped. However, the slight difference in the results suggests a

possible bias for datasets with too many females with single births or in general with too many open-ended birth intervals. This issue could be further investigated using simulations.

The estimated expected inter-birth interval for the second time period (3.93 years) was 12.5% smaller than that estimated using all 24 years of data (1989-2012). However, and based on the results of the simulations with sub-sampled datasets of 10 years, it is likely that the expected inter-birth interval and estimated fecundity rate based on only 9 years of data are negatively and positively biased, respectively, because of the lower probability of observing longer birth intervals (Barlow and Clapham, 1997).

Including gaps from the individual sighting histories into the estimation of expected inter-birth interval causes the same directional bias as if a large number of births were missed even when the females were sighted. As shown by the simulations, including gaps greatly overestimated expected inter-birth interval and underestimated fecundity rate, and thus justifies the data selection criteria in which gaps in the calving histories should not be included either for modelling the probability of birth or simply reporting observed birth intervals.

### **4.4.1.3.      *Application of the method in other populations***

This birth interval analytical approach requires individual reproductive data that have already been collected for many cetacean populations worldwide for different study periods (*e.g.* Mann *et al.*, 2000, Cooke *et al.*, 2001, Kraus *et al.*, 2001, Ward *et al.*, 2009, Wells, 2014), and thus should be applicable to any population study with comprehensive data on birth intervals. The approach could also potentially be applied to terrestrial mammal populations that have the required data on birth intervals. The approach benefits from longer rather than shorter datasets. Also, and in agreement with Barlow and Clapham (1997), the approach is more robust for populations in which capture probabilities are sufficiently high that females are commonly re-sighted and newborn calves can be associated correctly to their mothers. The results from the simulations using different capture probabilities and different study period lengths provide a reference for other studies, in particular the direction and size of bias that might result based on the number of years of data available and their probabilities of observing females and births.

The modelling approach is flexible in the sense that it may be modified to incorporate other parameters of interest into the modelling framework and so add valuable information to estimate the conditional probabilities of giving birth. For example, shorter observed inter-birth intervals are reported for females that lost their previous calf before weaning (*e.g.* Steiner and Bossley, 2008, Henderson *et al.*, 2014); information on the fate of the previous calf could be included in the modelling process as a fixed effect parameter to investigate how the probability of giving birth may be influenced by the survival of the previous calf. Also, changes in the length of inter-birth intervals have been observed with increased age of reproductive females in some odontocete species. In Sarasota Bay, observed calving intervals have been reported to lengthen later in the female's life (Wells, 2000), and a pattern of increased inter-birth intervals with age has also been reported in southern Alaskan resident killer whales (Matkin *et al.*, 2014) and British Columbia northern resident killer whales (Olesiuk *et al.*, 2005). The modelling framework could be then modified to include the age of the reproductive female as a fixed effect parameter and investigate whether changes in the probability of giving birth reflect a decrease in the fecundity due to age.

### **4.4.2. Inter-birth intervals and fecundity rate**

#### **4.4.2.1. *Inter-birth intervals***

Based on the observed data for this population, complete inter-birth intervals of 5, 6, and 7 years were less frequent than intervals of 2 and 3 years (Figure 4.2), which suggests that long inter-birth intervals of more than 7 years might be even less frequent. Longer intervals had less opportunity to be observed because of the length of the study period (Barlow and Clapham, 1997), however comparisons with the simulated datasets show a minimal bias in this respect. This is in good agreement with results from Cockcroft and Ross (1989), who concluded that mature females ovulate at least every third year in bottlenose dolphins from the Indian Ocean, which suggests that long intervals might not be common.

In this population, the shortest inter-birth interval observed was 2 years, observed in four different females and on seven different occasions. Two year birth intervals seem more likely to occur when a new born calf is lost, as seen in the study population on five occasions when the first calf died within the first year (Table 4.2). For example, female # 85 had two consecutive calves that died within their first year, and the female reproduced on a 2-year

cycle in both cases. Based on the photographs taken of #85 with and without the company of a new born calf, her calf #184 was born between July and November 1990 and died between April and May 1991. The next calf, #251, was born in September 1992, after an inter-birth interval of at least 22 months. This calf died in May 1993 and female #85 had a third calf #433 between July and August 1994 after an inter-birth interval of at least 22 months once again. Two year inter-birth intervals after the early death of the first calf have also been observed in bottlenose dolphins from the Adriatic Sea (Bearzi *et al.*, 1997), Doubtful Sound (Henderson *et al.*, 2014) and in Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Japan (Kogi *et al.*, 2004) and South Australia (Steiner and Bossley, 2008). Two year inter-birth intervals can also occur with a successfully weaned calf at the age of two, as seen in the study population on two separate occasions. Female #11 had calf #1109 in 2010, which was successfully weaned at age 2 in 2012 when the female had a second calf, #1144. Female #932 had calf #1101 in 2009 and a second one in 2011 (#1135), with the first one still alive in 2012. Two year inter-birth intervals with a surviving calf have also been reported in Sarasota, Florida (Connor *et al.*, 2000).

The estimated inter-birth interval of 4.49 years (95% CI = 3.94 - 4.93 years) is larger than the observed average birth intervals reported for bottlenose dolphins in North Carolina (2.9 yrs, SD=1.19 yrs, range: 2 to 7 yrs; Thayer, 2007) and in Cardigan Bay (3.3 yrs, range: 2 to 6 yrs; Feingold and Evans, 2013), but similar to the average reported in Shark Bay ( $4.55 \pm 1$  SE, range: 3 to 6.2 yrs; Mann *et al.*, 2000) and falls within the reported inter-birth interval range observed in Sarasota (3 to 6 years; Wells, 2014). The observed average birth interval reported for bottlenose dolphins in Doubtful Sound is larger than the estimated in this study when the previous calf survived more than a year (5.34 years - 95% CI = 4.96-5.73; Henderson *et al.*, 2014), but lower if the calf died within the first month or in the first year (2.1 years, 95% CI = 1.72-2.47 and 3.5 years, 95% CI = 2.93-4.06, respectively). It is highly likely that some of the observed inter-birth intervals reported for other populations may be underestimated due to biases related to short study periods (Barlow and Clapham, 1997) (*i.e.* study lengths of 11 and 12 years in Shark Bay and North Carolina), or overestimated if calves that died soon after birth were not observed (Baker, 1987).

Bottlenose dolphin females invest heavily in their calves, similar to terrestrial mammals such as chimpanzees and elephants, with offspring staying strongly associated with their mothers

for extended periods of time (Van Lawick-Goodall, 1968, Lee, 1987). A female's reproductive cycle is divided into gestation, lactation and resting period. The energetic costs associated with gestation seem to be relatively low but lactation incurs an elevated energy cost that can multiply by two to five times the energy intake during this period in most female mammals (Lee, 1996). Female bottlenose dolphins in captivity have been shown to increase their food intake by between 48% and 72% compared to similar periods in non-reproductive years (Kastelein *et al.*, 2002).

The duration of the lactation period is influenced by the needs of the offspring as well as the mother, with competing interests (Whitehead and Mann, 2000). The lactation period should be long enough to maximise offspring fitness and ability to feed itself, which will depend on food resources and the methods to find and catch them (Brodie, 1969). On the other hand, because lactation is a costly period for the mother, it puts a constraint on the female's ability to produce future offspring (Whitehead and Mann, 2000). The duration of the lactation period and the age at which calves are weaned varies among individuals of the same population and among populations (Whitehead and Mann, 2000). In Shark Bay, calves typically suckle for 3 to 6 years (Mann *et al.*, 2000), similar to observations in Sarasota Bay (Wells *et al.*, 1987) and Japan (Kogi *et al.*, 2004). Longer mother-calf associations of 8 to 10 years have also been observed in Sarasota and Shark Bay.

There is very limited information on the length of the resting period between weaning a calf and giving birth again for bottlenose dolphins. In Sarasota, calves separate from their mothers and thus are assumed to be weaned just before the birth of the next calf (Wells, 2014).

Simultaneously pregnant and lactating females have also been reported off Japan (Kasuya *et al.*, 1997) and Shark Bay, where calves continue nursing until or after half-way through the mother's pregnancy (Mann *et al.*, 2000).

For the study population there is currently no detailed information on the duration of the lactation period but the length of time that mother-calf pairs remain associated ranges from 3 to at least 8 years, with variation among individuals (Grellier *et al.*, 2003). The mean index of association between mother and calf was very high during the first 3 years of life (0.9 or greater), and then, although decreasing for years 4 to 8, it still remained high (approximately 0.7). Whether mother-calf pairs from the study population remain highly associated for longer periods compared to other populations is difficult to know with the available

information because data from Grellier *et al.* (2003) were only collected for eight years (1990-1997). However, the longer inter-birth intervals observed may reflect a longer weaning process, as suggested by Grellier *et al.* (2003).

Differences in the duration of the lactation period exist among odontocete species of different size, with calves of larger species generally suckling longer than smaller species, and the length of the inter-birth interval generally increasing with body size at the interspecific level (Whitehead and Mann, 2000). In bottlenose dolphins, body size varies geographically and seems to be inversely related to water temperature (Ross and Cockcroft, 1990) except in the eastern Pacific (Wells and Scott, 2009).

The Scottish east coast population of bottlenose dolphins represents the northern extreme of the coastal range of the species (Wilson, 1995). Water temperature in coastal areas off NE of Scotland between Aberdeen and the Firth of Forth ranges between 4-5°C in February to 13-16°C in August (monthly averaged sea surface temperature for 2002 to 2013 produced with the Giovanni online data system; Acker and Leptoukh, 2007). This represents a much colder temperature range compared to other locations such as Sarasota Bay, where water temperature ranges 13 to 35 °C seasonally (Wells, 2009). Individuals in study population exhibit some of the largest body sizes within the species (4.1 meters long; Lockyer and Morris, 1986), compared to body lengths of around 2.5 meters in females in Sarasota Bay, coastal waters of the Gulf of Mexico and North Western Atlantic (Read *et al.*, 1993), and to the even smaller Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) off the coast of South Africa (Ross and Cockcroft, 1990).

Inhabiting much colder waters, individuals from the study population not only have a larger size but also have a thicker fat layer. Data from stranded bottlenose dolphins in Scotland show blubber thickness layers up to 44 mm (Nick Davison, Scottish Marine Animal Stranding Scheme, *pers comm.*) compared to layers less than 22 mm from bottlenose dolphins in Sarasota biopsied during the winter (Montie *et al.*, 2008). These extreme variations in body size among different populations will substantially affect the energetic demands of the individuals, with larger and bigger females such as those in the study population likely to have higher metabolic demands for growth, maintenance and lactation of their calves, compared to smaller females from populations such as Sarasota Bay. It could therefore be that female bottlenose dolphins in the study population have longer lactation and

resting periods to meet their metabolic demands, which would be reflected in longer inter-birth intervals.

The ability to wean a calf successfully strongly influences the length of the inter-birth interval, with shorter birth-intervals generally occurring after the early death of a dependent calf and longer ones when the calf survives past the first year (Mann *et al.*, 2000, Steiner and Bossley, 2008, Henderson *et al.*, 2014). Longer inter-birth intervals may provide a female with more time to feed her calf and meet her own energetic demands during the lactation; however it also implies a prolonged energetic cost for the female to keep herself and the calf at optimum fitness for survival. Differences in the fitness of individual females may play an important role in the success of weaning a calf, because less fit females may compromise their calf's survival if they cannot meet their and their calf's energetic demands due to nutritional stress (Matkin *et al.*, 2014). On the other hand, calf survival has been observed to increase with the age of the mother, with calves from multiparous females having higher survival rates than calves from primiparous females (*e.g.* Wells, 2003, Henderson *et al.*, 2014). Also, longer inter-birth intervals may contribute to the probability of the calf surviving and being successfully weaned, but may also potentially limit the overall population growth by reducing the individual female's fecundity. In Doubtful Sound for example, multiparous bottlenose dolphin females have been categorised into three distinct groups of reproductive success based on their calves' survival (most successful, average and least successful multiparous females; Henderson *et al.*, 2014). Most successful multiparous females (30% of animals) showed a constant high calf survival but also tended to have the longest observed inter-birth intervals in the population (5 to 6 years), which had a strong influence on annual abundance fluctuations in such a small population (n=60) (Henderson *et al.*, 2014).

### **4.4.2.2. Fecundity rate**

In the study population, an average of 22% of the mature females were estimated to produce newborn calves (both male and female) annually. There are few estimates of fecundity rate available for bottlenose dolphins and they tend to differ in how they have been estimated, which limits the ability to make comparisons. The estimated fecundity rate for the study population is similar to that estimated for bottlenose dolphins in North Carolina (0.22, SD =

0.089; Thayer, 2007), but higher than estimates reported for Sarasota (0.144, SD=0.244; Wells and Scott, 1990) and the Adriatic Sea (0.171, SD=0.046; Fortuna, 2006).

The interpretation of the low fecundity rate from the bottlenose dolphins in the Adriatic Sea is partially limited because of the low number of years in which the study is based. On the other hand, both Thayer (2007) and Wells and Scott (1990) estimate the fecundity rate by dividing the number of calves surviving to the first year by the number of mature females in that year, and thus accounting for first year calf mortality. New born calf mortality was not accounted for in the estimation of inter-birth interval and fecundity rate in the study population (*i.e.* all data on calving histories was used in the estimation, regardless of the survival of the calf). Fecundity rates that account for calf mortality in the first year are expected to be much lower than fecundity rates that do not account for it (Wells and Scott, 1990). Also, Thayer (2007) and Wells and Scott (1990) differed in how they determined the reproductive status of females. Thayer (2007) could only determine the reproductive status of a female if she had given birth previously, while Wells and Scott (1990) included females that had given birth previously as well as females that had been ovulating for several breeding seasons and are thus considered to be mature. The inclusion of this extra category for mature females in Wells and Scott (1990) will lower the fecundity rate compared to other studies that do not have that type of information available. Notwithstanding this, the observed birth intervals for the bottlenose dolphins in Sarasota range between 3 and 6 years (Wells *et al.*, 1987), which do not correspond to such a low fecundity rate (Wells and Scott, 1990).

Changes in birth rate and juvenile survival have been identified as the main reflection of population density-dependent processes in cetacean populations (Fowler, 1984). It is possible that the lower fecundity rate estimated for the population in Sarasota is a reflection of the population reaching or being close to carrying capacity. This is likely because the population has been stable in abundance and composition for a long time (Wells and Scott, 1990, Wells, 2014). However, direct evidence of density-dependent changes in reproductive and survival parameters in cetacean populations is limited and remains unclear (*e.g.* Perrin and Henderson, 1984, Baker, 1987, Kraus *et al.*, 2001, Olesiuk *et al.*, 2005, Williams *et al.*, 2013, Matkin *et al.*, 2014). The Scottish east coast bottlenose dolphin population is currently thought to be either stable or increasing (Cheney *et al.*, 2014), compared to earlier predictions of negative population growth based on 1990 to 1997 data (Sanders-Reed *et al.*, 1999). The mean inter-

birth interval estimate based on data from 2004 to 2012 is indeed shorter than that estimated for the entire study period, by 12%, and the estimated fecundity rate is larger, by 9%, although both estimates have large 95% CI. However, as previously highlighted, both estimates are likely to be biased because they are based on a limited number of years of data. Notwithstanding this, it is possible that the true inter-birth interval for the second part of the study period is indeed smaller and reflects an increase in the fecundity rate in a population that is likely to be growing (Cheney *et al.*, 2014). However, more years of continued high photo-identification effort, and thus longer individual calving histories, are needed to ascertain whether the fecundity rate has actually changed over time for this population.

The research on bottlenose dolphins in Sarasota started in 1970, making this the longest running study of this species. In the absence of information on life-history parameters for other populations of bottlenose dolphins, other studies have used the information published by Wells and Scott (1990) when investigating the viability of small populations or potential growth rates in different scenarios using stochastic simulation models (*e.g.* Hall *et al.*, 2006, Englund *et al.*, 2007), including the study population (Sanders-Reed *et al.*, 1999, Thompson *et al.*, 2000). Using life-history parameters from other populations is sometimes the only option due to a lack of data on the study population. However, the fecundity rate estimated for the study population (0.22, 95% CI: 0.22-0.25) differs by a large amount (35%) from the estimated fecundity rate in Sarasota Bay (0.144, SD = 0.244; Wells and Scott, 1990). This illustrates well that life-history parameters from a different population may not be a representative reflection of the dynamics of a study population and thus may be inadequate and perhaps misleading when considering the viability of populations.

### **4.5. Conclusions**

An inter-birth interval of 4.49 years (95% CI = 3.94 to 4.93 years) was estimated for the Scottish east coast bottlenose dolphin population based on 24 years of photo-identification data. Based on this estimate, fecundity rate was estimated at 0.222 (95% CI = 0.218 to 0.253). The analytical approach and the most common data-driven biases were tested using simulated datasets of individual female calving histories. The results from the simulations showed that the analytical approach produced unbiased results, making it applicable to other populations with comprehensive data on birth intervals. The simulations also confirmed that

short study periods underestimate mean inter-birth interval (Barlow and Clapham, 1997) and generally produce highly imprecise estimates with short study periods of 5 years. The results also showed how including missing years when a female was not seen and thus births could have been missed overestimates inter-birth interval by 36%, on average. Additionally, the simulations provided an insight into the bias caused by different capture probabilities in the study population, with capture probabilities between 0.1-0.3, 0.4-0.6, and 0.7-0.9 producing average bias of 18.6%, 6.2% and 1.6%, respectively, compared to the estimated mean inter-birth interval with capture probability of 0.99.

The estimated inter-birth interval for the study population is larger than those reported for other populations of bottlenose dolphins, but falls well within the observed range. Although birth intervals reported from other population may be underestimated due to data-driven biases, density-dependent processes in different populations may account for differences in reproductive parameters. The estimated fecundity rate for the study population provides a key demographic parameter that was previously lacking and may be used in any future population viability analysis of this population of bottlenose dolphins.

## Chapter 5

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### **Distribution of bottlenose dolphins between Aberdeen and the Firth of Forth and habitat use of St Andrews Bay**

#### **5.1. Introduction**

Information on how animals are distributed in the environment and what leads them to choose certain habitats is fundamental to an understanding of the ecology of species (Guisan and Zimmermann, 2000, Begon *et al.*, 2006, Morrison *et al.*, 2006). Species live in patchy environments in which resources (*e.g.* food, refugia) are available at different spatial and temporal scales. This heterogeneous distribution of resources, other co-specifics, competitors and predators will all influence the use of space by animals (Wiens, 1976, Sinclair *et al.*, 2006, Matthiopoulos and Aarts, 2010), ultimately reflecting the trade-offs of costs versus benefits to maximize survival and reproduction (Southwood, 1977).

Species-habitat modelling is now widely used to quantify the relationship between populations and their environment, and has been applied to a wide range of terrestrial (*e.g.* Mladenoff *et al.*, 1999, Woolf *et al.*, 2002, López-López *et al.*, 2006) and marine species (*e.g.* Matthiopoulos, 2003, Bradshaw *et al.*, 2004, Bailey and Thompson, 2009, Scott *et al.*, 2010, Shillinger *et al.*, 2011). In cetaceans, habitat modelling has been used to study habitat partitioning between co-existing species (*e.g.* Parra, 2006, Praca and Gannier, 2008, Friedlaender *et al.*, 2009, Sasaki *et al.*, 2013), to understand the ecological needs of species and populations (*e.g.* Whitehead *et al.*, 2010, Dalla Rosa *et al.*, 2012), to identify areas of importance for populations (*e.g.* Hooker *et al.*, 1999, Cañadas *et al.*, 2005, Embling *et al.*, 2010) and to define effective management measures by predicting the effects on individuals of changes in the environment (*e.g.* Martins *et al.*, 2001, Lusseau and Higham, 2004, Notarbartolo-di-Sciara *et al.*, 2009).

In the marine environment, individuals' habitat use is influenced by a variety of factors, food availability probably being the main driver behind the distribution of species or populations (*e.g.* Hastie *et al.*, 2004, Friedlaender *et al.*, 2008). Other potentially

important factors include predator avoidance (*e.g.* Würsig and Würsig, 1980, Heithaus and Dill, 2002), reproduction and rearing of the young (*e.g.* Mann *et al.*, 2000, Loseto *et al.*, 2006), inter-specific competition (*e.g.* Gowans and Whitehead, 1995, Bearzi, 2005), and social structure (*e.g.* Ersts and Rosenbaum, 2003, Martin and Silva, 2004).

Data on cetacean prey abundance and distribution are generally not available because of the difficulty of measuring them. Instead, environmental variables are typically used as proxies for prey abundance or availability, which are expected to influence individuals' use of the habitat (Redfern *et al.*, 2006). Topographic (*e.g.* depth, slope, distance to the coast) and oceanographic (*e.g.* sea surface temperature, chlorophyll-*a* levels, frontal systems) variables have been closely linked to the distribution and habitat use of cetaceans, in whales (*e.g.* Johnston *et al.*, 2007, Panigada *et al.*, 2008, Gill *et al.*, 2011), porpoises (*e.g.* Johnston *et al.*, 2005, Booth *et al.*, 2013), and dolphins (*e.g.* Torres *et al.*, 2003, Cañadas *et al.*, 2005, Hastie *et al.*, 2005, de Stephanis *et al.*, 2008).

Data on the distribution and abundance of cetaceans are difficult to collect because they are typically highly mobile species that spend very little time at the surface. Data tend to be correlated temporally and spatially when individuals are followed for extended periods of time (*e.g.* via telemetry) or observations are recorded within the same area of interest over hours, days or months (*e.g.* in some surveys). This correlation between observations presents methodological issues in the study of habitat use, because analytical methods that are typically used assume independence among the model residuals, which is not always achieved in cetacean studies (Redfern *et al.*, 2006) and can lead to an underestimation of the true uncertainty, affecting model selection (Fieberg *et al.*, 2009).

There are different methods available to visualize and test for autocorrelation; some of the most commonly used include variograms (Cressie, 1992), an autocorrelation function implemented in R (ACF function; Gilbert and Plumber), and Moran's I index (Boots and Getis, 1988). Several approaches can be used to address autocorrelation in the data, each with advantages and disadvantages. One approach is to subset the data to eliminate correlated observations, so that the remaining data are separate enough in time and/or space to be considered independent (*i.e.* data-thinning) (*e.g.* Mendes *et al.*, 2002, Gannier and Praca, 2007). However this approach may not remove completely the

autocorrelation from the data, has the cost of discarding potentially important information, and of reducing the sample size (Rooney *et al.*, 1998, Redfern *et al.*, 2006).

Instead of removing the autocorrelation from the data, the effects of it can be investigated in statistical tests and taken into account in the models using more advanced statistical methods (Redfern *et al.*, 2006, Bailey *et al.*, 2013). These methods may involve a *post hoc* variance inflation to adjust the standard errors (Legendre, 1993), or the use of permutation tests, in which the statistical significance of the parameters is determined by random reassignments of the observations (*e.g.* Schick and Urban, 2000).

In studies in which the autocorrelation in the data is linked to unmeasured characteristics associated with individuals (*e.g.* telemetry studies), Generalized Additive Mixed Models (GAMMs) have been used (*e.g.* Aarts *et al.*, 2008, Sharples *et al.*, 2012). GAMMs can include between-individual variation as random effects within the mixed model and capture within-individual stochasticity in the variance of the fixed effects, and are most appropriate when the focus of the study is on the changes in the individuals' responses (Aarts *et al.*, 2008, Fieberg *et al.*, 2009). GAMMs require the definition of an explicit autoregressive error structure to account for the autocorrelation in the data (Wood, 2006). However, correlation structures commonly used (*e.g.* exchangeable, AR1; described in section 5.2.6. ) are unlikely to describe adequately the clustered data, leading to biased estimators of regression parameters (Fieberg *et al.*, 2010, Matthiopoulos and Aarts, 2010).

Another approach that is increasingly being applied in ecological studies is the use of Generalized Estimating Equations (GEEs), applied to either Generalized Linear Models (GLMs) or Generalized Additive Models (GAMs). GEEs assume non-independence and allow the use of a correlation structure to be defined within the modelling process, together with the estimation of robust standard errors for inference. Numeric problems can be encountered when using certain type of correlation structure (*i.e.* unstructured correlation) that imply estimating more parameters (Hardin and Hilbe, 2003). GEEs require a relatively large number of independent 'clusters' or blocks of data (*i.e.* the correlation structure is defined within each 'cluster', but independence is assumed between 'clusters'), and may fail to converge when the cluster size is large relative to the number of clusters (Bailey *et al.*, 2013). In general, the efficiency of the GEE

estimates and standard errors is improved when the correlation structure, cluster and the variance function are accurately modelled (Liang and Zeger, 1986). However, GEEs offer the advantage that the estimators of regression parameters are still unbiased even if the correlation structure is mis-specified (Liang and Zeger, 1986). This approach has been successfully applied in a number of cetacean habitat studies dealing with longitudinal datasets that are temporally and/or spatially correlated (*e.g.* Panigada *et al.*, 2008, Bailey *et al.*, 2014b, Pirodda *et al.*, 2014).

Bottlenose dolphins off the east coast of Scotland are primarily distributed from the Moray Firth to the Firth of Forth, containing a range of habitat characteristics, which include river estuaries, narrow channels in the firths, large sheltered bays or exposed coastal waters. Dolphins in this population are known to concentrate in particular regions of the distributional range and their presence is known to fluctuate seasonally (Wilson *et al.*, 1997a). Studies of habitat use and preferences in this population have focused in the area of the Moray Firth (*e.g.* Wilson *et al.*, 1997a, Mendes *et al.*, 2002, Hastie *et al.*, 2004, Bailey and Thompson, 2010), where concentrations of dolphin sightings have been linked to the narrow channels characterized by deep waters, steep seabed gradients and strong tidal currents. However, similar studies are lacking in areas outside the Moray Firth where bottlenose dolphins are known to occur, including the coast of Aberdeenshire, St Andrews Bay and the Firth of Forth (Stockin *et al.*, 2006, Cheney *et al.*, 2013).

This Chapter uses data from the dedicated surveys conducted in 2012 and 2013 to describe the distribution and occurrence of bottlenose dolphins off the east coast of Scotland between Aberdeen and the Firth of Forth. In a more extensive analysis, the bottlenose dolphin data collected during the surveys are analysed to investigate the use of St Andrews Bay and the entrance to the Firth of Tay in relation to environmental variables, and to define areas of high use, in an analytical framework that accounts for autocorrelation in the data.

## **5.2. Methods**

### **5.2.1. Study area**

Field work was conducted in coastal waters off eastern Scotland between Aberdeen and the Firth of Forth ( $57^{\circ} 9'$  to  $56^{\circ} 7'$  N and  $2^{\circ} 5'$  to  $2^{\circ} 44'$  W), extending across an area of approximately  $1500 \text{ km}^2$  and over a distance of 140km. The surveyed area covered coastal waters within 10 km from land and depths up to 50 meters, including coastal waters along the coast between Aberdeen and Arbroath, St Andrews Bay and the entrance to the Firth of Tay, and part of the Firth of Forth. To model bottlenose dolphin habitat use, the subarea of St Andrews Bay and the entrance to the Firth of Tay was selected. This area extended from Montrose in the north to Fife Ness in the south across the entrance to the Firth of Tay and St Andrews Bay, covering over  $500 \text{ km}^2$  and 50 km in length from the two most distant points (Figure 5.1).

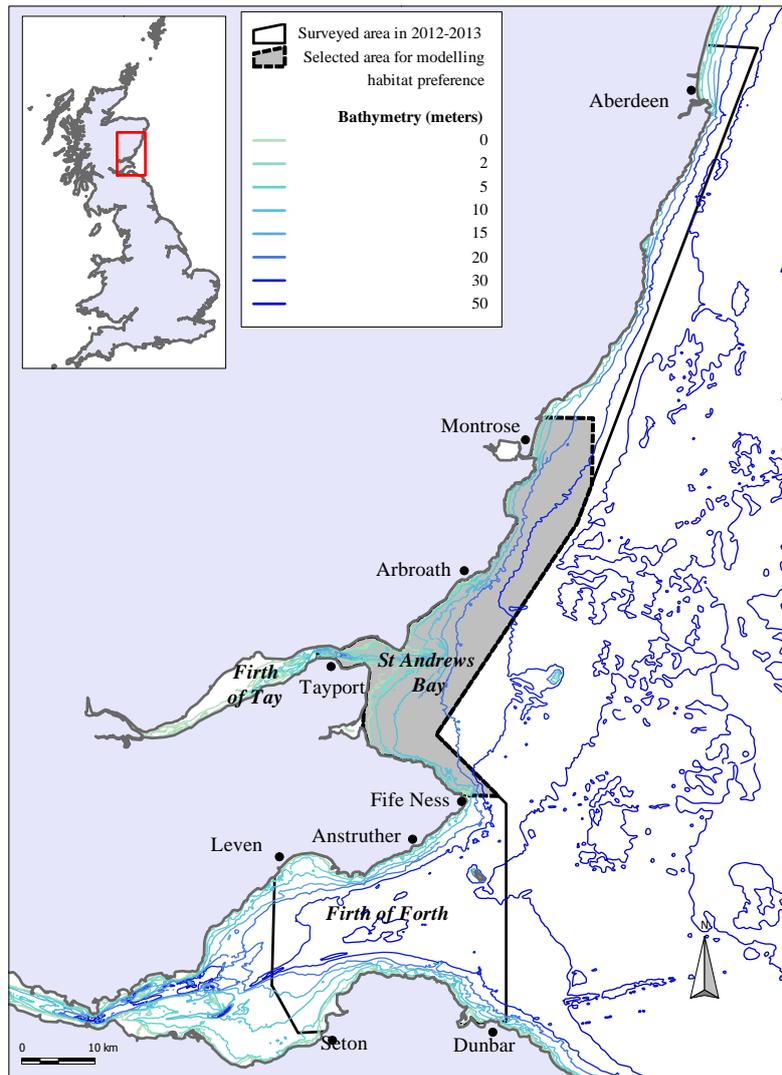


Figure 5.1. Study area off the NE coast of Scotland between Aberdeen and the Firth of Forth for the 2012 and 2013 surveys, and the subarea between Montrose and Fife Ness used to model the bottlenose dolphin habitat use (shaded).

### 5.2.2. Data collection

Dedicated boat-based surveys were conducted between May and September of 2012 and 2013. Surveys were conducted using the *Swordsman*, a 7.4 m aluminium planing-hull cruiser boat with a 225 hp outboard engine, when weather conditions were favourable (sea conditions Beaufort scale 0 to 3) and preferably when weather was dry. If weather conditions changed during a survey, data collection was aborted until weather improved or the survey was abandoned. For the duration of the trip, the boat position, sea surface temperature and depth were recorded *in situ* every minute using a Garmin GPS Map

551s GPS/Plotter/Sounder and a temperature sensor. A record of changes in the survey trip was kept by noting survey data in a daily trip record form every 15 minutes or if there was a change in the sea conditions or in survey activity. The boat was “On-effort” if searching for dolphins, on “Encounter” if following a group of dolphins, and “Off-effort” otherwise (see Appendix 1a).

Three different survey designs were conducted depending on the area surveyed: (1) Firth of Tay and St Andrews Bay, (2) Montrose to Aberdeen, and (3) Firth of Forth. Surveys started from Tayport harbour for the Firth of Tay and St Andrews Bay trips and for the Montrose to Aberdeen trips, and from Anstruther harbour for the Firth of Forth trips (Figure 5.1). Survey effort for the Firth of Tay and St Andrews Bay trips ran from Tayport out to the entrance of the Tay, extending south to St Andrews and north to Montrose. Survey effort for the Aberdeen trips ran from Montrose north up to Aberdeen. On those trips, bottlenose dolphin groups encountered between Tayport and Montrose were recorded but no photo-identification data were collected because of time constraints. On occasion, when weather and time allowed, photo-identification effort was extended south of Montrose to cover the area from Montrose back to Tayport harbour. Survey effort in the Firth of Forth covered an area between Leven and Fife Ness on the north side of the Forth and between Seton and Dunbar on the south side of the Forth, and included the associated water between (Figure 5.1).

Surveys were designed to ensure a good coverage of the study area. To do so, a grid of points separated 1 km apart was used to describe random survey lines following a zigzag pattern across the study area for St Andrews Bay and for the Firth of Forth. The surveys between Montrose and Aberdeen ran parallel to the coast to minimise the time needed to get to Aberdeen and back and instead maximise photo-identification effort when bottlenose dolphins were encountered. Realised survey effort is presented in Results (section 5.3.).

When bottlenose dolphins were encountered, groups were followed in order to collect photo-identification data, using a Canon EOS 50D with a 70-200 mm f2.8 USM Canon lens. Standardised protocols taken from the long running east coast of Scotland bottlenose dolphin project (Cheney et al. 2012) coordinated by the Lighthouse Field Station, University of Aberdeen and the Sea Mammal Research Unit, University of St

Andrews, were used at all times. This ensured that all data were standardised with, and incorporated into, the long-term central dataset for Scottish bottlenose dolphins. These protocols are summarized in Chapter 2. Each group encountered was followed until all photo-identification data were collected, constituting one encounter or follow. During each of these, the boat position, sea surface temperature and *in situ* depth were recorded every minute as done when the boat was on effort searching for dolphins. During all encounters, data on group size, behaviour, and the presence of calves, including new born individuals, were also recorded and noted in the ‘Encounter’ form (see Appendix 1b). All photo-identification data were collected under licence from Scottish Natural Heritage (SNH licence no.13292 and no.13855).

### 5.2.3. Covariate data

Spatial, temporal and environmental covariates were selected as potential predictors of bottlenose dolphin presence in the area of St Andrews Bay and the entrance to the Firth of Tay. Some covariates were collected *in situ* during the surveys and others were derived from a range of sources (Table 5.1).

*Depth* was measured in meters and collected *in situ* at each GPS fix using a depth sounder transducer connected to the GPS unit. Any missing values at points in which the transducer was not working were derived from bathymetry data extracted from EDINA Marine Digimap at a resolution of 200 m (SeaZone Hydrospatial Bathymetry). To do so, the function ‘Transfer Heights’ within the Geographic Information System (GIS) tool software Manifold (version 8.0. 64-bit, Manifold® System) was used to transfer the depth values from the Marine Digimap onto each missing value.

*Slope* was the slope gradient measured in degrees as the average change in depth over a grid of resolution 200x200 meters. Values were computed in Manifold from the bathymetry data extracted from EDINA Marine Digimap (SeaZone Hydrospatial Bathymetry) as a surface data file and transferred onto each GPS fix location using ‘Transfer Heights’ function.

## Chapter 5: Habitat modelling

Aspect was the orientation of the slope measured in degrees (ranging from – to + 180°) with respect to north. Values were also extracted from Marine Digimap and computed in Manifold as was done for *Slope*.

Sediment type data were provided by EDINA Geology Digimap / British Geological Survey service as a GIS shape file of categorical sediment classes. Sediment data were imported into Manifold and the values transferred to each GPS fix by means of the ‘Spatial Overlay’ function. The sediment types were reclassified in four new categories as (1) rock, (2) sand, (3) muddy sand /sandy mud, and (4) gravel / gravely sand / sandy gravel / gravel, mud, sandy.

Distance to land represented the linear distance to the nearest land, measured in meters, and calculated in Manifold using a script written by Clint Blight (SMRU) for each GPS fix in the data.

Distance to the Tay and Distance to Montrose were the shortest distance to the main two rivers in the study area (river Tay, and rivers South Esk and North Esk in Montrose), calculated for each GPS fix in the data using another script written by Clint Blight (SMRU) in Manifold. Prior to that, a network of points joined by lines was constructed to include all the GPS fixes, two separate points for the entrances to the two rivers (see Figure 5.5 for location of both entrances), and a grid of points separated by a distance of 500m from each other. To include information on the position of each GPS fix relative to the entrance of a river, distances to the Tay were negative for points located inside the Tay estuary and positive for points outside it. Similarly, distances to the Esk River in Montrose were negative for points north of Montrose and positive for points south of Montrose.

Sea surface temperature was collected *in situ* during the surveys and measured in degrees Celsius, using the built in temperature sensor from the boat connected to the GPS unit. To calibrate the boat’s temperature sensor, measurements were also taken during the surveys with a Fluke 51 II Single Input digital thermometer. Any missing values were averaged from all available *in situ* temperature values taken in that same month within a 500 m cell around the missing value.

Tidal state was defined as a categorical variable with four categories: ‘low’, ‘rising’, ‘high’, and ‘falling’, each representing a 3 hour block. ‘High’ and ‘low’ categories were delimited by 1.5 hours each side of high and low tide, respectively, and ‘rising’ and ‘falling’ categories were the remaining time from low to high tide and from high to low tide, respectively. To calculate the tidal state, the nearest tidal port had to be determined for each GPS fix, from which tidal data (high and low tide times between May and September of 2012-2013) could be then extracted from POLTIPS-3 (Version 3.4.0.3 / 10, Proudman Oceanographic Laboratory Applications Group). To do this, linear distances from each GPS fix to each of the four tidal ports in the study area (Dundee, Arbroath, Anstruther and Montrose) were calculated using the same script in Manifold used to calculate the distance to the nearest land. Then, a script was written in software R (R Core Team, 2014) to select the closest tidal port for each GPS fix and assign the time of the closest high or low tide to each data point based on the date and time. Finally, each GPS fix was assigned a tidal state category based on the difference in hours between the GPS fix and the nearest high or low tide time.

Current speed, Current level and Current direction were extracted from POLPRED (NERC National Oceanography Centre, Liverpool, UK) using the prediction function POL\_DoPrediction within the POLHydro32 model by means of an R script provided by Bernie McConnell and Clint Blight from SMRU. These current values were predicted based on the time and location of each GPS fix.

Year and Month were also included as potential covariates in order to investigate temporal variations in the probability of encountering bottlenose dolphins across years and across months within year.

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Table 5.1. List of all candidate covariates to model the presence of bottlenose dolphins in St Andrews Bay and the entrance to the Firth of Tay. Unit, summary statistics or number of data points (categorical covariates), resolution and source are shown for each covariate. POLPRED/POLTIPS are models for tidal data provided by Proudman Oceanographic Laboratory.

Covariate	Unit	Summary statistics				Resolution	Source
		Min	Median	Mean	Max		
<i>Depth</i>	meters	0.0	13.9	14.55	39.10	at each GPS fix	Collected <i>in situ</i>
<i>Slope</i>	degrees	0.0	0.33	0.51	3.15	200 m	EDINA Marine Digimap
<i>Aspect</i>	degrees	-178	94	65	180	200 m	EDINA Marine Digimap
<i>Distance to land</i>	meters	0	2019	2059	8711	at each GPS fix	Manifold
<i>Distance to the Tay</i>	meters	-13250	5879	8253	39990	at each GPS fix	Manifold
<i>Distance to Montrose</i>	meters	-8017	31880	27770	50940	at each GPS fix	Manifold
<i>Sea Surface Temperature</i>	Celsius degrees	6.2	12.20	11.89	17.20	at each GPS fix	Collected <i>in situ</i>
<i>Current speed</i>	meter/second	0.001	0.180	0.206	0.926	at each GPS fix	POLPRED
<i>Current level</i>	meters	-2.61	-0.32	-0.31	2.33	at each GPS fix	POLPRED
<i>Current direction</i>	degrees	0.03	139.0	146.0	359.9	at each GPS fix	POLPRED

Covariate	Number of data points by category				Resolution	Source	
	<i>Rock</i>	<i>Sand</i>	<i>Muddy Sand</i>	<i>Gravel</i>			
<i>Sediment</i>	1306	6720	643	1462	variable	EDINA Geology Digimap / British Geological Survey	
<i>Tidal state</i>	<i>High</i> 2378	<i>Falling</i> 2444	<i>Low</i> 2384	<i>Rising</i> 2925	at each GPS fix	POLTIPS	
<i>Month</i>	<i>May</i> 2041	<i>June</i> 2391	<i>July</i> 3031	<i>August</i> 1216	<i>September</i> 1452	at each GPS fix	-
<i>Year</i>	<b>2012</b> 5260		<b>2013</b> 4871		at each GPS fix	-	

#### 5.2.4. Modelling framework

The relationship between the presence/absence of bottlenose dolphins and the covariates described above was modelled in the framework of Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1990, Wood, 2006), an analytical approach that has been frequently used to model cetacean distribution and abundance (*e.g.* Forney, 2000, Ingram *et al.*, 2007, Cañadas and Hammond, 2008, Pirota *et al.*, 2011). GAMs were preferred to Generalized Linear Models (GLMs) (McCullagh and Nelder, 1998) because they are not restricted to parametric relationships between the response and explanatory variables, hence allowing for non-linear relationships that are typical of cetacean-habitat studies (*e.g.* Forney, 2000, Ferguson *et al.*, 2006a, Panigada *et al.*, 2008).

The GPS fixes taken every minute were used as the sample unit of analysis to model the habitat use of bottlenose dolphins. Only ‘On-Effort’ points were included in the analysis (*i.e.* when searching for dolphins or in an ‘Encounter’), excluding all other points (*i.e.* ‘Off-Effort’). All ‘On-Effort’ points recorded during an ‘Encounter’ were classed as 1 = ‘presence’, and all other ‘On-Effort’ points recorded while searching for dolphins were classified as 0 = ‘absence’.

The probability of presence of bottlenose dolphins was modelled using the presence/absence of animals at each GPS fix as the response variable in a binomial-based GAM with a logit link function:

$$p_i = \frac{e^{\eta_i}}{1 + e^{\eta_i}} + \varepsilon_i$$

Where  $p_i$  is the probability of bottlenose dolphin presence,  $\varepsilon_i$  is the binomial error and  $\eta_i$  is the linear predictor. In the GAM, the predictor is defined as the sum of smooth functions ( $f_q$ ) of covariates ( $x_q$ ) (Wood, 2006):

$$\eta_i = \beta_0 + f_1 x_{1i} + \dots + f_q x_{qi}$$

Each smooth function ( $f_q$ ) can be modelled as non-parametric, thus allowing for non-linear relationships (*i.e.* no assumption is made about the parametric form of the function fitted to the data).

### 5.2.5. Pre-modelling analysis

#### 5.2.5.1. *Exploratory analyses of covariates*

Prior to the modelling analysis, summary statistics were calculated for each candidate covariate showing the minimum, median, mean and maximum values. Boxplots were produced for all covariates against the presence/absence data to visualize the distribution of each covariate and detect potential outliers. Also, GAMs (Hastie and Tibshirani, 1990, Wood, 2006) were fitted to model the presence of bottlenose dolphins against each explanatory covariate separately, in order to investigate the nature of the relationship between the presence of dolphins and each covariate.

The existence of collinearity between covariates may affect the interpretation of model coefficients and it is advised to include only covariates that are uncorrelated (Redfern *et al.*, 2006). Multicollinearity among the covariates was inspected by means of Pearson's correlation coefficients using the 'cor' function in the package 'stats' in R, as well as generalized variance inflation factors (GVIF) using the 'vif' function in the package 'car' in R.

Two covariates showed evidence of collinearity: *Distance to the Tay* and *Distance to Montrose*, with GVIF > 3 and Pearson's correlation coefficient > 0.5. Only *Distance to the Tay* was included in the models because this was the main area of interest.

#### 5.2.5.2. *Dealing with autocorrelation in the residuals*

Regression techniques involve a number of assumptions that first need to be verified to ensure they are not violated (Redfern *et al.*, 2006, Zuur *et al.*, 2009). One critical assumption in linear regression and additive models such as GAMs is the independence of the model residuals, which can lead to unreliable model predictions if not accounted for (Matthiopoulos and Aarts, 2010). In this analysis, survey GPS fixes were one minute apart, meaning that the environmental characteristics at consecutive GPS locations are likely to be very similar and that the probability of encountering bottlenose dolphins at any one location may not be independent of the presence/absence at the previous location and time. Not accounting for this spatial and temporal autocorrelation between observations can result in a lower effective sample size, as new observations add little

or no information because they are very similar to information from near observations. Consequently, the uncertainty around the model coefficients can be underestimated, increasing the probability of obtaining Type I errors and increasing the chance that covariates are retained as significant in a model due to inflated  $p$ -values (Zuur *et al.*, 2009; *e.g.* Bailey *et al.* 2013).

As part of the pre-modelling analysis, a binomial-based GAM with a logit link function was fitted to model the presence/absence of bottlenose dolphins using the `mgcv` library (Wood, 2014) in R (R Core Team, 2014). Then, the level of autocorrelation in the residuals was visualized by means of an autocorrelation function (ACF) plot for the residuals of the fitted model, using the function ‘`acf`’ in the ‘`stats`’ package in R.

### 5.2.5.3. *Sub-setting the data*

The survey effort in St Andrews Bay and entrance to the Tay in 2012 and 2013 resulted in a total of 10131 GPS fixes recorded during on-effort mode, of which 6671 were recorded while searching for dolphins (*i.e.* absences) and 3460 while following dolphins during ‘Encounters’ (*i.e.* presences).

As expected, the ACF plot using all the GPS fixes (*i.e.* one every minute) showed a high level of autocorrelation in the model residuals. The autocorrelation between the residuals was still present at a lag of 8000 data points (Figure 5.2), resulting in all candidate explanatory covariates being retained in the fitted GAM.

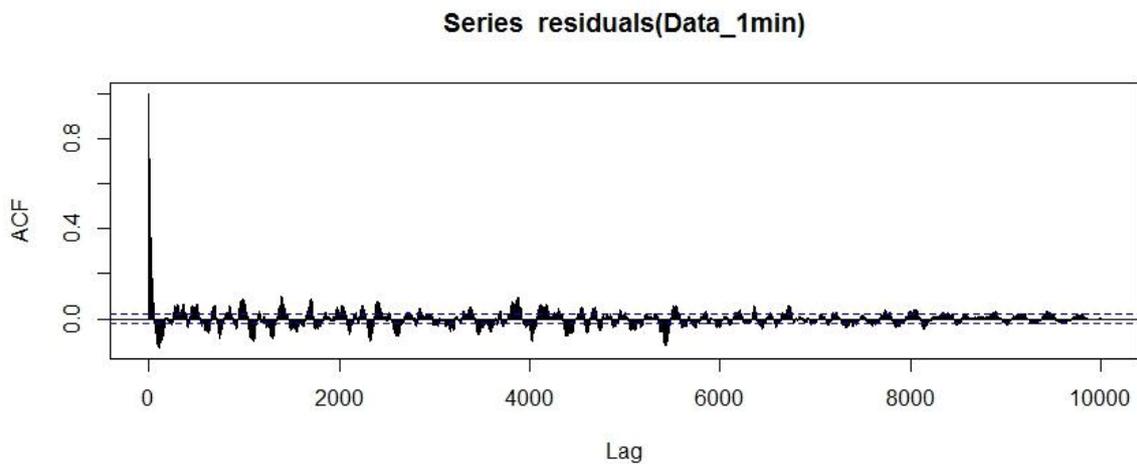


Figure 5.2. Autocorrelation function (ACF) plot for the residuals in the GAM fitted to the full dataset of one GPS fix every minute.

To investigate whether sub-setting the data (*i.e.* data-thinning) would eliminate the autocorrelation between observations, four data sub-sets were created from the original dataset by selecting one GPS fix every 5, 10, 15 and 20 minutes. A binomial-based GAM (with a logit link function) was fitted to each dataset to model the presence of dolphins and ACF plots were generated to determine whether, and at which point, the data points were separated enough in time and space to assume independence.

The ACF plots for sub-setted datasets with one GPS fix every 5, 10 and 15 minutes still showed autocorrelation in the residuals (see Appendix 3), and only the subset of the data of GPS fixes every 20 minutes showed low levels of autocorrelation. However, selecting only one GPS fix every 20 minutes resulted not only in a greatly reduced sample size (385 out of the original 6671 presence points), but also meant having one or few presence points for each follow. Bottlenose dolphin follows in 2012 and 2013 lasted an average of 29 minutes, during which time individuals crossed over a range of environmental covariates of interest (*e.g.* distance to the coast, depth or distance to the entrance of a river). With only one GPS fix every 20 minutes, most of the information on the habitat covariates related to the presence of the animals during the follows was missed. Thus, this was not considered a suitable option to deal with autocorrelation in the residuals, and Generalized Estimating Equations were considered next to account for autocorrelation in the residuals while keeping all the data (see below).

#### 5.2.5.4. *Generalized Estimating Equations*

Generalized Estimating Equations (GEEs) are an extension of generalized linear models that relax the assumption of independence by modelling the correlation between residuals, and can be used with non-normally distributed data such as binary (presence/absence) data (Liang and Zeger, 1986). Based on this approach, data points are grouped into blocks or panels, allowing for observations within each block to be correlated, based on a specified correlation structure, but assuming independence between blocks of data.

For this analysis, GPS fixes of presence/absence data points were classified into ‘follow blocks’ and ‘searching blocks’. A ‘follow block’ was comprised by consecutive ‘presence’ points recorded from the start to the end of a single encounter; a ‘searching block’ was comprised by consecutive ‘absence’ points, either between two encounters, between ‘Off-Effort’ points, or between an encounter and ‘Off-Effort’ (and *vice versa*). These blocks were used to select an appropriate autocorrelation structure, as described in the next section, to account for the lack of independence in the observations.

#### 5.2.6. **Model fitting**

The presence/absence of bottlenose dolphins were modelled using GAMs (Wood, 2006) with a binomial distribution for the error structure and a logit link function. GEEs (Liang and Zeger, 1986) were used to model a working correlation structure based on the blocks of consecutive presence/absence points (see below). Models were fitted using the R library *geepack* (Højsgaard *et al.*, 2006) together with the library *splines* (Bates and Venables, 2012) to extend the GEE-generalized linear models to GEE-GAMs.

The Akaike Information Criterion (AIC; Akaike, 1973) is a criterion typically used to evaluate goodness of fit of likelihood-based models. Because GEEs are quasi-likelihood based, the AIC cannot be used. Instead, the *quasi-likelihood under the independence model criterion* (QIC; Pan, 2001) was used to select the most appropriate correlation structure for the residuals. The QIC is a modified extension of the AIC criterion that accounts for the fact that GEEs are quasi-likelihood based and generalizes the penalty

term to be analogous to the one in the AIC. This criterion is interpreted in the same way as the AIC, with smaller QIC values for the models that are most supported by the data.

Three different autocorrelation structures were compared using the QIC: an autoregressive correlation structure (AR1), an exchangeable structure and a working independence structure. In the AR1 structure, the correlation between observations decreases as the lag or distance between the observations increases; in the exchangeable structure, the correlation between observations in the same block is uniform; and in a working independence structure (Liang and Zeger, 1986, Pan, 2001), the correlation matrix is an identity matrix, but still produces realistic standard errors by using robust modified sandwich variance estimators that account for the observed lack of independence in the data (Hardin and Hilbe, 2003). In other words the model is fitted as though the observations were independent, generating model coefficients identical to those of a GAM, but then the estimated standard errors are adjusted (*i.e.* inflated) to account for the lack of independence. This approach tends to be efficient and produce robust standard errors of the model coefficients (McDonald, 1993), and is recommended when applying GEEs to habitat use analysis (Fieberg *et al.*, 2010). The QIC was used to compare models that were identical except for their different correlation structures, selecting the correlation structure with the smallest QIC value.

### 5.2.6.1. *Model selection*

An approximation of the QIC, known as the  $QIC_u$  (Pan, 2001) was used to compare models which had the same correlation structure, but different sets of covariates. As with the QIC, models with the smallest values of the  $QIC_u$  were preferred.

The spline structure (*i.e.* the number of degrees of freedom in the spline) defining the smooth function for each of the candidate explanatory covariates has to be defined when using the packages `geepack` and `splines` in R. Previous to fitting a model with all candidate covariates, the  $QIC_u$  was used to choose the best form for each covariate to enter the model. Specifically, each non-categorical covariate could enter the model as a linear term, as a *B*-spline with four degrees of freedom (d.f.) (with one internal knot at the average value of that covariate), or as a *B*-spline with five d.f. (with two internal knots, positioned at the lower and upper quartiles of that covariate). The  $QIC_u$  of a null

model (*i.e.* with only the intercept) was compared against the  $QIC_u$  scores of three other models, each containing a different spline structure for the same covariate. For each covariate, the spline structure in the model with the lowest  $QIC_u$  was chosen as the best form to enter the model.

The best subset of covariate predictors to model the presence of bottlenose dolphins was selected by applying a manual backwards stepwise selection based on the  $QIC_u$  criterion. Starting with a full (saturated) model with all candidate covariates, a set of reduced models were fitted, dropping a different covariate in each reduced model of the set. In each round, the model with the lowest  $QIC_u$  was selected as the starting model for the next round. This process was repeated until removing any more covariates did not lower the  $QIC_u$  score anymore (*i.e.* did not improve the model), representing the final model.

### 5.2.6.2. *Evaluation of the final model*

The significance of each covariate retained in the final model was evaluated by applying repeated Wald's tests and dropping the least significant covariate each time ( $p$ -value > 0.05) (Hardin and Hilbe, 2003, Zuur *et al.*, 2009) using the function 'anova' within the geepack in R. However, non significant covariates retained in the model selection were still kept in the final model because they improved the model fit. The R package 'ggplot2' (Wickham, 2009) was used to generate partial residual plots to visualize the relationship between the presence of bottlenose dolphins (on the link scale) with each covariate retained in the final model, with associated confidence intervals.

The goodness-of-fit of the final model was evaluated by means of a confusion or error matrix, which compares observed and the predicted values of presences and absences (Fielding and Bell, 1997). A confusion matrix is generally presented as percentages of correctly and incorrectly classified presences/absences by the fitted model. The classification is normally based on a cut-off probability, generally fixed at 0.5, meaning that probabilities greater than 0.5 predicted by the model are classified as a predicted presence in the matrix, and probabilities less than 0.5 are classified as predicted absence. Choosing between different cut-off levels has been shown to affect the accuracy of the classification in the matrix if the chosen threshold is not optimal (Boyce

*et al.*, 2002). An alternative is to choose the cut-off level based on a receiving-operating characteristic (ROC) curve (Pearce and Ferrier, 2000, Praca *et al.*, 2009, Pirota *et al.*, 2011).

The ROC curve (Figure 5.3) evaluates the proportion of correctly and incorrectly classified predictions over a range of thresholds (Swets, 1988, Zweig and Campbell, 1993). Sensitivity values for true positive fraction, *i.e.* fraction of presences well predicted, are plotted against 1-specificity values for false positive fraction, *i.e.* fraction of presences incorrectly predicted, for a continuous range of cut-off probability thresholds.

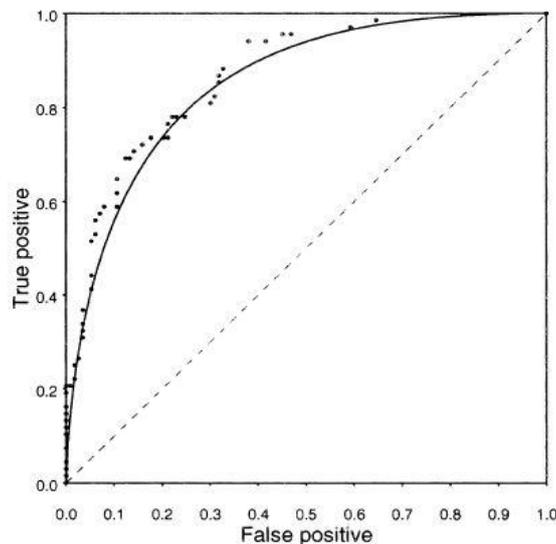


Figure 5.3. Example of a ROC curve. Sensitivity values (true positive proportion) are plotted against the false positive proportion values for a range of threshold probabilities. The 45° line represents the sensitivity and specificity values expected to obtain by chance for each threshold (taken from Pearce and Ferrier (2000)).

The ROC curve from a model with good performance will maximize the sensitivity values for low 1-specificity values, *i.e.* maximizing the correctly classified presences and minimizing the incorrectly classified ones. The point in the ROC curve that maximises the distance from a 45° diagonal line (*i.e.* worst model predictive

performance) was chosen as the best cut-off probability to create the confusion matrix. To do so, distances between each point of the ROC curve and the 45° diagonal line were calculated, using a trigonometric relationship provided in the annotated R code available from Pirotta *et al.* (2011). For each point with coordinates (x; y) of the ROC curve, the code calculates the length of the line ( $L$ ) from the origin to the point (x; y) and the angle between the diagonal and this line ( $\varphi$ ). The distance from each point of the ROC curve to the diagonal line ( $d$ ) is calculated as:

$$d = L \sin \varphi$$

The area under the ROC curve (AUC) provides a measure of overall accuracy of the model predictions that can be used to assess the model and its predictive power (Boyce *et al.*, 2002). AUC can range from 0.5 when the ROC curve is a 45° line in a model with no predictive power, up to an AUC of 1 for a perfect model. The R library ‘ROCR’ (Sing *et al.*, 2005) was used to build the ROC curve plot, calculate the AUC and extract the best cut-off probability, and the R library ‘PresenceAbsence’ (Freeman and Moisen, 2008) was used to compute the confusion matrix.

### 5.2.6.3. *Predictions*

The final model was used to predict the probability of presence of bottlenose dolphins in the study area. To do so, a grid of 1x1 km cells was created in the study area and values of the covariates retained in the final model were associated to the centroid of each cell in the grid. Only grid cells within the surveyed area were included to avoid predicting in areas with covariate values outside the range observed in the data used in the modelling (*e.g.* cells with deeper waters than the deepest point in the data). Dynamic covariates such as the current and tidal covariates were averaged for each centroid at the temporal scale of interest based on the categorical covariates retained in the final model (*e.g.* tidal state, month, year), so that multiple prediction maps could be created to predict the presence of dolphins at each temporal state. The functions ‘Transfer Heights’ and ‘Spatial topology’ in Manifold were used to associate averaged values of the covariates to each centroid.

The resulting data with the latitude and longitude for each centroid and all associated covariate values was used to predict the probability of dolphin presence in each

location. Predictions were made to cover combinations of the different temporal covariates. The presence of dolphins at each location was predicted on the response scale (*i.e.* a value between 0 and 1) using the function `predict` in R. The predicted probability of dolphin presence for each temporal combination was visualized in Manifold by first creating a map of the probabilities of presence associated to each centroid and then generating a smoothed surface of probabilities across the area using the Kriging method to interpolate between centroids. A palette of colours was used to identify areas of higher and lower probability of dolphin presence. Maps of predicted presence/absence (*i.e.* 1 or 0) of bottlenose dolphin based on the best cut-off probability from the ROC curve were also created.

### **5.3. Results**

#### **5.3.1. Summary of survey data**

Between May and September of 2012 and 2013, 50 trips were conducted (22 and 28 trips, respectively), covering a total of 6294 km of on-effort survey. Twenty-eight trips were conducted in St Andrews Bay and the entrance to the Firth of Tay, 12 in the Firth of Forth, and 10 between Tayport and Aberdeen. The number of trips conducted each month was mainly driven by weather conditions (Table 5.2). In 2012, the month of July had the best weather conditions and allowed a total of eight trips; there were three or four trips in other months. In 2013, the weather was generally better and June had the best weather conditions allowing a total of eight trips. There were four to seven trips in the other months. In total, 322 hours were spent on the water. A detailed summary of each trip can be found in Appendix 4.

## Chapter 5: Habitat modelling

Table 5.2. Summary of survey effort in 2012/13, showing monthly number of trips, on-effort km, survey time, number of bottlenose dolphin encounters and average group size.

Year 2012					
Month	# Trips	On-effort (km)	Survey time (hrs)	# Enc	Average group size and range
May	3	376	20.92	6	10 (2-25)
June	4	512	26.50	5	10 (5-25)
July	8	887	51.95	22	17 (4-35)
August	3	465	22.65	10	12 (2-25)
September	4	427	22.48	10	10 (2-30)
<b>Total 2012</b>	<b>22</b>	<b>2667</b>	<b>144.50</b>	<b>53</b>	<b>14 (2-35)</b>
Year 2013					
Month	# Trips	On-effort (km)	Survey time (hrs)	# Enc	Average group size and range
May	5	599	13.36	10	14 (2-28)
June	8	1037	49.17	25	9 (2-25)
July	7	1080	55.38	21	9 (2-22)
August	4	438	22.15	19	8 (3-25)
September	4	473	24.17	13	10 (1-28)
<b>Total 2013</b>	<b>28</b>	<b>3627</b>	<b>178.43</b>	<b>88</b>	<b>10 (1-28)</b>
<b>Total 2012/13</b>	<b>50</b>	<b>6294</b>	<b>322.93</b>	<b>141</b>	<b>11 (1-35)</b>

### 5.3.2. Bottlenose dolphin encounters between Aberdeen and the Firth of Forth

Bottlenose dolphins were sighted on 43 of the total 50 trips (86%). Of the 28 trips in St Andrews Bay and the entrance to the Firth of Tay, dolphins were sighted on 27 trips (96%). Of the 12 trips in the Firth of Forth, dolphins were sighted on 6 trips (50%) and of the 10 trips to Aberdeen dolphins were sighted on all trips (100%). Bottlenose dolphins were seen in all months in which a survey took place in St Andrews Bay and the entrance to the Firth Tay and on Aberdeen trips. For the Firth of Forth trips, dolphins were seen in all months except May (see Appendix 4).

Between one and nine separate groups were encountered during each trip in which bottlenose dolphins were seen. Each encounter lasted on average 29 minutes, giving a total of 68 hours spent with bottlenose dolphins, representing 21% of the total survey time. Most of the groups were encountered in St Andrews Bay (89 groups), especially

around the entrance to the Firth of Tay, from its outer entrance in waters approximately 15 meters deep to Tayport (Figure 5.4). Dolphins were also often encountered along the coast between St Andrews Bay and Aberdeen, with most of the encounters occurring off Montrose and Aberdeen. In the Firth of Forth, dolphins were only seen on the north side of the Forth, within 1 km off the coast line, mostly between Anstruther and Fife Ness. No groups were encountered on the south side of the Firth or in the deeper waters in between. Only one group was encountered per trip except on one trip in which four different groups were encountered close to Fife Ness.

Estimates of group sizes on all encounters varied between 1 and 35 individuals (Table 5.2), with an estimated mean group size of 11 individuals for all areas. In the Firth of Tay and St Andrews Bay, estimates of group size ranged between 1 and 35 individuals (mean = 11 individuals). Between Montrose and Aberdeen estimated group size ranged between 2 and 28 individuals (mean = 11 individuals) and in the Firth of Forth estimates of group size ranged between 2 and 29 individuals (mean = 12 individuals). All age classes including young of the year and older calves, were sighted in all areas.

A range of behaviour was observed in all locations. Feeding and foraging behaviour was inferred from observing long dives at the same place, fast swimming under the surface chasing fish, individuals tossing fish or with fish in the mouth at the surface. Groups were seen travelling slowly and relatively quickly, normally forming tight groups and swimming very close to the shore line in all locations except in St Andrews Bay. Dolphins were often seen socializing in all locations. Individuals were seen milling at the surface, rolling over, playing with bits of sea weed and even tossing jelly fish, and were also seen chasing each other and displaying a wide range of aerial jumps.

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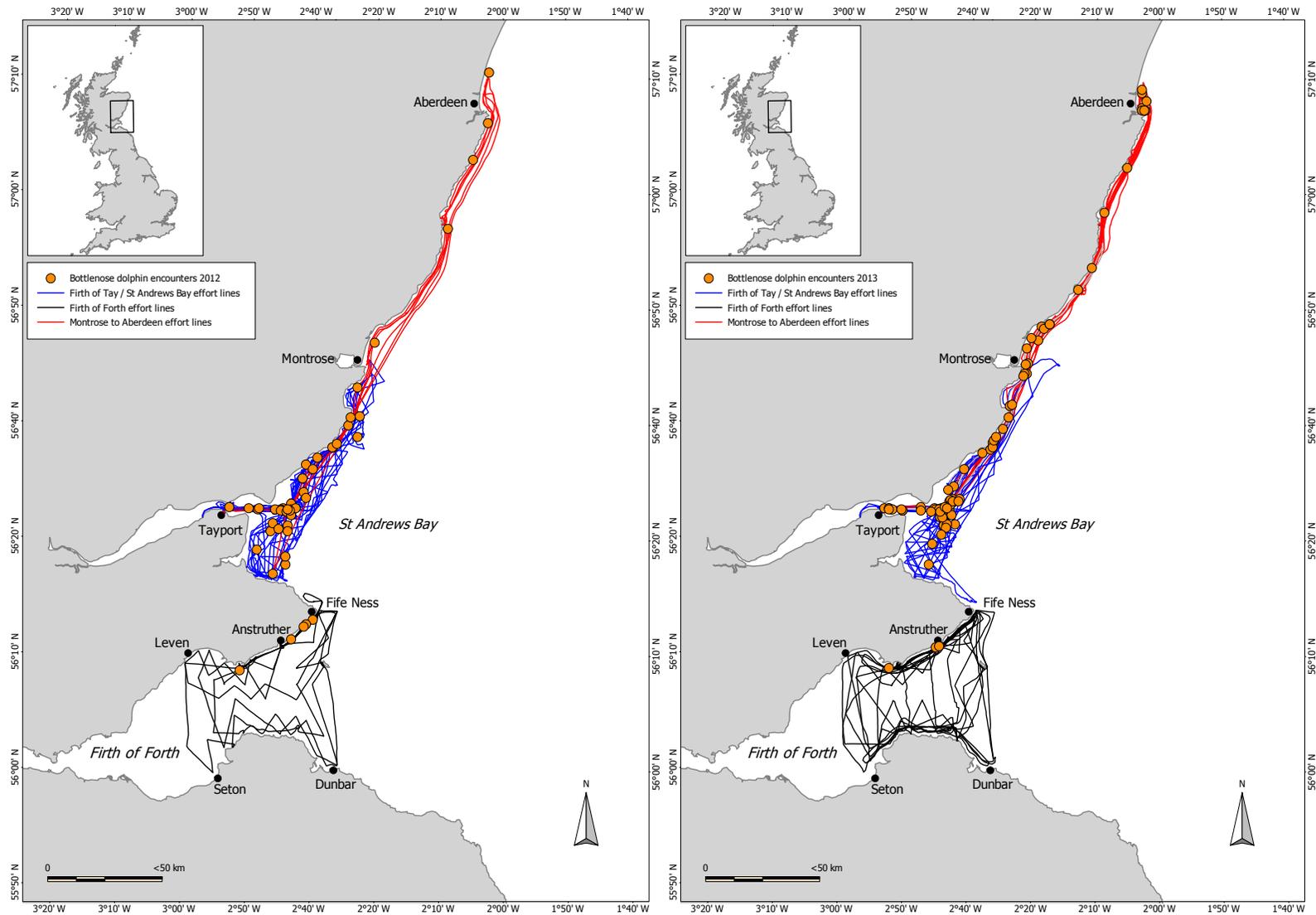


Figure 5.4. Survey effort in 2012 and 2013 and bottlenose dolphin encounters in the Firth of Tay / St Andrews Bay (blue), the Firth of Forth (black), and Montrose to Aberdeen (red).

### 5.3.3. Modelling bottlenose dolphin presence in St Andrews Bay and the entrance to the Firth of Tay

Over the two years, 3782 km of survey effort in St Andrews Bay and the entrance to the Firth of Tay were used to model the presence of bottlenose dolphins. In total, 128 groups were encountered and animals were followed for 325 km (Table 5.3, Figure 5.5 and Figure 5.6). A detailed summary of each trip is given in Appendix 4.

Table 5.3. Summary of field work effort, photo-ID follows, and number of encounters in 2012 and 2013, in the area of St Andrews Bay and entrance to the Tay.

Month	2012			2013		
	On-effort (km)	Follow (km)	No. Encounters	On-effort (km)	Follow (km)	No. Encounters
May	376	34	6	414	37	10
June	358	20	5	602	45	17
July	628	90	21	402	25	13
August	225	15	5	243	16	18
September	214	30	7	320	13	26
<b>Total</b>	<b>1801</b>	<b>189</b>	<b>44</b>	<b>1981</b>	<b>136</b>	<b>84</b>
	<b>Total 2012/13</b>			<b>3782</b>	<b>325</b>	<b>128</b>

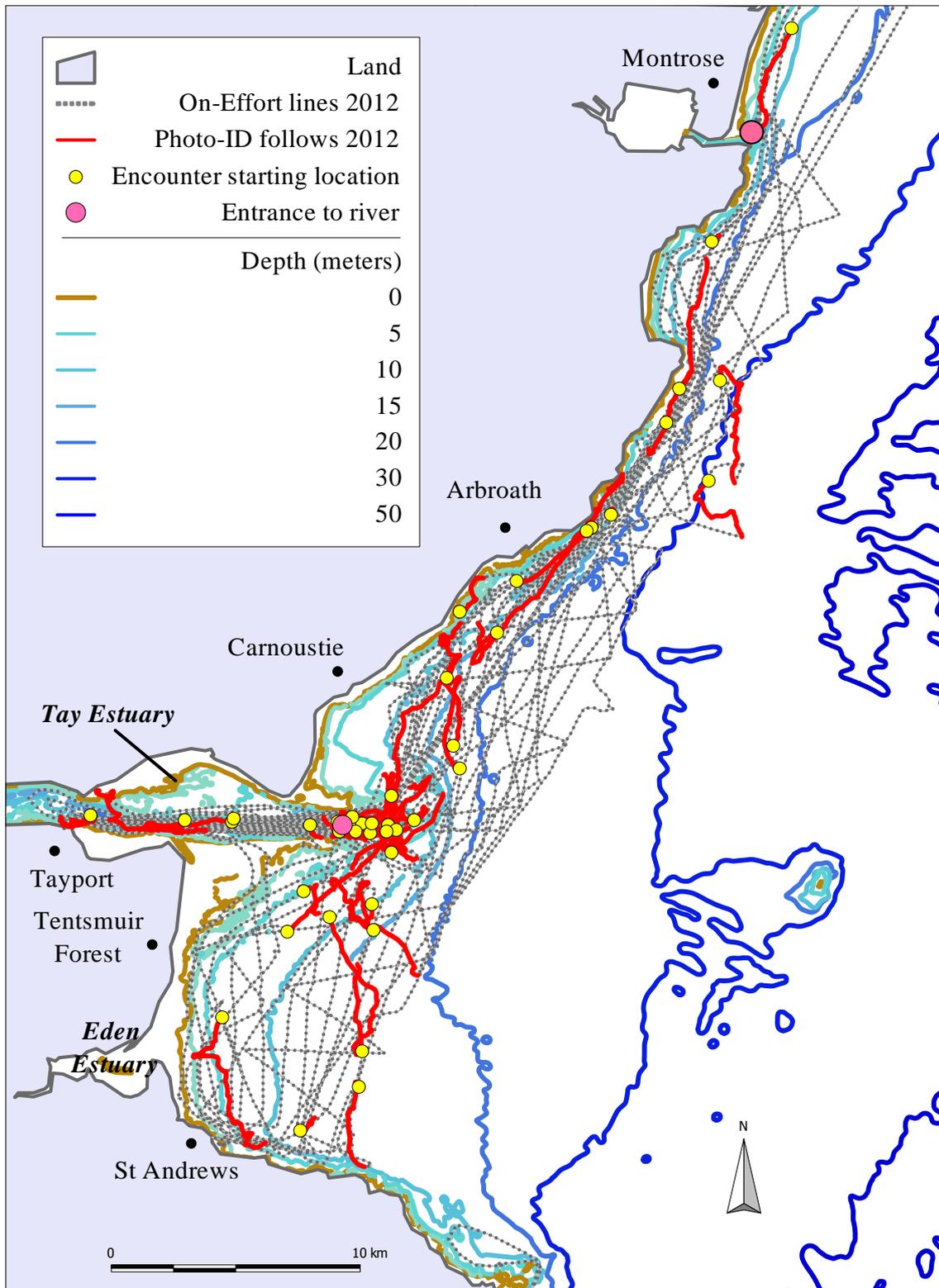


Figure 5.5. On-effort survey tracks, starting encounter locations and photo-ID follow tracks used to model the presence of bottlenose dolphins in St Andrews Bay and entrance to the Firth of Tay in 2012. The 0 meter contour defines the sandbar exposed at low tide.

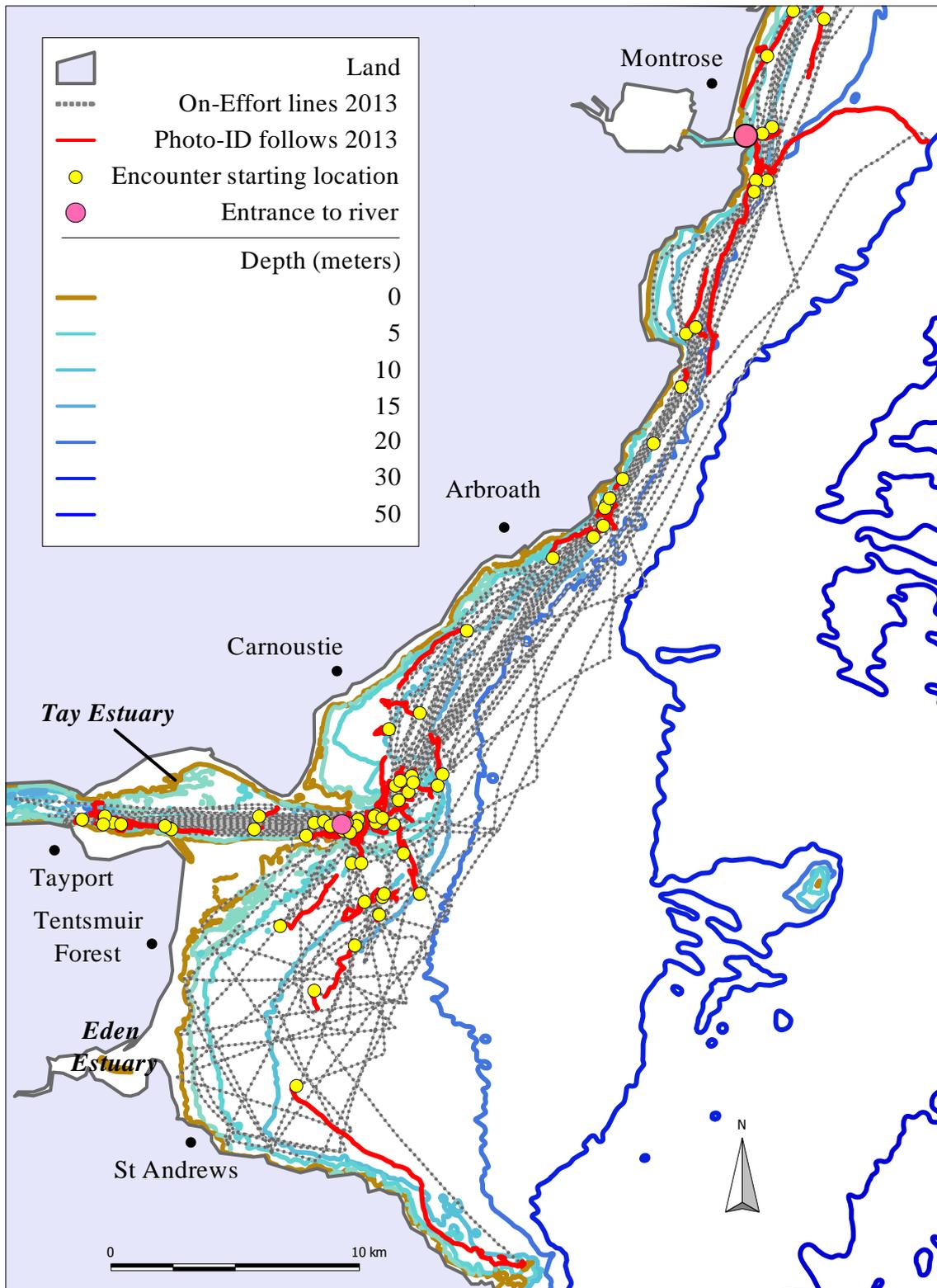


Figure 5.6. On-effort survey tracks, starting encounter locations and photo-ID follow tracks used to model the presence of bottlenose dolphins in St Andrews Bay and entrance to the Firth of Tay in 2013. The 0 meter contour defines the sandbar exposed at low tide.

### 5.3.3.1. *Model fitting and model selection*

Tidal data sourced from POLPRED/POLTIPS (*current speed, current level, current direction*) were not available in areas very close to the coast because the tidal model is not able to predict in those locations. Thus, a subset of the data excluding missing values for tidal covariates was used for the modelling, including 7758 GPS fixes with 5019 absence points and 2739 presence points.

Based on the *quasi-likelihood under the independence model criterion* (QIC; Pan, 2001), the working independence structure was preferred with a criterion value much smaller (QIC = 10088) the one when the model was fitted with an autocorrelation structure of order 1 (AR1 structure) (QIC = 10172) or with the exchangeable autocorrelation structure (QIC = 10151).

A fully saturated model was fitted with all candidate covariates included as categorical variables or as *B*-splines with either 4 or 5 degrees of freedom (d.f.), with the best form for each covariate previously selected based on the  $QIC_u$ . The covariates included *depth* (5 d.f.), *sea surface temperature* (4 d.f.), *distance to land* (5 d.f.), *slope* (5 d.f.), *aspect* (5 d.f.), *distance to the Tay* (5 d.f.), *current level* (4 d.f.), *current speed* (4 d.f.) and *current direction* (5 d.f.), and the categorical covariates *year* (2 factors levels), *month* (5 factor levels), *sediment* (4 factor levels), and *tidal state* (4 factor levels).

The manual backwards stepwise selection based on the  $QIC_u$  retained *distance to the Tay, current speed, current direction, temperature, month* and *year*. Repeated Wald's test on the final model confirmed that *distance to the Tay* was significant ( $p$ -value <0.05); all covariates were retained in the final model to predict the presence of bottlenose dolphins (Table 5.4). Tidal stream patterns for St Andrews Bay are shown in Figure 5.7 at mid-flood and mid-ebb tidal state. Figure 5.8 shows a scatterplot of the values of *current speed* plotted against *current direction*, to visualize how these two tidal covariates are related. Figure 5.9 shows the photo-ID follows of presence points plotted with the covariate *distance to the Tay* retained in the final model.

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Table 5.4. Wald's test on the final model to test for covariate significance. Each covariate is expressed as a factor covariate or a B-spline (bs) with one or two knots, positioned at the mean or at the upper and lower quartiles of each covariate, respectively. Significant covariates are marked with one asterisk when  $p$ -value  $< 0.05$  (d.f. = degrees of freedom).

Covariate	d.f.	$\chi^2$	$p(>  \chi^2 )$
bs(distTay,knots=quantile(tayinout,p=c(1/3, 2/3)))	5	13.90	0.01622*
bs(current.dir, knots=quantile(current.dir, p=c(1/3, 2/3)))	5	5.36	0.37379
bs(current.speed,knots=mean(current.speed))	4	5.85	0.21053
as.factor(month)	4	4.79	0.30893
bs(temperature,knots=mean(temp))	4	3.55	0.47197
as.factor(year)	1	0.71	0.39866

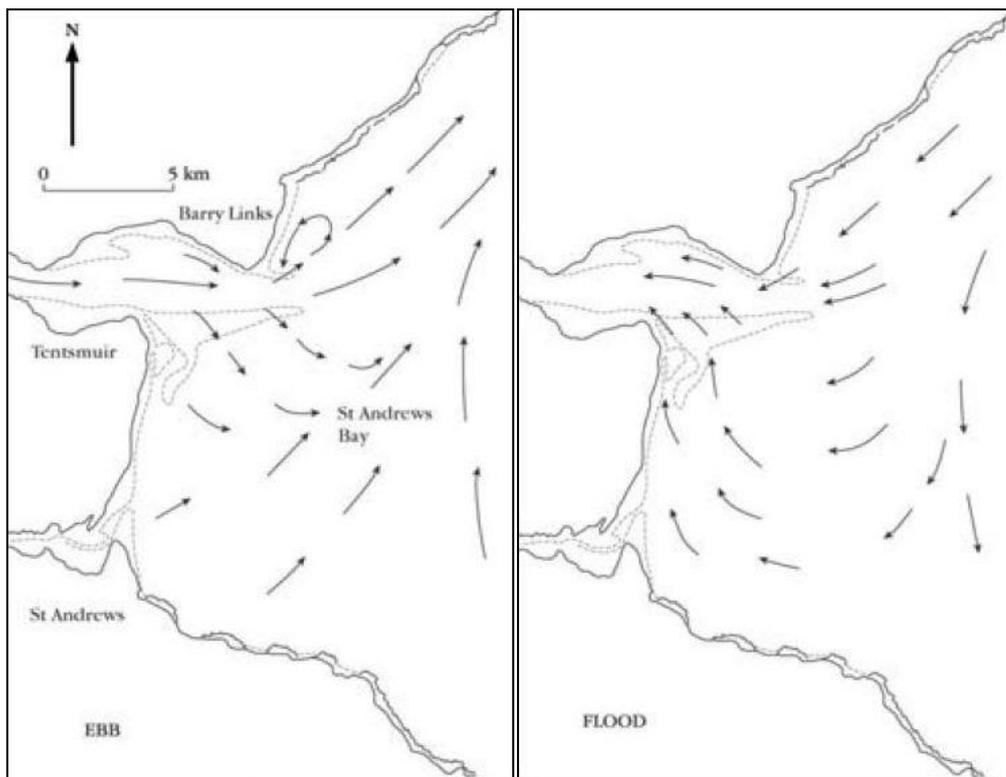


Figure 5.7. Tidal stream patterns at mid-ebb and mid-flood tidal states for St Andrews Bay from direct measurements and hydraulic modelling (extracted from Ferentinos and McManus (1981)).

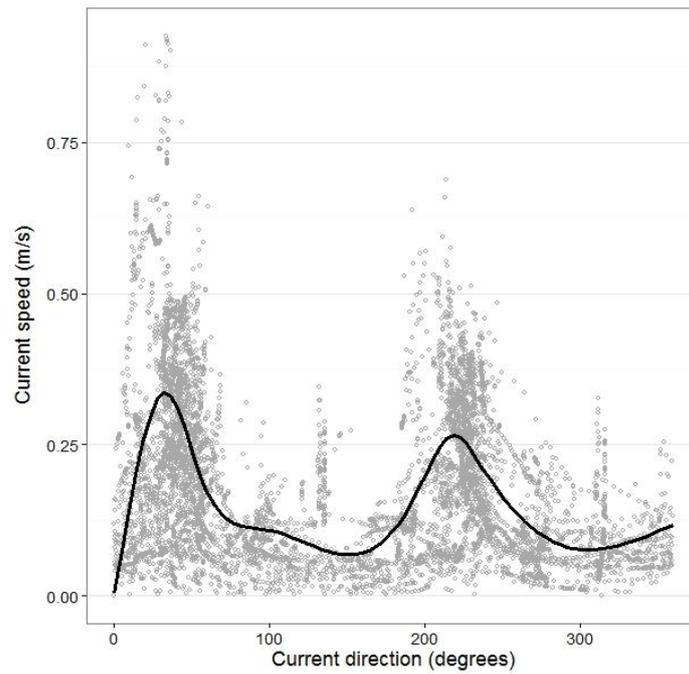


Figure 5.8. Scatterplot and smooth line of current direction (in degrees) versus current speed (in m/s) from the data used to model the probability of presence of dolphins.

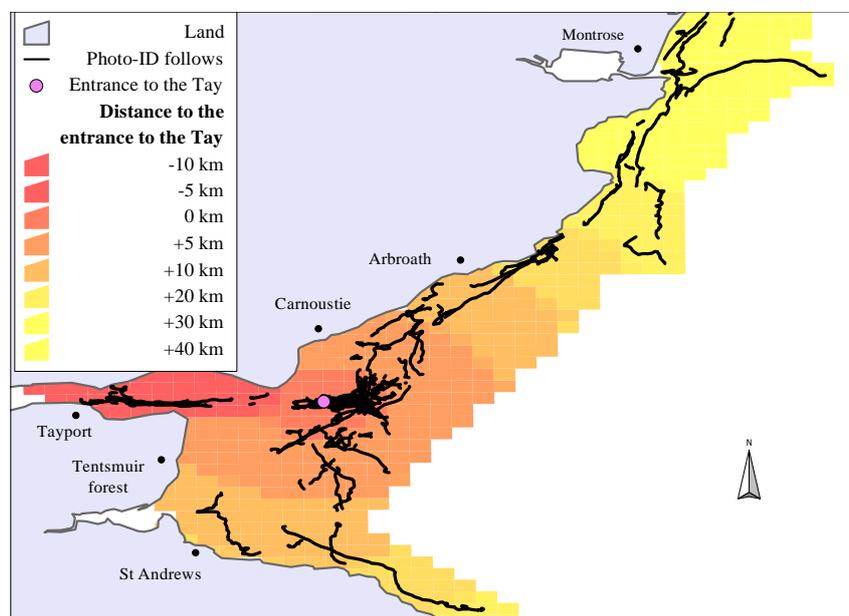


Figure 5.9. Photo-ID follows plotted with the values of the covariate *distance to the Tay* (km). The location of the entrance to the Firth of Tay is shown, and negative and positive distances are from locations inside and outside the Tay.

Partial residual plots for all covariates retained in the final model are shown in Figure 5.10, to visualize the relationship between the response variable (on the link scale) and each covariate. The coefficients with associated standard errors estimated in the best model for all retained covariates are shown in Table 5.5. Bottlenose dolphins were more likely to be encountered close to Tayport and around the entrance to the Tay, approximately within a distance of 7 km east of the entrance. The probability of dolphin presence decreased further away from the Tay except for a second presence peak greater than 30 km away from the entrance, which, based on the data, would correspond to the area close to Montrose. Very low current speeds (0.0 to 0.15 m/s) and very high current speeds (0.5 to 0.8 m/s) were associated with a higher probability of presence of bottlenose dolphins, compared to current speeds between those two extremes (0.15 to 0.5 m/s). The probability of presence of bottlenose dolphin varied with the direction of the current. Current direction flowing towards the NE (*i.e.* 10 to 60 degrees) and towards the WSW (*i.e.* 220 to 300 degrees) was associated with a higher probability of dolphin presence, compared to other current directions. These ranges are approximately the current directions associated with higher current speed, as shown in Figure 5.8. The probability of encountering dolphins varied slightly between months, with September having the highest probability of dolphin presence. Between the two years, probability of encountering dolphins was slightly higher in 2012. The 95% confidence intervals around the modelled relationships between the response variable and the retained covariates were generally wide (Figure 5.10).

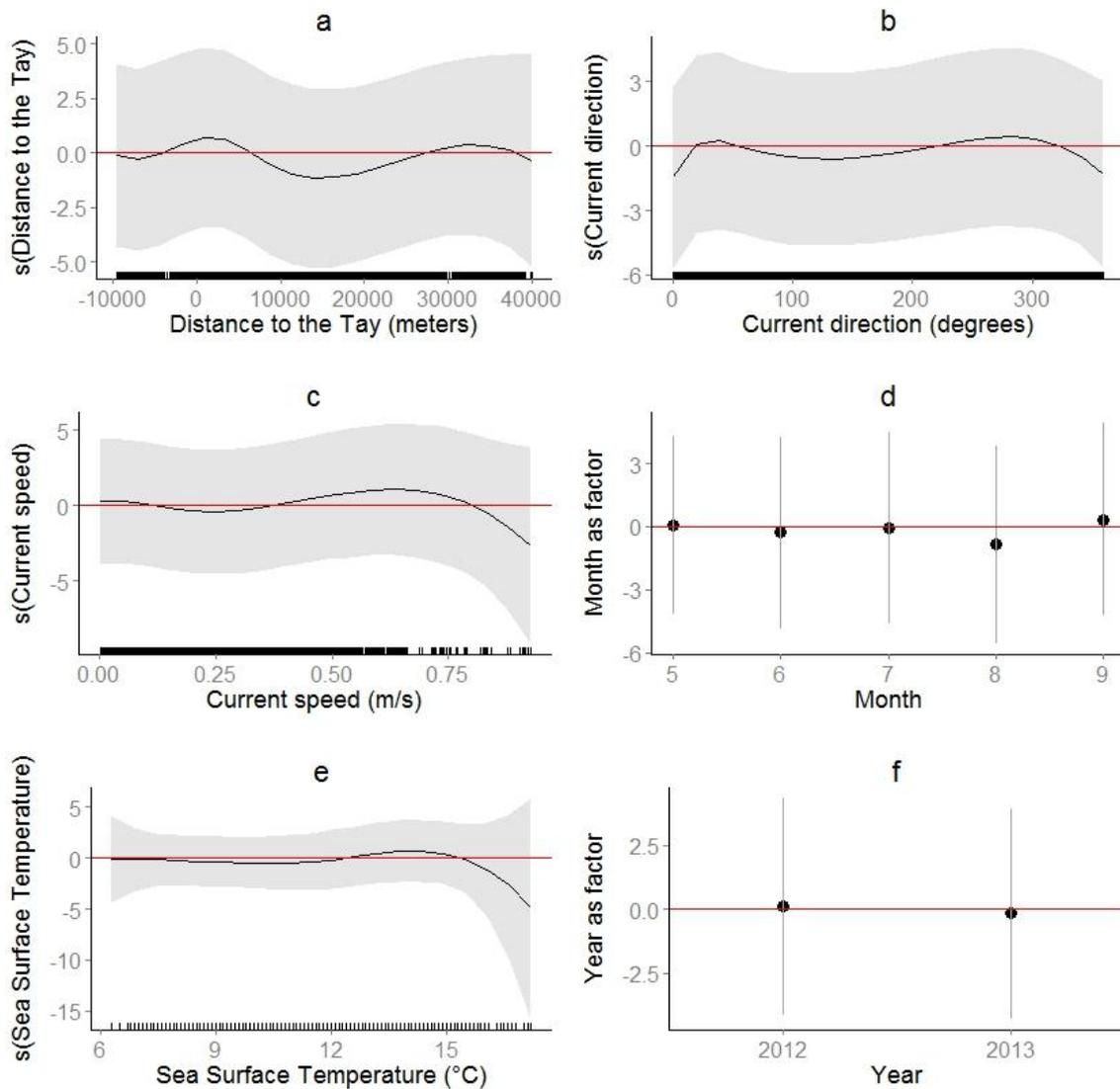


Figure 5.10. Partial residual plots of the relationship between presence of bottlenose dolphins (on the link scale) and the retained covariates (a) distance to the Tay (meters), (b) current direction (0-360 degrees), (c) current speed (m/s), (d) month, (e) sea surface temperature (°C) and (f) year. The shaded areas are the GEE-based 95% confidence intervals and a rug plot with the actual data values is shown at the bottom of each plot.

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Table 5.5. Output summary for best model showing estimates for each model coefficient, and associated standard errors. Multiple coefficients are shown for each covariate, one for each degree of freedom of that covariate.

<b>Coefficients</b>	<b>Estimate</b>	<b>Standard Error</b>
(Intercept)	-1.795	2.1336
bs(distTay) 1	-0.7818	1.4943
bs(distTay) 2	2.0617	0.8425
bs(distTay) 3	-3.6562	1.5485
bs(distTay) 4	2.2417	1.6684
bs(distTay) 5	-0.2727	1.3858
bs(current.dir) 1	2.3074	1.0425
bs(current.dir) 2	0.2713	1.3745
bs(current.dir) 3	1.3145	1.2641
bs(current.dir) 4	2.4821	1.295
bs(current.dir) 5	0.1192	0.887
bs(current.speed) 1	0.1554	1.0458
bs(current.speed) 2	-2.834	1.3656
bs(current.speed) 3	4.2327	2.5913
bs(current.speed) 4	-2.9795	2.8066
as.factor(month) 6	-0.3309	0.836
as.factor(month) 7	-0.1293	0.941
as.factor(month) 8	-0.8948	1.0522
as.factor(month) 9	0.2649	0.9685
bs(temperature) 1	0.1536	3.1022
bs(temperature) 2	-1.8823	2.2903
bs(temperature) 3	2.9844	3.2772
bs(temperature) 4	-4.7486	5.2472
as.factor(year) 2013	-0.2797	0.3313

### 5.3.3.2. *Model evaluation*

The confusion matrix showed that the model correctly predicted 70% of the dolphin presences and 70% of the dolphin absences based on a cut-off probability of 0.381 in the ROC curve (Figure 5.11). The area under the ROC curve (AUC) was equal to 0.741, which supported the good performance of the final model ( $AUC > 0.7$ ).

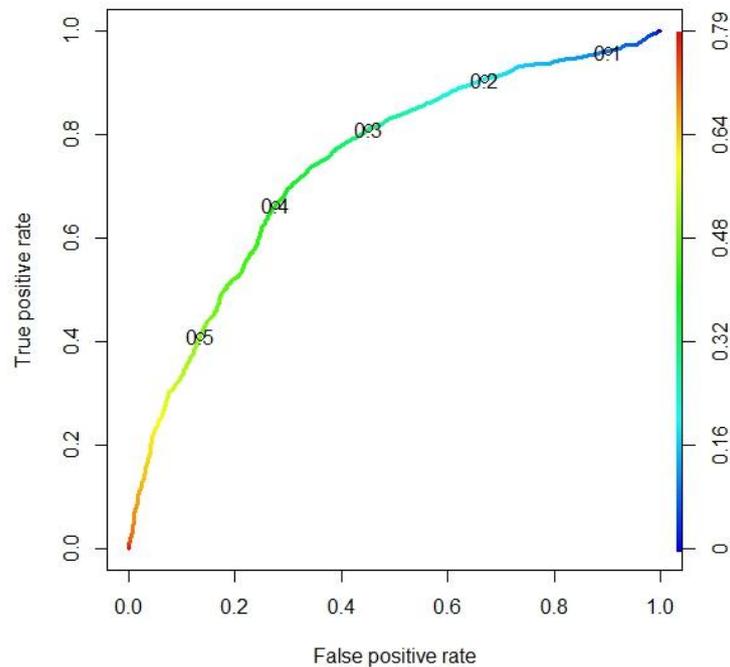


Figure 5.11. ROC curve plot for the final model, showing the locations of 0.1 to 0.5 cut-off probability levels. The best cut-off probability was at 0.381, and the area under the curve (AUC) was 0.741.

### 5.3.3.3. *Predicted presence of bottlenose dolphins*

The probability of presence of bottlenose dolphins was predicted at different range values of the retained tidal covariates, *current speed* and *current direction*. Because those two covariates are not independent from each other, not all combinations of values from both covariates are realistic (*i.e.* high speeds of more than 0.5 m/s only occur at certain current directions, as seen in Figure 5.8). The classification of the covariate values into each range was based on the visual inspection of the raw tidal data (*i.e.* how *current speed* varies with *current direction* and *vice versa*) (Figure 5.8) as well as on the

modelled relationships between the probability of presence of dolphins and those two tidal covariates (Figure 5.10). *Current direction* was divided into four value ranges: 10-60 degrees, 60-220 degrees, 220-300 degrees, and 300-10 degrees. *Current speed* was divided into three value ranges: 0-0.15 m/s, 0.15-0.5 m/s, and 0.5 m/s or over.

To predict the probability of presence of bottlenose dolphins, data for each tidal covariate were selected for each value range, together with the corresponding data values of the other tidal covariate. Averaged values were then generated for each cell. Because the retained categorical covariates *year* and *month* have the effect of increasing or decreasing the predicted probability of presence of dolphins equally over all prediction cells, the year and month with the highest coefficient values were selected for the predictions (*i.e.* 2012 and September, Table 5.5). *Sea surface temperature* was averaged for that temporal scale.

The prediction maps identified the entrance of the Firth of Tay as an area with high probability of presence of bottlenose dolphins in all value ranges of current direction and current speed (Figure 5.12 and Figure 5.13). The area around Montrose was also predicted to have a high probability of presence of bottlenose dolphins. On the contrary, the southern half of St Andrews Bay and the waters between Carnoustie and north of Arbroath had a smaller probability of presence of dolphins.

The predicted probability of presence of dolphins was lowest when the current was flowing towards 60-220 degrees, and highest at the other current directions, although the area with the highest predicted probability shifted slightly along the entrance to the Tay at different current directions (Figure 5.12). The effect of current speed on the probability of presence of dolphins was more differentiated among the three ranges of values. Bottlenose dolphins were more likely to occur at very low (0-0.15 m/s) or at very high (>0.5 m/s) current speeds. Very high current speeds (>0.5 m/s) only occurred at the very entrance to the Tay in St Andrews Bay and waters north along the coast. The predicted probability of dolphins was highest at those high current speeds. At intermediate values of current speed (0.15-0.5 m/s) the predicted probability of presence of dolphins was generally much lower.

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The effect of current speed and current direction on the presence of bottlenose dolphins was also reflected in the presence/absence maps (Figure 5.14 and Figure 5.15) based on the cut-off probability in the ROC curve. It can again be seen that bottlenose dolphins were present at the entrance to the Firth of Tay and the area around Montrose at all current directions but less when the current was flowing towards 60 to 220 degrees (Figure 5.14). Dolphins were present in those two areas at low or high current speeds, but were mostly absent at intermediate speeds (Figure 5.15).

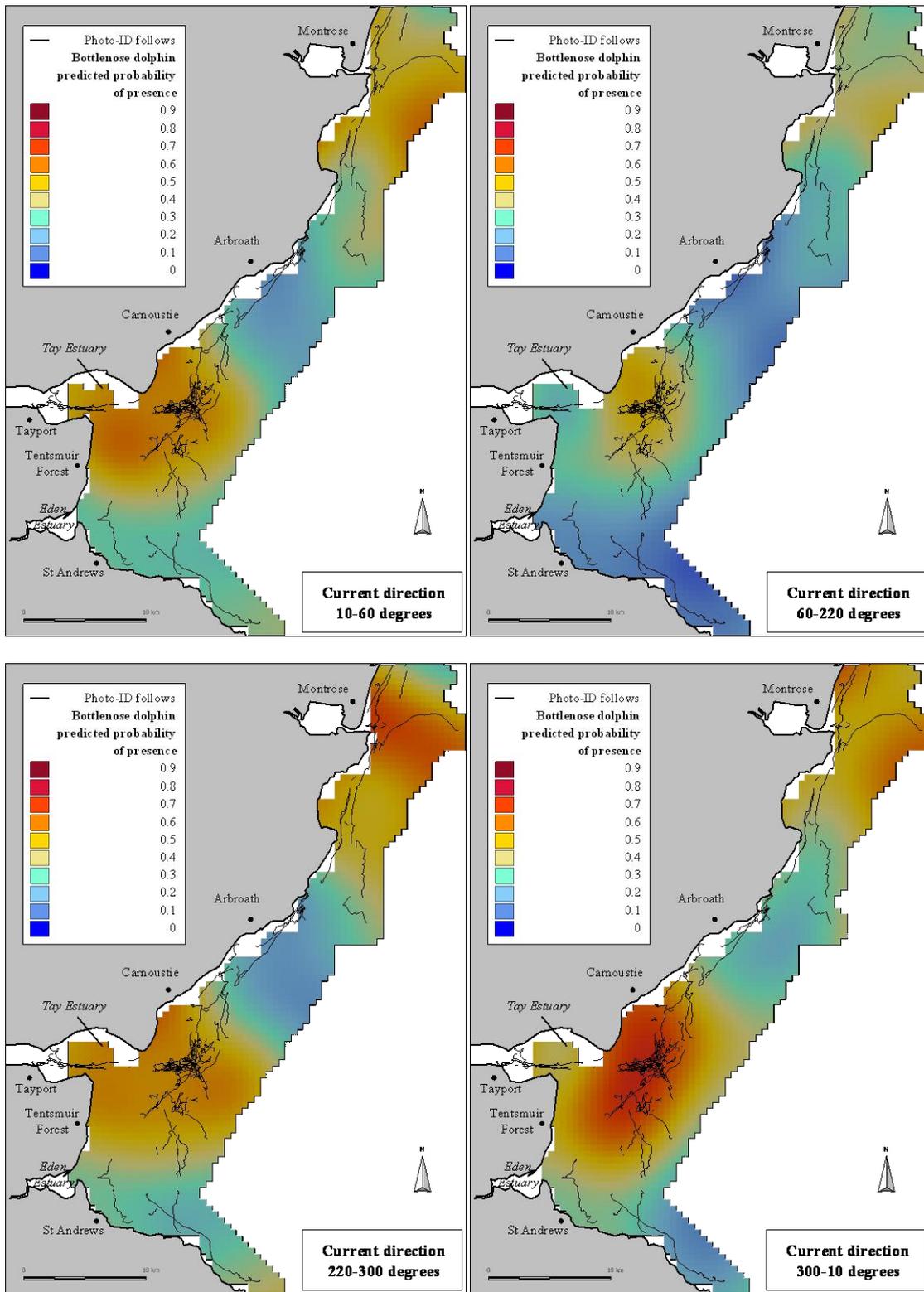


Figure 5.12. Prediction maps of probability of presence of bottlenose dolphins for different current direction ranges (10-60 degrees, 60-220 degrees, 220-300 degrees and 300-10 degrees).

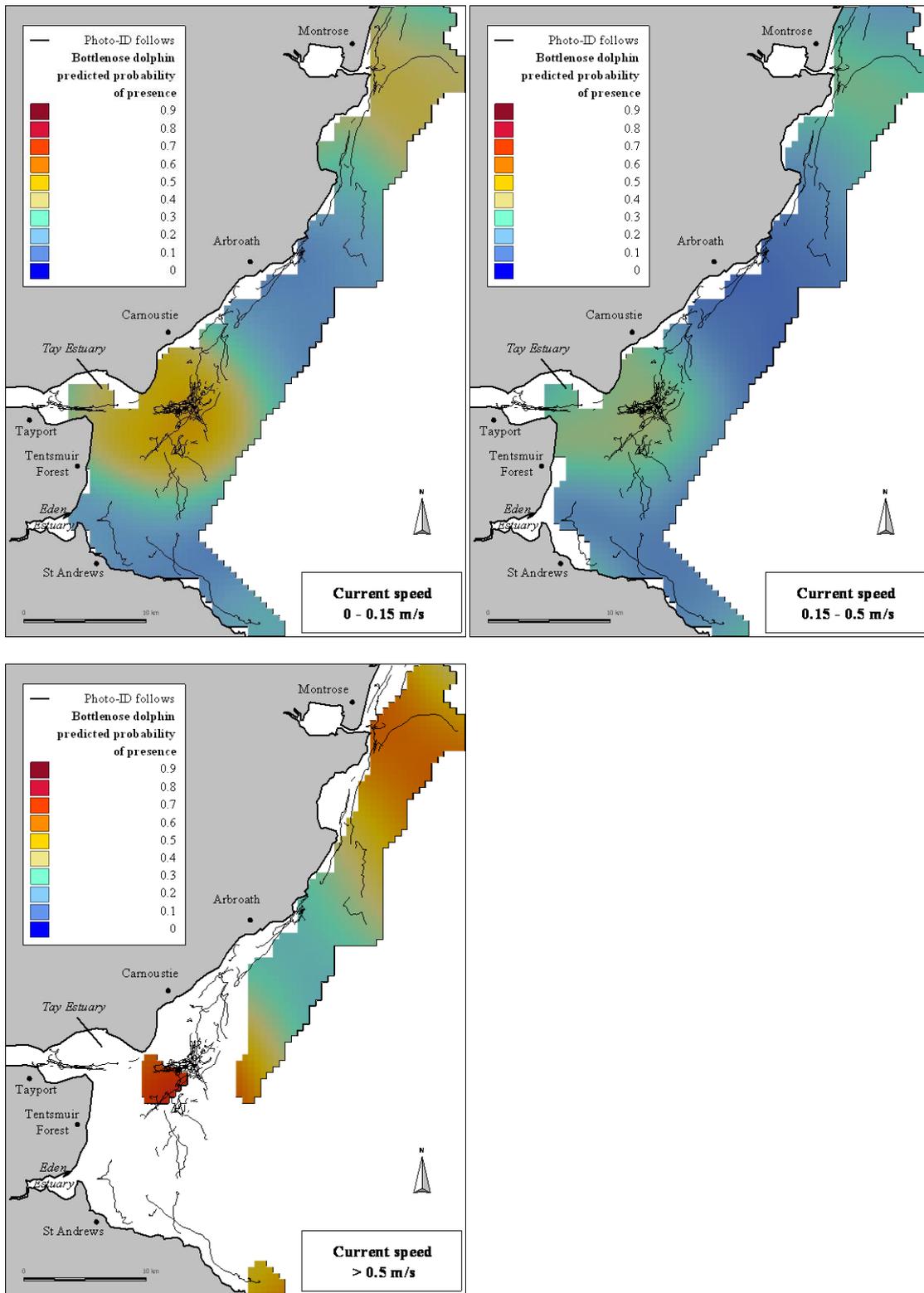


Figure 5.13. Prediction maps of probability of presence of bottlenose dolphins for different current speed ranges: low speed (0-0.15 m/s), intermediate speed (0.15-0.5 m/s) and high speed (>0.5 m/s).

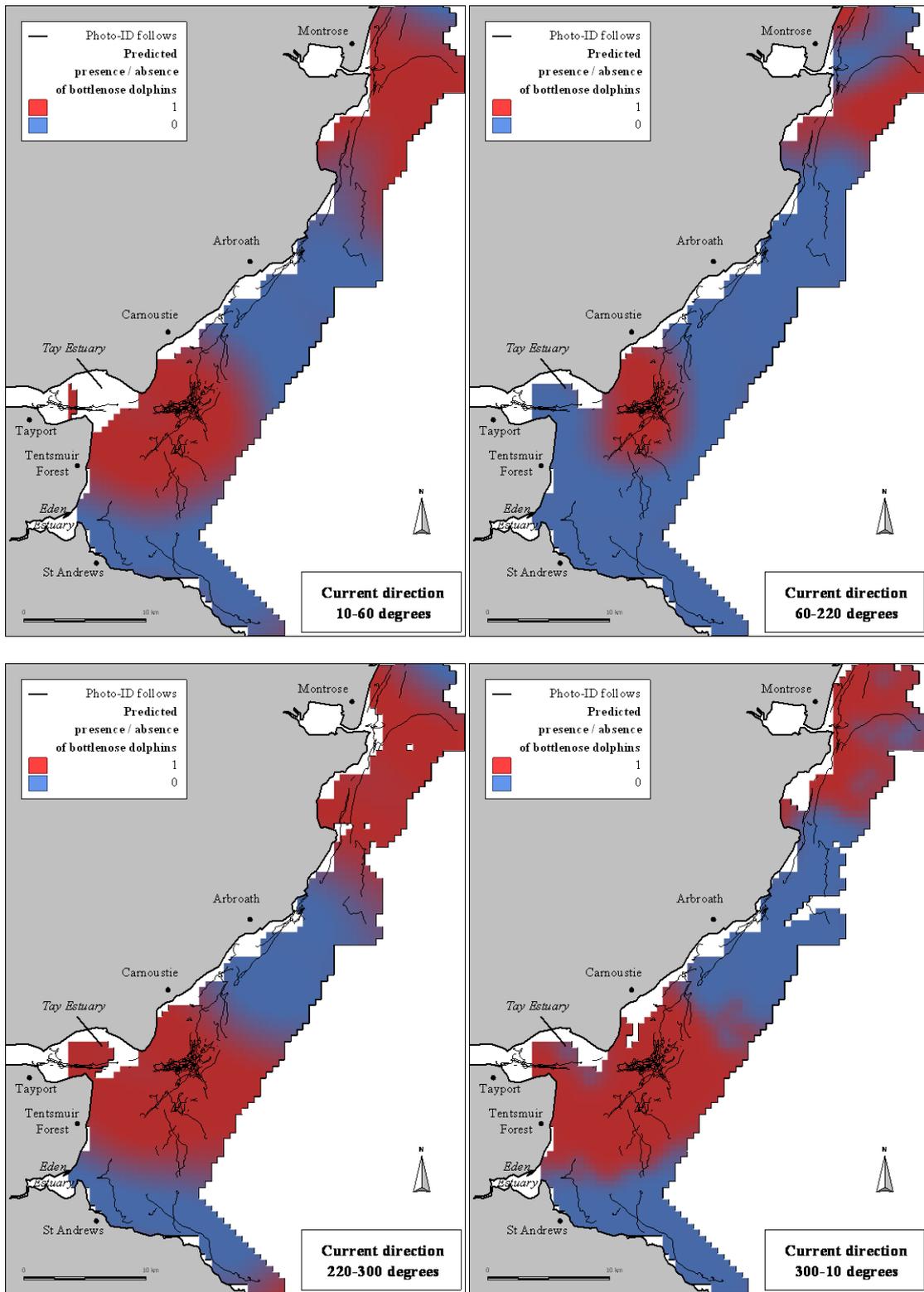


Figure 5.14. Prediction maps of presence / absence of bottlenose dolphins for different current direction ranges (10-60 degrees, 60-220 degrees, 220-300 degrees and 300-10 degrees).

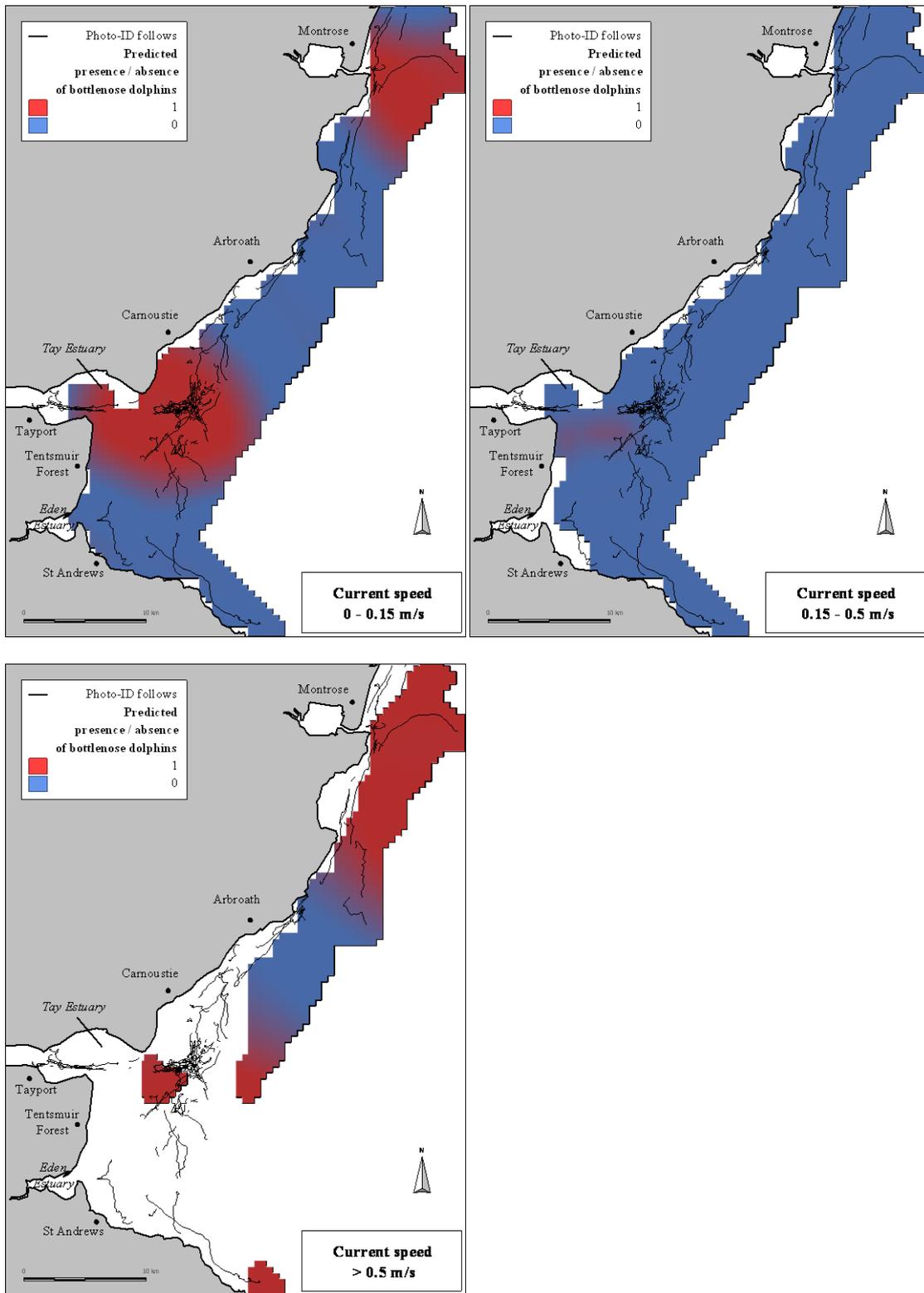


Figure 5.15. Prediction maps of presence / absence of bottlenose dolphins for different current speed ranges: low speed (0-0.15 m/s), intermediate speed (0.15-0.5 m/s) and high speed (>0.5 m/s).

## 5.4. Discussion

### 5.4.1. Distribution of sightings between Aberdeen and Firth of Forth

The survey effort conducted in 2012 and 2013 covered an extensive area of the coastal waters off the east coast of Scotland, with 140 km between the most distant locations of Aberdeen and the south side of the Firth of Forth. Survey effort between Montrose and Aberdeen and in the Firth of Forth was not included to model the habitat use of bottlenose dolphins for various reasons. First, the number of trips in each of those areas was much smaller than in St Andrews Bay, resulting in a much smaller sample size of presence/absence points that might have limited the ability to fit models. Secondly, priority was given to increase the chances of encountering dolphins and maximise the time available to photograph them, especially between Montrose and Aberdeen, where effort was not consistently made to cover the range of environmental covariates needed to model habitat use. In the Firth of Forth, coverage was good in the sense that transects were designed to cover coastal and deep waters, but the low number of encounters resulted in very small proportion of presence points.

Bottlenose dolphins were encountered in waters within 2 km of the coast between Montrose and Aberdeen and within 1 km of the coast in the Firth of Forth. The groups encountered between Montrose and Aberdeen were observed travelling up or down the coast but also feeding, especially just north of Montrose, around Stonehaven and in Aberdeen, suggesting that these are all important areas used by the dolphins. In Aberdeen, dolphins were seen feeding at the entrance of the harbour, between the north and the south pier, in accordance with observations from previous studies (Sini *et al.*, 2005, Pirotta *et al.*, 2013), that define that area as an important feeding spot. In the Firth of Forth, sighting data prior to this study are limited, but bottlenose dolphins have been recorded in the area from stranding and sighting data (summarized in Cheney *et al.* (2013)). The low number of groups encountered despite the fairly extensive survey effort, and the fact that all encounters occurred on the north side indicate that although the Firth of Forth is used by at least part of the population, it is likely to represent the southern limit of the usual distributional range.

### 5.4.2. Presence of dolphins

The predicted presence of bottlenose dolphins was not uniform across the study area. Bottlenose dolphins were more likely to be present at the entrance of the Firth of Tay and in the waters around Montrose at the extreme north of the modelled area. This pattern of predicted high probability of presence was maintained across different current speeds and current directions, although the probability of presence did vary at different values of those tidal covariates. The model predicted a much lower presence of bottlenose dolphins in other areas including the southern half of St Andrews Bay from the Eden Estuary to Fife Ness at the southern end of the area, and in waters between Carnoustie and north of Arbroath (Figure 5.12 and Figure 5.13). The presence/absence predictive maps based on the best cut-off probability of 0.381 from the ROC curve confirmed the importance of the entrance of the Tay and the area around Montrose (Figure 5.14 and Figure 5.15)

The final model identified a temporal difference in the presence of dolphins between the two years of data, with 2012 having a higher probability of presence than 2013. The final dataset that was used to predict the presence of dolphins contained a similar number of on effort data points for each year (5260 in 2012 and 4871 in 2013), but the percentage of observed presences in 2012 (56%) was slightly higher than in 2013 (48%), which could account for part of the temporal variation in the predicted presence of dolphins. The reason behind this might be related to an increased efficiency in taking photographs between the first and the second year, which would translate into shorter periods following groups and thus less presence points per encounter.

Month was also retained as a covariate in the best model, reflecting a temporal variability in the probability of presence of dolphins among months, although the differences were small. Bottlenose dolphins were seen in all surveyed months (May to September) in both years, in accordance with past years of survey effort during the summer in St Andrews Bay (Cheney *et al.*, 2013). Seasonal differences in the presence of bottlenose dolphins exist in the Moray Firth, with the greatest numbers occurring from May to September and the lowest October until April (Wilson *et al.*, 1997a). In St Andrews Bay and the north side of the Firth of Forth there are anecdotal records of sightings of bottlenose dolphins all year round. Winter data are very limited for St Andrews Bay; winter boat surveys were only conducted in 2008, during

which no bottlenose dolphins were encountered (Thompson *et al.*, 2011). However, acoustic detections data from C-PODs and T-PODs deployed in Arbroath and Fife Ness in 2007 and 2008 confirmed the presence of dolphins year round but with a lower occupancy rate in winter (Thompson *et al.*, 2011), reflecting the same seasonal pattern observed in the Moray Firth.

The presence and distribution of bottlenose dolphins off eastern Scotland has been mainly linked to the availability of food resources (*e.g.* Mendes *et al.*, 2002, Hastie *et al.*, 2004, Bailey *et al.*, 2013). Predator avoidance, which has been found to affect the habitat use of bottlenose dolphins in other populations (*e.g.* Heithaus and Dill, 2002), has been discounted for the eastern Scotland population because there is no evidence of predation (Wilson, 1995). Preference for specific calving areas was suggested for some places in the inner Moray Firth (Wilson *et al.*, 1997a), although mother and newborn pairs are seen throughout the study area with no obvious definition of specific calving grounds (Grellier, 2000). This was also seen in the observations during the 2012-13 surveys, during which mother-calf pairs were observed in all areas between Aberdeen and the Firth of Forth.

In the Moray Firth, the increase in the presence of bottlenose dolphins during the summer months has been linked to seasonal migrations of salmonids (Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*) through the area (Wilson *et al.*, 1997a). Salmonids are known to be important prey for bottlenose dolphins in this population based on stomach contents (Santos *et al.*, 2001) and direct observations of dolphins feeding on salmon (*e.g.* Wilson *et al.*, 1997a, Janik, 2000, Hastie *et al.*, 2004). In St Andrews Bay, bottlenose dolphins were also observed chasing or with salmon in the mouth in the 2012-2013 surveys, indicating salmonid species are part of their diet at least during the summer months.

Salmon data are difficult to quantify; they are generally provided for the different Scottish regions and districts, summarized by method (rod and line catches, net catches and fixed engine), catches and releases, and species (salmon, grilse and sea trout). The River Tay is an important river for salmon and sea trout within Scotland (ASFB & RAFTS, 2014). In 2012, the total catch and release of salmon, grilse and sea trout in that river was greater than 40 tonnes, representing 11% of the total catches and releases in Scotland for 2012 (Marine Scotland Science, *unpublished data*, available at <http://www.scotland.gov.uk/Topics/marine/Publications/stats/SalmonSeaTroutCatches>).

Those data only reflect salmonids migrating through the river and have not been corrected for non-returns or incomplete information, but they are indicative of the abundance of those prey species in the area. Salmon and sea trout that do not migrate upstream also approach the Tay estuary at different stages of their life cycle (Mills, 1986). It is therefore likely that salmon plays an important role in the ecology of bottlenose dolphins in St Andrews Bay as seen in other areas off the east coast of Scotland.

Similarly, the rivers by Montrose (North Esk and South Esk rivers) are also important for sea trout and salmon (Marine Scotland Science, 2012). The seasonality in the presence of those prey species is also likely to determine the presence of bottlenose dolphins in the area. Other prey species important in the diet of bottlenose dolphins from this population include cod, saithe, whiting, haddock and cephalopods (Santos *et al.*, 2001). All of these are found in south east of Scotland North Sea waters, where the dominant fish species based on fisheries assessment are flatfish, gadoids (cod, haddock, whiting, pollock) and sandeels (Callaway *et al.*, 2002). A study on seal diet in St Andrews Bay found that despite sandeels being the main prey in their diet, seals were also feeding on gadoid fish (whiting and cod) and flatfish. In the Firth of Tay, harbour seal diet was dominated by salmonids except in the winter, representing 78% of the diet in the spring (salmon, smelt and sea trout), 47% in the summer (only salmon), and 40% in the autumn (sea trout only) (Sharples *et al.*, 2009).

### **5.4.3. Influence of the tidal cycle**

Predictive maps showed that the presence of dolphins at the entrance of the Firth of Tay and around Montrose varied with current speed and direction. Because these covariates vary together throughout the tidal cycle, it is impossible to completely separate their effects on the probability of presence of dolphins. Dolphins were more likely to be present in areas with low current speeds or high current speeds, compared to intermediate values. The highest current speeds tend to occur half way between flood and ebb tides, while low current speeds generally occur close to the slack high and low waters. On the other hand, the probability of presence of dolphins was highest when the current was flowing approximately towards the NE or WSW (Figure 5.10), which corresponds to falling and rising tides, although dolphins were also predicted to be present when the current was flowing towards the WNW (Figure 5.12). Interpretation of these results is difficult for the area of the entrance to the Tay Estuary.

That area is influenced by offshore tidal currents and by the estuarine currents, which have different phase relationships with respect to high water, causing complex circulations of the water and system of fronts (Ferrier and Anderson, 1997).

The tidal cycle has been seen to influence the movements of bottlenose dolphins in other populations (*e.g.* Shane *et al.*, 1986, Scott *et al.*, 1990, Shane, 1990, Acevedo, 1991, Gregory and Rowden, 2001, Fury and Harrison, 2011) and in areas within the distributional range of the eastern Scotland population (*e.g.* Mendes *et al.*, 2002, Bailey *et al.*, 2013). In Chanonry Channel, located in the inner Moray Firth, dolphins are more likely to be present at low and flooding tides (Bailey *et al.*, 2013). Nearby, in the Kessock Channel, dolphins are also more abundant during the flood tide (Mendes *et al.*, 2002). Those two locations have narrow channels with deep water and steep seabed gradients, and are characterized by strong tidal currents. The presence of dolphins in areas with such habitat characteristics have been linked to foraging in the Moray Firth (Wilson *et al.*, 1997a, Hastie *et al.*, 2003b, Hastie *et al.*, 2004, Pirota *et al.*, 2014). The deep waters, steep seabed gradient and strong tidal fronts have been suggested to increase the foraging efficiency of the dolphins as prey may accumulate in these areas and the deep waters may facilitate the location of prey (Wilson *et al.*, 1997a, Mendes *et al.*, 2002, Hastie *et al.*, 2004).

The outside part of the River Tay Estuary channel is characterized by depths that range from 2 to 20 meters, with a generally flat seabed ( $0^\circ$  to  $3^\circ$  of slope). The entrance to the channel is delimited by sandbars that extend eastwards on the north (off Buddon Ness at the Barry Links) and south sides (Abertay Sands off Tentsmuir point) of the channel (Figure 5.5). The sandbars are exposed at low tide, most obviously the sandbar from Tentsmuir point that extends for more than 5 km eastwards. The distance across the entrance of the Tay between the two zero meter depth contours at each side (*i.e.* exposed at low tide) is just over one kilometre, making the entrance into the Tay relatively narrow at low tide. Despite having shallower waters than some of the above mentioned channels in the Moray Firth and having a flat seabed, the area experiences fast and complex tidal currents. The mouth of the Tay estuary is characterized by a complex system of fronts caused by the highly variable tidal mixing between sea water moving into the Tay and the fresh water moving out of it throughout the tidal cycle (Ferrier and Anderson, 1997). The spring tidal range reaches 4.4 meters at the entrance to the Tay, with spring tidal flows of greater than 1.2 m/s (Hansom *et*

*al.*, 2011). These tidal characteristics are comparable or even exceed those in other locations such as Kessock channel (4.1 meters at spring tides and tidal current flow rates of greater than 0.75 m/s; Mendes *et al.*, 2002). This dynamic and complex tidal mixing may accumulate prey and improve the foraging efficiency of dolphins in the area, as suggested for the narrow channels in the inner Moray Firth with similar highly complex tidal dynamics (*e.g.* Mendes *et al.*, 2002, Hastie *et al.*, 2004).

The exposure of the sandbars at either side of the entrance of the Tay Estuary may also increase foraging efficiency at low tide by confining and concentrating prey in the area or acting as a physical barrier that the dolphins can use to herd fish. In 2012 and 2013 individual dolphins were seen in many encounters next to the exposed sand bar, especially on the south side, feeding or attempting to feed (*i.e.* long dives on the same spot, chasing prey under the water, tossing fish at the surface or with fish in the mouth). Individuals were also seen just over or next to the sandbar at other tidal states when it was not exposed, where the waves would be breaking at times of the day closer to low tide.

Bottlenose dolphins from other populations have also been observed using physiographic natural features such as sand bars, estuarine mudflats and sandy beaches to isolate and catch prey. For example, bottlenose dolphins in Florida feed along the edge of sand bars, oyster bars or the shoreline where fish are known to aggregate, exhibiting what is known as a ‘feeding rush’ (*i.e.* sudden acceleration and splash as the dolphin spins or turns to catch the prey) (Shane, 1990). In Georgia and South Carolina, bottlenose dolphins are known for their ‘strand-feeding’ techniques in mud banks in which they cooperate in group to create a wave to strand small fish on the mud bank and then strand themselves to catch them (Duffy-Echevarria *et al.*, 2008). A similar feeding strategy called ‘beach hunting’ occurs in bottlenose dolphins (*Tursiops sp.*) in Shark Bay, in which dolphins herd fish against sandy beaches to catch them (Sargeant *et al.*, 2005). Estuarine mudflats are also used by bottlenose dolphins in different locations in the southern USA (Hoese, 1971, Rigley, 1983, Petricig, 1993), the Colorado river delta (Silber and Fertl, 1995), and in Portugal (dos Santos and Lacerda, 1987, Harzen, 1998) (summarized in Sargeant *et al.*, 2005). Similar feeding strategies are also used by other delphinid species, including the humpback dolphins near Bazaruto Archipelago in the Indian Ocean (Peddemors and Thompson, 1994). Individuals from that location have been observed feeding in the channels between sandbanks at ebb

tides, trapping fish against the sandbank and beaching themselves after causing fish to wash onto the sandbank.

### 5.4.4. Analytical considerations

#### 5.4.4.1. *Covariate data limitations*

Tidal covariates were retained as important predictors by the model selection. However, values of current speed, height and direction extracted from the model POLPRED (NERC National Oceanography Centre, Liverpool, UK) were not available for some areas very close to the coast. Limitations in the availability of environmental data at different temporal or spatial scales is a not uncommon issue in cetacean habitat use studies, and it generally requires excluding part of the effort data from the analysis (*e.g.* Embling *et al.*, 2010, Pirotta *et al.*, 2014), as done in this analysis, or limiting the analysis to the temporal scale at which covariates are available (Redfern *et al.*, 2006). On some occasions, *in situ* data can be collected to obtain detailed covariate data at the necessary scale, as done in this study by collecting *in situ* sea surface temperature. *In situ* data can also be of interest to characterize the water column dynamics, information that is not available from satellite-derived data (Redfern *et al.*, 2006). For example, Mendes *et al.* (2002) recorded observed surface features of the tidal fronts to investigate bottlenose dolphin spatial and temporal distribution in relation to the tidal cycle. Bailey and Thompson (2010) also characterized the changes in the tidal fronts and collected *in situ* current speed to investigate dolphin foraging movements related to fine-scale oceanographic features. In both cases, the relatively small size of the study area and landscape around it allowed for both land-based and boat-based surveys to collect data.

A finer-scale characterization of the tidal current dynamics at the Tay entrance as well as the effect of the tidal exposure of the sand bar would allow a better understanding of the effects of hydrographic features on the habitat use of the dolphins in that area. Unfortunately, the entrance to the Tay in St Andrews Bay lacks elevated land points in the vicinity to implement an experimental set up to obtain tidal dynamics data similar to what has been done in some of the above mentioned studies in the inner Moray Firth.

#### 5.4.4.2. *GAMs and GEEs approach*

The pre-modelling exploratory analysis showed that all covariates were to be fitted in the models as *B*-splines rather than linear terms. This is not surprising because most relationships between the distribution and abundance of cetaceans and environmental variables tend not to be parametric (*e.g.* linear or quadratic form) (*e.g.* Forney, 2000, Ferguson *et al.*, 2006a, Pirotta *et al.*, 2011). Allowing for smoothed relationships within a GAM framework was thus justified to model bottlenose dolphin habitat use in St Andrews Bay. Overall, the model predicted correctly 70 % of both the presences and the absences, which together with an area under the ROC curve (AUC) of 0.741 is interpreted as a good model performance (Swets, 1988, Manel *et al.*, 2001).

Spatial and temporal autocorrelation is an inherent issue in cetacean ecological data, because presence/absence or abundance of animals in nearby locations or times are likely to be more similar than if locations or times were randomly selected (Redfern *et al.*, 2006). Data-thinning methods are used in some studies to eliminate the correlation by deleting in between observations; this is not recommended because it tends to reduce sample size considerably and eliminate important information (Rooney *et al.*, 1998, Redfern *et al.*, 2006). On occasions, the selection of a sample unit of analysis at a specific spatial (*e.g.* grid cell size) or temporal scale (*e.g.* duration of the observations) is enough to minimize the autocorrelation in the data (*e.g.* Gordon *et al.*, 2000, Ferguson *et al.*, 2006a, Azzellino *et al.*, 2008). Other studies have taken no account of spatial autocorrelation after testing for it and finding no evidence for significant autocorrelation in the model residuals (*e.g.* Cañadas *et al.*, 2005, Tynan *et al.*, 2005, Marubini *et al.*, 2009, Sasaki *et al.*, 2013), or when accounting or not accounting for autocorrelation in the data makes no difference in the results (*e.g.* predictions) (Whitehead *et al.*, 2008).

Other than data-thinning methods, there are three main approaches to address the presence of autocorrelation in cetacean data. One option is to simply continue with the analysis knowing that the assumption of independence of model residuals might be violated and then acknowledge the potential limitations of the modelling results. For example, Ferguson *et al.* (2006b) and Gregr and Trites (2001) modelled the distribution of cetacean species in relation to environmental variables. These authors acknowledged the likely presence of

autocorrelation in their data, but stated that the problems associated with violating the assumption of independence were irrelevant when the purpose of the study was prediction rather than investigation of ecological relationships or hypothesis testing (Forney, 2000, Hamazaki, 2004). A second option is to account for the autocorrelation within the analysis when testing for the significance of the different candidate environmental covariates used to explain cetacean distribution. For example, simple and partial Mantel tests (Mantel, 1967, Smouse *et al.*, 1986) have been frequently used in cetacean habitat use studies to assess the effect of covariates on the species distribution while accounting for autocorrelation and for multicollinearity (*e.g.* Legendre, 1993, Schick and Urban, 2000, Torres *et al.*, 2008, Rayment *et al.*, 2010). However, concerns regarding the ability of the simple and partial Mantel tests to account for autocorrelation (*i.e.* inflated type I error or low power) have been raised (Guillot and Rousset, 2013).

A third option is to define a correlation structure within the modelling framework and explicitly account for the autocorrelation, as described in the introduction to this Chapter. In this study, data collected during each encounter with bottlenose dolphins were expected to be highly correlated, as shown by the ACF plots. Data-thinning, although attempted, resulted in a greatly reduced sample size with observations separated by 20 minutes, thus containing few presence data points for each encounter. The use of GEEs within the modelling framework avoided removing data and allowed autocorrelation to be accounted for. A simple independent working correlation structure was selected based on QIC. In fact, a working independence structure is generally preferred when unsure about the true underlying dependency structure between the residuals (Pan, 2001), and GEEs have the advantage of estimating robust standard errors even when the correlation structure is mis-specified (Liang and Zeger, 1986). The sandwich-based variance estimators used in the GEEs produce robust and realistic standard errors, but it means that the 95% confidence intervals around the model coefficient estimates tend to be very wide (Hardin and Hilbe, 2003), as happened in this case (Figure 5.10). The robust standard errors ensure that the retained covariates are important predictors for dolphin presence, but the resulting wide 95% confidence intervals limit the interpretation of the shape of the relationships (Pirotta *et al.*, 2011). Despite these limitations, the use of GEEs and GAMs allowed the use of detailed data collected during the encounters to predict dolphin presence in the study area and identify areas of high probability of dolphin presence, which was the main objective in this analysis.

## 5.5. Conclusions

Bottlenose dolphins were seen in all months between May and September throughout the study area, although groups were encountered more frequently in certain areas. Bottlenose dolphins were always encountered in Aberdeen harbour, where feeding behaviour was frequently observed in agreement with other studies. Other important areas of occurrence were the entrance to the Firth of Tay, and off Montrose and Stonehaven. The Firth of Forth seems to define the southern end of the typical range of this population.

The habitat use modelling analysis identified the entrance to the River Tay and the waters around Montrose as high use areas for bottlenose dolphins. The presence of dolphins was influenced by current speeds and directions, with more dolphins predicted to be in these areas at either low or high current speeds, compared to intermediate speeds, and current flowing towards the NE or WSW. The results suggest that the topography of the entrance to the Tay, with strong complex tidal currents and the exposure of sandbars on either side, may increase the foraging efficiency of the dolphins at least during the summer when salmonid prey species are in the area, as also suggested for areas in the inner Moray Firth.

This analysis demonstrates that the spatial and temporal variation of bottlenose dolphin presence collected during photo-ID follows can be modelled by means of GEEs to account for autocorrelation. The predictions provide information on bottlenose dolphin habitat use that was previously lacking for this part of the distributional range, and highlights the importance of St Andrews Bay and the entrance to the Firth of Tay for at least a part of the population.

## Chapter 6

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### General Discussion

#### 6.1. Thesis synthesis

Cetacean populations inhabiting coastal waters tend to have small and restricted distributional ranges, often overlapping considerably with human activities, which exposes them to numerous simultaneous, and potentially cumulative, anthropogenic impacts (Reeves and Reijnders, 2002). The life histories of marine mammals (*e.g.* low reproductive potential and slow population growth rate) make them especially vulnerable to such threats (Merrick *et al.*, 2009), especially in small populations that are more affected by demographic stochasticity (Townsend *et al.*, 2003). Reliable information on population parameters such as survival, fecundity and abundance is essential to assess the conservation status of a population, detect and investigate changes or trends in population size and ultimately provide the best information towards effective conservation and management (Read, 2010).

The population of bottlenose dolphins off the east coast of Scotland has been studied for more than 25 years, providing one of the few long-term individual-based datasets for this species. This long-term dataset has encompassed changes in the population's range (Wilson *et al.*, 2004) and also subsequent changes in sampling effort, as the population expanded outside the Moray Firth into Aberdeenshire, St Andrews Bay and the Firth of Forth. The population parameters that have been used in the past to investigate the conservation status and trajectory of this population have either been taken from the literature (*e.g.* fecundity rate) or have been estimated based on relatively short time periods, from the data available at the time of those studies (Sanders-Reed *et al.*, 1999, Thompson *et al.*, 2000, Corkrey *et al.*, 2008). In addition, most of the studies to understand what determines the occurrence of dolphins in certain areas and to identify which areas may be more important for this population have focused on the inner Moray Firth where the SAC was designated (Wilson *et al.*, 1997a, Mendes *et al.*, 2002, Hastie *et al.*, 2003a, Hastie *et al.*, 2004, Bailey and Thompson, 2006, Bailey and Thompson, 2010, Bailey *et al.*, 2013, Pirotta *et al.*, 2014). In this thesis, the currently available 25 years of data have been used to fill gaps in our knowledge and understanding of the biology and ecology of this population of bottlenose

dolphins. Key results from this thesis include new estimates of survival and fecundity rate, new estimates of the size of the total population and the number of animals using two areas outside the Moray Firth SAC, and new information on the usage by the dolphins of the area incorporating St Andrews Bay and the entrance to the Firth of Tay.

In Chapter 2, I provided an updated estimate for adult and sub-adult survival rate based on capture-recapture models fitted to 25 years of photo-identification data. Temporary emigration in the data caused by the population's range expansion was able to be modelled using the robust design (Pollock, 1982, Kendall *et al.*, 1995, Kendall *et al.*, 1997), and thus minimize potential bias in the estimates of survival probability. Using the available information about the sex of the individuals I also provided the first sex-specific estimates of survival for this population, using an analytical framework to minimize the bias caused by individuals of unknown sex (Nichols *et al.*, 2004).

The approaches commonly used to estimate reproductive parameters based on photo-identification re-sighting data in cetaceans tend to be biased (Barlow and Clapham, 1997), and the only attempts to model birth intervals in cetacean species have been with right whales and humpback whales (Barlow, 1990, Payne *et al.*, 1990, Barlow and Clapham, 1997, Cooke *et al.*, 2001). In Chapter 4, I developed a new analytical approach to estimate fecundity rate from inter-birth intervals that should be applicable to any population study with comprehensive data on birth intervals. The use of simulations indicated how short study periods, missing data years and low capture probabilities can lead to large bias in estimates of inter-birth interval and fecundity rate, providing a reference on the direction and size of bias for other studies. Applied to the study population, I provided an unbiased estimate of fecundity rate that was previously lacking for this population.

Total population abundance estimates for this population are available for different short study periods and based on a variety of analytical approaches (Wilson *et al.*, 1999b, Durban *et al.*, 2005, Corkrey *et al.*, 2008, Cheney *et al.*, 2013). In Chapter 3, I provided annual estimates of total population size for the period 1990-2013, using mark-recapture models that accounted for heterogeneity of capture probabilities and for temporary emigration. The results showed that both sources of unequal catchability, which cause opposite bias in abundance estimates, were minimized in the most recent years (2009-2013) to negligible levels, as a result of increased sampling effort covering the whole known population range.

Thus, the estimates from 2009-2013 provide the most accurate indication of the current size of the Scottish east coast population, at around 200 individuals.

Estimates of abundance of bottlenose dolphins using the Moray Firth SAC are available since 1990 (Cheney *et al.*, 2012), most recently as part of the monitoring programme designed for the Moray Firth SAC. Outside the Moray Firth, information on abundance of animals was previously very limited, even though those areas were known to be used by individuals from this population since the 1990s. In Chapter 3, I provided annual abundance estimates for St Andrews Bay for 2009-2013 and an estimate of abundance in Aberdeenshire for 2012-2013, both in summertime. These new results fill a gap on the knowledge of the usage of areas outside Moray Firth, and indicate that approximately half of the population uses St Andrews Bay in summer on an annual basis.

Knowledge on the distribution and habitat usage of bottlenose dolphins off the east coast of Scotland has primarily focused on the Moray Firth SAC, in which dolphins are known to concentrate in areas with narrow inshore channels characterized by deep waters, steep seabed gradients and strong tidal currents (Wilson *et al.*, 1997a, Mendes *et al.*, 2002, Hastie *et al.*, 2004, Bailey and Thompson, 2010). The data collected during 2012 and 2013 added important information on the distribution and occurrence of dolphins in areas outside the Moray Firth, from Aberdeen to the Firth of Forth (Chapter 5). The modelling approach I used to investigate the dolphins' use of St Andrews Bay and the entrance to the Firth of Tay in relation to a range of environmental variables highlighted the importance of that area, especially at certain stages of the tide, for at least a part of the population. As part of this work, I also showed that the spatial and temporal variation of bottlenose dolphin presence collected during photo-ID follows can be modelled by means of GEEs to account for serial autocorrelation (Chapter 5).

### **6.2. Use of population parameters to inform conservation**

Accurate information on life-history parameters is essential to evaluate a population's status and viability, and consequently to provide the best information towards effective conservation and management (*e.g.* Kraus *et al.*, 2001, Runge *et al.*, 2004, Currey *et al.*,

2011). A common tool used to predict the future status of a population is to quantify the probability of extinction by using population viability analysis (PVA) (Boyce, 1992, Caswell, 2001). PVA estimate the viability of small populations under different scenarios with population models that use life history parameters from the population. Applications of this analytical method include investigating which life stages are most sensitive to different threats, predicting the effects of demographic, environmental, catastrophic and stochastic events on a given population, as well as identifying the potential risks associated with different management scenarios (Thompson *et al.*, 2000, Beissinger and McCullough, 2002).

Population viability analysis has often been criticized and its reliability debated because of concerns about the precision of predictions of events and the sensitivity of estimates of extinction risk to the uncertainty associated with the parameters used for those predictions (Coulson *et al.*, 2001, McCarthy *et al.*, 2001, Beissinger *et al.*, 2002, Ellner *et al.*, 2002, Reed *et al.*, 2002, Lindenmayer *et al.*, 2003). A key part of PVA is to have reliable estimates of demographic parameters used to predict future viability of a population (Coulson *et al.*, 2001, White *et al.*, 2002). Obtaining unbiased and precise estimates of population size and life history parameters is essential to PVA, but depends greatly on the number of years of data available, especially for long-lived species such as cetaceans (Ralls *et al.*, 2002).

Motivated by the proposal of the Moray Firth as a candidate Special Area of Conservation (cSAC) under the Annex II of the EU Habitats Directive (92/43/EEC), a PVA was developed for the study population based on data collected between 1990 and 1997 (Sanders-Reed *et al.*, 1999). The authors used a model based, where possible, on data collected from the bottlenose dolphins occurring in the Moray Firth. They used 8 years of data to estimate adult survival and birth rate, and 4 years to estimate calf survival; information on other required life history parameters was taken from the literature. That model predicted a population decline and a median of 45 years to quasi-extinction (Sanders-Reed *et al.*, 1999). A few years later, Corkrey *et al.* (2008) conducted a Bayesian-based population modelling analysis based on data collected between 1990 and 2002 which suggested the likelihood of a decline but with weak evidence (Corkrey *et al.*, 2008). The authors were concerned that the detected decline could have been confounded with temporary emigration caused by the population's range expansion (Wilson *et al.*, 2004).

The use of robust design mark-recapture models in Chapter 2 allowed the expected bias in the estimates of survival probability due to temporary emigration in the data to be minimized. The results indicated that the bias was actually small, with an estimated apparent survival probability (0.946, SE=0.005) very similar to that reported in Sanders-Reed *et al.* (1999) (0.942, SE=0.015), and slightly higher than that in Corkrey *et al.* (2008) (0.93, SE=0.029). However, differences are more obvious in the mortality rates, needed for a PVA. The mortality rate estimated in this study of 5.4% (SE=0.5%) is 7% smaller than that from Sanders-Reed *et al.* (1999) (5.81%, SE=1.48%), but 23% smaller than that from Corkrey *et al.* (2008) (7%, SE=2.9%). As well as reducing bias, the use of a much larger dataset (25 years) in this thesis also greatly improved the precision of the estimates, which would improve the overall ability of a PVA to predict the trajectory of this population with accuracy and precision (Beissinger *et al.*, 2002) (see section 6.5. below on future work).

Other outcomes from this thesis also contribute information to the conservation of this population. The sex-specific apparent probability of survival estimated in Chapter 2 showed a slight difference in mortality rate between males (4.9%, SE=1.3%) and females (4.4%, SE=1.1%). The previous population modelling (Sanders-Reed *et al.*, 1999, Corkrey *et al.*, 2008) used a single survival rate for both sexes because information on sex-specific mortality rates was completely lacking for the study population. However, information on sex-specific life history parameters may be important in population viability analyses (*e.g.* Galimberti *et al.*, 2001). In a wider context, the results from Chapter 2 contribute by adding valuable information to the very limited data available on sex-specific survival rates for wild populations of bottlenose dolphins (see summary of available information in Table 2.1 in Chapter 2).

The results from Chapter 2 did not seem to uphold the suspicion of a bias in the estimate of survival due to temporary emigration, which was previously thought to influence the predicted trajectory of this population in previous PVAs (Sanders-Reed *et al.*, 1999, Corkrey *et al.*, 2008). An update of the Corkrey *et al.* (2008) model now suggests that there is a greater than 99% probability that the study population is either stable or increasing (Cheney *et al.*, 2014). This leads to the need to pose the question whether other population parameters used in the earlier analyses were biased.

Sanders-Reed *et al.* (1999) estimated crude birth rate per female based on the available data from the study population at that time. The estimated mean crude birth rate per female (19.3%, SE=2.77%), corresponding to a birth interval of 5.2 years, was likely biased because of missing births in some years as well as because of bias in the population size estimate upon which it was based (crude birth rate was calculated by dividing the number of births by the minimum number of adult dolphins observed annually) (Sanders-Reed *et al.*, 1999). The estimated fecundity rate from Chapter 4 (22.2 %) is higher by 15% compared to that used by Sanders-Reed *et al.* (1999), and should be unbiased according to the results from the simulations (Chapter 4). Other life-history parameter values used in that population viability analysis were calf mortality rate and age at first reproduction for males and females. The calf mortality rate that was estimated for the study population (38.3 %, SE=6.28%) was much higher than that from the Sarasota Bay population (18.9%, SE=6.44%) (Wells and Scott, 1990), which has been used in studies when data for the population of interest are lacking (*e.g.* Thompson *et al.*, 2000, Englund *et al.*, 2008). The currently available long-term dataset now includes information on breeding age for a number of females, and on capture histories for over 90 calves first sighted in their year of birth during 1990-2013, which would allow the estimated calf mortality in Sanders-Reed *et al.* (1999) to be updated (see section 6.5. ).

### **6.3. Management to achieve conservation**

The conservation objectives for the Moray Firth SAC with regards to bottlenose dolphins are to avoid deterioration of the habitats of, or significant disturbance to, bottlenose dolphins, and thus to ensure that the SAC is maintained to make an appropriate contribution to achieving favourable conservation status of this species, ensuring the long-term maintenance of the distribution and viability of the population within the site (Thompson *et al.*, 2006). These conservation objectives translate into the monitoring of a series of targets about the number of individual dolphins using the SAC, the importance of the SAC to the population, and the total population trends (Thompson *et al.*, 2006, Cheney *et al.*, 2012).

Current knowledge of this population (Cheney *et al.*, 2013) shows that the Moray Firth SAC represents a very small proportion of its total distributional range. The SAC is still used by a high proportion of the current population, *i.e.* greater than 60% of the population used the SAC in 16 of the 21 years between 1990 and 2010 (Cheney *et al.*, 2012). However, the use of

the SAC by the population has been estimated to have decreased from 100% in 1990 (*i.e.* start of the study period) to 64% in 2010, while the overall population size is thought to be stable or increasing (Cheney *et al.*, 2012).

Outside the SAC, dolphins from the study population occur in other areas of the distributional range, from the Moray Firth to the Firth of Forth (Cheney *et al.*, 2013), including the outer Moray Firth (Robinson *et al.*, 2007, Culloch and Robinson, 2008), the Aberdeenshire coast (Weir and Stockin, 2001, Stockin *et al.*, 2006, Anderwald and Evans, 2010), and St Andrews Bay (Quick, 2006, Thompson *et al.*, 2011). But how important are these areas to this population? That is, what proportion of the population uses areas outside the SAC on an annual basis?

The analysis from Chapter 3 contributes to filling in some of those gaps. The results highlight the importance of St Andrews Bay, which is used on an annual basis by approximately half of the estimated total population. The results also provide the first abundance estimate for the area of Aberdeenshire, indicating that greater than 25% of the estimated total population used that area in the period 2012-2013. Observations made during the surveys in 2012-2013 suggest that the area between Stonehaven and Aberdeen is important both as a transiting area between the most distant extremes of the population's distributional range, as well as a foraging area, which supports the findings of previous studies (Sini *et al.*, 2005, Stockin *et al.*, 2006). For St Andrews Bay, even though sightings of dolphins have been increasingly reported in that area since the mid-1990s (Wilson *et al.*, 2004, Anderwald and Evans, 2010), there has been a lack of knowledge of how the dolphins may be using the area and whether there are high use areas of particular importance. The results from Chapter 5 identify the entrance to the Firth of Tay as a high use area for bottlenose dolphins, and suggest that the topography of the entrance to the Tay, with strong complex tidal currents and the exposure of sandbars on either side, may increase the foraging efficiency of the dolphins, at least during the summer when salmonid prey species are in the area.

The results regarding areas such as St Andrews Bay in terms of number of animals and specific high use areas question whether the Moray Firth SAC as a management tool is still affording the initially envisaged protection of this population, a point that has been highlighted in the past (Wilson *et al.*, 2004, Culloch and Robinson, 2008, Weir *et al.*, 2008). The change in the distributional range could not have been predicted when the Moray Firth

cSAC was proposed in 1996 (Wilson, 2008), but the degree of protection offered by the current SAC for the long-term viability of this population is clearly limited, especially considering potential threats from the expansion of the marine renewable energy industry in Scottish waters in the coming years (see section 6.4. ). Responsibility for managing the Moray Firth SAC is shared by the ‘relevant authorities’, which are organizations with statutory responsibilities through licensing or consenting the various activities or developments taking place in the Moray Firth. A Management Scheme was published to facilitate the management of the SAC (Moray Firth Partnership, 2009), as well as to direct and co-ordinate efforts towards long-term conservation of the population whilst taking into account economic and social interests. Again, the scheme’s capacity to achieve those objectives is limited as a result of the population’s current distribution and use of other areas outside the SAC (Wilson, 2008).

The limitations of the Moray Firth SAC to afford the protection for which it was designed have also been highlighted for other designated areas. In Cardigan Bay, an SAC for bottlenose dolphins was proposed in 1995 and designated in 2001 to cover the southern part of Cardigan Bay, which was the portion that had been surveyed at that time. Additional information and studies over the following years show now that dolphins range over a much wider area outside the SAC boundaries, questioning the ability of the SAC to protect the population on the long-term (Evans and Pesante, 2008).

SACs are intended to protect vulnerable species in particularly important parts of their range. The area-based management approach of marine protected areas (MPAs) is intended to protect both the species of interest as well as the entire ecosystem, and has been increasingly used in the marine environment (Hooker and Gerber, 2004). However, this poses a number of difficulties for highly mobile species such as cetaceans which can range widely over areas that are too large to be encompassed by an MPA. Even though the number of MPAs for cetacean populations has been increasing at a global scale (Hoyt, 2009a), there has been an increased debate on their ability to achieve their conservation goals, questioning whether such area-based management is appropriate for cetacean species (Notarbartolo-Di-Sciara *et al.*, 2008, Game *et al.*, 2009, Hoyt, 2009a).

The success of an MPA to protect a cetacean population will largely depend on the ability to define appropriate boundaries around critical areas, as well as to invest enough attention and

resources to address the real threats to the population (*e.g.* by-catch, noise, habitat degradation) (Agardy *et al.*, 2011, Silva *et al.*, 2012). Examples of MPAs that fail to protect the species they were intended to protect include those for the vaquita in the Upper Gulf of California (Mexico) and the Pelagos Sanctuary in the Mediterranean Sea. For the vaquita, the Vaquita Refuge Area covers only a part of its distributional range and the unsustainable mortality due to by-catch from gillnets outside the MPA is likely to drive this endemic species to extinction in the near future (Jaramillo-Legorreta *et al.*, 2007, Gerrodette and Rojas-Bracho, 2011). The Pelagos Sanctuary was designated to protect critical habitat for cetacean species in the Mediterranean Sea. However, after a decade of negotiations between the countries involved, the final delimitation of the sanctuary boundaries comprises large areas of low conservation value for cetacean species but excludes other higher value areas (Notarbartolo-Di-Sciara *et al.*, 2008, Agardy *et al.*, 2011).

Harbour porpoises are listed under Annex II of the EU Habitats Directive, requiring the designation of SACs, but there are currently none designated for the UK. This is another clear example of cetacean species for which area-based conservation management poses difficulties. Harbour porpoises are widely distributed around the UK (Reid *et al.*, 2003, Hammond *et al.*, 2013), mainly ranging over continental inshore shelf waters (Embling *et al.*, 2010, Booth *et al.*, 2013). The main threat to harbour porpoises in European waters is by-catch in gill and tangle net fisheries (Hammond *et al.*, 2013). Even if SACs are proposed for harbour porpoises around the UK after identifying the most critical areas for this species (Embling *et al.*, 2010), they will not contribute towards the long-term conservation of this species unless efforts are also put to minimize the by-catch.

Natura 2000 is a network of Special Areas of Conservation (SACs) and Special Protection Areas (SPAs) intended to assure the long-term survival of Europe's most valuable and threatened species and habitats. Given the current information on the importance of St Andrews Bay, and specifically the entrance to the Firth of Tay, for a large part of the bottlenose dolphin population off the east coast of Scotland, this area could be a good candidate for a second SAC for the study population. However, designating an entirely new SAC is a major task that would take a number of years (Wilson, 2008). A more realistic option might be to modify the existing SAC for harbour seals (*Phoca vitulina*) in the Firth of Tay and Eden Estuary (see Figure 1.2 in Chapter 1) to include bottlenose dolphins as a new

feature to the site. The current SAC for harbour seals extends to the entrance of the Firth of Tay just past the Barry Links. Based on the results from Chapter 5 from the habitat use modelling analysis, the current SAC for harbour seals includes part of the high use area identified at the entrance to the River Tay, although ideally the boundaries of a hypothetical SAC in that area should extend a few kilometres further east.

#### **6.4. Dolphins and marine renewable energy plans in Scotland**

The plans for expansion of offshore renewable energy extraction along the east coast of Scotland in the near future raise a wide range of environmental concerns, including impacts upon the population of bottlenose dolphins in the area. Offshore wind farms are planned to be developed in the offshore waters of the outer Moray Firth (MORL, 2012), off Aberdeenshire (Vattenfall and Aberdeen Renewable Energy Group, 2012, Statoil Wind Ltd, 2013), and off St Andrews Bay and the Firth of Forth (SeaEnergy Renewables Limited, 2010, SeaGreen Wind Energy, 2011a, Mainstream Renewable Power, 2014) (see Figure 1.2 in Chapter 1). The location of those developments ranges between 2.4 and 25 km from the coast.

Environmental concerns arising from the development of marine wind farms relate to direct effects on coastal species of cetaceans due to the exposure to increased underwater noise, as well as to indirect effects due to alterations to the habitat or potential changes in prey resources (Dolman and Simmonds, 2010, Thompson *et al.*, 2010, Bailey *et al.*, 2014a). The construction phase is likely to have the biggest impact, due to the increased underwater noise generated from the pile-driving and increased vessel traffic (David, 2006, Madsen *et al.*, 2006). Exposure to the increased levels of noise during pile-driving has the potential to cause short-term behavioural changes in the bottlenose dolphins of the study population, potentially displacing them from those areas more exposed to the pile-driving sound (Thompson *et al.*, 2010). Such a behavioural change has already been observed in harbour porpoises. Studies showed how harbour porpoises left the construction area of an offshore wind farm in Denmark (Carstensen *et al.*, 2006), and suggest long-term impacts on the population because the harbour porpoises' echolocation activity inside the wind farm has not fully recovered yet after a decade (Teilmann and Carstensen, 2012). Similar patterns of avoidance in response to pile-driving have been observed during the construction of another wind farm in Germany (Dähne *et al.*, 2013). For bottlenose dolphins off the east coast of Scotland, studies indicate

they may exhibit behavioural disturbance within 50 km of pile-driving (Bailey *et al.*, 2010), which would include parts of the distributional range of the bottlenose dolphins in the study population for all planned offshore developments, including parts of the Moray Firth SAC.

Environmental Impact Assessments (EIA) have been or are planned to be conducted for each of the above mentioned marine renewable energy developments, to specify the potential environmental impacts for the habitat and different species, including bottlenose dolphins. All these EIAs correctly assume that the bottlenose dolphins found in different areas of the coast belong to the same population found in the Moray Firth SAC, that individuals move across the distributional range, and that a large proportion of the estimated total population may be occurring in the coastal waters of St Andrews Bay, based on the available information (*e.g.* Quick and Cheney, 2011, Thompson *et al.*, 2011, Cheney *et al.*, 2013). Temporary displacement of the dolphins during and possibly after the piling activity is described as the main impact on the bottlenose dolphins as specified by the EIAs from the renewable developments in Scottish Territorial waters (Vattenfall and Aberdeen Renewable Energy Group, 2011, Mainstream Renewable Power, 2012, Inch Cape Offshore Ltd, 2013).

There is also the potential for impacts on prey species to indirectly affect marine mammals. Bottlenose dolphin diet off the east coast of Scotland (Santos *et al.*, 2001) includes gadoid fish (*e.g.* whiting, saithe, cod, haddock, pollock), and salmonids (sea trout and Atlantic salmon), which are thought to be moderately sensitive to noise and might be displaced during the construction phase, although no long-term impacts are predicted (Mainstream Renewable Power, 2012). In the case of the EOWDC development in Aberdeen Bay, a potential barrier effect to movement north and south of the wind farm caused by the increased underwater sound during the piling is also suggested. The above mentioned EIAs state that impacts from piling exercises are likely to be short-term during construction operations, and that they will be mitigated by dolphins moving into other areas within the distributional range along the coast.

If all areas along the distributional range were of similar importance to the dolphins, temporary displacement from a certain area might not have long-term consequences at the individual and/or population level. However, the dolphins in this population are known to concentrate in certain areas, mainly linked to the availability of food resources and foraging efficiency (*e.g.* narrow channels in the inner Moray Firth and Aberdeen Harbour; Wilson *et*

*al.*, 1997a, Mendes *et al.*, 2002, Hastie *et al.*, 2004, Sini *et al.*, 2005, Pirotta *et al.*, 2013). In the EIA from the Neart na Gaoithe wind farm off Fife Ness it is stated that ‘it is not known whether the Firth of Tay area is of significant importance to bottlenose dolphins’ referring to the consequences of a displacement from the area of the Tay and St Andrews Bay to other areas within the distributional range (page 13 in Mainstream Renewable Power, 2012). Results presented here (Chapter 5) demonstrate clearly that the Firth of Tay is indeed important for a large part of this population.

An important additional point is that of in-combination effects, given the multiple offshore renewable energy projects planned and the likely overlapping construction activity (*e.g.* EOWDC and Neart na Gaoithe wind farms; Mainstream Renewable Power, 2012). Animals displaced from one area by increased underwater noise from piling may move into other areas that area also exposed to noise and other impacts. For example, animals in the Tay Estuary may be displaced north towards Aberdeen, where the construction phase of the EOWDC might also be occurring. In addition, different parts of the population might be affected simultaneously at different sites within the distributional range.

Most importantly though, activities such as pile-driving are likely to occur in conjunction with other anthropogenic activities that can negatively impact bottlenose dolphins, raising concerns for cumulative impacts from simultaneous different sources. European conservation legislation requires regulators to assess cumulative impacts as part of the EIA process in order to infer population consequences (Cooper and Sheate, 2002). For example, increased vessel activities and operational noise is expected to occur during the construction phase of the different proposed wind farms, in conjunction with pile-driving activities (Mainstream Renewable Power, 2012). An increase in the number of boats might require modifications in the main harbours along the east coast (*e.g.* Aberdeen, Montrose, Dundee), which would likely involve dredging, which has been found to displace bottlenose dolphins from important foraging areas (Pirotta *et al.*, 2013). Other potential impacts may add to all of the above mentioned, including impacts of piling activities on the dolphins main prey resources, disturbance impacts from increased helicopter traffic or cable-laying activities, as well as potential impacts from other activities in the area. These include the refurbishment of the Tay rail bridge between 2014-2017, the development of the Dundee Waterfront between 2009-

2016 or the Forth Bridge replacement crossing to be completed in 2016 (Mainstream Renewable Power, 2012).

It is difficult to predict at this point the consequences that these effects may have at the population level, including for the viability of this population in the long term. How may these behavioural changes affect demographic parameters such as survival and reproductive rates? The uncertainty around the effects at the population level and the potential for in-combination cumulative impacts require flexible and adaptive management during the construction phase of the different offshore wind farms, to minimize the impact on individuals and, potentially, the impact on the long-term viability of the population.

### **6.5. Future work**

Continuation of the photo-identification surveys in the area of St Andrews Bay and the Firth of Tay is highly recommended to monitor the population in the future, given the importance of that area as shown in Chapters 3 and 5. As shown in Chapters 2 and 3, the uninterrupted effort in recent years over most of the known distributional range of this population minimized biases in the estimation of population parameters and abundance of animals, improving our understanding of the population and the quality of the data needed to inform conservation. Currently, 6 years of uninterrupted comprehensive photo-identification effort exist for this area (2009-2014). The build up of a long-term dataset of individual histories of dolphins in that area would benefit the future monitoring of the entire population, given the individual ranging preferences within the population (Cheney *et al.*, 2013).

The upcoming development of various offshore wind farms has the potential to affect individual dolphins in different areas of the distributional range, with uncertain impacts at the population level. Thus, continued monitoring through photo-identification surveys in the future years in different areas of the population's range is highly recommended.

Estimation of survival rates for calves is needed because it is an important population parameter required to make the best use of population viability analysis (PVA). Given the long-term dataset currently available, survival of calves can be estimated, not only to inform conservation of this population but also to increase the limited knowledge on calf survival rate in bottlenose dolphins. Together with the estimates of adult and sub adult survival and

fecundity rates estimated in this thesis, there is now an opportunity to model the long-term viability of this population. This could include using the same methods as in Sanders-Reed *et al.* (1999) to allow for comparisons, and should investigate the sensitivity of predicted population growth rate and viability to different scenarios relating to the impact of anthropogenic activities such as the development of offshore wind farms.

The estimation of calf survival is of special interest for this population because of the presence of a number of young individuals with very obvious scoliosis malformations. This type of vertebral column malformation has previously been observed in different cetacean species (Berghan and Visser, 2000), including the bottlenose dolphin (Berrow and O'Brien, 2006, DeLynn *et al.*, 2011). More than 15 individuals with scoliosis have been observed in this population since the late 1980s, of which only two were identified as adults, and the capture histories of the other individuals suggest their survival might be lower than in individuals without those deformities. A further investigation of the occurrence of such malformations in the population is needed, in order to investigate the potential effects to the long-term viability of this population if individuals with scoliosis have a lower survival rate.

Finally, the increased availability of long-term datasets of individual histories in different species of cetaceans offers a good opportunity to apply the approach developed in Chapter 4 to estimate fecundity rates from inter-birth intervals in other populations of bottlenose dolphins or other cetacean species. The obvious bottlenose dolphin long-term dataset would be that from Sarasota Bay (Florida), which contains unique detailed data on individual reproductive histories covering up to 5 generations (Wells and Scott, 1990, Wells, 2014). The approach could also be tested in long-term longitudinal studies of other cetacean populations such as Hector's dolphins (Burkhart and Sloaten, 2003, Currey *et al.*, 2009), Indo-Pacific bottlenose dolphins (Mann *et al.*, 2000), killer whales (Olesiuk *et al.*, 1990), humpback whales (Clapham, 1996) or right whales (Payne *et al.*, 1990, Cooke *et al.*, 2001).

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# Appendices

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**Appendix 1a:** “Daily Trip” form used to record information during a boat-based trip, including information on GPS locations, logged waypoints (Wpt#), activity (survey, encounter, off), boat heading, encounter number within each trip (Enc #), and sea state.

<b>Daily Trip Record</b>				Date:.....			
Crew:.....				Wind Direction: .....			
Time start:.....				Time end: .....			
Time	Location	GPS	Activity	Initial Heading °	Enc #	Sea State	Wpt #

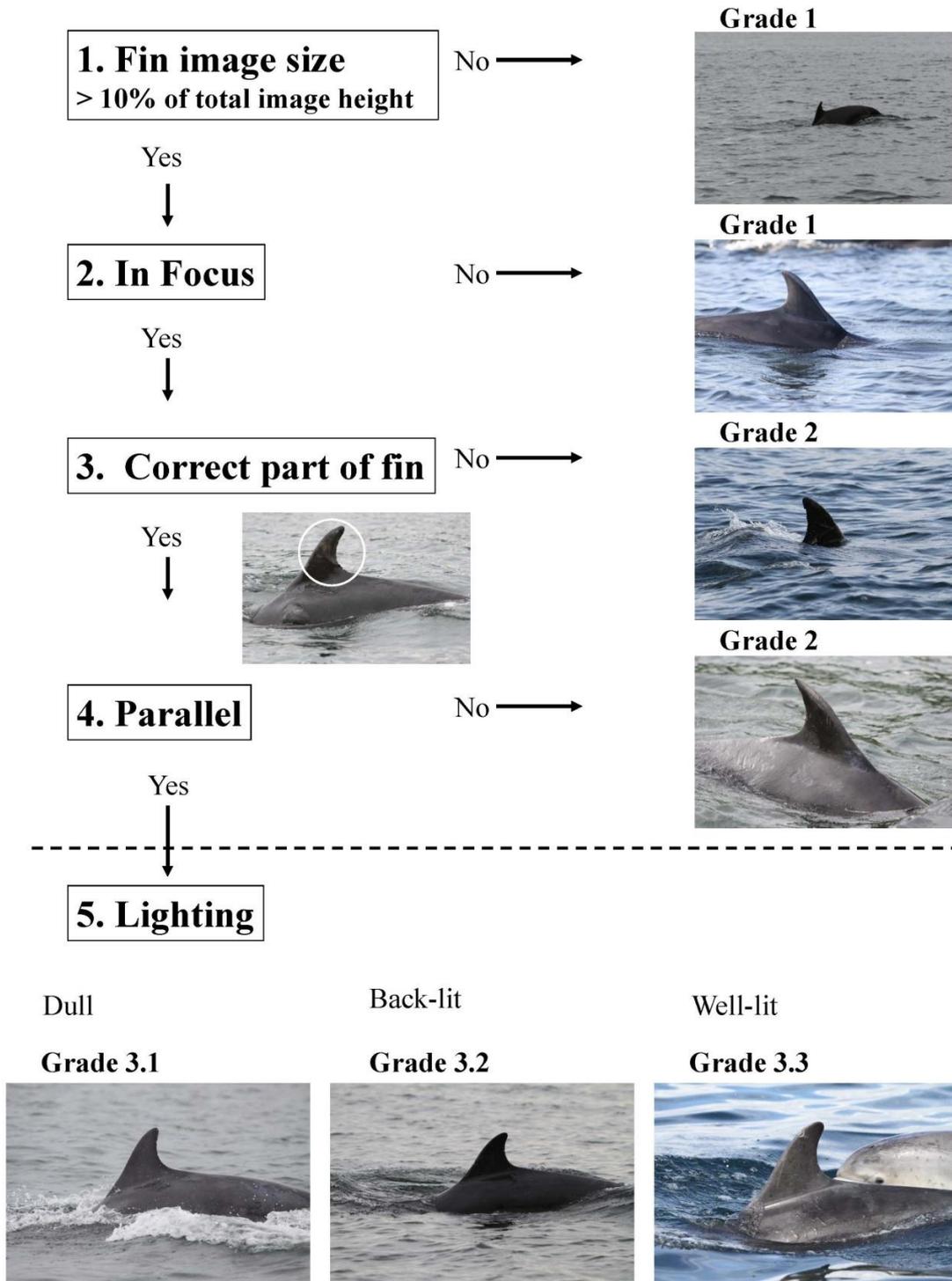
Appendices

**Appendix 1b:** “Encounter” form used to record information during each encounter with a group of bottlenose dolphins. Data include starting and ending time and GPS location from the encounter, estimate of the number of individuals encountered, notes on behaviour and extra comments relevant to the encounter.

<b>Date:</b> ___/___/___		<b>Start Time (BST) :</b> _____		
<b>Daily Encounter No:</b> _____		<b>Depth (m):</b> _____		
<b>Lat/long: N</b> _____		<b>Sea State:</b> _____		
<b>W</b> _____		<b>Wpt no.</b> _____		
<b>No of Individuals: MIN</b> ___ <b>MAX</b> ___ <b>BEST</b> ___ <b>Complete: Y/N</b>				
<b>Notes:</b>				
<b>SURFACING</b> slow medium rushing	<b>DIVES</b> long short altern	<b>GROUP</b> bunched subgroups dispersed	<b>MOVEMENT</b> progress same spot fish	<b>Bowriding</b> play / fight tailslap jumps
<b>End time (BST):</b> _____		<b>End shot: Frame</b> _____		
<b>Location: N</b> _____		<b>W</b> _____		
<b>Wpt no.</b> _____		<b>Depth (m):</b> _____		<b>Sea State:</b> _____
<b>Photographer(s)</b> _____		<b>Crew</b> _____		
<i>FOR OFFICE USE ONLY</i>				
<b>Encounter No.:</b> _____		<b>Trip No. :</b> _____		

**Appendix 1c:** Criteria for grading pictures based on the photographic quality

## Quality Grading Criteria



## Appendices

**Appendix 2:** Model selection of multistate models to estimate survival ( $\varphi$ ), capture ( $p$ ), and transition ( $\psi$ ) probabilities. Models are ordered by their AICc.  $\Delta$ AICc: difference in the AICc of any given model from that of the minimum AICc model; (.)=constant; (T)=time-specific; (sex) = state-specific (M, F, and U); (U=M $\neq$ F; M=F $\neq$ U; M=F $\neq$ U) (continues on next page)

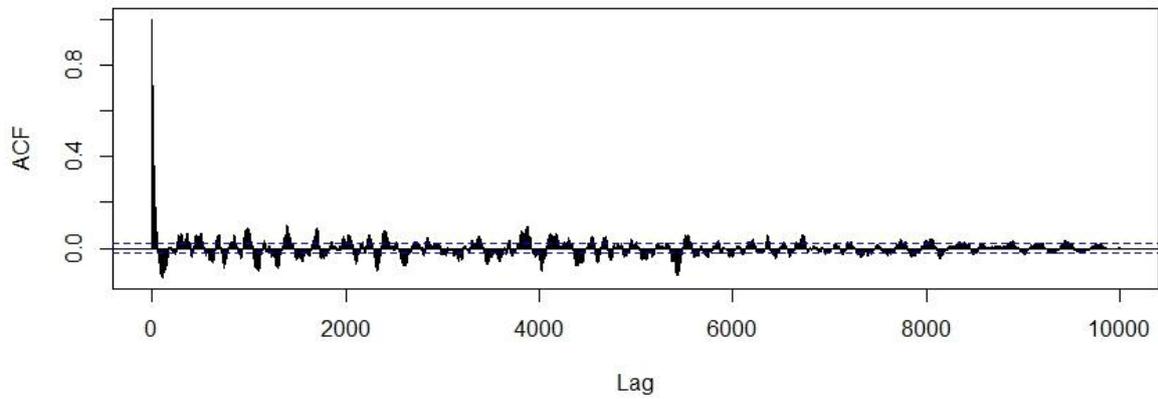
Model #	Model	AICc	AICc	AICc Weights	Model Likelihood	Num Par	Deviance
1	$\varphi$ (F=M<>U)p(F=U<>M, T) $\psi$ (., T)	13710.17	0	0.36877	1	42	12939.04
2	$\varphi$ (M=U<>F)p(F=U<>M, T) $\psi$ (., T)	13711.12	0.956	0.22864	0.62	42	12940
3	$\varphi$ (.) p(F=U<>M, T) $\psi$ (., T)	13711.65	1.4782	0.1761	0.4775	41	12942.65
4	$\varphi$ (sex) p(F=U<>M, T) $\psi$ (., T)	13712.23	2.067	0.13119	0.3558	43	12938.98
5	$\varphi$ (F=U<>M) p(F=U<>M, T) $\psi$ (., T)	13713.26	3.093	0.07854	0.213	42	12942.13
6	$\varphi$ (F=M<>U)p(F=U<>M,T) $\psi$ (sex, T)	13718.85	8.6807	0.00481	0.013	49	12932.74
7	$\varphi$ (M=U<>F)p(F=U<>M, T) $\psi$ (sex, T)	13719.81	9.6387	0.00298	0.0081	49	12933.7
8	$\varphi$ (.) p(F=U<>M,T) $\psi$ (sex, T)	13720.36	10.1896	0.00226	0.0061	48	12936.4
9	$\varphi$ (sex) p(F=U<>M, T) $\psi$ (sex, T)	13720.93	10.766	0.00169	0.0046	50	12932.68
10	$\varphi$ (F=U<>M) p(F=U<>M,T) $\psi$ (sex, T)	13721.99	11.8247	0.001	0.0027	49	12935.89
11	$\varphi$ (F=M<>U) p(sex, T) $\psi$ (., T)	13722.63	12.4617	0.00073	0.002	60	12912.67
12	$\varphi$ (M=U<>F,.) p(.,T) $\psi$ (., T)	13722.85	12.681	0.00065	0.0018	39	12958.09
13	$\varphi$ (M=U<>F) p(sex, T) $\psi$ (., T)	13723.57	13.3997	0.00045	0.0012	60	12913.61
14	$\varphi$ (F=M<>U) p(.,T) $\psi$ (.,T)	13723.57	13.406	0.00045	0.0012	39	12958.82
15	$\varphi$ (.)p(.,T) $\psi$ (., T)	13724.01	13.8447	0.00036	0.001	38	12961.37
16	$\varphi$ (.) p(sex, T) $\psi$ (.,T)	13724.12	13.9508	0.00034	0.0009	59	12916.34
17	$\varphi$ (sex) p(sex, T) $\psi$ (., T)	13724.75	14.5789	0.00025	0.0007	61	12912.6
18	$\varphi$ (sex) p(.,T) $\psi$ (., T)	13724.88	14.7075	0.00024	0.0007	40	12958
19	$\varphi$ (F=U<>M) p(sex, T) $\psi$ (., T)	13725.8	15.6307	0.00015	0.0004	60	12915.84
20	$\varphi$ (F=U<>M)p(.,T) $\psi$ (., T)	13726.13	15.959	0.00013	0.0004	39	12961.37
21	$\varphi$ (M=U<>F) p(F=M<>U, T) $\psi$ (., T)	13727.94	17.7759	0.00005	0.0001	57	12924.53
22	$\varphi$ (F=M<>U) p(F=M<>U, T) $\psi$ (., T)	13728.16	17.9909	0.00005	0.0001	57	12924.75
23	$\varphi$ (M=U<>F) p(.,T) $\psi$ (sex, T)	13728.94	18.7774	0.00003	0.0001	45	12951.42
24	$\varphi$ (.) p(F=M<>U, T) $\psi$ (., T)	13729.17	19.0039	0.00003	0.0001	56	12927.93
25	$\varphi$ (F=M<>U) p(.,T) $\psi$ (sex, T)	13729.7	19.5364	0.00002	0.0001	45	12952.18
26	$\varphi$ (sex) p(F=M<>U, T) $\psi$ (.,T)	13729.82	19.6482	0.00002	0.0001	58	12924.22
27	$\varphi$ (.) p(.,T) $\psi$ (sex, T)	13730.13	19.9601	0.00002	0.0001	44	12954.74
28	$\varphi$ (sex) p(.,T) $\psi$ (sex, T)	13731	20.831	0.00001	0	46	12951.33
29	$\varphi$ (F=U<>M) p(F=M<>U, T) $\psi$ (.,T) }	13731.31	21.1389	0.00001	0	57	12927.89
30	$\varphi$ (F=M<>U) p(sex, T) $\psi$ (sex, T)	13731.69	21.5205	0.00001	0	67	12906.34
31	$\varphi$ (F=U<>M) p(.,T) $\psi$ (sex, T)	13732.26	22.0914	0.00001	0	45	12954.73
32	$\varphi$ (M=U<>F) p(sex, T) $\psi$ (sex, T)	13732.63	22.4645	0	0	67	12907.29

## Appendices

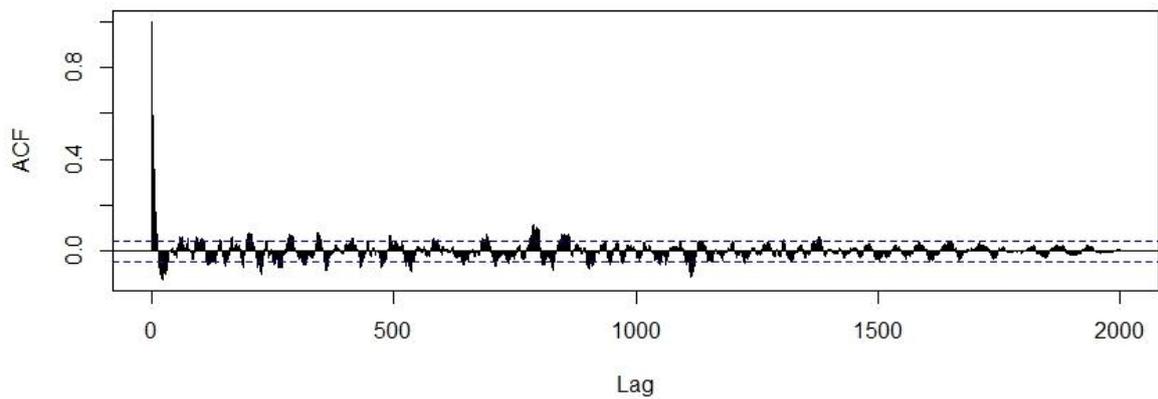
Model #	Model	AICc	AICc	AICc Weights	Model Likelihood	Num Par	Deviance
33	$\varphi (\cdot) p(\text{sex}, T) \psi(\text{sex}, T)$	13733.21	23.0384	0	0	66	12910.07
34	$\varphi (\text{sex}) p(\text{sex}, T) \psi(\text{sex}, T)$	13733.83	23.659	0	0	68	12906.27
35	$\varphi (M=U<>F) p(F=M<>U, T) \psi(\text{sex}, T)$	13734.41	24.2471	0	0	63	12917.88
36	$\varphi (F=M<>U) p(F=M<>U, T) \psi(\text{sex}, T)$	13734.65	24.4861	0	0	63	12918.12
37	$\varphi (F=U<>M) p(\text{sex}, T) \psi(\text{sex}, T)$	13734.91	24.7385	0	0	67	12909.56
38	$\varphi (\cdot) p(F=M<>U, T) \psi(\text{sex}, T)$	13735.65	25.4803	0	0	62	12921.31
39	$\varphi (\text{sex}) p(F=M<>U, T) \psi(\text{sex}, T)$	13736.32	26.1482	0	0	64	12917.59
40	$\varphi (F=U<>M) p(M=F<>U, T) \psi(\text{sex}, T)$	13737.81	27.6391	0	0	63	12921.27
41	$\varphi (F=M<>U) p(M=U<>F, T) \psi(\cdot, T)$	13741.39	31.2242	0	0	58	12935.8
42	$\varphi (M=U<>F) p(M=U<>F, T) \psi(\cdot, T)$	13741.45	31.2842	0	0	58	12935.86
43	$\varphi (\cdot) p(M=U<>F, T) \psi(\cdot, T)$	13742.14	31.9719	0	0	57	12938.73
44	$\varphi (\text{sex}) p(M=U<>F, T) \psi(\cdot, T)$	13743.26	33.0888	0	0	59	12935.48
45	$\varphi (F=U<>M) p(M=U<>F, T) \psi(\cdot, T)$	13744.21	34.0442	0	0	58	12938.62
46	$\varphi(F=M<>U) p(M=U<>F, T) \psi(\text{sex}, T)$	13747.91	37.7452	0	0	64	12929.18
47	$\varphi(M=U<>F) p(M=U<>F, T) \psi(\text{sex}, T)$	13747.94	37.7752	0	0	64	12929.21
48	$\varphi (\cdot) p(M=U<>F, T) \psi(\text{sex}, T)$	13748.66	38.4911	0	0	63	12932.13
49	$\varphi (\text{sex}) p(M=U<>F, T) \psi(\text{sex}, T)$	13749.78	39.6127	0	0	65	12928.85
50	$\varphi(F=U<>M) p(M=U<>F, T) \psi(\text{sex}, T)$	13750.76	40.5912	0	0	64	12932.03

**Appendix 3:** Autocorrelation function (ACF) plots for GAM residuals of datasets with GPS fixes every 1, 5, 10, 15, and 20 minutes (continues on next page)

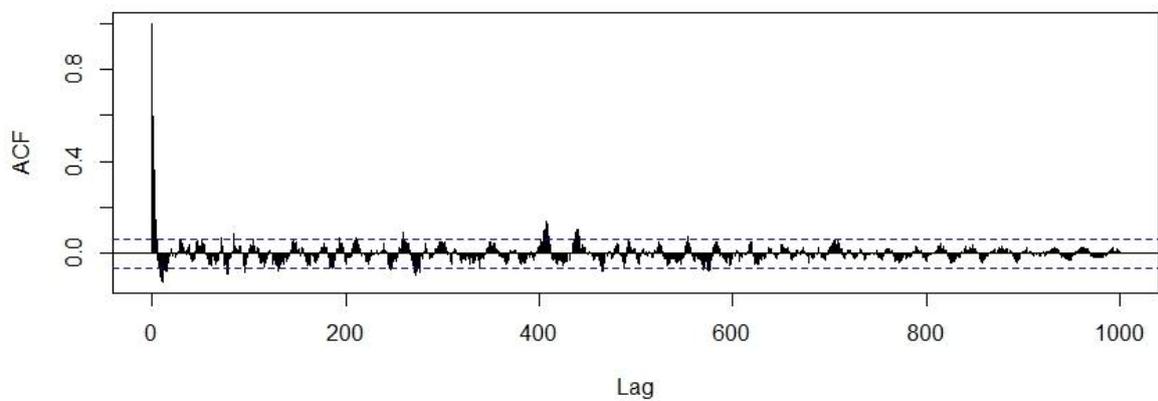
**Series residuals(Data\_1min)**



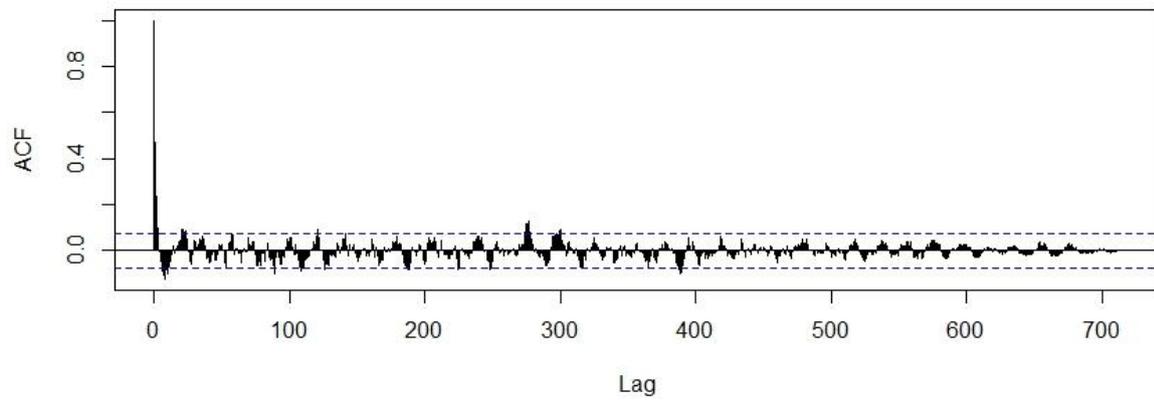
**Series residuals(Data\_5min)**



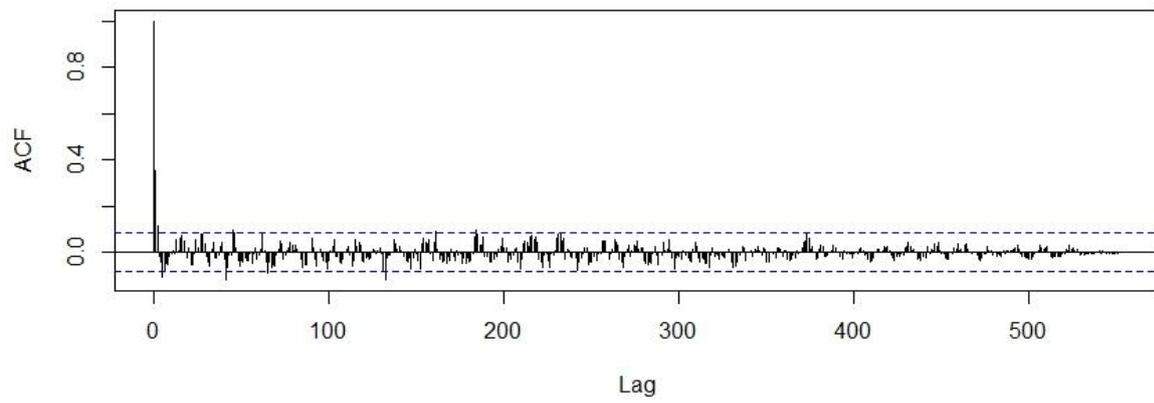
**Series residuals(Data\_10min)**



**Series residuals(Data\_15min)**



**Series residuals(Data\_20min)**



## Appendices

**Appendix 4:** Summary of the photo-ID surveys carried out during 2012 and 2013 in the three core areas. Survey time, area and number of bottlenose dolphin encounters. Species seen: BND = bottlenose dolphin; HP = harbour porpoise; MW = minke whale; RD = Risso's dolphin; WD = Whitebeaked dolphin (continues on next page).

Trip	Date	Month	Area	Survey time (hours)	No. encounters	BND	HP	MW	Other species
1449	09-May-12	May	St A Bay	6.75	2	yes	yes	-	-
1451	22-May-12	May	St A Bay	7.30	2	yes	yes	-	-
1453	25-May-12	May	St A Bay	6.87	2	yes	-	-	-
1456	05-Jun-12	June	St A Bay	6.25	0	-	-	-	-
1457	12-Jun-12	June	Forth	7.98	0	-	-	-	-
1458	13-Jun-12	June	St A Bay	4.72	1	yes	-	-	-
1461	25-Jun-12	June	St A Bay	7.55	4	yes	-	-	-
1463	02-Jul-12	July	St A Bay	5.12	3	yes	-	-	-
1464	10-Jul-12	July	St A Bay	7.03	2	yes	-	-	-
1466	12-Jul-12	July	St A Bay	5.40	2	yes	-	-	-
1467	14-Jul-12	July	Aberdeen*	9.77	5	yes	yes	-	-
1468	17-Jul-12	July	St A Bay	5.68	4	yes	-	-	-
1470	20-Jul-12	July	Forth	6.83	0	-	-	-	-
1472	25-Jul-12	July	St A Bay	7.05	4	yes	-	-	-
1475	31-Jul-12	July	St A Bay	5.07	2	yes	-	-	-
1476	08-Aug-12	August	Aberdeen*	8.72	2	yes	yes	-	-
1478	09-Aug-12	August	Forth	7.18	4	yes	-	-	-
1479	19-Aug-12	August	St A Bay	6.75	4	yes	yes	yes	-
1483	07-Sep-12	September	St A Bay	4.37	3	yes	-	-	-
1484	20-Sep-12	September	Aberdeen*	9.17	4	yes	yes	-	-
1486	22-Sep-12	September	Forth	5.70	1	yes	yes	-	-
1487	27-Sep-12	September	St A Bay	3.25	2	yes	-	-	-
1490	07-May-13	May	St A Bay	5.30	1	yes	yes	-	-
1492	16-May-13	May	St A Bay	4.17	2	yes	-	-	-
1494	20-May-13	May	St A Bay	5.80	4	yes	-	-	-
1496	21-May-13	May	Forth	4.43	0	-	-	-	-
1498	31-May-13	May	Aberdeen*	7.87	3	yes	-	-	-
1499	03-Jun-13	June	St A Bay	4.37	3	yes	-	-	-
1501	08-Jun-13	June	Forth	5.27	0	-	-	-	-
1502	09-Jun-13	June	Aberdeen*	9.20	7	yes	yes	-	-
1504	10-Jun-13	June	St A Bay	3.78	1	yes	-	-	-
1506	18-Jun-13	June	Forth	5.78	1	yes	yes	-	-
1507	19-Jun-2013	June	St A Bay	4.53	2	yes	-	-	-
1509	25-Jun-2013	June	Aberdeen*	9.08	7	yes	-	-	-
1510	26-Jun-2013	June	St A Bay	7.15	4	yes	yes	-	-
1512	08-Jul-2013	July	St A Bay	6.87	3	yes	yes	-	-
1513	09-Jul-2013	July	Aberdeen*	10.80	5	yes	yes	-	-
1514	10-Jul-2013	July	Forth	6.53	1	yes	yes	-	-
1516	18-Jul-2013	July	Aberdeen*	11.18	7	yes	yes	-	RD, WD
1517	19-Jul-2013	July	Forth	5.82	1	yes	yes	-	-
1519	26-Jul-2013	July	St A Bay	6.33	3	yes	-	-	-
1520	27-Jul-2013	July	Forth	7.85	1	yes	-	-	-

## Appendices

<b>Trip</b>	<b>Date</b>	<b>Month</b>	<b>Area</b>	<b>Survey time (hours)</b>	<b>No. encounters</b>	<b>BND</b>	<b>HP</b>	<b>MW</b>	<b>Other species</b>
1523	05-Aug-2013	August	St A Bay	4.50	5	yes	yes	yes	-
1524	10-Aug-2013	August	St A Bay	6.67	9	yes	-	yes	-
1525	13-Aug-2013	August	Aberdeen*	7.53	5	yes	yes	-	-
1528	22-Aug-2013	August	Forth	3.45	0	-	-	-	-
1533	13-Sep-2013	September	St A Bay	4.60	6	yes	-	-	-
1535	24 Sep-2013	September	St A Bay	6.17	3	yes	yes	-	-
1536	26 Sep-2013	September	Forth	5.28	0	-	-	-	-
1538	27 Sep-2013	September	Aberdeen*	8.12	4	yes	yes	-	-

\* The number of encounters for the Aberdeen trips includes all encounters between Tayport and Aberdeen

**Appendix 5:** Binomial based GAMs to explore the relationship between the presence of dolphins and each explanatory covariate, including depth, slope, aspect, distance to land, distance to the Tay, to Montrose, sea surface temperature, current level, current speed and current direction.

