# DEMOGRAPHY AND BREEDING PHENOLOGY OF A MARINE TOP PREDATOR

**Line Søltoft Cordes**

M.Sc. Marine & Fisheries Science, University of Aberdeen (2007)
B.Sc. Marine Science, Coastal Carolina University (2005)

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# THESIS CONTENTS

# AUTHOR'S DECLARATION

I declare that the work presented in this thesis has been composed by myself. I carried out all photo-identification surveys during my M.Sc. degree and Ph.D. study, apart from the 2006 data which were collected by Helen Wheeler. I collected the year-round count data from 2008, whereas all earlier land-based and aerial count data were collected by various researchers and staff at the Lighthouse Field Station and more recent aerial survey data were provided by Callan Duck and Beth Mackey at the Sea Mammal Research Unit, University of St. Andrews. I was also involved in the catching of harbour seals from Loch Fleet for deploying GPS tags to investigate changes in foraging areas. I alone analysed all mark-recapture and count data, incorporating advice from Alex Douglas, University of Aberdeen, on generalised linear mixed modelling. Chapter II was published in a peer-reviewed journal and therefore includes contributions from co-authors. No part of this work has been accepted in any previous application for a degree. All quotations have been distinguished by quotation marks and all sources of information have been specifically acknowledged.

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# SUMMARY

Worldwide harbour seal populations are showing differing and fluctuating trends in abundance, but the drivers of change remain uncertain. Within the Moray Firth, NE Scotland, count surveys carried out over the last 20 years highlighted the development of a new breeding site, providing a unique opportunity to carry out an individual-based study of harbour seal demography and pupping phenology using photo-identification techniques within a mark-recapture framework.

Sightings of individual seals suggested that a large proportion of harbour seals are year-round residents at haul-out sites. Both sexes displayed high levels of between-year breeding site fidelity as well as seasonal variation in their haul-out behaviour. Apparent sex-specific survival rates (0.89♂, 0.97♀) and birth rates (0.88) were high. There was a strong correlation between lactation durations and the timing of pupping, suggesting that shifts in pupping phenology are a result of energetic constraints. This highlights the potential for using the timing of pupping as an indicator of ecosystem conditions.

This study provided the first concurrent real-time estimates of survival and fecundity in a naturally regulated population of harbour seals. Demographic parameters and physiological responses indicate that prevailing conditions within the Moray Firth are favourable, and that this population should be recovering. However, observed patterns may also be an artefact of the long-term decline having caused an increase in per capita food availability through the reduction in intra-specific competition. This study highlights the current and long-term importance of individual-based data in understanding population dynamics. Through the identification of sentinel sites around the world, harbour seals could provide a single-species indicator of coastal ecosystem conditions in the Northern Hemisphere.

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And finally, to mum and dad for caring so much and their continuous effort in trying to understand what I have been doing over the last four years.

Et stort tak til alle for nogle dejlige år.

# CHAPTER I

## GENERAL INTRODUCTION

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Marine ecosystems around the world have undergone dramatic changes over the last few decades as a result of climate change (Walther *et al*. 2002), regime shifts (Edwards & Richardson 2004; Perry *et al*. 2005), overfishing (Pauly *et al*. 1998; Heath 2005) and other anthropogenic impacts such as pollution (Halpern *et al*. 2008; Doney 2010) or the introduction of invasive species (Molnar *et al*. 2008). Several approaches have been applied to monitor ecosystem health, from multispecies to entire ecosystem modelling, but these have been met with mixed success due to the costs and challenges involved in acquiring the necessary data (Yodzis 1998; Boyd, Wanless & Camphuysen 2006).

Marine top predators are now widely recognised as important indicators of ecosystem condition and performance (Boyd, Wanless & Camphuysen 2006) particularly as their demographic and behavioural responses are likely to reflect dynamics at lower trophic levels (Wanless *et al*. 2007). Worldwide, populations of top predators are showing varying population trends, with some suffering dramatic declines due to climate and anthropogenic impacts (Baum *et al*. 2003; Myers & Worm 2003; Österblom *et al*. 2008). This is of great concern in ecosystem management, as these species form a critical component of ecosystem health and stability (Frank *et al*. 2005; Heithaus *et al*. 2008; Estes *et al*. 2011). The use of marine top predators as bio-indicators often involves several different species, which may occupy different regions, making within and between ecosystem comparisons difficult to draw (Boyd, Wanless & Camphuysen 2006). Regional multispecies approaches would be ideal, but this is often unrealistic for the same reasons that fisheries and ecosystem modelling approaches have failed (Boyd, Wanless & Camphuysen 2006). Alternatively, single species with wide distributions could provide reliable indicators of environmental conditions across different geographical regions (Frederiksen, Harris & Wanless 2005). One such top predator, the harbour seal, has a circumpolar distribution across temperate regions in the northern hemisphere, and hence, is the widest distributed pinniped.

Based on geographic distribution, the harbour seal comprises five subspecies, two of which occur in the North Pacific, namely *Phoca vitulina stejnegeri* with a range that stretches from Japan to the western Aleutians, and *Phoca vitulina richardii*, which occurs from the eastern Aleutians to California. The three subspecies of the North Atlantic include *Phoca vitulina vitulina* distributed along the European coast and also found in the Barents Sea, *Phoca vitulina concolor* located along the east coast of the USA and Canada as well as southern Greenland and Iceland, and finally *Phoca vitulina mellonae* which is found in freshwater lakes and rivers in north-eastern Canada. Harbour seals therefore present an interesting case study for worldwide single-species comparative studies.

The structure of harbour seal populations consist of clusters of subpopulations which are made up of several smaller breeding groups. Early tagging studies were restricted to pups and revealed some long distance movements (Thompson, Kovacs & McConnell 1994), whereas later telemetry studies of adults showed more localised movements indicating that subpopulations may be relatively discrete (Bonner & Thompson 1990; Lowry *et al.* 2001). However, as tags are shed during the annual moult these studies are often confined to a single breeding season. Whereas the structure of subpopulations is well understood, less information exists about the finer-scale dynamics of breeding groups, constraining the ability to identify suitable functional units for describing population dynamics (Härkönen & Harding 2001). A long-term study of freeze branded harbour seals in Skagerak indicated both between-year site fidelity and a degree of natal site fidelity (Härkönen & Harding 2001). This behaviour was stronger in females compared to males. Gene flow within and between populations may therefore largely be due to male dispersal (Greenwood 1980). However, this study was carried out during a period of population growth where space was relatively unrestricted and there was no pressure to disperse. Understanding age and sex-specific differences in migration rates have important implications for conservation management, genetic diversity and the spread of diseases. Worldwide genetic analyses have revealed differentiation between harbour seal populations, both at the broad scale across the Pacific and Atlantic (Stanley *et al.* 1996; Goodman 1998; Burg, Trites & Smith 1999; Westlake & O'Corry-Crowe 2002), as well as on the smaller scale, highlighting the implications of genetic differentiation within regions for identifying appropriate management units (Westlake & O'Corry-Crowe 2002; Herremann *et al.* 2009).

*Worldwide monitoring efforts*

The utilisation of temperate coastlines by harbour seals has resulted in a long history of conflict between seals and fisheries (Bonner 1989). More recently conservation concerns have led to the protection of harbour seals under the Marine Mammal Protection Act (MMPA) (1972) in the USA, and the Habitats Directive in Europe. These conflicts and subsequent conservation efforts led to extensive monitoring programs of harbour seal abundance. These indicate that populations worldwide have shown differing and fluctuating trends in abundance as illustrated in Figure 1 and discussed in the sections below. However, in spite of the extensive monitoring programs, the proximate causes of change are often uncertain, due to the limited understanding of the dynamics of harbour seal populations.

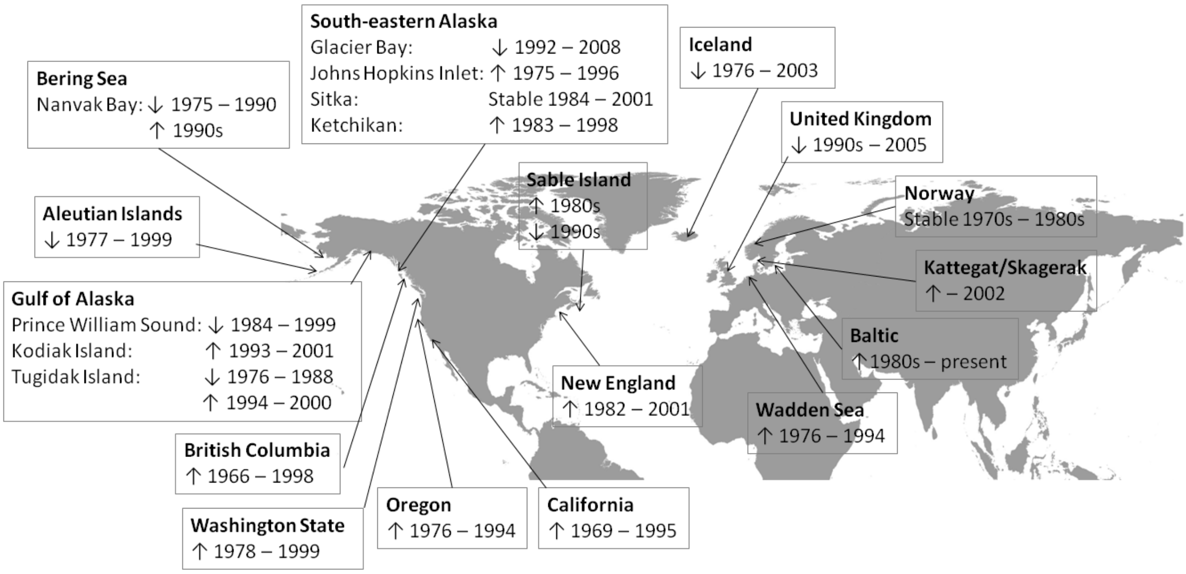

*Figure 1. Map showing worldwide trends in abundance of harbour seal populations since the late 1960s.*

*Eastern North Pacific coast*

Alaskan harbour seal populations have varied regionally over several decades, some suffering dramatic losses of up to 85%, despite the implementation of the MMPA (Pitcher 1990; Mathews & Pendleton 1997; Jemison & Kelly 2001; Small, Pendleton & Pitcher 2003; Jemison *et al*. 2006; Mathews & Pendleton 2006; Small *et al*. 2008). Parallel and contrasting trends in other marine top predators in Alaska indicated that this complex system was driven by a number of factors, including larger scale oceanic processes and inter-specific competition (Pitcher 1990; Jemison & Kelly 2001; Small, Pendleton & Pitcher 2003; Mathews & Pendleton 2006; Small *et al*. 2008; Womble *et al*. 2010). In 1977 a climate-regime shift resulted in the replacement of a shrimp-dominated crustacean community by a gadids and flatfish dominated community (Hirons, Schell & Finney 2001). This led to the hypothesis that pinnipeds were feeding on leaner fish causing nutritional stress, reduced body condition and lower fecundity (Trites & Donnelly 2003).

In contrast, most populations from south-eastern Alaska to California increased post 1972, and some recovered to pre-bounty levels (Olesiuk, Bigg & Ellis 1990; Sydeman & Allen 1999; Baird 2001; Jeffries *et al*. 2003; Grigg *et al*. 2004; Brown *et al*. 2005; Mathews & Pendleton 2006; Womble *et al*. 2010). In south-eastern Alaska, one exception was the animals in Glacier Bay (Mathews & Pendelton 2006), but genetic data suggests this population may be demographically isolated (O'Corry Crowe, Martien & Taylor 2003; Matthews & Pendleton 2006; Herreman *et al.* 2009). Furthermore, and in contrast to Alaskan populations, Brown *et al*. (2005) argued that the 1970s oceanic regime shift had created more favourable conditions for harbour seal prey and the regions carrying capacity had increased as a result.

### *Western North Atlantic coast*

In the north-western North Atlantic harbour seal populations have also shown contrasting and fluctuating trends in abundance. On Sable Island, Canada, the population increased during the 1980s but suffered dramatic declines during the 1990s (Lucas & Stobo 2000). Although the causes for the decline were not fully understood there were several plausible hypotheses including increased predation by sharks, inter-specific competition with grey seals and changing ocean temperatures causing a shift in the distribution of prey fishes (Lucas & Stobo 2000; Bowen *et al*. 2003). Along the New England coast, several pinniped populations, including harbour seals, have shown exponential growth since the implementation of the MMPA (Baraff & Loughlin 2000; Gilbert *et al*. 2005). Although harbour seals are present further north in the St. Lawrence, Newfoundland and the coast of Labrador little is known about trends in abundance (Stenson 1994; Gagnon 1998).

### *Northern European coast*

In parts of Europe, harbour seals constituted an important resource during the 18th and 19th century and were hunted for fur and food. In addition, they were also considered competitors by fisheries which resulted in long-term bounty programs whereby culling depleted several local populations (Bjørge 1991; Bonner, Vaughan & Johnston 1973; Heide-Jørgensen & Härkönen 1988; Bonner 1989; Reijnders 1994; Reijnders, van Dijk & Kuiper 1995; Harding & Härkönen 1999). Only by the end of the 20th century did hunting cease due to a change in public opinion concerning marine mammals. However, the conflict between fisheries and seals has persisted to this day and remains a concern for the conservation of the species (Hansen & Harding 2006; Thompson *et al*. 2007; Butler *et al*. 2008). Following reduction in hunting, most harbour seal populations around mainland Europe, Scandinavia and the Baltic started to recover (Heide-Jørgensen & Härkönen 1988; Helander & Bignert 1992; Reijnders & Lankester 1990; Teilman, Rigét & Härkönen 2010), although this was interrupted by the phocine distemper (PDV) outbreak in 1988 which spread rapidly across Europe causing the death of approximately 18,000 seals or ~60% of the population (Härkönen *et al*. 2006). Mortality varied regionally as populations in Scotland and the Baltic only suffered minor losses (Thompson & Miller 1992; Härkönen *et al*. 2006). Post epidemic, populations increased again until a second outbreak of PDV in 2002 (Reijnders *et al*. 1997; Härkönen *et al*. 2006; Teilman, Rigét & Härkönen 2010). Mortality rates were generally lower compared with 1988, which could be a result of increased immunity (Härkönen *et al*. 2006). In most areas recovery resumed with the exception of the Wash and some areas in the Kattegat/Skagerak, which have remained at reduced post epidemic levels (Thompson, Lonergan & Duck 2005; Teilman, Rigét & Härkönen 2010).

In contrast to the general increase around mainland Europe, Scandinavia and the Baltic, harbour seals in the westernmost area of the Wadden Sea declined from the 1950s to the 1980s due to high hunting pressure until this ceased in the 1960s and 70s, pollution causing reproductive failure (Reijnders 1985, 1986), and loss of habitat and disturbance due to construction (Mees & Reijnders 1994; Reijnders 1994). The differing population trends within the Wadden Sea may be a result of the population occupying coastlines of three different countries causing distinct regional differences in anthropogenic impacts (Reijnders 1981, 1983). Towards the northern limit of the species range recent information on the abundance and distribution is somewhat limited. Norwegian populations appear to have been stable during the 1970s and 1980s (Bjørge 1991), whereas Icelandic harbour seals have shown a dramatic decline from 1976 to 2003 (Hauksson *et al*. 2006).

In northern parts of the United Kingdom, harbour seals have suffered long-term and widespread declines over the last 10-20 years (Lonergan *et al*. 2007; Thompson *et al*. 2007), despite conservation measures being put in place for their protection (Baxter 2001). The most dramatic declines occurred in Orkney and Shetland where the population was reduced by 40% (Thompson, van Parijs & Kovacs 2001; Lonergan *et al*. 2007), similar in magnitude to the declines previously observed in Iceland (Hauksson *et al*. 2006). On the east coast of Scotland, the Moray Firth constitutes the largest colony of harbour seals and this population has been studied intensively over the past 20 years (Thompson & Miller 1992; Thompson *et al*. 1996a, 1997a&b, 2007). Here numbers of seals declined by 2-5% per year from the mid 1990s to 2005 (Thompson *et al*. 2007). Although the proximate causes for the Scottish declines are not fully understood, the widespread nature suggests that larger scale oceanic processes may be playing an important role (Lonergan *et al*. 2007). Other factors, such as culling due to conflict with fisheries (Thompson *et al*. 2007) are also likely to have contributed locally.

Several of the European harbour seal populations are located around the boundaries of the North Sea. This ecosystem has undergone dramatic changes over the last four decades as a result of climate and fisheries altering the structure and function of food webs. In the late 1970s and late 1980s regime shifts occurred within the wider North Sea as a result of changes in salinity and temperature, respectively (Weijerman, Lindeboom & Zuur 2005). The 1980s shift was characterised by an inflow of warmer Atlantic nutrient rich water. However, warmer sea surface temperatures led to a mismatch in the phenology of temperature and light dependent planktonic cycles (Edwards & Richardson 2004). In addition, warm winter temperatures cause poor sandeel recruitment, which is an important prey item for seals (Thompson *et al.* 1996b; Tollit & Thompson 1996; Sharples, Arrizabalaga, Hammond 2009), and several species of seabirds (Frederiksen *et al*. 2004b). Intensive fisheries have operated in the North Sea for several decades and fishing down the food web has significantly altered the abundance and structure of fish populations in many systems (Pauly *et al*. 1998). Removal of large predatory fish resulted in increased abundance of smaller prey fishes, such as sandeel. However, in the 1990s, sandeel became the target of the largest single species fishery in the North Sea (ICES 2003), leading to direct competition between fisheries and marine top predators (Frederisken *et al*. 2004b). The breeding success of seabirds in this region is believed to have suffered as a result of both climate change and the impacts of fisheries (Furness & Tasker 2000; Frederiksen *et al.* 2004b).

### *Understanding drivers of population change*

It is now widely accepted that individual-based studies offer important ecological and evolutionary insights into the drivers of population dynamics (Clutton-Brock & Sheldon 2010). Studies of passerine and seabirds in the 1950s and 1960s were the catalyst of individual-based studies (Klujvier 1951; Dunnet *et al*. 1990) and today this approach is being applied to a variety of species (Harris 1970; Goodall 1986; Clutton-Brock, Albon & Guinness *et al*. 1988; Scott 1988; Festa-Bianchet 1989; Mann *et al.* 2000). Most long-term studies have involved initial physical capture of individuals for marking and sample size is therefore constrained by the number of individuals caught. Tags may also be lost over time limiting the possibility for monitoring individual life histories. In contrast, photo-identification techniques are now widely used on species with natural individual markings. This involves species that accumulate nicks, cuts, or scrapes over time, such as elephants (Moss 2001), manatees (Langtimm *et al*. 2004) and dolphins (Mann *et al*. 2000), and species with natural consistent markings such as manta rays (Kitchen-Wheeler 2010), tigers (Karanth *et al.* 2006), killer whales (Baird & Stacey 1988) and whale sharks (Holmberg, Norman & Arzoumanian 2008). These offer unique opportunities for following individuals over time as sightings can be carried out remotely, marks are consistent over time, and all individuals present in the study area are available for sampling. Individual-based studies of long-lived marine vertebrates present additional challenges due to their aquatic lifestyle and potential for wide dispersal. However, the dependency and fidelity of some species - such as pinnipeds and seabirds - on terrestrial sites during important stages of their life history provide better opportunities to follow individuals over time.

For pinnipeds, long-term individual-based studies are generally biased towards colonial otariids (e.g. Lunn, Boyd & Croxall 1994; Pendleton *et al*. 2006) and larger phocids (e.g. Le Boeuf & Reiter 1988) that have extended nursing periods or remain on land during lactation. All of these studies have depended on initial physical capture for tagging or branding. Species of pinnipeds with natural markings are generally found within the family Phocidae, but many of these occupy remote and inaccessible habitats in the Arctic or Antarctic. The harbour seal, however, with its distinct markings in the pelage that have previously proved successful for the identification of individuals (Cunningham *et al.* 2009; Hastings, Hiby & Small 2008; Mackey *et al.* 2008; Thompson & Wheeler 2008), coupled with their wide temperate distribution, offer a suitable candidate species. Nevertheless, individual-based studies of harbour seals are limited due to the fact that haul-out sites are often inaccessible and, with the exception of Sable Island (Bowen *et al.* 2003), easily disturbed. Furthermore, the use of inter-tidal breeding sites, results in mother-pup pairs spending a significant amount of time in the water, and therefore not always available for sighting. These factors have constrained the development of individual-based studies of harbour seals and limited our understanding of their demography and behavioural responses to environmental variation.

### *Harbour seal demography*

Population rate of change in long-lived species is most sensitive to variation in adult survival (Caswell 1978; Gaillard, Festa-Bianchet & Yoccoz 1998) and so obtaining accurate measures of survival rates is critical for understanding longer-term changes in population dynamics. Furthermore, fecundity and costs of reproduction have been shown to vary in response to population density and weather conditions, where high population density and poor weather conditions caused reduced fecundity and increased costs of reproduction (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005; Hadley, Rotella & Garrott 2007). Hence, these parameters provide more sensitive and short-term indicators of population dynamics (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005; Hadley, Rotella & Garrott 2007). Harbour seals are long-lived iteroparous mammals whereby females generally reproduce annually after the age of 4 to 6 years and due to their small body size females make short foraging trips during lactation in order to sustain the energy demand of the pup (Boness, Bowen & Oftedal 1994).

For harbour seals, estimates of survival and fecundity have mainly been obtained from analysis of teeth and ovaries from dead animals collected after disease outbreaks or scientific harvesting (Boulva & McLaren 1979; Härkönen & Heide-Jørgensen 1990; Heide-Jørgensen & Härkönen 1992). However, such samples of animals are rare and constrained by ethical and conservation considerations. Furthermore, these instantaneous and cross-sectional samples do not capture the temporal variation in survival and reproductive rates that are crucial for understanding population dynamics. Despite long-term individual-based work being carried out on Sable Island, Canada (e.g. Bowen, Oftedal & Boness 1992, Bowen *et al.* 2001, 2003), no individual-based estimates of survival rates are published for this population and the subsequent dramatic decline of harbour seals on Sable Island prohibited the continuation of the research (Lucas & Stobo 2000). Mackey *et al.* (2008) published the first photo-identification based estimate of survival for any pinniped, which also represented the first ever survival estimate for UK harbour seals. Unfortunately this study was not ideal for long-term monitoring because only a small proportion of seals at the site were close enough to photograph, resulting in low recapture rates, and preventing robust estimates of fecundity.

### *Shifting breeding phenology as an indicator of variation in environmental conditions*

Climate change and environmental variation can cause shifts in the timing of seasonal resources. Some species have shown the ability to plastically adjust their timing of breeding accordingly using certain environmental and climatic cues (Forchhammer, Post & Stenseth 1998; Réale *et al*. 2003; Frederiksen *et al*. 2004a; Møller, Flensted-Jensen & Mardal 2006; Love *et al*. 2010), whereas others suffer reduced breeding success due to the mismatch between resources and the arrival of offspring (Visser & Both 2005; Post & Forchammer 2008).

Shifts in the timing of the seasonal activities of plants and animals, such as the flowering of trees (Menzel & Fabian 1999), spawning of amphibians (Beebee 1995), the emergence of butterflies (Roy & Sparks 2000) and the egg-laying of birds (Crick *et al*. 1997), may be some of the simplest processes in which to track species responses to changes in the environment (Menzel & Fabian 1999; Walther *et al*. 2002). Temperate regions are typically characterised by distinct seasonal peaks in resources and several long-lived marine top predators (e.g. pinnipeds and seabirds) occupying these areas have adapted a relatively short and synchronised breeding season that coincides with the time of year when resources are most abundant or conditions most favourable for rearing offspring. Seabirds synchronise egg-laying with distinct peaks in resources, such as the timing of the spring plankton bloom (Vermeer 1981), herring migration (Durant, Anker-Nilssen & Stenseth 2003) or peaks in sandeel abundance (Rindorf, Wanless & Harris 2000). For pinnipeds, the time of year when food availability is most important is more difficult to determine, and may depend on their lactation strategy. Otariids generally forage during an extended nursing period, and so food availability during this period is important. Meanwhile, phocids fast throughout or during part of the nursing period and therefore must gain the required fat stores during pregnancy. In addition to monitoring climate-induced shifts in breeding phenology, it is also crucial to understand whether these responses have consequences on breeding success and survival (Visser & Both 2005). Nutritional stress as a result of variation in the abundance of resources or changes in population density can also cause shifts in breeding phenology, whereupon the timing of breeding is typically delayed during years of low food availability or high population density and offspring survival is reduced (Clutton-Brock, Albon & Guinness 1988; Sydeman *et al.* 1991; Lunn, Boyd & Croxall 1994; Boyd 1996; Catry, Ratcliffe & Furness 1998; Ratcliffe, Furness & Hamer 1998). Furthermore, changes in the age-structure of populations of long-lived mammals as a result of age-specific mortality from disease outbreaks or harvesting can also shift the timing of breeding because older females tend to give birth earlier than younger females (Lunn, Boyd & Croxall 1994; Loe *et al*. 2005).

In harbour seals, delayed implantation (whereby blastocyst implantation is initiated by photoperiod) ensures a highly synchronised pupping season (Mead 1989; Temte 1993).

The timing of pupping in harbour seals varies geographically but this is likely an adaptation to a seasonal environment (Temte 1994). Both individual- and population-level studies of harbour seal pupping phenology in other parts of the world revealed significant delays in the timing of pupping during population declines and advances during population growth (Bowen *et al*. 2003; Jemison & Kelly 2001). Additionally, a recent study of harbour seals in the southern part of the North Sea suggested the timing of pupping had significantly advanced over the last 35 years due to an improved forage base (Reijnders *et al*. 2010). This study used the timing of max pup count as an indicator of the actual timing of pupping, but the use of such a proxy for the timing of pupping has not been tested. Nevertheless, the proposed improved conditions for harbour seals in this area are of particular interest as other populations in the North Sea have undergone long-term declines during the same period (Lonergan *et al*. 2007).

### *Aims and objectives*

The overall aim of this study was to gain insights into the population dynamics of harbour seals by estimating demographic parameters and investigating between-year variation in physiological responses. Below I detail the specific aims and objectives of each chapter.

Chapter II aims to provide context for the individual-based approach through an investigation of population-level changes in distribution and abundance within the study area using 20 years of count data. This chapter also describes the study area in Loch Fleet National Nature Reserve and the nearby Dornoch Firth and Morrich More Special Area of Conservation. The objectives were to determine temporal changes in the relative use of haul-out sites and associated foraging areas in relation to the long-term efficacy of Special Areas of Conservation that were put in place to protect harbour seals.

Chapter III aims to acquire an understanding of the dynamics and stability of harbour seal breeding groups by investigating site-use at the individual level. This chapter outlines how photo-identification has been used at the Loch Fleet study site to collect the individual-based data used throughout the thesis. The first objective of this chapter was to use sightings of individual seals over five consecutive breeding seasons from 2006 to 2010, and throughout the year in 2008 and 2009 to estimate sex-specific haul-out probability and site fidelity at different temporal scales. Secondary objectives included investigating how haul-out probabilities obtained from sightings of individuals compared with those previously obtained from telemetry data, and examining the accuracy of count data in depicting seasonal variation in the importance of haul-out sites by comparing these data with novel mark-resight models that take into account individual variation in haul-out probability.

Chapter IV aims to provide the first concurrent estimates of survival and reproductive rate from a naturally regulated population of harbour seals. The objectives were to use multistate and robust design analyses, which take into account individuals occupying unknown states (unidentified sex or uncertainty in breeding state), for estimating sex-specific survival rates, reproductive rates and costs of reproduction on survival.

Chapter V aims to investigate the use of temporal variation in pupping dates and lactation durations of individual harbour seals as an indicator of environmental conditions. The objectives were to estimate the extent of variation in pupping dates and lactation durations between years, to understand whether the timing of pupping had an influence on lactation duration and to compare direct and indirect estimates of the timing of pupping.

Finally Chapter VI aims to develop a cost-effective sampling regime for the long-term continuation of the study. The objectives were to estimate the costs and efficacy of three reduced sampling regimes in estimating survival and reproductive rates as well as detecting temporal variation in pupping dates.

The general discussion summarises the consequences of key findings in terms of population dynamics and makes recommendations for the directions of future research.

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# CHAPTER II

## LONG-TERM PATTERNS IN HARBOUR SEAL SITE-USE AND THE CONSEQUENCES FOR MANAGING PROTECTED AREAS

Cordes, L.S., Duck, C.D., Mackey, B.L., Hall, A.J., & Thompson, P.M.

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# CHAPTER II

## LONG-TERM PATTERNS IN HARBOUR SEAL SITE-USE AND THE CONSEQUENCES FOR MANAGING PROTECTED AREAS

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### Introduction

The designation of marine protected areas is commonly used as a management tool in the conservation of threatened or declining animal populations (Hooker, Whitehead & Gowans 1999; Balmford *et al*. 2004), but its success can be highly dependent upon the factors considered during their design (Agardy 1994; Sala *et al*. 2002). Protected areas for marine species offer unique challenges in their designation due to high levels of connectivity between areas and widespread dispersal of individuals within a population (Roberts 1997; Mora & Sale 2002). To maximize the conservation potential of protected areas, it is necessary to understand the longer-term stability of distribution patterns of target species (Grech & Marsh 2008).

Globally, many pinniped populations are declining or threatened, emphasizing the need to improve conservation measures for these species (Reijnders *et al*. 1993; Estes *et al*. 2009). Harbour seals are the most widespread of pinnipeds. Their populations show marked regional variations in their dynamics, with some populations increasing over recent decades (Jeffries *et al*. 2003; Brown *et al*. 2005) whereas others have declined (Bowen *et al*. 2003; Lonergan *et al*. 2007; Small *et al*. 2008). In Europe, harbour seals are protected under the European Commission Habitats Directive (Council Directive 92/43/EEC), requiring the designation of Special Areas of Conservation (SACs) to protect both their terrestrial haul-out sites and associated foraging areas (Baxter 2001; Cunningham *et al*. 2009). Harbour seals have a wide distribution and come ashore (or ‘haul out’) on a variety of substrates such as inter-tidal sandbanks, skerries and ice floes. The dependence of seals on terrestrial haul-out sites for resting (da Silva & Terhune 1988) and rearing pups (Thompson 1989) has provided good opportunities for assessing patterns of terrestrial distribution and abundance, underpinning the identification of key clusters of haul-out sites for protection as SACs (Cunningham *et al*. 2009). Intensive short-term studies have shown that harbour seals display high levels of site fidelity to such areas over periods of months to years (Härkönen & Heide-Jørgensen 1990; Thompson *et al*. 1997; Cunningham *et al*. 2009). However, less is known about the stability of distribution patterns over decadal scales that are more likely to be relevant to the long-term management of protected areas. Furthermore, most attention has been paid to identifying and protecting key terrestrial sites whereas little is known about their use of foraging areas. A number of studies have shown that the seals' selection of haul-out sites can be influenced by changes in prey distribution (Montgomery, Ver Hoef & Boveng 2007; Womble, Sigler & Willson 2009). Given this, an understanding of the factors that may influence changes in the use of protected haul-out sites also requires information on the seals' foraging areas.

In recent years, there have been marked declines of harbour seals across much of Scotland (Lonergan *et al*. 2007). As with pinniped declines in other regions (e.g. Trites & Donnelly 2003; Estes *et al*. 2009) the key drivers underlying these declines are uncertain, but include factors such as predation (Springer *et al*. 2003; Bolt *et al*. 2009), human persecution (Thompson *et al*. 2007), disease (Hall *et al*. 2006) and changes in food availability (Trites & Donnelly 2003). The designation of SACs in response to the EU Habitats Directive was put forward before this period of decline in Scottish harbour seal populations. In north-east Scotland, the importance of the northern region of the Moray Firth as a harbour seal breeding site during the 1990s led to the designation of the Dornoch Firth and Morrich More SAC (see Fig. 1) in 2000 (Butler *et al*. 2008). However, the abundance of harbour seals in this area has declined by 2–5% per year since the early 1990s (Thompson *et al*. 2007).

The Moray Firth is the only UK region where long-term harbour seal population studies have been conducted in parallel with detailed studies of foraging ecology. We used this unique opportunity to investigate long-term changes in the distribution and seasonal use of haul-out sites over a 20-year period. In particular, we aimed to assess whether the criteria used for SAC designation have adequately protected key pupping areas, and whether observed changes in the use of pupping areas are likely to have been driven by wider scale changes in their foraging areas or by local changes in conditions within haul-out areas.

## Materials and methods

### *Study area*

The Dornoch Firth and Morrich More SAC covers 8700 ha and stretches 19km inland from the mouth of the Firth to the westernmost haul-out site (Thompson *et al*. 2007; http://www.jncc.gov.uk/ProtectedSites/SACselection). Systematic surveys between 1988 and 2008 have shown that harbour seals haul-out on 11 inter-tidal sandbanks within this SAC (Fig. 1). For the purposes of this study, haul-out sites within the Dornoch Firth and Morrich More SAC were grouped into three regions: the inner, mid and outer Dornoch Firth (Fig. 1). Loch Fleet National Nature Reserve (NNR) is 10km north of the mouth of the SAC (Fig. 1). This is a smaller site, covering just over 1000 ha and stretching only 2.5 km from the mouth to the innermost haul-out site. Seals haul-out regularly on two inter-tidal sandbanks within Loch Fleet, whereas a third sandbank is used occasionally.

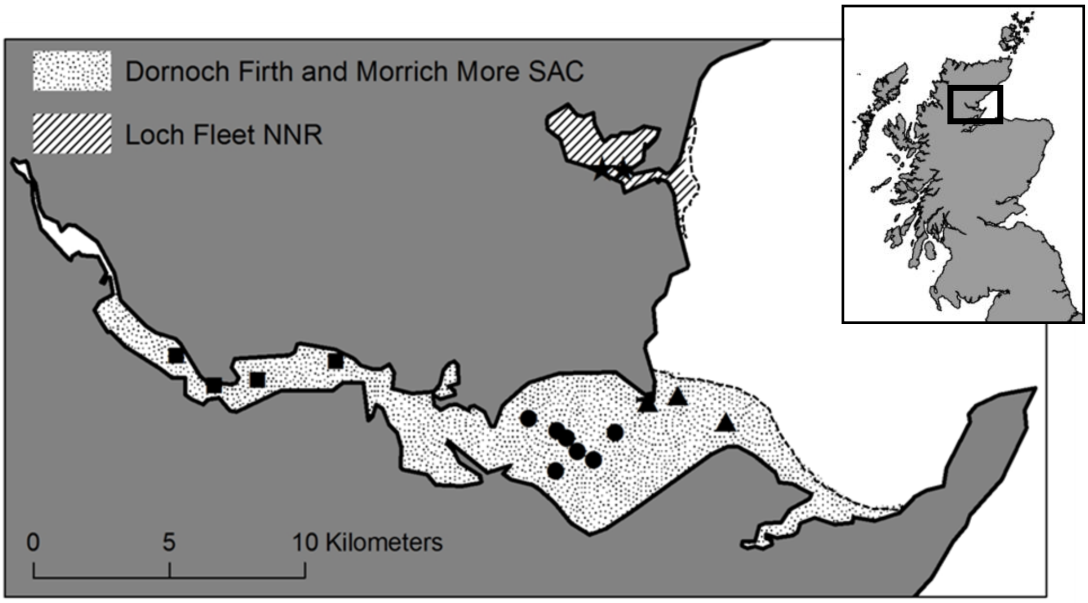

*Figure 1. Map showing locations of inter-tidal haul-out sites in the Dornoch Firth and Morrich More SAC (including sub-areas: inner■, mid● and outer▲) and Loch Fleet NNR.*

### *Distribution of seals at terrestrial haul-out sites*

At least two land-based counts of harbour seals in the SAC and Loch Fleet NNR were carried out during each pupping season (15 June to 15 July) between 1988 and 2005 (see Thompson *et al*. 2007) and in 2008 (Table 1). In 2006 and 2007, comparable data were collected from aerial surveys carried out during the same time-period (Table 1). Detailed investigation of variability in these counts indicated that the CV of mean estimates was <0.12 (Thompson *et al*. 2007). In the present study, these data were used to investigate long-term changes in the relative abundance of seals at different haul-out sites during the pupping season. Harbour seals typically continue to come ashore regularly at local haul-out sites to rest throughout the year, although seasonal patterns of abundance can differ between sites. To investigate whether there had been long-term changes in seasonal patterns at these Moray Firth sites, we conducted twice-monthly year-round surveys throughout 2008 for comparison with similar surveys that had been made in 1988 (Table 1). Full details of the methods used for these surveys are provided in Thompson *et al*. (1996). In brief, low tide haul-out counts were made by experienced observers from the nearest coastal vantage point using 30-80mm telescopes. These counts provided reliable estimates of the total number of adult (i.e. non-pup) seals. In the SAC, the distance between some haul-out sites and observer made it difficult to accurately estimate the number of young pups as they could be obscured by their mothers. However, sandbanks in Loch Fleet were close to shore (120–250 m); allowing pups to be counted accurately (see Thompson & Wheeler 2008). Unless stated otherwise, all pupping season counts of seals do not include pups of the year. Counts made outside the pupping season include seals of all ages.

To provide accurate data on the number of pups born in all areas, aerial surveys were carried out during the pupping seasons of 1989, 2006 and 2007 (Table 1). In 1989, three surveys were carried out on 23 June, 29 June and 3 July. These surveys were made at a height of c. 100m from a single-engine helicopter, and groups of seals were photographed using oblique 35mm photography, a 75–300mm zoom lens and colour transparency film. Numbers of pups with mothers, and all other seals >1 year of age were later counted over a light table using a binocular microscope. In 2006, five surveys were carried out, on 18 June, 23 June, 29 June, 7 July and 15 July. In 2007, four surveys were carried out, on 15 June, 29 June, 8 July and 13 July. These surveys were made from a height of 275m using a fixed wing aircraft and a digital SLR with a 70–300mm lens. All surveys were carried out within two hours before and after low tide. In all 3 years, data on the relative distribution of mothers and pups were based on the survey that contained the highest pup count.

### *Identification of foraging areas*

Foraging areas of individual female seals caught in the Dornoch Firth in 1989 and females caught in Loch Fleet in 2009 were compared (Table 1). In 1989, five females were caught and equipped with VHF radio tags during late May (Thompson *et al*. 1994). In April 2009, five females were caught and equipped with GPS Fastloc/GSM tags (SMRU, Scottish Oceans Institute, University of St Andrews, UK). The methods for catching and handling the seals are described in Thompson & Miller (1990) and Thompson *et al*. (1992). Capture and handling was carried out under Licence from the Scottish Government and the Home Office, respectively, and followed current guidelines for the use of marine mammals in field research (Gales *et al*. 2009). To compare foraging areas used by adult females in 1989 and 2009, we used data from May 27 until 20 July. In 1989, a single position for each VHF tagged seal was obtained by triangulation once a day, 6 days a week, and the duration of offshore foraging trip determined using automated receiving stations overlooking haul-out areas (Thompson *et al*. 1994). Unless seals were underwater or ashore, the GPS–GSM tags used in 2009 were programmed to record a GPS position accurate to within 30m every 20min. These data were subsequently transmitted to the Scottish Oceans Institute via GSM (McConnell *et al*. 2004; Cronin & McConnell 2008), resulting in an average of 40 locations per seal per day and a detailed track of each foraging trip. To balance sample sizes for comparison between the two datasets, we randomly selected a single data point for each seal on each day in 2009. In both 1989 and 2009, any data points within 2 km from the haul-out site were excluded as these were likely to be associated with periods of haul-out rather than with foraging activity (see Thompson *et al*. 1994). Foraging areas for each female were then defined through kernel analysis (Worton 1989) of remaining locations using the Hawth’s Tools module (available at http://www.spatialecology.com) within ArcGIS 9.3.

To compare foraging distances in 1989 and 2009, we estimated the mean distance between each of the daily locations that were obtained during foraging trips and the central location of the haul-out area being used in each year of study (1989, Dornoch Firth: 57.84901N, 4.03351W; 2009, Loch Fleet: 57.93521N, 4.03341W). Whereas animals did not always haul-out at their exact capture sites, all individuals did continue to return to the same general haul-out area (i.e. either Dornoch Firth or Loch Fleet).

*Table 1. Information on methodology and timing of surveys conducted in different years and where data were collected (AU, Aberdeen University; SMRU, Sea Mammal Research Unit).*

| Year(s) | Period | Method | Custodian |
|---|---|---|---|
| 1988-2005, 2008 | Pupping season | Land-based counts | AU |
| 1989 | Pupping season | Aerial survey counts | AU |
| 2006-2007 | Pupping season | Aerial survey counts | SMRU |
| 1988, 2008 | Year-round | Land-based counts | AU |
| 1989 | Summer | VHF Radio tracking | AU |
| 2009 | Summer | GPS tracking | AU |

## Results

### *Temporal changes in distribution of seals during the breeding season*

Although harbour seal counts in the northern region of the Moray Firth have been declining since the mid 1990s (Thompson *et al.* 2007), trends within the Dornoch Firth and Morrich More SAC and Loch Fleet differed markedly during this period (Fig. 2). During the pupping season, mean counts at haul-out sites in the SAC declined by 4–7% per year. In contrast, numbers in Loch Fleet increased by an average of 12% per year since the mid 1990s (Fig. 2). As a result there was a notable decline in the proportion of seals using the SAC over the 20-year period. In 1988, 100% of animals were located within the SAC whereas by 2008 only 70% used this area.

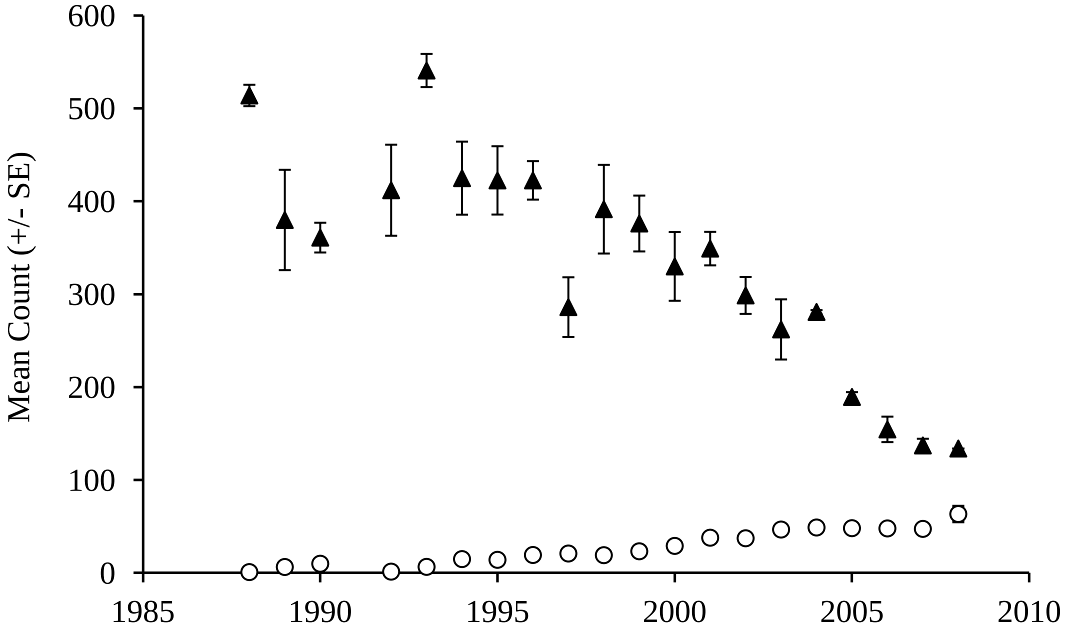

*Figure 2. Trends in abundance of harbour seals within the Dornoch Firth and Morrich More SAC ▲ and Loch Fleet ○. Data are means (+/- 1SE) of counts made during land-based surveys carried out between 15 June and 15 July in each year with the exception of 2006 and 2007 where data were obtained from aerial surveys.*

There was often considerable inter-annual variability in both abundance and the relative importance of different sub-areas within the SAC (Fig. 3). Trends in the proportion of animals in each sub-area were also examined. The lowest numbers of seals were consistently counted in the inner Dornoch Firth, whereas the highest numbers of animals were counted in the mid Dornoch Firth. Numbers of seals in the inner Dornoch Firth were least variable over the 20-year period, whereas numbers in the mid and outer Dornoch Firth showed more inter-annual variation. However, there was no indication of any long-term change in relative distribution within the Dornoch Firth during the 20-year period (Fig. 3).

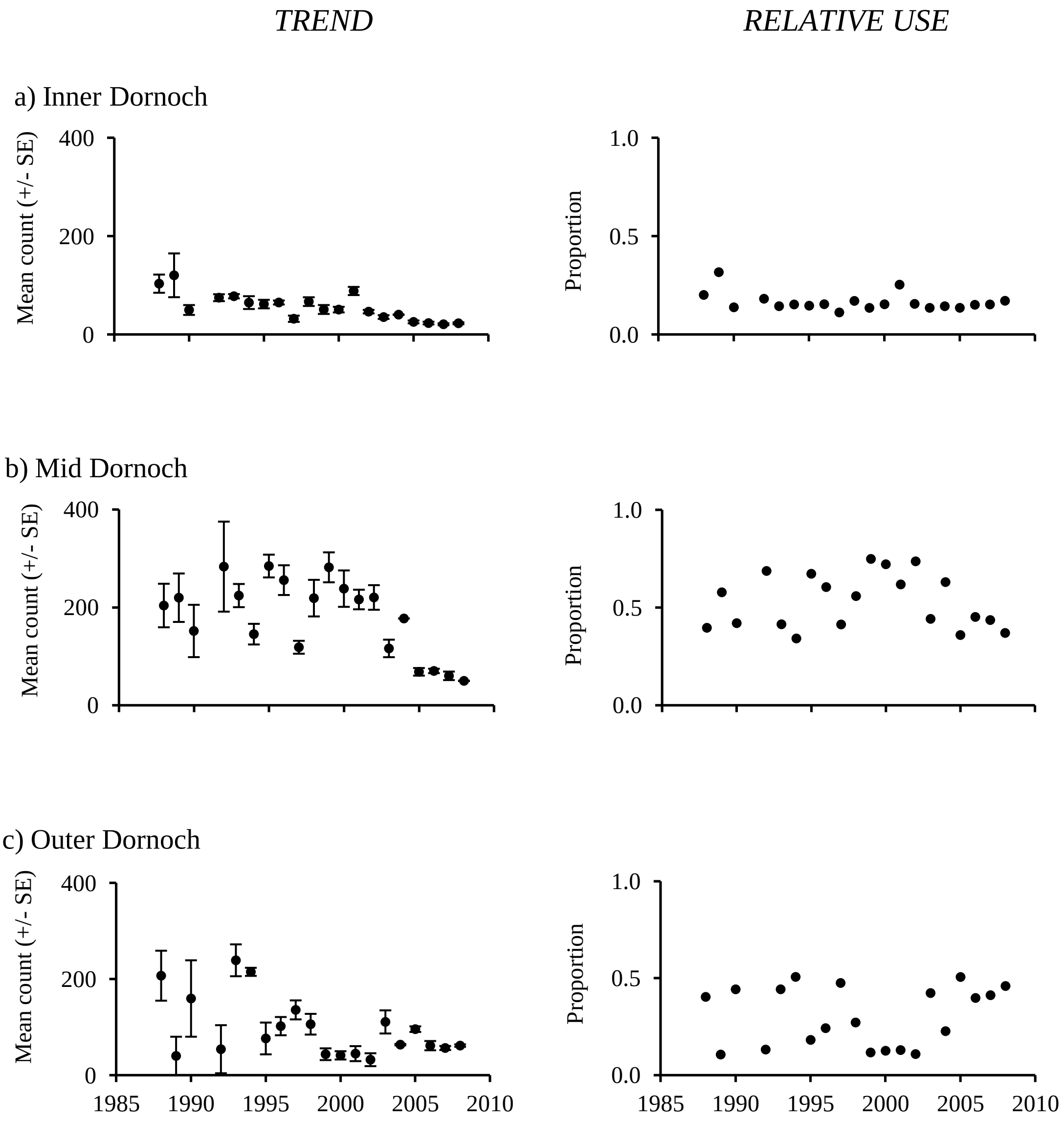

*Figure 3. Trends in annual mean counts and relative usage of the a) inner Dornoch, b) mid Dornoch and c) outer Dornoch. Data collected from land-based surveys carried out between 15 June and 15 July in each year apart from 2006 and 2007 where data were collected from aerial surveys.*

### *Long-term consistency of seasonal patterns*

In 1988, year-round counts suggested that the inner Dornoch Firth was an important area for harbour seals in both the pupping season and the winter (Fig. 4a). The mid Dornoch Firth was used year-round but was especially important during the pupping season (June and July) and moult (August and September) (Fig. 4b). The outer Dornoch Firth did not show the same year-round use as the inner and mid Dornoch Firth, but was characterized by a strong peak from the start of the pupping season through moult (Fig.

4c). In 1988, numbers in Loch Fleet were low, and this appeared to be used primarily as a winter site (Fig. 4d).

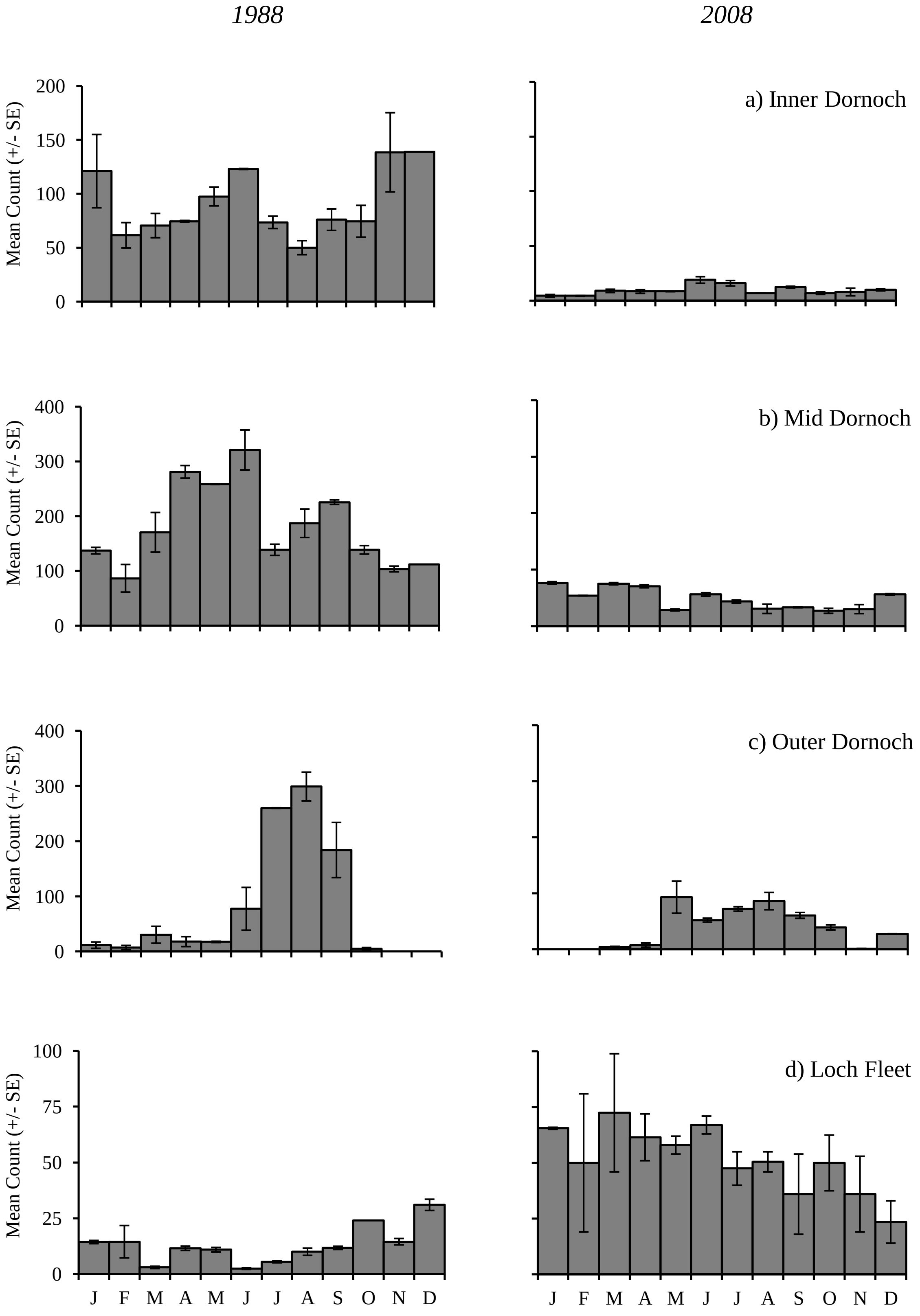

*Figure 4. Monthly mean counts from the a) inner Dornoch, b) mid Dornoch, c) outer Dornoch and d) Loch Fleet in 1988 and 2008. Data collected from year-round twice-monthly land-based surveys.*

By 2008, numbers at all sites within the SAC had declined. In the inner Dornoch Firth, there was a slight increase in abundance during the pupping season, but no evidence of the winter peak seen in 1988 (Fig. 4a). In the mid Dornoch Firth, numbers remained more similar throughout the year compared with 1988, with no obvious peak during the pupping and moult seasons (Fig. 4b). The outer Dornoch Firth was still characterized by one distinct peak. However, instead of being confined to the pupping and especially the moult season, use of this area was higher in spring and autumn (Fig. 4c). In 2008, Loch Fleet showed a considerable increase in numbers throughout the year. Seasonal usage was highest from late winter, through the pupping season to the end of the moult, and then decreased slightly through early winter (Fig. 4d).

### *Changes in the relative importance of different pupping sites*

The maximum number of pups counted in the northern region of the Moray Firth was similar in 1989 (n=84 pups, 29 June), 2006 (n=84 pups, 29 June) and 2007 (n=78 pups, 29 June). Data from aerial surveys indicated that in 1989 the SAC contained 100% of the pups born within the northern region of the Moray Firth. However, by 2006 and 2007, the importance of the SAC as a pupping site had fallen by *c.* 37% with max pup count reduced to 54 in 2006 and 49 in 2007. This difference in the relative number of pups born in the SAC and Loch Fleet was significant ($X^2$=51.232, df=6, p<0.001).

Annual land-based counts at Loch Fleet were used to explore the development of this new pupping site in more detail. In the late 1980s and early 1990s, no pups were observed in this area. Since then pup production has increased steadily year by year (Fig. 5), indicating that there has been a gradual shift in importance from the SAC to Loch Fleet.

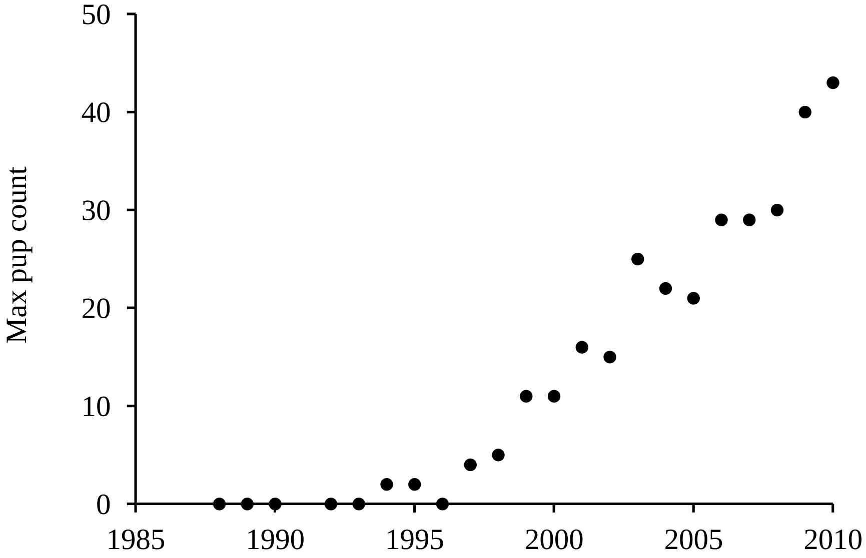

*Figure 5. Maximum annual pup counts from Loch Fleet. Data were collected from land-based surveys carried out between 15 June and 15 July in each year, although in 2006 and 2007 data from aerial surveys were used.*

### *Comparison of foraging areas in 1989 and 2009*

Adult females foraged in broadly similar areas in 1989 and 2009. Individual seals tagged in 1989 (n=5) showed some overlap in foraging areas, whereas seals caught in 2009 (n=5) displayed less overlap (Fig. 6). Analysis showed no significant difference in the distance travelled by seals in 1989 (17–22 km) and 2009 (7–22 km) (Welch test, t=1.038, df=5, p>0.05) (Table 2).

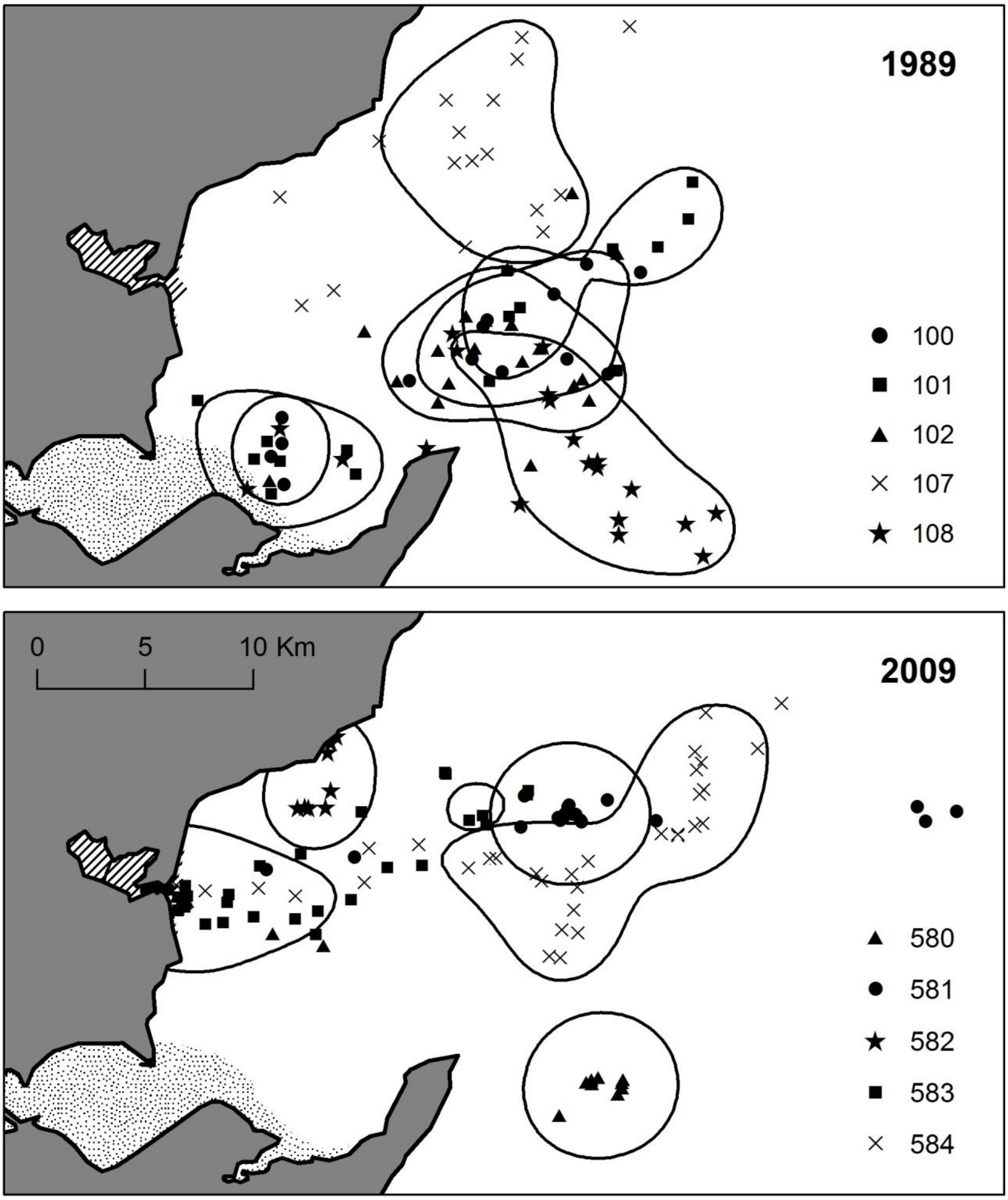

*Figure 6. Comparison of adult female foraging locations in 1989 (n=5) and 2009 (n=5). The solid lines show the 50% contours for individual foraging areas as calculated by Kernel analysis. Individuals 100 and 101 (1989), and 583 (2009) each had two separate 50% contours.*

*Table 2. Summary of the distance between haul-out and foraging areas for 10 females tagged in 1989 and 2009. n = the number of daily locations >2km from haul-out areas.*

| ID | Year | n | Max | Mean | 95% CI |
|---|---|---|---|---|---|
| 100 | 1989 | 14 | 25.8 | 16.5 | 13.0-20.0 |
| 101 | 1989 | 16 | 29.7 | 16.5 | 12.2-20.9 |
| 102 | 1989 | 20 | 25.1 | 18.4 | 16.5-20.3 |
| 107 | 1989 | 17 | 31.5 | 21.8 | 19.4-24.2 |
| 108 | 1989 | 20 | 27.4 | 19.3 | 16.7-21.9 |
| 580 | 2009 | 14 | 24.6 | 18.4 | 13.9-23.0 |
| 581 | 2009 | 19 | 38.4 | 21.9 | 18.5-25.3 |
| 582 | 2009 | 8 | 11.7 | 10.0 | 9.1-10.8 |
| 583 | 2009 | 35 | 18.9 | 7.3 | 5.3-9.2 |
| 584 | 2009 | 34 | 31.2 | 19.3 | 16.6-22.1 |

## Discussion

### *Temporal changes in haul-out distribution*

Observations in many regions have shown that harbour seal pupping sites are used consistently in successive years (Frost, Lowry & Ver Hoef 1999; Small, Pendleton & Pitcher 2003; Lonergan *et al*. 2007), despite high levels of disturbance or hunting at some locations (Bonner, Vaughan & Johnston 1973). In contrast, zoo-archaeological and genetic studies have provided evidence for longer-term changes in the abundance and distribution of harbour seals in the Baltic region (Härkönen *et al*. 2005; Schmölcke 2008). However, data on the consistency of site-use at the intermediate timescales of interest to conservation biologists are sparse. Fine-scale studies of haul-out site use have typically been conducted over only a few years, and longer time-series of abundance estimates generally present aggregated data at larger scales (Jeffries *et al*. 2003; Brown *et al*. 2005; Lonergan *et al*. 2007) or use a sub-set of sites for trend monitoring (Frost *et al*. 1999; Small *et al*. 2003). The results from this study are the first to present data on fine-scale patterns of harbour seal haul-out site use over a period of two decades.

Previous studies have provided some evidence for the loss of certain haul-out sites in industrialized estuaries (Allen 1991), but there is little information on whether these represented previously important pupping areas, or sites that were used only occasionally. In other pinniped populations, the developments of new pupping sites tend to have occurred as a consequence of population growth (Payne 1977; Pomeroy, Twiss & Duck

2000). The changes in site-use observed in our study are of particular interest to conservation managers because the development of the new pupping site occurred during a period when harbour seal populations across this and many other parts of Scotland underwent significant declines (Lonergan *et al*. 2007). Furthermore, over this same period, there was a reduction in the importance of nearby pupping sites that had recently been designated as an SAC to protect this species. An understanding of the mechanisms driving changes in the relative importance of different sites within this intensively studied area could provide important insights into the likely success of different management measures at this and other protected haul-out areas. Unfortunately, an absence of individual-based studies during the late 1990s mean that it is not possible to say whether the increase in pup production in Loch Fleet resulted from an influx of new recruits, or whether adult females from the SAC switched to new breeding sites. But whatever the proximate cause for this change, there are several possible reasons why haul-out sites in Loch Fleet may now be more attractive to adult females than the sites within the SAC.

Increases in anthropogenic disturbance have been shown to influence haul-out site choice of harbour seals (Suryan & Harvey 1999). Shooting of seals is known to have occurred regularly within the Dornoch Firth (Thompson *et al*. 2007), but is believed to have been rare in Loch Fleet in recent decades. This may have driven observed changes in site-use, although it does not explain why the increase in Loch Fleet did not occur until the mid 1990s, well after shooting had been restricted in this area. Similarly, boat-based mussel fisheries regularly operate close to the haul-out sites within the SAC, but this fishery has been in operation for over 500 years and this also seems unlikely to explain recent changes in distribution. The only major development in the area during this period was the construction in 1991 of a bridge across the narrows between the inner and mid Dornoch Firth that now carries over a million vehicles a year. Whereas it is impossible to directly assess whether seals responded to this development, the lack of any other obvious changes in habitat quality within the SAC suggests that the potential for in-air or underwater traffic noise to influence seal movements and site-use deserves further investigation at a broader range of sites.

Changes in the distribution and/or abundance of prey are other possible explanations for the observed changes in site use within the northern Moray Firth. Changes in prey distribution could cause seals to forage further offshore, potentially using haul-out sites nearer those resources to reduce travel costs. However, although sample sizes were small and individual variability high, foraging adult females were located in broadly similar areas and travelled similar distances in 1989 and 2009. The relative local foraging seen in both years is consistent with previous tracking work of harbour seals in the Moray Firth (Tollit *et al*. 1998) and elsewhere (Lesage, Hammill & Kovacs 2004).

*Long-term consistency of seasonal patterns*

Typically, information on long-term trends in abundance and distribution are based on summer surveys during either the pupping or moulting seasons. However, the use of haul-out sites may vary seasonally, and the potential conservation importance of certain sites may be overlooked when surveys are limited to one period of the year. Furthermore, the assessment of potential impacts from new developments will also be constrained unless there is a clear understanding of seasonal patterns in the seals' use of different protected areas. We carried out year-round surveys at the beginning and end of our time series. Comparison of these data suggests that harbour seals in the SAC have shown some changes in their seasonal pattern of site-use over this period. For example, sites in the inner Dornoch Firth previously showed a winter peak in abundance, whereas recent counts peaked in the summer (Fig. 4a). Changes in seasonal patterns were also evident in Loch Fleet. In the late 1980s, Loch Fleet was used primarily as a winter site, with any seals present at other times typically being small groups of juveniles (P. M. Thompson, *Unpublished data*). More recently, Loch Fleet has become increasingly important during the summer. Pupping season and moult surveys will remain an important tool for abundance estimates (Thompson *et al*. 1997; Small *et al*. 2003; Gilbert *et al*. 2005), but year-round surveys are often also required to provide conservation managers with the information needed to mitigate the impact of potential developments. Our results highlight that seasonal patterns may vary over time, and care should be taken when drawing conclusions from short-term or older survey data.

*Management implications*

The population dynamics of long-lived vertebrates are most sensitive to changes in adult mortality (Caswell 1978; Gaillard, Festa-Bianchet & Yoccoz 1998) and efforts to reduce mortality due to hunting, persecution or by-catch should be the first priority when managing the restoration of declining populations. The development of a management plan to control the numbers of seals shot in the Moray Firth (Butler *et al*. 2008) was therefore an appropriate response to reported declines in this population, particularly as estimates of the numbers of seals shot were sufficient to explain a large part of this decline (Thompson *et al*. 2007). Nevertheless, wider scale declines in areas where there is little documented persecution suggest that other drivers are involved (Lonergan *et al*. 2007; Hall & Frame

2010), and the development of SACs through the EU Habitats Directive offers a framework for protecting key habitats and controlling other threats. The nature and extent of these potential threats remain unclear, but reductions in the use of pupping sites within the SAC suggest that subtle changes in the quality of these haul-out sites compared with those in the adjacent Loch Fleet NNR have influenced female site choice. Of the monitored sites in Scotland, Loch Fleet is the only site where pup production has increased. Fortuitously, this area was designated as a NNR in 1998 due to its broad biodiversity interest, and management of the NNR can be adapted to encompass the area's increasing importance as a seal pupping site.

Efforts to designate protected areas for seal and seabird populations have traditionally focussed on key terrestrial breeding sites, primarily due to the limited information available on the foraging areas used by animals from these colonies. Methods for following the at-sea movements of these marine top predators have been developed only relatively recently, meaning that information on long-term variation in the use of different feeding areas is rare. This can be a particular constraint when managing breeding colonies, because it is unclear whether the site's importance depends upon its intrinsic characteristics or its proximity to suitable feeding areas. Although sample sizes were small, our results indicate that harbour seal foraging areas remained similar, despite changes in their use of breeding sites. This does not rule out the possibility that broader scale changes in haul-out site use may be driven by changes in foraging conditions. However, it does suggest that subtle temporal and spatial changes in the characteristics of their breeding sites, or surrounding tidal waters, have influenced site selection. In contrast, the key features of these areas that affect the seals site selection remain elusive to conservation managers. More detailed assessments of the environmental conditions at sites with contrasting trends in pup production may now provide an opportunity to develop better site selection criteria, and identify key management measures for conserving viable populations within this and other harbour seal SACs.

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# CHAPTER III

## AN INDIVIDUAL-BASED APPROACH TO ESTIMATING FINE-SCALE SITE FIDELITY AND ABUNDANCE IN HARBOUR SEALS: IMPLICATIONS FOR CONSERVATION MANAGEMENT

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### Introduction

Monitoring trends in the abundance of pinniped populations typically involves counting seals at their terrestrial haul-out sites during the breeding season or moult when seals are most likely to be hauled out (Bowen, McMillan & Mohn 2003; Jeffries, Huber & Calambokidis 2003; Baker & Johanos 2004). At other times of the year, counts of seals are generally lower (Sullivan 1980; Thompson *et al*. 1996, 1997), but it is largely unknown whether fewer individuals are present, or whether temporal variation in counts reflects a change in haul-out probability. Seasonal variation in the importance of haul-out sites may therefore be misinterpreted, and management decisions based on count data alone could have significant implications for the populations in question.

Broad conservation measures have been put in place to protect European harbour seal populations, including the designation of protected areas in order to conserve their vital habitat (Baxter 2001). Nonetheless, long-term monitoring of harbour seal abundance at key haul-out sites during the pupping season indicates that the UK harbour seal population has been declining over the last two decades for reasons that are not fully understood (Thompson *et al*. 1997; Lonergan *et al*. 2007). The UK harbour seal population consists of clusters of subpopulations (Lonergan *et al*. 2007), which may be relatively discrete (Thompson *et al*. 1996). However, less is known about the structure and dynamics of the breeding groups within these subpopulations.

High levels of site fidelity may have implications for the degree of genetic isolation between potentially discrete breeding groups. Tagging and telemetry studies have shown that individual harbour seals typically demonstrate high levels of site fidelity over the course of a single breeding season (Thompson *et al*. 1997; Cunningham *et al*. 2009b) particularly as adult females are likely to be constrained by the presence of a pup, whereas adult males defend their mating territory. Other studies have found high levels of between-year breeding site fidelity, as well as age and sex-specific differences (Härkönen & Harding 2001; Mackey *et al*. 2008). Although Sharples, Mackenzie & Hammond (2009) estimated haul-out probabilities throughout the year using telemetry, this did not involve the same individuals and sample size was relatively small. Therefore, until now, no estimates of continuous year-round haul-out probabilities exist for individual harbour seals.

Despite more attention often being paid to key demographic parameters, such as survival and fecundity, site fidelity can provide equally important information on population dynamics (Hestbeck, Nichols & Malecki 1991), including crucial insights into levels of inbreeding as well as the mechanisms driving the spread of disease. Nevertheless, a major constraint in developing long-term studies of site fidelity in harbour seals, as with many other species, is that it requires the ability to follow individuals over time. Capture of seals for tagging is logistically difficult, sample sizes are typically small, tags are shed during the moult or lost over time, and recapturing the same individuals for re-tagging is difficult. However, harbour seals have natural and distinctive individual markings which offer a unique and low cost opportunity to follow individuals over time using photo-identification techniques. Nevertheless, haul-out sites are often inaccessible or easily disturbed, and only a few sites in the world have proved suitable for this type of data collection (Hastings, Hiby & Small 2008; Mackey *et al*. 2008; Cunningham 2009a). On the north east coast of Scotland, within the Moray Firth, Loch Fleet National Nature Reserve has recently become a preferred haul-out and breeding site for harbour seals (Chapter II). The proximity of the main sandbank within this estuary has permitted accurate photographic identification of individual seals (Thompson & Wheeler 2008).

Here, I aim to estimate sex-specific site fidelity and haul-out probability of harbour seals across a range of temporal scales that include within the breeding season, throughout the year, and between years. I also investigate how haul-out probabilities obtained from re-sightings of individuals compare with those previously obtained from tagging and telemetry data. Finally, I use novel mark-resight models to examine the extent to which count data provides a useful indicator of the seasonal variation in the number of seals that used this site.

## Methods

### *Photo-identification surveys*

The study was carried out in Loch Fleet National Nature Reserve, a tidal estuary on the north east coast of Scotland within the Moray Firth (see Chapter II). At low tide several sandbanks were exposed, two of which were used frequently by harbour seals for resting, giving birth and nursing pups. The proximity of the main sandbank to an onshore observation point (130m) allowed individual seals to be recognised by photographic identification (Fig. 1).

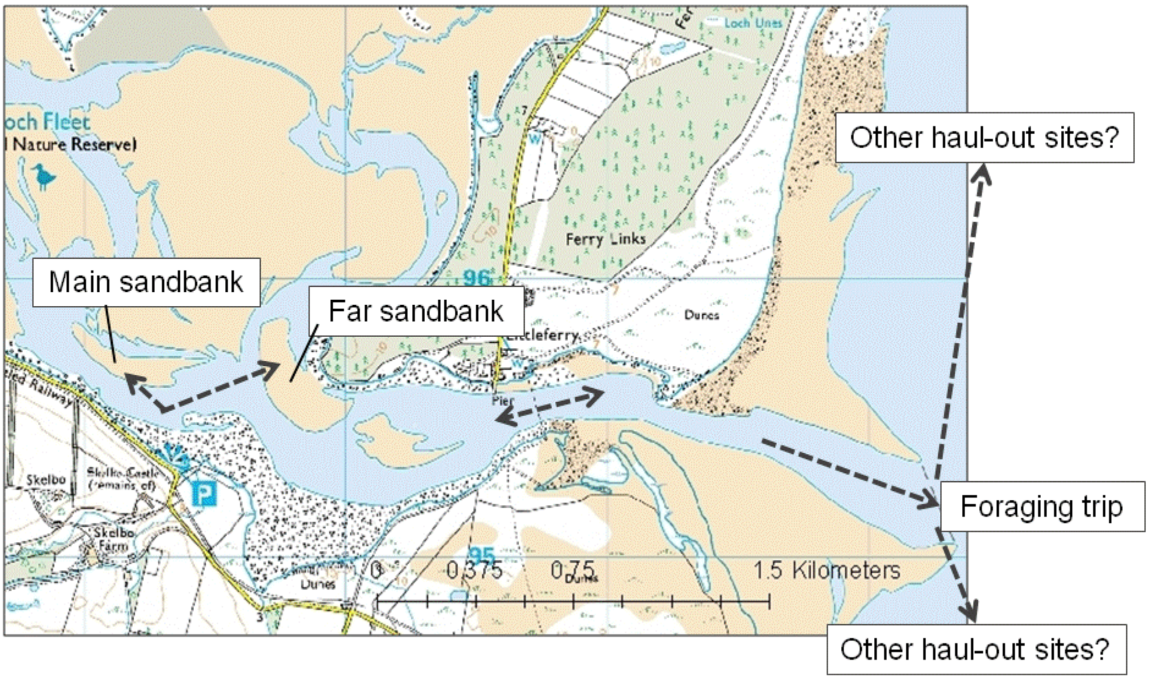

*Figure 1. Map of the Loch Fleet study area illustrating movement of seals within and outside the estuary.*

Surveys were carried out using a digital camera (Nikon Coolpix 5100) attached to a telescope (20-60x80mm Swarowski HD-ATS 80). The main sandbank was exposed prior to low tide. However, surveys were started an hour after low tide to allow seals to settle on the sandbank. Left and/or right side headshots were taken of all seals hauled out (Fig. 2), and matched by eye to a catalogue containing left and right headshots of all seals photographed at this site since 2006 (Appendix I). From 2006 to 2010, photo-identification surveys were carried out on a daily basis during the pupping season from the end of May to the end of July. During 2008 and 2009 one to five surveys (mean=3.2 ±0.3 SE) were carried out each month throughout the year. August surveys were excluded because the majority of individuals were moulting, making individual identification difficult and inconsistent. During photo-identification surveys, counts of adult seals (defined as all individuals except pups) were carried out simultaneously.

*Figure 2. Original photographs indicating typical body positions of harbour seals for photo-identification.*

*Re-sighting rates*

The probability of detecting individuals during photo-identification surveys depends upon a number of factors. Within Loch Fleet, sightings of individuals depend upon the individual’s preference for a particular sandbank, as well as the orientation of the seals when hauled out on the main sandbank. On any particular low tide, individuals may be in the water moving between banks and therefore not necessarily sighted despite being in the study area. Individual seals may also be outside the study area, e.g. on foraging trips, and therefore not available for sighting. While out foraging other haul-out sites may be used occasionally for resting, such as Brora to the north or the Dornoch Firth to the south, before returning to Loch Fleet. Recapture probabilities (*p*) from mark-recapture analyses were used as a proxy for the minimum values of haul-out probabilities (within a breeding season or month) and levels of site fidelity (between years).

*Determining sex*

Males and females were sexed from photographs of their ventral side. In addition to the umbilical scar, the penile opening was visible on males, and the pair of nipples was visible on females. Females were also sexed when seen with a pup between May - July (Fig 3).

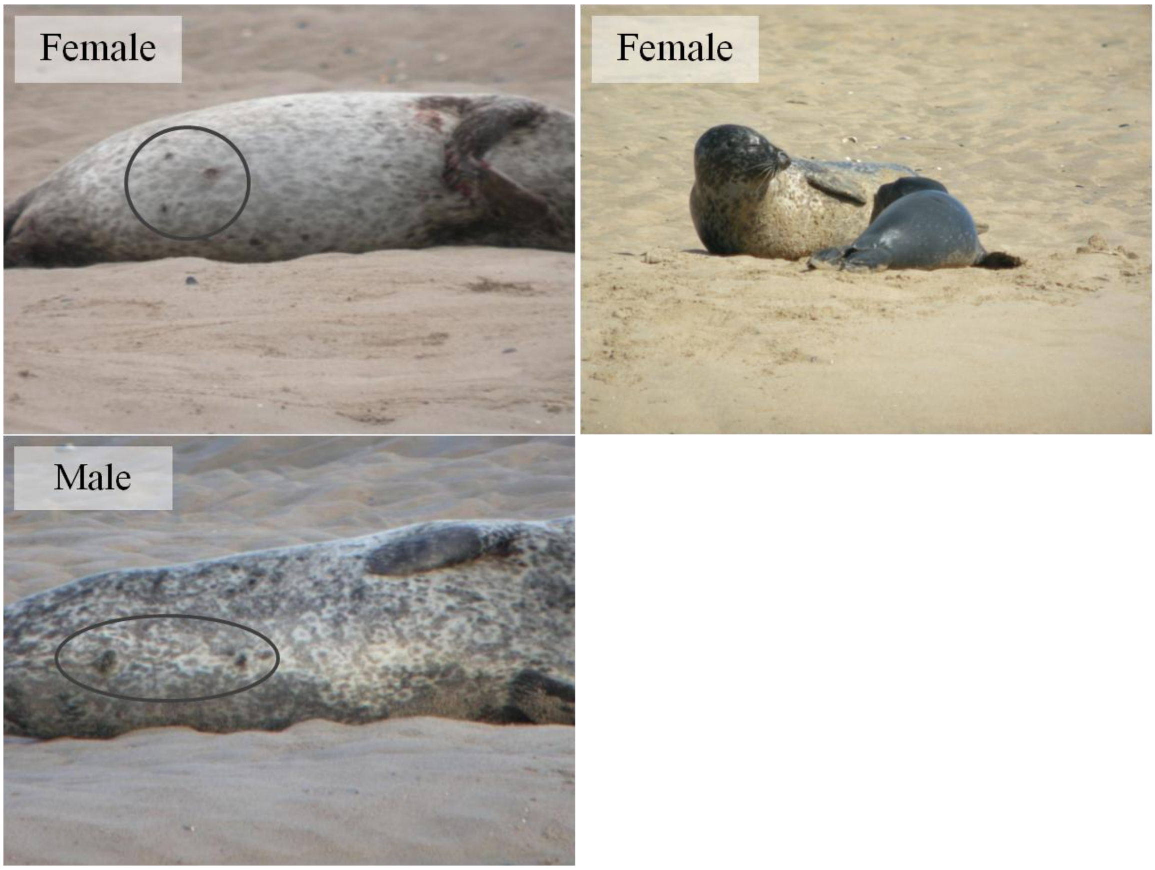

*Figure 3. Photographs illustrating the identification of male and female harbour seals.*

**Statistical analysis**

All statistical analyses were carried out in the program MARK (Gary White, Colorado State University, White & Burnham 1999), using statistical models as described below. A summary of all model parameters involved is included in Table 1. Within each analysis the best model was chosen based on $AIC_c$ scores, adjusting for small samples size (Burnham & Anderson 1998). Goodness of fit for Cormack-Jolly-Seber (CJS) and multistate models were tested in the program U-CARE.

*Table 1. Summary of parameters in CJS and multistate models (Nichols et al. 2004; McClintock et al. 2009).*

| | | | | |
|---|---|---|---|---|
| *CJS & Multistate* | Phi or $S_i$ | Survival | - | Probability that an individual in sampling period *i* survives to period *i+1* and remains part of the population |
| | $p_i$ | recapture | - | Probability that an individual alive and in the population is sighted in period *i* |
| | $\psi_i$ | Psi | - | Probability of an individual in a specific state in period *i* will transition to another state in period *i*+1 |
| Mark-resight | $U_i$ | | - | Number of unmarked animals in the population during primary occasions |
| | $\alpha_i$ | alpha | - | Intercept for mean re-sighting rate during primary occasions |
| | $\sigma_i^2$ | zigma | - | Individual heterogeneity level |
| | $\phi_i$ | Phi | - | Apparent survival between primary occasions |
| | $\gamma_i'$ | Gamma’ | - | Probability of transitioning from an observable state to an unobservable state |
| | $\gamma_i''$ | Gamma’’ | - | Probability of remaining in an unobservable state when at an unobservable state |
| | $\lambda_i$ | Lamda | - | Overall mean re-sighting rate for primary occasions |
| | $N_i$ | $U_i+n_i$ | - | Total population size during primary occasions |

### *Between-year site fidelity*

There is a risk of positively biasing parameter estimates when using simple models such as CJS in estimating sex-specific recapture rates when sex is not always known, as known sex individuals are likely to be sighted more frequently (Nichols *et al*. 2004), and CJS models do not take into account individuals changing states over time (i.e. from unidentified sex to identified male or female). I therefore considered a multistate model (Nichols *et al*. 2004) which yields unbiased and precise results for males and females, but may include some bias for individuals of unknown sex due to the heterogeneous behaviour of a group containing both males and females (Nichols *et al.* 2004). Capture histories of individuals were constructed based on the individual’s state, male (M), female (F) or of unidentified sex (U). Sightings until the sex of an individual had been determined were recorded as “U”. Once sex was determined (M or F) the individual remained in that state for every future re-sighting (Table 2).

*Table 2. Summary of the total number of males, females and individuals of unknown sex in the catalogue for each year.*

| | 2006 | 2007 | 2008 | 2009 | 2010 |
|---|---|---|---|---|---|
| Males | 3 | 3 | 24 | 34 | 38 |
| Females | 42 | 49 | 60 | 72 | 73 |
| Unknown | 63 | 71 | 55 | 40 | 41 |
| Total | 108 | 123 | 139 | 146 | 152 |

The state (M, F, or U) of each individual in each of the five years, including non-sightings (0), made up the individual sightings histories. The final data set contained 152 individuals, which had at least one sighting in one of the five years. Given the three states an individual could occupy, $S^M$, $S^F$ and $S^U$ were the probabilities of an individual in a particular state surviving from time $t$ to time $t+1$. Similarly, $p^M$, $p^F$ and $p^U$ are the probabilities that an individual in a particular state is recaptured from time $t$ to time $t+1$. Transitions between states were restricted to occur from “U” to either “M” or “F” ($\psi^{UM}$, $\psi^{UF}$), whereas all other transitions were fixed to zero ($\psi^{MF}$=0, $\psi^{FM}$=0, $\psi^{FU}$=0, $\psi^{MU}$=0). Since the sum of the $\psi$ for each state should add up to one, a MLogit(x) link function was applied to transition probabilities.

### *Monthly haul-out probability*

A Cormack-Jolly-Seber (CJS) model was used to estimate overall monthly haul-out probabilities for all individuals using the sightings (1) and non-sightings (0) from the year-round surveys carried out in 2008 and 2009. To balance sample sizes, two surveys were randomly selected for each month (using random number generator) and individual sightings within months were pooled. The final data set consisted of sighting histories from 133 individuals. Survival (*S)* and recapture probabilities (*p)* were estimated from time *t* to time *t+1,* and the importance of variation in recapture probabilities across time were evaluated for both sexes. However, in time-dependent CJS models no estimate can be obtained for the first occasion (January 2008).

Next, a multistate model was used to estimate sex-specific monthly haul-out probabilities, using the same sighting histories as above but converting sightings into states (M, F, U) alternative to 0-1 data. This analysis was similar to that estimating between-year site fidelity (see details above). The data set consisted of sightings histories from 34 males, 66 females, and 33 individuals of unidentified sex.

### *Within pupping season haul-out probability*

CJS models were used to estimate within pupping season haul-out probabilities of males and females in each year from 2006 to 2010, using daily sighting histories from the 15 June to 15 July. In CJS models sightings and non-sightings are recorded as ones and zeros which do not incorporate information on the individual sex, in contrast to multistate model, and sex has to be defined as a grouping after the sightings histories. The final data set included sighting histories from 35 males and 70 females. Estimated haul-out probabilities were compared to estimates obtained from telemetry data from the same period (Thompson *et al*. 1997).

### *Estimating monthly abundance from re-sightings data*

Mark-resight models estimate abundance using sightings of known marked individuals that transition between observable (individuals present in the study area) and unobservable states (individuals outside the study area), while also incorporating information on the number of unmarked seen and marked unidentified individuals (McClintock & White 2010). In this study, a large proportion of the unmarked individuals are juveniles which due to their coat characteristics are difficult to identify consistently. Marked unidentified individuals include adults and some juveniles (with defined coat patterns), which occasionally due to their position on the sandbank cannot be positively identified as their markings are obscured. I chose the poisson-log normal mark-resight model developed by McClintock *et al*. (2009) to estimate the monthly abundance of harbour seals in Loch Fleet in 2008 and 2009. This model was selected because the number of marked individuals in the population at any one time was not known. This is often the case when individuals are recognised by natural markings rather than caught for tagging prior to sampling. Seals could be photographed more than once both within secondary (surveys) and primary occasions (months), also referred to as sampling with replacement. This model assumed closure within primary occasions (month), whereas periods between primary occasions were open to births, deaths, and movement. As seals were identified by markings in their pelage, I assumed that no marks were lost over time. As harbour seals are not highly sexually dimorphic or have obvious sex-specific characteristics, the sex of the unmarked and marked unidentified individuals was not known, and abundance estimates could not be obtained separately for males and females.

The sightings data from twice-monthly randomly selected surveys were used to estimate monthly abundance and compare variation in monthly abundance between years. The total number of unmarked individual sightings and marked but unidentified sightings were summarized in Table 3. The mark-resight model included constancy for parameterization of mean re-sighting rate, α(.), and individual heterogeneity, σ(.). The six parameter model {alpha(.), sigma(.), U(.)} was used to estimate population size (N) for each primary occasion (month), incorporating apparent survival, ϕ, and the transition probabilities, γ' and γ'' (Table 1).

*Table 3. Summary of the total number of sightings of marked identified, marked unidentified and unmarked individuals in each month of 2008 and 2009.*

| | Month | Marked identified | Marked unidentified | Unmarked seen |
|---|---|---|---|---|
| | Jan | 19 | 0 | 0 |
| | Feb | 25 | 5 | 3 |
| | Mar | 46 | 3 | 4 |
| | Apr | 36 | 0 | 4 |
| | May | 50 | 3 | 11 |
| 2008 | Jun | 53 | 4 | 14 |
| | Jul | 37 | 3 | 14 |
| | Sep | 36 | 0 | 3 |
| | Oct | 44 | 6 | 2 |
| | Nov | 26 | 4 | 3 |
| | Dec | 21 | 3 | 4 |
| | Jan | 22 | 0 | 3 |
| | Feb | 34 | 5 | 6 |
| | Mar | 46 | 3 | 6 |
| | Apr | 51 | 3 | 5 |
| | May | 53 | 6 | 15 |
| 2009 | Jun | 63 | 6 | 13 |
| | Jul | 32 | 3 | 4 |
| | Sep | 44 | 6 | 17 |
| | Oct | 41 | 4 | 14 |
| | Nov | 24 | 3 | 1 |
| | Dec | 27 | 3 | 4 |

### *Estimating abundance from count data*

In previous studies, breeding season abundance estimates have been produced for the period 15 June to 15 July, by combining mean counts of adult seals with haul-out probabilities estimated from telemetry data. See equation 1, where n is the mean low tide count during the sampling period, and $h_1$ and $h_2$ are the proportion of low tides on which tagged males (0.521) and females (0.698) were hauled out (from Thompson *et al*. 1997). In 2008 and 2009, mean counts were obtained from ten randomly selected surveys (random number generator) carried out within the period 15 June to 15 July. Variation around the abundance estimate was calculated using equation 2 (see Thompson *et al*. 1997).

$$N = \frac{2 \times n}{(h_1 + h_2)} \qquad Equation\ 1$$

$$var(N) = N^2 \left[ \frac{var(n)}{n^2} + \frac{var(h_1) + var(h_2)}{(h_1 + h_2)^2} \right] \qquad Equation\ 2$$

**Results**

A total of 347 photo-identification and count surveys were carried out during the course of the study. Surveys were most intensive during the breeding season from the end of May to the end of July (Table 4).

*Table 4. Summary of the number of visits (photo-identification surveys) and number of different individuals identified in each month.*

| | 2006 | | 2007 | | 2008 | | 2009 | | 2010 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Visits | IDs | Visits | IDs | Visits | IDs | Visits | IDs | Visits | IDs |
| Jan | | | | | 2 | 19 | 4 | 35 | | |
| Feb | | | | | 3 | 26 | 4 | 45 | | |
| Mar | | | | | 4 | 62 | 3 | 51 | | |
| Apr | | | | | 4 | 58 | 4 | 61 | | |
| May | 13 | 78 | 14 | 87 | 11 | 108 | 9 | 102 | 6 | 106 |
| Jun | 30 | 103 | 26 | 100 | 30 | 112 | 29 | 114 | 29 | 111 |
| Jul | 19 | 78 | 21 | 87 | 18 | 83 | 17 | 75 | 17 | 76 |
| Aug | | | | | 3 | 38 | 3 | 38 | | |
| Sep | | | | | 6 | 63 | 3 | 49 | | |
| Oct | | | | | 2 | 44 | 3 | 45 | | |
| Nov | | | | | 4 | 55 | 3 | 31 | | |
| Dec | | | | | 1 | 21 | 2 | 27 | | |

During these surveys I photographed between 159-162 individually identified harbour seals, of which 147 had photographs of both left and right side. Of the individuals with only one side photographed, 12 individuals had left-side head shots (2 males, 2 females, 8 of unknown sex), whereas only three individuals (unknown sex) had right-side head shots. Thus there were a minimum of 159, and a maximum of 162 unique individuals.

A total of 74 females, 41 males and 47 individuals of unknown sex were identified during the study. In summary, almost 80% of females were seen in all five years, whereas around 74% of males were seen in four or more years, and nearly 50% of the individuals of unknown sex were seen in three or more years. However, not all individuals were seen since the beginning of the study which may negatively bias these percentages. To explore this, the number of years between sightings was plotted (Fig. 5). These data indicate that the majority of individuals were seen in every year following their first sighting, particularly females (81%) and males (72%).

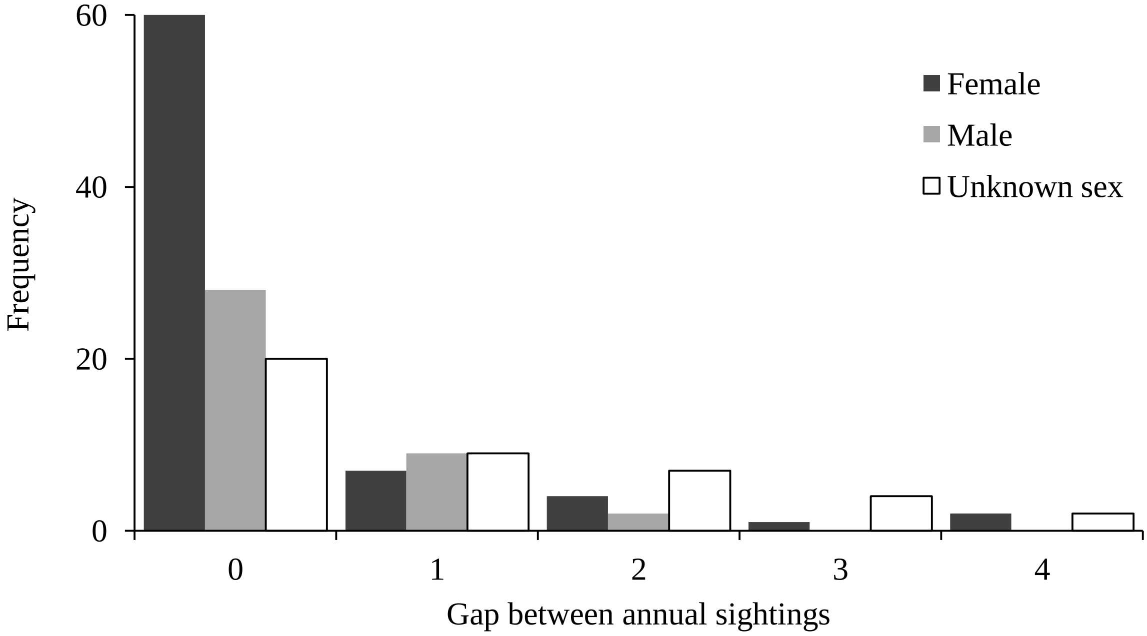

*Figure 5. Frequency distribution of the number of years between sightings of males, females and individuals of unknown sex over the five-year study period.*

*Residents*

Forty-three percent of individuals were sighted within the study area in ≥6 months of the year. Of these, 64% were female, 27% male and 16% individuals of unidentified sex. Most females were seen both during and outside the pupping season (n=65, 92%), and there were no females sighted only outside the pupping season (Fig. 6). Similarly, most males were seen both during and outside the pupping season (n=31, 78%), and only a few were only seen outside the pupping season (n=3, 8%) (Fig. 6). In contrast to confirmed males and females, a large proportion of individuals of unknown sex were only seen outside the pupping season (n=13, 33%) (Fig. 6). These differences in sightings during and outside the pupping season of males, females and individuals of unknown sex were analysed in a 3x3 contingency table and showed a highly significant difference (Fisher's

Exact Test, p<0.0001). However, to explore whether this was purely a result of the unknown group, a 2x3 contingency table including only males and females was analysed. This revealed a moderate significant difference (Fisher's Exact Test, p=0.03). These results indicate that males and females behave differently compared to individuals of unknown sex, whereas females also behave slightly differently compared to males.

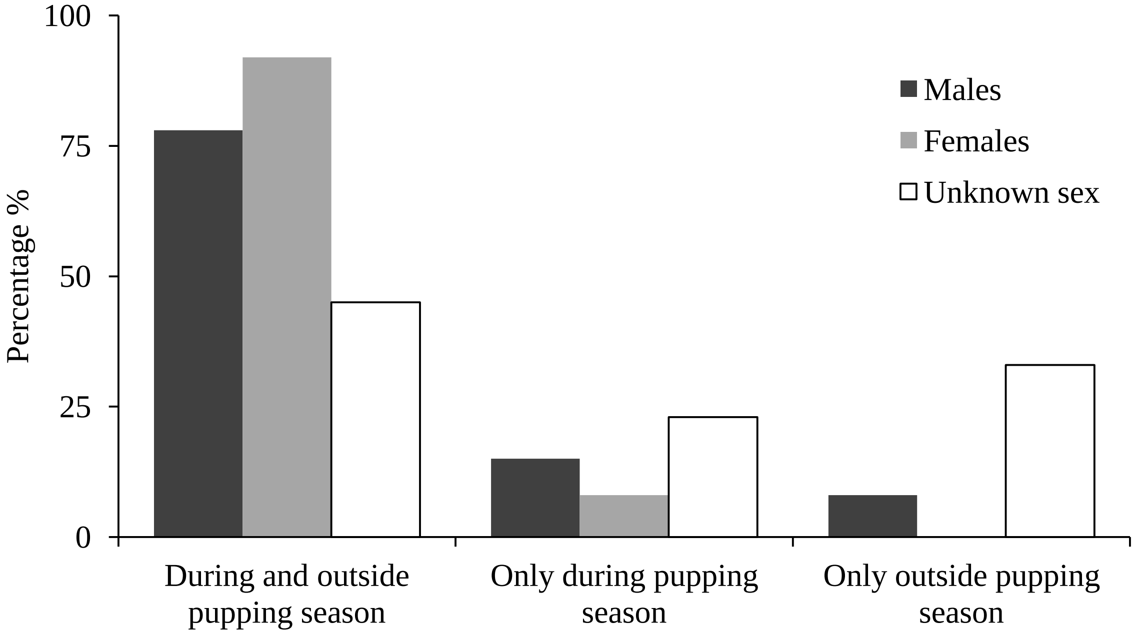

*Figure 6. The percentage of males, females and individuals of unknown sex that were seen during and outside the pupping season, only seen during the pupping season, or only seen outside the pupping season.*

*Between-year fidelity to breeding sites*

The multistate model was applied to the sightings data. The most general model that was fit was {S(*g*,*t*), p(*g*,*t*), ψ(*g*,*t*)}, allowing variation across states (*g*=M, F, U) and time (*t*) for apparent survival (*S*), recapture probability (*p*) and transition probability (*ψ*). Goodness of fit was tested in the program U-CARE and revealed a moderate lack of fit with a variance adjustment factor, c-hat, of 2.19 ($X^2$=46, df= 21), which was used to adjust AIC$_c$ scores and standard errors (Table 5).

*Table 5. Comparison of fit for multi-state models for estimating between-year site fidelity.*

| *Model* | | | *No. Par.* | *ΔQAIC<sub>c</sub>* | *QAIC<sub>c</sub> Weight* | *Model likelihood* |
|---|---|---|---|---|---|---|
| S(.,.) | p(g,.) | ψ(.,.) | 5 | 0.00 | 0.49 | 1.00 |
| S(g,.) | p(g,.) | ψ(.,.) | 6 | 0.12 | 0.46 | 0.94 |
| S(.,.) | p(.,.) | ψ(.,.) | 3 | 5.13 | 0.04 | 0.08 |
| S(.,.) | p(.,.) | ψ(g,.) | 4 | 7.04 | 0.01 | 0.03 |
| S(g,.) | p(.,.) | ψ(g,.) | 6 | 10.14 | 0.00 | 0.01 |
| S(g,t) | p(g,t) | ψ(g,t) | 24 | 15.20 | 0.00 | 0.00 |

The two top models were within one $AIC_c$ score of each other, and far better than any of the other models. The first top model was {S(.,.), p(*g*,.), ψ(.,.)} which included no variation in survival across time or between states (.,.), variation in recapture probabilities between states but not across time (*g*,.), and no variation in transition probabilities between states (sexes) or across time (.,.), $\Delta QAIC_c$=0.00. The second top model was {S(*g*,.), p(*g*,.), ψ(.,.)} which in contrast to the first top model included variation in survival between states (*g*,.), $\Delta QAIC_c$=0.12. These two models accounted for 0.49 and 0.46 of the $QAIC_c$ weight, respectively. Recapture probabilities from the first model were $p^M$ = 0.97 (±0.05 SE), $p^F$ = 0.98 (±0.01 SE) and $p^U$ = 0.84 (±0.05 SE), and for the second model $p^M$ = 1.00 (±0.00 SE), $p^F$ = 0.98 (±0.02 SE) and $p^U$ = 0.84 (±0.05 SE).

*Comparison of haul-out probabilities obtained from re-sightings data and telemetry*

CJS models were applied to sightings histories of males and females from the 15 June to 15 July in each year (Table 6). The most general model fit was {S(*g*,*t*), p(*g*,*t*)} allowing variation in survival (*S*) and recapture probabilities (*p*) between groups (M, F) and across time (*t*). Goodness of fit for each of the models were tested and the variance adjustment factor (c-hat) used to adjust $AIC_c$ scores and standard errors ($X^2$=205, df=139, c-hat$_{2006}$=1.47; $X^2$ =319, df=122, c-hat$_{2007}$=2.61; $X^2$ =259, df=119, c-hat$_{2008}$=2.18; $X^2$ =308, df=124, c-hat$_{2009}$=2.48; $X^2$ =338, df=136, c-hat$_{2010}$=2.49). The best fitting models were selected based on $AIC_c$ scores.

*Table 6. Comparison of fit for CJS models in estimating within breeding season haul-out probabilities for each year.*

|  | *Model* | *No. Par.* | $\Delta QAIC_c$ | $QAIC_c$ *Weight* | *Model likelihood* |
|---|---|---|---|---|---|
| 2006 | S(g,.) p(g,.) | 6 | 0.00 | 0.70 | 1.00 |
|  | S(.,.) p(g,.) | 4 | 1.78 | 0.29 | 0.41 |
|  | S(g,.) p(.,.) | 4 | 50.14 | 0.00 | 0.00 |
|  | S(.,.) p(.,.) | 2 | 56.56 | 0.00 | 0.00 |
| 2007 | S(g,.) p(g,.) | 6 | 0.00 | 0.81 | 1.00 |
|  | S(.,.) p(g,.) | 4 | 2.85 | 0.19 | 0.24 |
|  | S(g,.) p(.,.) | 4 | 39.93 | 0.00 | 0.00 |
|  | S(.,.) p(.,.) | 2 | 48.81 | 0.00 | 0.00 |
| 2008 | S(.,.) p(g,.) | 4 | 0.00 | 0.87 | 1.00 |
|  | S(g,.) p(g,.) | 6 | 3.83 | 0.13 | 0.15 |
|  | S(g,.) p(.,.) | 4 | 49.68 | 0.00 | 0.00 |
|  | S(.,.) p(.,.) | 2 | 55.99 | 0.00 | 0.00 |
| 2009 | S(g,.) p(g,.) | 6 | 0.00 | 0.50 | 1.00 |
|  | S(.,.) p(g,.) | 4 | 0.03 | 0.50 | 0.98 |
|  | S(g,.) p(.,.) | 4 | 57.55 | 0.00 | 0.00 |
|  | S(.,.) p(.,.) | 2 | 63.23 | 0.00 | 0.00 |
| 2010 | S(.,.) p(g,.) | 4 | 0.00 | 0.54 | 1.00 |
|  | S(g,.) p(g,.) | 6 | 0.28 | 0.46 | 0.87 |
|  | S(g,.) p(.,.) | 4 | 86.76 | 0.00 | 0.00 |
|  | S(.,.) p(.,.) | 2 | 92.31 | 0.00 | 0.00 |

In each year, the two top models were stronger than any of the others, and these consistently supported variation in recapture probabilities (*p*) between sexes (Table 6). The estimates of recapture probability for males and females are summarised and compared with published estimates of haul-out probability from telemetry data for the same period (Table 7; Thompson *et al*. 1997). Haul-out probabilities of females in 2009 and 2010 were similar to telemetry estimates, whereas male haul-out probabilities were consistently much lower (Table 7).

*Table 7. Comparison of haul-out probabilities between 15 June and 15 July estimated in this study using sightings of individual seals and estimates from radio tagged seals (from Thompson et al. 1997).*

| | | Male | | Female | |
|---|---|---|---|---|---|
| | | Estimate | SE | Estimate | SE |
| Telemetry | 1993 | 0.52 | 0.04 | 0.70 | 0.04 |
| Re-sightings | 2006 | 0.22 | 0.03 | 0.47 | 0.02 |
| | 2007 | 0.18 | 0.04 | 0.51 | 0.02 |
| | 2008 | 0.24 | 0.03 | 0.51 | 0.02 |
| | 2009 | 0.29 | 0.04 | 0.67 | 0.02 |
| | 2010 | 0.22 | 0.04 | 0.65 | 0.02 |
| | Mean | 0.23 | 0.04 | 0.56 | 0.02 |

*Monthly haul-out probabilities*

A CJS model was applied to the monthly sighting histories (Table 8). The most general model that was fit was {S(*t*), p(*t*)} allowing variation in survival (*S*) and recapture probabilities (*p*) across time (*t*). The model revealed a moderate lack of fit with a variance adjustment factor of 1.91 ($X^2$=174, df= 91), which was used to correct $AIC_c$ scores and standard errors. According to $AIC_c$, the top model {S(.), p(*t*)}, indicating variation in recapture probabilities (*p*) across time (*t*), was far better than any of the others, accounting for 0.99 of $AIC_c$ weight (Table 8). This model gave strong support for variation in recapture probabilities across months (Fig.7).

*Table 8. Comparison of fit of CJS models for estimating overall monthly haul-out probabilities in 2008 and 2009.*

| *Model* | | *No. Par.* | *$\Delta AIC_c$* | *$AIC_c$ Weight* | *Model likelihood* |
|---|---|---|---|---|---|
| S(.) | p(t) | 22 | 0.00 | 0.99 | 1.00 |
| S(.) | p(.) | 2 | 14.75 | 0.00 | 0.00 |
| S(t) | p(t) | 41 | 30.89 | 0.00 | 0.00 |
| S(t) | p(.) | 22 | 41.25 | 0.00 | 0.00 |

A multistate model was applied to the monthly sighting histories for males, females and individuals of unidentified sex. The most general model was {S(*g*,*t*), p(*g*,*t*), ψ(*g*,*t*)} allowing variation in survival (*S*), recapture probabilities (*p*) and transition probabilities (*ψ*) between states (g=M, F, U) and across time (*t*). The model showed a good fit (c-hat=1.09). The two top models were within one $AIC_c$ score of each other, and far stronger than any of the other models. These were {S(.,.), p(*g*,*t*), ψ(.,*t*)} with $\Delta$QAIC$_c$=0.00, and {S(*g*,.), p(*g*,*t*), ψ(.,*t*)} with $\Delta$QAIC$_c$=0.89. Of the QAIC$_c$ weight these two models accounted for 0.61 and 0.39, respectively. Both of these models indicate variation in recapture probabilities between states (M, F, and U) and across time (*t*) (Table 9).

*Table 9. Comparison of fit of multi-state models for estimating monthly haul-out probabilities of males, females and individuals of unknown sex in 2008 and 2009.*

| *Model* | | | *No. Par.* | *ΔQAIC$_c$* | *QAIC$_c$ Weight* | *Model likelihood* |
|---|---|---|---|---|---|---|
| S(.,.) | p(g,t) | ψ(.,t) | 169 | 0.00 | 0.61 | 1.00 |
| S(g,.) | p(g,t) | ψ(.,t) | 171 | 0.89 | 0.39 | 0.64 |
| S(.,.) | p(.,t) | ψ(.,t) | 127 | 34.88 | 0.00 | 0.00 |
| S(g,.) | p(g,t) | ψ(g,t) | 192 | 56.87 | 0.00 | 0.00 |
| S(.,.) | p(g,.) | ψ(g,t) | 130 | 66.80 | 0.00 | 0.00 |
| S(g,t) | p(g,t) | ψ(g,t) | 252 | 253.87 | 0.00 | 0.00 |

Both males (Fig. 8) and individuals of unknown sex (Fig. 10) showed more variability in their levels of haul-out probabilities within months, compared to females (Fig. 9). Male haul-out probability peaked in May ($p_{2008}$=0.70 ± 0.1 SE; $p_{2009}$=0.52 ± 0.1 SE), after which it dropped to its lowest levels at the onset of the mating season in July ($p_{2008}$=0.18 ± 0.1 SE; $p_{2009}$=0.11 ± 0.1 SE) (Fig. 8). Similarly, haul-out probabilities of individuals of unknown sex were also lowest during July (Fig. 10). Females displayed the highest haul-out probability during June ($p_{2008}$=0.68 ± 0.1 SE; $p_{2009}$=0.85 ± 0.1 SE), the month when all pups are born (Chapter V; Fig. 9).

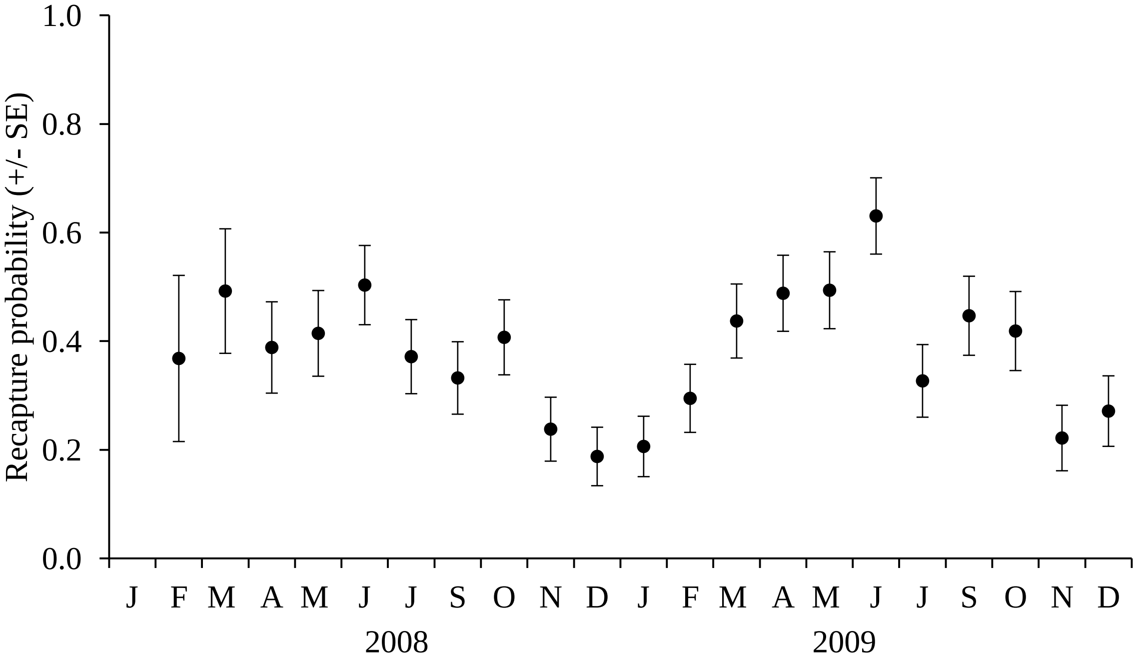

*Figure 7. CJS model output showing overall monthly haul-out probabilities (p) for all individuals in 2008 and 2009.*

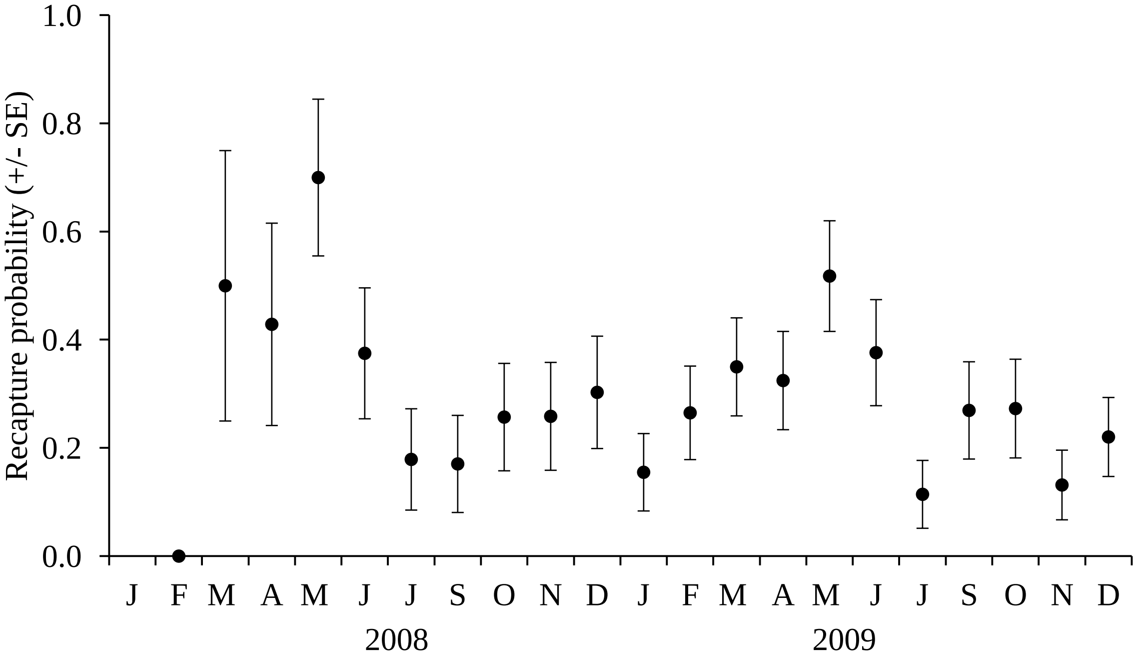

*Figure 8. Multistate model output showing monthly haul-out probabilities (p) for males in 2008 and 2009.*

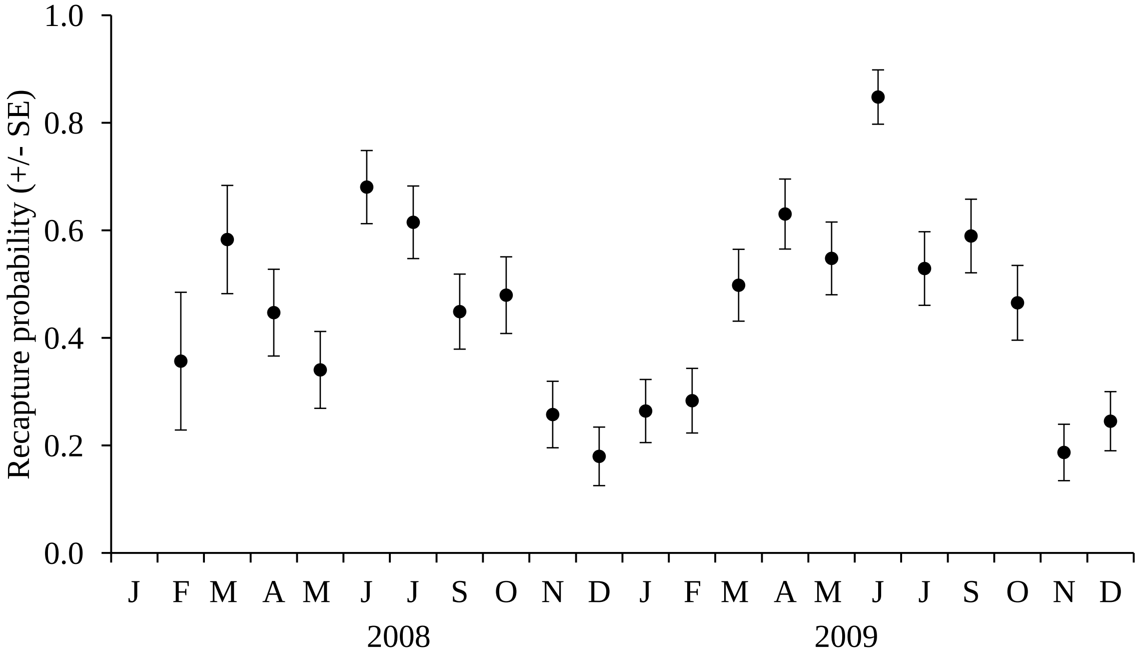

*Figure 9. Multistate model output showing monthly haul-out probabilities (p) for females in 2008 and 2009.*

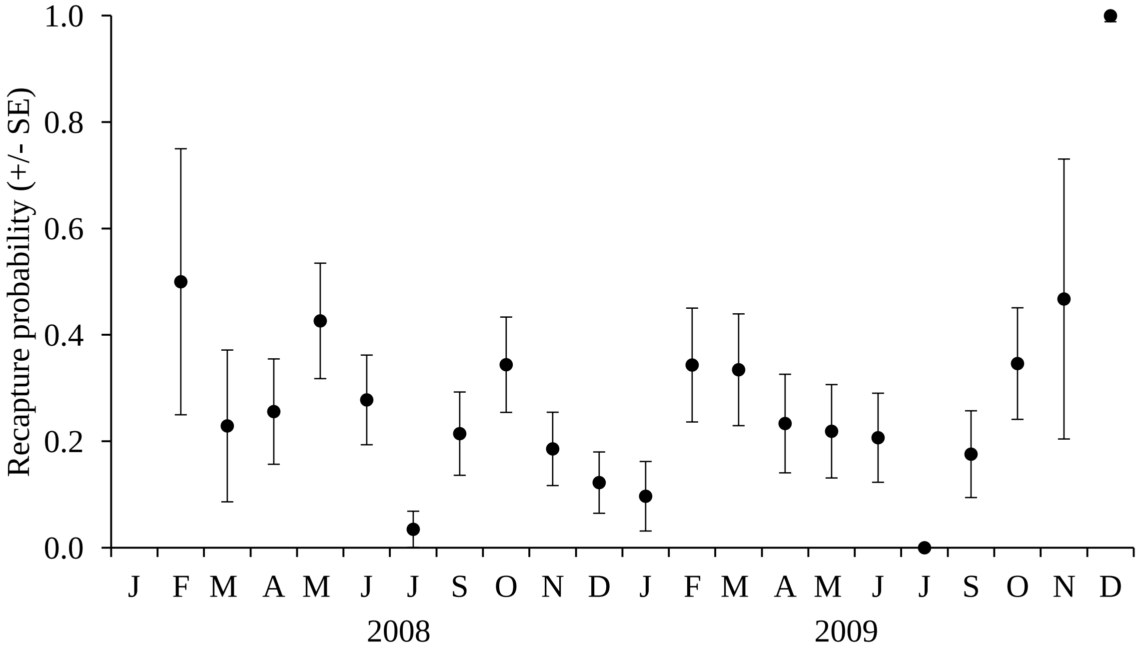

*Figure 10. Multistate model output showing monthly haul-out probabilities (p) for individuals of unknown sex.*

*Comparison of abundance estimates obtained from analysis of re-sightings and count data*

For comparison, twice monthly sightings and count data were used to estimate monthly abundance of adult seals. Abundance estimates from both count data (Fig. 11) and re-sightings data (Fig. 12) peaked during the early breeding season (May-June), although counts of seals showed a less defined pattern. Monthly mark-resight abundance estimates showed defined peaks during May and June in each year, but dropped in July.

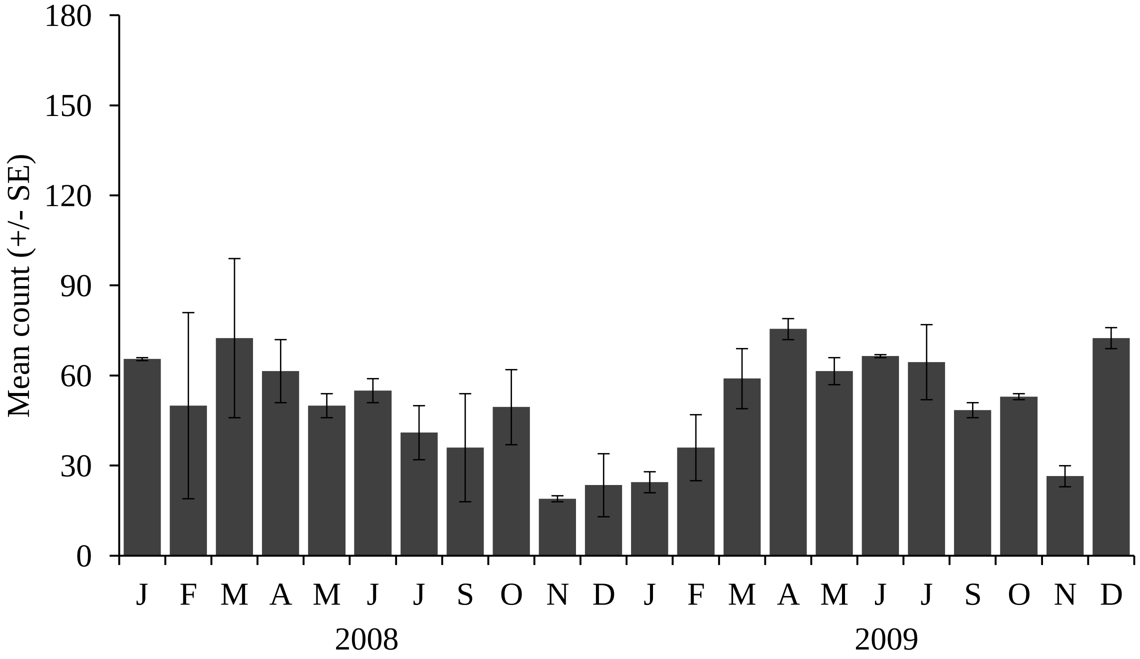

*Figure 11. Twice monthly mean count of harbour seals from land-based surveys.*

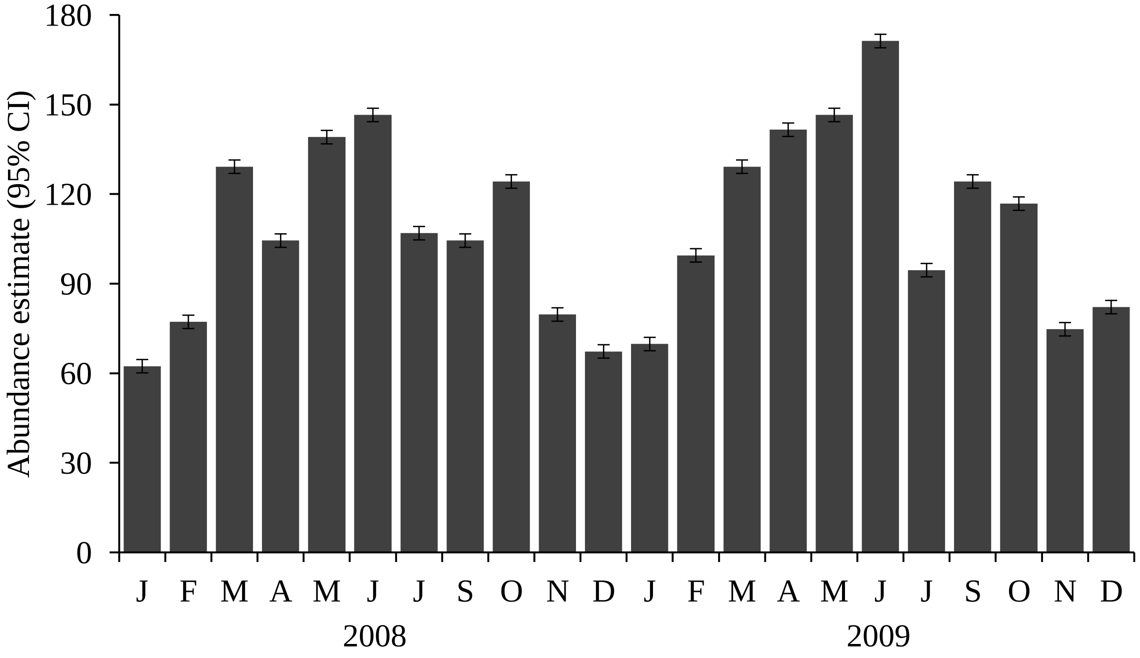

*Figure 12. Monthly abundance estimates from mark-resight model, using sightings data from twice-monthly photo-identification surveys.*

In 2008 and 2009, mean counts of adults between 15 June and 15 July were 61 (±3.3 SE) and 67 (±2.8 SE), respectively. Using equations 1 and 2, abundance from count data was estimated at 100 seals (±23.39 SE) in 2008 and 110 seals (±25.67 SE) in 2009.

For direct comparison, using sightings data from the same days that the count data was obtained, the mark-resight model estimated abundance at 110 seals (±1.71 SE) in 2008 and 117 seals (±1.71 SE) in 2009.

## Discussion

Site fidelity is characteristic of many colonial species, both sedentary and migratory (Blancher & Robertson 1985; Cooch *et al*. 1993; Ganter & Cooke 1998; Pomeroy, Twiss & Redman 2000; Matthiopoulos, Harwood, & Thomas 2005; Gamble, McGarigal & Compton 2007). In the literature this concept is mainly described in relation to between or within-year breeding season site fidelity, whereas less is known about the function and use of these sites at other times of the year. This is less relevant for migratory species that move to wintering grounds. However, many pinnipeds rely on terrestrial sites for resting throughout the year. Here we present the first concurrent estimates of harbour seal site fidelity and haul-out probability across a range of temporal scales.

Between-year breeding site fidelity was extremely high for both males (0.97 ±0.05 SE) and females (0.98 ±0.01 SE). Individual males showed more variation in their site faithfulness than females, which could be a result of some males, particularly younger ones, prospecting for other breeding sites (Dobson 1982; Burg, Trites & Smith 1999; Herremann *et al*. 2009). Individuals of unidentified sex showed lower levels of site fidelity compared to males and females (0.84 ±0.05 SE), but it may be that these individuals are more faithful to other sandbanks within Loch Fleet, or are younger seals that naturally display lower levels of site fidelity (Härkönen & Harding 2001). A previous photo-identification study in the nearby Cromarty Firth revealed lower levels of breeding season site fidelity ($p^F$=0.71, and $p^M$=0.46; Mackey *et al*. 2008). However, these lower estimates were likely to be at least partly due to the difficulty of getting close enough to the seals at these sites (Mackey *et al*. 2008), resulting in a lower probability of detecting individuals that were actually present. A long-term study of branded harbour seals in Swedish waters revealed higher levels of breeding season site fidelity in older versus younger individuals, and similar to this study, higher levels of site fidelity in females compared to males (Härkönen & Harding 2001).

Almost all pinniped species have a synchronised annual breeding cycle and aggregate in large colonies during the breeding season (Payne 1977; Pomeroy, Twiss & Duck 2000). Both genetic and re-sighting studies of these species have shown evidence of site fidelity or philopatry to certain sites or areas (Kretzmann *et al*. 1997; Pomeroy, Twiss & Redman 2000; Fabiani *et al*. 2006; Hoffman, Trathan & Amos 2006; Campbell *et al*.

2008) as well as stronger site fidelity in females compared to males (Allen *et al*. 1995; Burg, Trites & Smith 1999; Hoffman, Trathan & Amos 2006). These studies also indicate that, although a population may appear continuous, sub-structuring and genetic differentiation may still occur, which has implications for the efficacy of management if this has not been identified (Hoffman, Trathan & Amos 2006).

A high percentage of individuals, particularly females, hauled out within the study area throughout most of the year, indicating that it is not uncommon for harbour seals to be year-round residents. Some individuals were only seen during the pupping season, or at other times of the year. This may suggest that some individuals have adopted a different strategy to those who remain residents by making inter-seasonal movements to other haul-out sites. However, there was a difference in effort between pupping season surveys and surveys at other times of the year, which may influence detection probabilities of individuals outside the pupping season.

Male haul-out probability was highest during May, just before the onset of pupping, after which male haul-out probability dropped reaching the lowest level in July (Fig. 8). This pattern is likely to reflect the onset of the mating season when males spend more time in the water near corridors or foraging areas where they are likely to encounter receptive females (Van Parijs *et al*. 1997). Estimates of male haul-out probability obtained from telemetry were much higher (Thompson *et al*. 1997) than those estimated in this study using re-sightings (Table 7). This is likely due to the fact that estimates from telemetry measure the individual likelihood of hauling out, whereas re-sightings in this study are site-specific, not taking into account that males may be hauling out on the far sandbank or using haul-out sites outside the study area. Over the course of the year females exhibited the highest haul-out probability during June, the pupping period (Fig. 9). Haul-out probabilities were lower during July, when females make short foraging trips during late lactation or forage intensively to replenish depleted fat stores post weaning (Bowen, Oftedal & Boness 1992; Boness, Bowen & Oftedal 1994; Thompson *et al*. 1994). Breeding season haul-out probabilities of females estimated from re-sightings increased over the five years, but only in recent years were they similar to those previously obtained from telemetry (Thompson *et al*. 1997). Since older females tend to display higher levels of site fidelity (Härkönen & Harding 2001), this increase in female haul-out probability over the course of the study may indicate that females within this breeding group are ageing, particularly as Loch Fleet is a recently established haul-out and breeding site (Chapter II).

Previously, Thompson *et al*. (1997) suggested that June and July was the optimal timing for count surveys in this region, however, this sampling approach may no longer capture the highest number of animals. The seasonal patterns in male and female haul-out probabilities obtained here suggest that a surveys design covering the early part of the breeding season in May and June would capture the highest number of individuals. Furthermore, this peak in haul-out probabilities during the early part of the breeding season also indicated that elevated breeding season counts may simply be the result of a seasonal change in haul-out probability, rather than an actual increase in the number of individuals using a site. Nevertheless, monthly abundance estimates using re-sightings data still suggested that more individuals use the site during this period (May-June; Fig. 12). Re-sightings abundance estimates showed a consistent and defined seasonal pattern in the number of individuals using the site. Monthly mean counts displayed a similar pattern, although the clarity varied between years (Fig. 11), highlighting the sensitivity and care that should be taken when using sparse count data. Comparison of breeding season abundance estimates from count and re-sightings data revealed similar results.

The tendency to remain faithful to one site may have consequences for genetic structuring, particularly in declining or threatened populations, as this may reduce genetic diversity and individual fitness (Westlake & O'Corry-Crowe 2002). Genetic analyses in European harbour seals revealed six distinctly differentiated units, two of which were located within the UK, namely Scotland-Ireland and the English east coast (Goodman 1998). The structure of the Scottish harbour seal population consists of clusters of subpopulations (Longeran *et al*. 2007) within a metapopulation framework (Swinton *et al*. 1998). Tagging and telemetry studies have revealed that harbour seals generally only make local movements up to 75km, indicating that subpopulations may be relatively discrete (Thompson *et al*. 1996; Thompson *et al*. 1998; Sharples, Mackenzie and Hammond 2009), although on the west coast of Scotland and in the Pacific, seals have shown occasional long distance movements (Brown & Mate 1983; Yochem *et al*. 1987; Cunningham *et al*. 2009b). The high levels of fine-scale site fidelity observed here suggest that within subpopulations, breeding groups may also be relatively discrete. Since pups and juveniles are difficult to identify consistently, I was not able to investigate site fidelity or philopatry in these younger seals, which would have more direct consequences for genetic structuring. However, continued studies of site fidelity and individual histories will provide these opportunities to investigate age-specific differences in site fidelity over time.

Indications of site fidelity from genetic studies suggested that structuring of harbour seal populations occurs at a regional scale of several hundred kilometres (Goodman 1998), and telemetry revealed that approximately 20% of harbour seal pups travelled several hundred kilometres from the site they were born (Thompson, Kovacs &

McConnell 1994). The rapid spread of the phocine distemper virus across the whole of northern Europe in both 1988 and 2002 (Härkönen *et al.* 2006) gave further indiciations of the level of movement of seals. The disease was mainly thought to be transported by juveniles and pups dispersing from natal grounds (Thompson, Kovacs & McConnell 1994), although grey seals where more likely responsible where larger geographical “jumps” occurred (Härkönen *et al*. 2006). This level of regional philopatry and dispersal should be sufficient in preventing genetic differentiation and inbreeding among breeding groups.

Whereas breeding season counts are important for monitoring trends in abundance (Bowen, McMillan & Mohn 2003; Jeffries, Huber & Calambokidis 2003; Baker & Johanos 2004), less is known about the use and function of haul-out sites at other times of the year. Here we have shown that whereas counts and abundance estimates peak during the breeding season, a large proportion of harbour seals remained faithful to haul-out sites throughout the year. Furthermore, the high levels of site fidelity between years indicate that breeding groups may be relatively discrete which could have implications for their viability, growth and genetic fitness, and highlights the need for site-specific management.

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# CHAPTER IV

## AN INDIVIDUAL-BASED STUDY OF HARBOUR SEAL SURVIVAL AND REPRODUCTIVE FITNESS: INSIGHTS INTO THE REGIONAL DECLINE OR AN EXCEPTION TO THE RULE?

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### Introduction

The broad temporal scales at which demographic and ecological processes operate present a key challenge in studies of population dynamics in long-lived species (Clutton-Brock & Sheldon 2010). Long-term research of natural populations has therefore been essential for understanding the ecological factors that drive demographic change in these species (e.g. Clutton-Brock, Albon & Guinness 1987; Cooch *et al*. 1991; Boyd *et al*. 1995; Clutton-Brock *et al*. 1996; Bronikowski *et al*. 2002). Whereas population-level studies are important for monitoring species abundance and distribution, it is individual-based studies that generally offer the greatest insights into the behavioural, physiological and life-history responses of individuals to changes in the environment, which in turn can help understand the drivers of population change (Grimm 1999; Clutton-Brock & Sheldon 2010).

As population rate of change in long-lived species is most sensitive to changes in adult survival (Caswell 1978; Gaillard, Festa-Bianchet & Yoccoz 1998), obtaining accurate measures of this demographic parameter is particularly important for understanding longer-term changes in population dynamics. At the same time, variation in fecundity and costs of reproduction can provide more sensitive indicators of short-term responses to environmental change. High population density or poor weather conditions have been shown to cause lower reproductive rates and increased costs of reproduction (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005; Hadley, Rotella & Garrott 2007). In the past, estimates of these demographic parameters have typically been obtained from the analysis of dead animals that have either been targeted directly for scientific purposes (Bjørge 1992), harvested or culled (Harwood & Prime 1978; Boulva & McLaren 1979; Harwood, Smith & Melling 2000), or collected after disease outbreaks (Härkönen & Heide-Jørgensen 1990; Heide-

Jørgensen & Härkönen 1992). Ethical and conservation considerations now constrain studies of this type (Baker and Palumbi 1994). But even where such data are available, this instantaneous and cross-sectional sampling is unlikely to capture temporal variation in survival and reproductive rates. In contrast, following individuals throughout their lives as they age, reproduce, and adapt within a naturally varying environment, provides a continuous demographic record. Such individual-based studies have proved particularly successful where populations exist in relatively discrete areas and the characteristics of the study area or study population mean that all individuals can be detected regularly with a relatively high probability. Typically these tend to be terrestrial species (Clutton-Brock, Albon & Guinness 1988; Clutton-Brock *et al*. 1996), although some marine species, such as seabirds and pinnipeds which return regularly to terrestrial breeding sites are amenable to study (Dunnet & Ollason 1978; Le Boeuf & Reiter 1988; Boyd *et al*. 1995).

Of the individual-based studies of pinnipeds carried out to date, all have used initial physical capture for tagging or branding as the primary means of following individuals over time. Therefore age and sex-specific survival and age-specific reproductive rates can only be estimated for the marked individuals in the population. Furthermore, tagging studies have to correct for tag loss and sighting probabilities are often low (Croxall & Hiby 1983). Species with natural markings allow sightings and re-sightings to be obtained remotely, and physical capture is therefore not required (Stevick *et al*. 2001). However, as a consequence, particularly in species that do not exhibit pronounced sexual dimorphism, sex is not always known. Incorporating this unknown proportion of the population in sex-specific survival rate estimation has been shown to positively bias survival rates of known-sex individuals (Nichols *et al*. 2004). Furthermore, in some pinnipeds, non-breeders are often not present at breeding sites, and it is therefore assumed that any female not seen during the pupping season is a non-breeder that has temporarily emigrated. This framework may work well for otariids or fasting phocids that have extended nursing periods or remain on land throughout lactation. However, for species with relatively short lactation durations, where mother-pup pairs spend time in the water (Boness, Bowen & Oftedal 1994) and are therefore not always observable, or where non-breeders may be detected at the breeding site during pupping, this may not be the case. Indeed, this situation requires more advanced models to obtain robust estimates of fecundity by incorporating these females as occupying an uncertain breeding state.

Long-term individual-based studies of pinnipeds are biased towards a few species of otariids and larger phocids (Le Boeuf & Reiter 1988; Boyd *et al*. 1995; Pistorius *et al*. 2004; Beauplet *et al*. 2006; Pendleton *et al*. 2006). These are typically species that haul-out in large social groups on land during the breeding season and either fast or have a prolonged lactation period with short foraging bouts out to sea. Less is known about smaller phocids such as harbour seals. The difficulty involved in studying harbour seals is largely due to the nature of their haul-out sites, including inter-tidal sandbanks, skerries, and ice floes, which are often remote, inaccessible or easily disturbed. Information on harbour seal demography has therefore largely been derived from analysis of dead animals (Boulva & McLaren 1979; Härkönen & Heide-Jørgensen 1990; Heide-Jørgensen & Härkönen 1992). Long-term individual-based studies of harbour seal demography have been limited to one study population on Sable Island, Canada. However, the dynamics of this population are quite unique as mothers and pups remain on land throughout lactation and may therefore not be directly comparable with other populations. Also, despite the long-term individual-based work at this colony, no survival or reproductive rates have yet been published. More recently, the Sable Island population suffered dramatic declines constraining the continuation of the study (Bowen *et al*. 2003). Other harbour seal populations around the world are showing varying trends in abundance (see Chapter I; Gilbert *et al*. 2005; Jemison *et al*. 2006; Mathews & Pendleton 2006; Lonergan *et al*. 2007) but the lack of information on temporal and spatial variation in survival and fecundity hinders an understanding of the dynamics of these populations.

The UK harbour seal population has been declining over the past 10-20 years for reasons that are not fully understood (Lonergan *et al*. 2007). The magnitude of the decline suggested either a sustained high level of reproductive failure, increased mortality rates or a combination of the two (Lonergan *et al*. 2007). The long history of conflict between seals and salmon fisheries led to regular shooting of seals and is likely to have played a role in some areas (Thompson *et al*. 2007). In the Moray Firth, for example, the harbour seal population declined by 2-5% per year from 1993 to 2004 (Thompson *et al.* 2007). It was believed that between 66 and 327 harbour seals were culled each year from 1994 to 2002, which would have been sufficient to explain the magnitude of decline in this area. However, uncertainty surrounding the species identity and the exact number of seals that were shot means that other factors, such as changes in food availability and/or quality may have played a contributing role (Thompson *et al*. 2007). In order to balance the conservation of seals and salmon fisheries, the Moray Firth Seal Management Plan was implemented in 2005 (Butler *et al*. 2008). The plan limited the number of harbour seals that could be shot each year to 60, although from 2005 to 2009, this maximum limit was not reached (Butler *et al*. 2008; The Scottish Government, *Unpublished data*).

Here we use a unique site where individual harbour seals could be remotely identified by their pelage patterns to obtain the first individual-based estimates of sex-specific survival and reproductive rates. This study was carried out after shooting had been restricted in the area, and I took this opportunity to model the influence of different estimated levels of culling on population trends. I discuss whether these modelled estimates help gain insights into the long-term decline or whether harbour seals in Loch Fleet may be an exception to the rule.

## Methods

### *Species characteristics*

The harbour seal is a long-lived capital breeder. Females reach sexual maturity between the ages of three to five years after which they generally produce one pup every year during a highly synchronised pupping season. Females nurse their pups on fat rich milk, but are not able to store sufficient energy to sustain the energy demands of the pup, and often make foraging trips during the latter period of lactation (Boness, Bowen & Oftedal 1994). This optimises the pup’s chances of survival and reduces the risk of the female compromising her own future survival and reproductive success. Nevertheless as females can lose around 35% of their body mass during lactation some costs are likely to be involved (Härkönen & Heide-Jørgensen 1990). Adult harbour seals show high levels of site fidelity. However, these have mainly been estimated within year, typically during a single pupping season (see Chapter III; Godsell 1988; Thompson *et al*. 1996; Cunningham *et al*. 2009). Only on rare occasions has this been confirmed between years (see Chapter III; Härkönen & Harding 2001; Mackey *et al*. 2008), and only once throughout the year (see Chapter III).

### *Study site and data collection*

The study was carried out in Loch Fleet National Nature Reserve in the Moray Firth on the north-east coast of Scotland (Chapter II). During low tide several sandbanks are exposed, separated by deep-water channels, two of which are regularly utilised by seals for hauling out. During the pupping season the main sandbank within Loch Fleet is used intensively by harbour seals for resting, giving birth and nursing pups. The proximity of this sandbank to the shoreline observation point (approximately 130m) allowed individual seals to be recognised using photo-identification (Thompson & Wheeler 2008). Photographic-identification survey data were collected over five consecutive years (2006 – 2010). During each pupping season (from the end of May to the end of July) the site was visited daily, resulting in a total of 272 surveys (2006= 57, 2007= 54, 2008= 55, 2009= 54, and 2010= 52). On each day photographs were taken to identify all the seals hauled out on the main sandbank. Typically, seals hauled out soon after the sandbanks were exposed. Surveys were therefore started an hour after low tide to allow seals to settle, and were continued for two to three hours to ensure that photographs were obtained of all individuals using the sandbank. Photographs were taken of the head and neck region using a digital camera and a telescope (Nikon Coolpix 5100 camera, 20-60x80mm Swarowski HD-ATS 80 telescope). These photographs were matched against a catalogue of the best images (left and right side of the head) of all seals photographed during the study. Sex was determined from photographs of genetalia for both males and females, whereas females were also sexed if seen with a pup. Photographs were also used to record whether or not individually identified females were seen with or without a pup on each day. Visual observations of females looking pregnant were recorded, but not used as an indication of her breeding state.

### Mark-recapture analysis

Sightings data were analysed in the program MARK (Gary White, Colorado State University, White & Burnham 1999), using statistical models as described below. Models were built including different scenarios of group (*g*) and/or time (*t*) effects of estimated parameters. Model selection was based on $AIC_c$ scores in agreement with the guidelines for dealing with small sample sizes (Lebreton *et al*. 1992; Bolker *et al*. 2009). Definitions of model parameters are included in Table 1. The goodness of fit of the global models was tested in the program U-CARE and in the case of a lack of fit the c-hat (variance adjustment factor or value of overdispersion parameter) was adjusted in MARK.

*Table 1. Summary of multistate and robust design model parameters (Kendall, Hines & Nichols 2003).*

| | | | |
|---|---|---|---|
| $S_i$ | Survival | - | Probability that an individual in sampling period i survives to period i+1 and remains part of the population |
| $p_i$ | recapture | - | Probability that an individual alive and in the population is sighted in year i |
| $\psi$ | Transition | - | Probability of an individual in a specific state in period i will transition to another specific state in period i+1 |
| $\pi_i$ | pi | - | Proportion released in a specific state |
| $\omega$ | State structure | - | Proportion of the population in the study area in period i that occupy a given state |
| $\delta$ | Delta | - | Probability of correctly classifying a specific state |
| *pent* | | - | Probability of entry to the study area |
| $\Phi$ | Phi | - | Probability of remaining on the study area |

*Estimating sex-specific survival using a multistate model*

Studies of this kind typically use the Cormack-Jolly-Seber models to estimate sex-specific survival (Croxall & Hiby 1983; Pistorius *et al*. 2004; Baker & Thompson 2007). However, when sex is not always known, these simple models can positively bias survival estimates and related parameters of males and females, as known-sex individuals are often seen more frequently (Nichols *et al*. 2004). To reduce bias, we considered a multistate model (Nichols *et al*. 2004) that contains three states: male (M), female (F) and unknown (U). The multistate model yields unbiased and precise results for males and females, but there may be some bias for individuals of unknown sex due to the heterogeneous behaviour of a group containing both males and females (Nichols *et al*. 2004). Until the sex of an individual had been determined, sightings were recorded as "U". Once sex was determined the individual remained in that state (M or F) for every future re-sighting. Sighting histories were constructed for each individual including non-sightings (0). The final data set consisted of sighting histories of 152 individuals. Given the three states, $S^F$, $S^M$ and $S^U$ are the probabilities of an individual surviving from time $t$ to time $t+1$. Similarly, $p^F$, $p^M$ and $p^U$ are the probabilities that an individual is recaptured from time $t$ to time $t+1$. Transitions between states were restricted to occur from U to either M or F ($\psi^{UM}$, $\psi^{UF}$), whereas all other transitions were fixed to zero. To ensure the sum of $\psi$ for each state added up to one, a MLogit(x) link function was applied to transition probabilities.

*Estimating reproductive rate and costs of reproduction on survival using the open robust design multistate model with misclassification*

The nature of harbour seal breeding behaviour means that successful mothers may not always be detected with their pup and therefore misclassified as non-breeders, similar to that demonstrated by a study of manatees (Kendall, Hines & Nichols 2003, Kendall *et al.* 2004). This is due to harbour seals using inter-tidal sites for breeding, meaning that mothers and pups often spend a significant amount of time in the water. This may result in some females only being sighted on a few occasions, apparently without a pup, but it is not known whether they may in fact be suckling a pup on another sandbank. Furthermore, due to their small body size, females also undertake short foraging trips during lactation to sustain the energy demands of the pup, which may result in females being sighted alone upon returning to the haul-out site. Similarly, some pups inevitably die or become separated from their mother soon after birth, in which case the female may not be sighted with the pup within that short period of time. All these scenarios can lead to breeders being misclassified as non-breeders.

Consequently the use of traditional multistate models could cause reproductive rates to be underestimated (Nichols *et al*. 1994) and mask differences in survival between breeders and non-breeders (Kendall *et al*. 2004). To adjust for the probability of misclassifying breeders as non-breeders, estimates of reproductive rate and costs of reproduction on survival were obtained using the robust design multistate model with misclassification (Kendall, Hines & Nichols 2003, Kendall *et al.* 2004). The "open" model was chosen as capture probabilities of females varied with pupping date, whereby females were seen occasionally pre-birth and post-weaning, and more regularly seen during lactation. This also allows for the estimation of both conditional (the probability that a non-breeder at time *t*, breeds at time *t+1*) and unconditional reproductive rates (the proportion of females breeding).

To account for misclassification, multiple secondary occasions (daily surveys) within each primary occasion (year) were used. However, due to the extensive number of secondary occasions (>50 per primary occasion) these were reduced to weekly occasions, resulting in six secondary occasions (week) for each of the five primary occasions (year). Within the primary occasions (year) females could occupy one of two states, breeder (B) if seen with pup on one or more occasions, and non-breeder (N) if seen without a pup on one or more occasions. When a female was seen without a pup but there was uncertainty surrounding whether or not she actually had one, instead of recording the sighting as “N”, a “u” was input instead. This is not an actual state as described in the multistate model, but an unobservable event (Kendall, Hines & Nichols 2003). It was assumed that a pup could not be assigned to the wrong female and there was no restriction on transition probabilities.

The ages of 12 females (estimated from tooth growth rings, Appendix II) and visual observations indicated that not all females were reproductively mature from the start of the study, but recruited into the breeding group over the course of the five years. Reproductive rates were therefore likely to be underestimated for the first years. In 2009 and 2010, all females had given birth to at least one pup, and estimates for these years were therefore thought to give the best representation of reproductive rate.

A sighting history was constructed for each female. This consisted of its non-sightings (0) and sightings with (B) or without a pup (N). Within each primary occasion, females could only occupy one state across all secondary occasions, so if a female was seen with a pup on just one occasion, all other sightings were recorded as “B”. The final data set contained sighting histories of 65 females which had given birth to at least one pup. Sightings of these females are summarised for each year in Table 2.

*Table 2. Summary of the number of observed breeders, non-breeders and apparent non-breeders (“unknowns”) in each year.*

| | *2006* | *2007* | *2008* | *2009* | *2010* |
|---|---|---|---|---|---|
| Breeders | 39 | 39 | 42 | 50 | 50 |
| Non-breeders | 5 | 7 | 6 | 8 | 7 |
| “unknown” | 3 | 2 | 3 | 4 | 4 |

Given the two states, $S^B$ and $S^N$ are the probabilities that a female with or without a pup at time *t* survives to time *t+1*. The conditional reproductive rate ($\psi^{NB}$) is the probability that a female without a pup at time *t*, survives from *t* to *t+1*, will be with a pup at *t+1*. The state structure ($\omega^B$) represents the unconditional reproductive rate or its complement depending on which state is presented first, describing the proportion of females that are breeding. Delta illustrates the probability of correctly classifying breeders and non-breeders.

*Population modelling*

Population viability analysis was run in the program Vortex 9.99 using the demographic parameters estimated in MARK to explore how different levels of culling might influence population trends: 1) no culling, 2) maximum culling levels set by the Moray Firth Seal Management Plan (60 harbour seals shot per year), 3) the most probable average level of culling estimated in Thompson *et al*. 2007 (137 harbour seals shot per year), 4) the average of the maximum level of culling (172 harbour seals shot per year), 5) the maximum estimate of culling in any year (327 harbour seals shot per year).The models were based on an initial population size of 1650 estimated for the Moray Firth (Thompson *et al*. 1997). Vortex reports population growth rate as the exponential growth (r) rather than the arithmetic growth rate (λ). The exponential growth rate indicates the percent increase per year. The mean exponential growth rate over time is equal to the long-term r. The mean growth rate is calculated from the mean population estimate in one year over the population estimate from the previous year.

## Results

In this study 152 individuals were identified, 73 of which were female, 38 were male, and 41 individuals were not sexed. Of the 73 females, 66 were known to have produced at least one pup. Re-sightings of individuals within each pupping season were high averaging 12 sightings per individual per season, ranging from 1 to 42 sightings (Fig. 1).

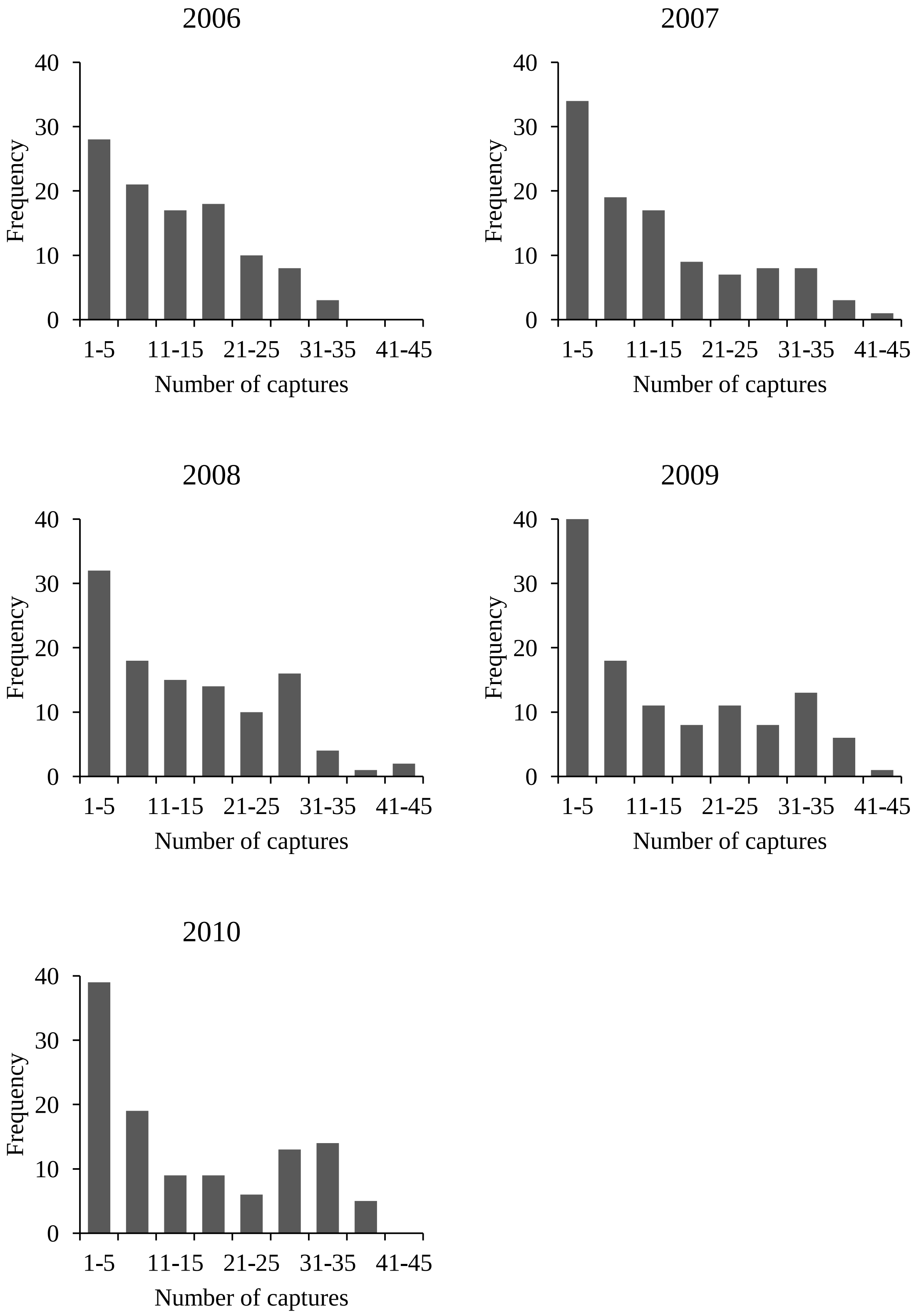

*Figure 1. Sighting frequencies of individuals seen at least once during each pupping season from 2006 to 2010.*

*Estimating sex-specific survival*

The multistate model was applied to the sightings data. The most general model that was fit was {S(*g,t*), p(*g,t*), ψ(*g,t*)}, allowing variation across breeding and non-breeding states (*g*=B or N) and time (*t*) for survival (*S*), recapture rate (*p*) and transition probability (*ψ*). Goodness of fit was evaluated in the program U-CARE and revealed a moderate lack of fit with a variance adjustment factor of 2.19 (Chi-square=46, df= 21). This was used to adjust the $AIC_c$ and standard errors. The best fitting models were selected based on $AIC_c$ scores (Table 3).

*Table 3. Comparison of fit of multi-state models for estimating survival rate (c-hat=2.19).*

| *Model* | | | *No. Par.* | *$\Delta QAIC_c$* | *$QAIC_c$ Weight* | *Model likelihood* |
|---|---|---|---|---|---|---|
| S(.,.) | p(g,.) | ψ(.,.) | 5 | 0.00 | 0.69 | 1.00 |
| S(g,.) | p(g,.) | ψ(.,.) | 7 | 2.19 | 0.23 | 0.34 |
| S(.,.) | p(.,.) | ψ(.,.) | 3 | 5.13 | 0.05 | 0.08 |
| S(.,.) | p(.,.) | ψ(g,.) | 4 | 7.04 | 0.02 | 0.03 |
| S(g,.) | p(.,.) | ψ(g,.) | 6 | 10.14 | 0.00 | 0.01 |
| S(g,t) | p(g,t) | ψ(g,t) | 32 | 33.37 | 0.00 | 0.00 |

The two top models were within two $AIC_c$ scores of each other, and far better than any of the other models. The first model was {S(.,.), p(*g*,.), ψ(.,.)} with $\Delta QAIC_c$=0.00. The model indicated no variation in apparent survival between states (*g*) or across time (*t*), variation in recapture probabilities between states but not across time, and no variation in transition probabilities between states or across time. The second model was {S(*g*,.), p(*g*,.), ψ(.,.)} with $\Delta QAIC_c$=2.19. In contrast to the first model, this indicated variation in apparent survival between states (*g*). Of the $QAIC_c$ weight these two models accounted for 0.69 and 0.23, respectively. Apparent survival probability from the first model was $S^{MFU}$ = 0.95 (±0.02 SE), and for the second model $S^{M}$ = 0.89 (±0.06), $S^{F}$ = 0.97 (±0.02) and $S^{U}$ = 0.95 (±0.02).

*Estimating reproductive rate and costs of reproduction on survival*

The maximum observed inter-birth interval was two years, but most females who had become breeders tended to remain in that state the following year (Fig. 2).

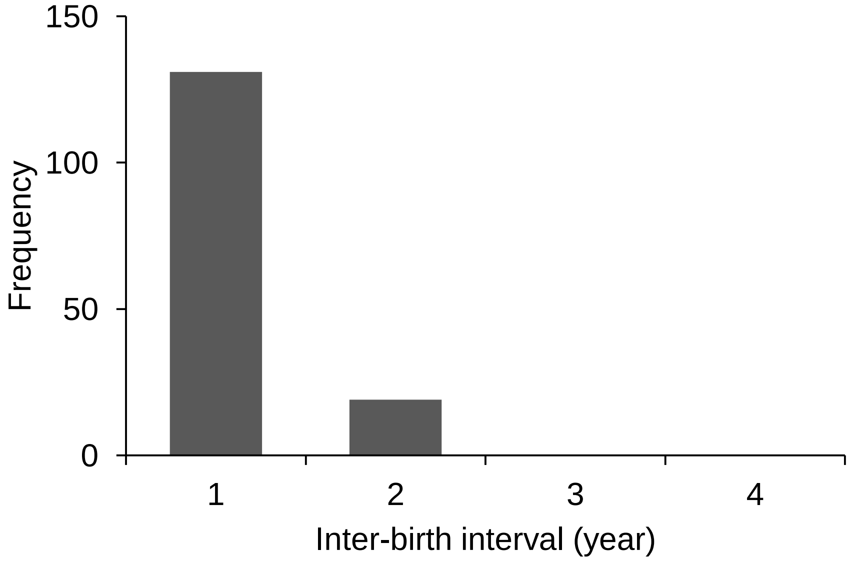

*Figure 2. Frequency of years between observed breeding attempts of all mature females.*

The most general model fitted was {S(*g*,*t*), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), p(*g*,*t*), δ(*g*,*t*), pent(*g*,*t*), Φ(*g*,*t*)}, which indicated state (*g*) and time (*t*) variation across all parameters (Table 4). This model showed good fit with a variance adjustment factor of 0.85 ($X^2$=16.78, df=20). The two top models accounted for most of the AIC$_c$ weight, 0.96 and 0.04, respectively. According to AIC$_c$ scores, the best supported model was {S(*g*,.), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), p(*g*,.), δ(*g*,.), pent(*g*,*t*), Φ(*g*,.)}, which indicates variation in survival between breeders and non-breeders (*g*), as well as state and time variation on conditional (*ψ)* and unconditional (*ω)* reproductive rates. The second best model {S(.,.), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), p(*g*,.), δ(*g*,.), pent(*g*,*t*), Φ(*g*,.)} was within seven AIC$_c$ scores and indicated no variation between states on survival. Although survival probabilities for breeders and non-breeders appeared similar, 0.99 (±0.01 SE) and 0.99 (±0.02), there was more variation in the confidence intervals surrounding survival probability of non-breeders (0.81-0.9995), compared to breeders (0.95-0.996). Conditional ($\psi^{NB}$) and unconditional reproductive rates (*ω*) increased over time. However, this was most likely due to some females being immature in the early years, but recruited into the breeding group over the course of the study. This was consistent with ages obtained from teeth and visual observations of females as juveniles. The inclusion of these immature females as non-breeders, when in fact they were not capable of breeding, would ultimately bias reproductive rates low. By 2009, all females in the sample had given birth to at least one pup. Estimates of reproductive rate in 2009 and 2010 were therefore thought to best represent the true reproductive rate. In 2009, $\psi^{NB}$= 0.94 (±0.06), and in 2010, $\psi^{NB}$= 0.86 (±0.13). Unconditional reproductive rates were $\omega_{09}$=0.87 (±0.04) and $\omega_{10}$=0.89 (±0.04). Since conditional reproductive rate does not include transitions from breeder to breeder, the average unconditional reproductive rate from 2009 and 2010 was used as the reported reproductive rate (0.88). Delta$^N$ was 1 (±0.00) as expected as no non-breeders were misclassified as breeders, whereas delta$^B$ = 0.97 (±0.01), highlighting the misclassification probability of breeders as non-breeders.

*Table 4. Comparison of fit of open robust design multi-state models for estimating reproductive rate.*

| *Model* | *No. Par* | *ΔAIC$_c$* | *AIC$_c$ Weight* | *Model Likelihood* |
|---|---|---|---|---|
| S(g,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) Φ(g,.) | 75 | 0.00 | 0.96 | 1.00 |
| S(.,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) Φ(g,.) | 74 | 6.38 | 0.04 | 0.04 |
| S(.,.) p(g,.) ψ(g,.) π(g,t) ω(g,t) δ(g,.) Φ(g,.) | 68 | 12.51 | 0.00 | 0.00 |
| S(g,.) p(g,.) ψ(g,.) π(g,.) ω(g,.) δ(g,.) Φ(g,.) | 62 | 14.03 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) π(g,t) ω(g,t) δ(g,t) Φ(g,t) | 241 | 212.31 | 0.00 | 0.00 |

### *Population modelling*

The survival and reproductive rates estimated in MARK were included in the population viability model to estimate population trends within the Moray Firth including different levels of culling. Survival and reproductive rates were assumed stable on a regional and temporal scale. Other harbour seal life-history information to be included in the model was obtained from a variety of sources (Table 5).

*Table 5. Summary of life-history parameters (and sources) used for population modelling.*

| ***Parameter*** | ***Values used*** | ***Source*** |
|---|---|---|
| Initial population size | 1650 | Thompson *et al.* 1997 |
| Age at first reproduction ♂ | 5 ♂, 4 ♀ | Härkönen & Heide-Jørgensen 1990 |
| Inter-birth interval | 1-2 years | This study (Fig. 2) |
| Mating system | Polygynous | Boulva & McLaren 1979 |
| Number of broods | 1 | |
| Number of young | 1 | |
| Sex ratio of young | 0.5 | Boulva & McLaren 1979 |
| Reproductive rate | 88% | This study |
| Annual mortality (age 0-1) | 25% ♂; 25% ♀ | Harding *et al*. 2005; Härkönen & Heide-Jørgensen 1990 |
| Annual mortality (age 1-2) | 11% ♂; 9% ♀ | |
| Annual mortality (age 2-3) | 11% ♂; 9% ♀ | |
| Annual mortality (age 3-4) | 11% ♂; 9% ♀ | |
| Annual mortality (age 4-5) | 11% ♂; 3% ♀ | |
| Annual mortality (age 5-6) | 11% ♂; 3% ♀ | |
| Annual mortality adults | 11% ♂; 3% ♀ | This study |
| Maximum age | 25 | Härkönen & Heide-Jørgensen 1990 |

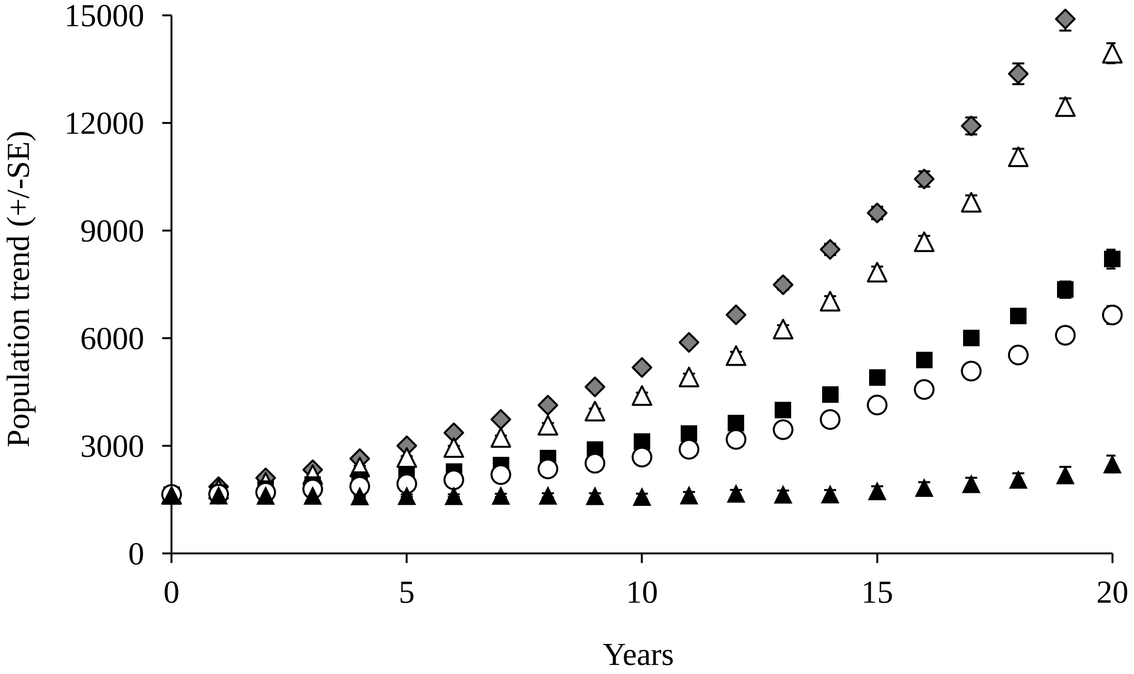

*Figure 3. Predicted population trends using the current survival and reproductive rates without harvesting (grey ♦), with harvesting by the quota set in the Moray Firth Seal Management Plan (60/yr, white ▲), with harvesting at most probable levels (137/yr, black ■), with maximum mean harvesting (172/yr, white ●), and harvesting at the maximum number (327/yr, black ▲).*

Without culling the harbour seal population within the Moray Firth should be growing by ~12% per year (Fig. 3, Table 6). Even under the maximum levels of culling introduced by the Moray Firth Seal Management Plan, the population growth was estimated at ~11% per year (Fig. 3, Table 6). By increasing culling to the most probable average level and average maximum level estimates during the period 1995-2005 the population still increases, by ~8% and ~7% per year respectively (Fig. 3, Table 6). Only when culling levels were increased to the maximum number of seals shot does the population decline, by ~2% per year (Fig. 3, Table 6).

*Table 6. Predicted population growth from population viability analysis.*

| *Scenario* | *Growth rate (r)* | *Standard deviation* |
|---|---|---|
| No harvesting | 0.115 | 0.056 |
| MFSMP harvesting quota (60/yr) | 0.106 | 0.057 |
| Most probable harvesting levels (137/yr) | 0.079 | 0.061 |
| Mean max harvesting levels (172/yr) | 0.068 | 0.064 |
| Maximum number harvested (327/yr) | -0.015 | 0.113 |

## Discussion

Here, I present the first concurrent real-time estimates of apparent survival and reproductive rates obtained from harbour seals within a naturally regulated population. Adult survival rates were high, particularly for females (0.89 ♂; 0.97 ♀). Individuals of unknown sex showed high survival rates (0.95) similar to that of females indicating that a large proportion of these may be sub-adult females that have not bred yet, and therefore not sexed. The disparity in sample sizes of males and females is partly due to the bias in the ability of determining sex. Females would be sexed either from photographs taken of their ventral side or when seen in the presence of their pup. In contrast, males could only be sexed from photographs taken of their ventral side. In addition, studies have shown that harbour seal populations are typically female biased, like many other long-lived polygynous mammals (Bigg 1969; Boulva & McLaren 1979; Clutton-Brock, Major & Guinness 1985; Härkönen & Heide-Jørgensen 1990; Clutton-Brock & Lonergan 1994; Clutton-Brock *et al*. 2002). The recapture rate of individuals of unknown sex was lower than those estimated for males and females, indicating that these are individuals that either typically use other haul-out sites, or are younger animals that naturally show lower levels of site fidelity (Härkönen & Harding 2001).

Estimates of survival and reproductive rates for harbour seals are sparse in the published literature (Table 7). The only comparative sex-specific survival rates have been obtained from analysis of dead animals collected after the northern European phocine distemper virus outbreak in 1988 that resulted in the deaths of c. 23,000 harbour seals (Härkönen & Heide-Jörgensen 1990; Heide- Jörgensen & Härkönen 1992). These survival rates were estimated at 0.91 and 0.95 for males and females respectively, similar to those estimated in this study. However, survival rates were estimated based on a known population growth rate and pregnancy rates obtained from analysis of ovaries. Only one other estimate of survival has been obtained from live harbour seals, also the first ever estimate of survival obtained using photo-identification for any species of pinniped (Mackey *et al*. 2008). This study was carried out in the Cromarty Firth, *c.* 50 km south of Loch Fleet, from 1999 to 2002. The sample of individuals in this study was female biased with 95 females, 10 males, and 57 individuals of unknown sex, creating too much uncertainty to estimate male survival (Mackey *et al*. 2008). Recapture rates were low with just eight females and one male seen in all four years. This was largely due to the relatively long distance between observer and seals, weather limitations and only being able to photograph seals hauled-out in a certain position. Due to the sparse data, a Bayesian approach was implemented to estimate survival, although, with some uncertainty surrounding estimated parameters. When using photo-identification data only, their model estimated adult survival as 0.98, and when incorporating an informative prior distribution from previously published survival estimates survival was estimated as 0.97.

*Table 7. Comparative survival and reproductive rates of harbour seals (n) in the literature.*

| Estimate<br>*Male* | <br>*Female* | Site | Method | Source |
|---|---|---|---|---|
| **Survival** | | | | |
| 0.89 *(38)* | 0.97 *(73)* | Loch Fleet, Scotland | Photo-ID | *This study* |
| -- | 0.97 *(162)* | Cromarty Firth, Scotland | Photo-ID | Mackey *et al*. 2008 |
| 0.91 | 0.95 | Kattegat & Skagerak | Dead seals | Härkönen & Heide-Jørgensen 1990; Heide-Jørgensen & Härkönen 1992 |
| **Reproductive rate** | | | | |
| -- | 0.88 *(66)* | Loch Fleet, Scotland | Photo-ID | *This study* |
| -- | 0.92 | Kattegat & Skagerak | Dead seals | Härkönen & Heide-Jørgensen 1990 |
| -- | 0.95 *(38)* | Eastern Canada | Dead seals | Boulva & McLaren 1979 |
| -- | 0.93 *(58)* | Svalbard, Sweden | Live captures | Lydersen & Kovacs 2005 |
| -- | 0.90 *(81)* | Norway | Dead seals | Bjørge 1992 |

The reproductive rate estimated for females in Loch Fleet (0.88) was only slightly lower than those obtained from analysis of seals harvested in eastern Canada (0.95 for prime-aged females; Boulva & McLaren 1979) as well as those collected after the 1988 epizootic in the Kattegat and Skagerak (0.92; Härkönen & Heide-Jørgensen 1990). These previous estimates were obtained from counting placental scars, corpus luteum and corpus albicans, which develop in the ovaries after ovulation (Boyd 1984). The reliability of counting stained placental scars for estimating reproductive rates has been tested in relatively few species (e.g. Strand, Skogland & Kvam 1995; Elmeros & Hammershøj 2006). Furthermore, as corpus albicans may originate from sources other than corpus luteum of successful pregnancy, reproductive rates estimated using this method are likely to be over rather than underestimated (Boyd 1984). Here, reproductive rate was obtained from re-sightings of females with pups, and might therefore better represent birth rate. Nevertheless, despite the difference in methodology, the use of re-sightings of females with pups provided accurate and robust estimates of reproductive rate. One study in Svalbard estimated reproductive rate from live captures at 0.93 (Lydersen & Kovacs 2005). However, these females were caught during the pupping season, potentially causing bias in the sample as lactating or heavily pregnant females are likely to be easier to catch or may preferably use certain areas.

Long-lived iteroparous mammals and birds are faced with the challenge of balancing energy allocation between current reproduction and future survival, which often varies with phenotype and environmental variation (Albon, Clutton-Brock & Guinness 1987; Clutton-Brock, Albon & Guinness 1987; Gomendio 1990). Under optimal environmental conditions the costs of reproduction on survival are likely to be minimal, particularly for prime-aged females. However, unfavourable environmental conditions (e.g. low food availability, increased density) may incur increased costs, particularly in young females that are still allocating energy into growth, and old senescent females that are more susceptible to resource scarcity (Newcomb, Rodriguez and Johnson 1991; Clutton-Brock *et al*. 1996; Mayor 2004; Tavecchia *et al*. 2005; Penn & Smith 2007; Descamps *et al*. 2009). Studies of costs of reproduction in pinnipeds are limited to Antarctic fur seals (Boyd *et al*. 1995), Weddell seals (Hadley, Rotella & Garrott 2007) and sub-Antarctic fur seals (Beauplet *et al*. 2006). Reproductive females of Antarctic fur seals and Weddell seals suffered lower survival rates and reduced fecundity in the following year (Boyd *et al*. 1995; Hadley, Rotella & Garrott 2007). In Antarctic fur seals between 40-50% of mortality was explained by pregnancy (Boyd *et al*. 1995). The opposite was observed in Sub-Antarctic fur seals where non-breeders had lower survival rates than breeders and showed higher probability of being non-breeders in the following year (Beauplet *et al*. 2006). Females showed consistency in breeding performance over years, indicating that non-breeding tended to occur among lower quality females (Beauplet *et al*. 2006). In this study, breeders and non-breeders showed similar and very high survival rates, although for non-breeders they were more variable. This suggests that there were no costs of reproduction on survival, and that breeding may be an indication of quality (Aubry *et al*. 2011). Poor condition, younger or older senescent females may skip years or abort their pregnancy as a strategy for not compromising future survival and reproductive success.

The decline of harbour seals within the northern region of the Moray Firth may have resulted in an increase in per capita food availability, thereby reducing intra-specific competition. The improved forage conditions could explain the high adult survival rates at Loch Fleet, although estimates of survival were similar at the Cromarty Firth during the decline (Mackey *et al*. 2008), indicating that low pup and juvenile survival rates may have played a significant role. Reproductive rates of ungulates have been shown to decline with increasing population density, and females only conceived at higher body weights, reducing the risk of dying from pregnancy or lactation as well as maximising the probability of survival for their young (Albon, Mitchell & Staines 1983). In our study, reproductive rates were also high, which would be expected due to the currently low population levels. Other factors such as a biased age-structure may also influence reproductive rates. The harbour seal breeding site in Loch Fleet has only recently been established and the number of pups did not begin to increase until the mid 1990s (Chapter II). It is therefore possible that these individuals are biased towards young prime-aged females. The lack of any costs of reproduction on survival could also be explained by improved food availability after a reduction in intra-specific competition. Reproductive rate and reproductive costs on survival may therefore provide more sensitive indicators of environmental conditions (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005; Hadley, Rotella & Garrott 2007).

The survival and reproductive rates obtained in this study provide important information for understanding the current dynamics of harbour seal populations on the north-east coast of Scotland. Given the overlap in foraging areas used by seals at other haul-out sites in the Moray Firth (see Chapter II; Thompson *et al*. 1994; Thompson *et al*. 1996), these parameters are unlikely to vary significantly across the region, unless local factors (e.g. shooting) have caused fine-scale variation in age-structure. However, the changes in shooting pressure and intra-specific competition may have caused temporal variation in survival and reproductive rates over the last few decades. Furthermore, harbour seals co-habit with the larger grey seal and it is possible that inter-specific competition has played a contributing role. However, the recent implementation of a limited quota of seals which can be shot should have reduced mortality (Butler *et al*. 2008). The levels of harvesting proposed in the Moray Firth Seal Management Plan (Butler *et al*. 2008) did not appear to drastically affect population growth. Neither did the estimated most probable levels of shooting from Thompson *et al*. 2007, apart from delaying the time in which carrying capacity was reached. Only when culling levels were increased to the maximum number estimated to have been shot in a single year did the population decline. This indicates that if estimated mean harvesting levels are correct, then other processes, such as variation in ecosystem conditions, must have contributed to the decline.

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# CHAPTER V

## TIMING MATTERS: THE INFLUENCE OF BREEDING PHENOLOGY ON LACTATION PERFORMANCE AND OFFSPRING SURVIVAL

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### Introduction

In temperate regions, many long-lived mammals and birds have adapted their timing of breeding to occur when conditions are most favourable for rearing offspring. However, climate change and environmental variation can cause shifts in the timing of seasonal peaks in resources resulting in a potential mismatch with the birth of young (Visser & Both 2005; Post & Forchammer 2008). A number of species of birds, amphibians and mammals have shown the ability to plastically adjust their timing of breeding in anticipation of such temporal shifts in resources (Forchhammer, Post & Stenseth 1998; Réale *et al*. 2003; Frederiksen *et al*. 2004a; Møller, Flensted-Jensen & Mardal 2006; Love *et al*. 2010;), whereas others, often mammals, face potential energetic constraints and lower offspring survival (Post & Forchammer 2008). Similarly, variation in food availability or population density can lead to a shift in the timing of breeding. For example, a number of studies have shown that the timing of breeding was delayed during years of limited food availability or high population density (Clutton-Brock, Albon & Guinness 1988 (*deer*); Sydeman *et al.* 1991; Lunn, Boyd & Croxall 1994; Boyd 1996 (*pinnipeds*); Ratcliffe, Furness & Hamer 1998 (*seabird*)). The effects of these energetic responses are likely to vary between species, depending on factors such as metabolic demands, foraging costs, as well as the ability to switch diet (Furness & Tasker 2000). In addition, age-specific culling or disease mortality can cause changes in population age-structure which may also influence breeding phenology because older or more experienced females typically give birth earlier than younger females (Lunn, Boyd & Croxall 1994; Loe *et al*. 2005). Whereas shifts in breeding phenology have been well documented, less is known about their long-term consequences on population dynamics, particularly when these are caused by environmental variation or climate change (Walther *et al*. 2002; Parmesan & Yohe 2003; Edwards & Richardson 2004).

The North Sea is a temperate region currently under significant pressure from both climate change and anthropogenic impacts (Furness 2002; Edwards & Richardson 2004; Perry *et al*. 2005). Warming sea temperatures over the last few decades have resulted in a mismatch in the timing of different spring planktonic cycles upon which successive trophic levels depend (Edwards & Richardson 2004; Perry *et al*. 2005), as well as a change in the distribution, abundance and condition of demersal fish (Beaugrand *et al*. 2003; Perry *et al*. 2005). Furthermore, intensive fisheries have altered the abundance and structure of fish populations as a result of fishing down the food web (Heath 2005). However, the dynamics of plankton species and demersal fishes are often costly or difficult to monitor due to their inconspicuous nature. In contrast, some marine top predators, such as seabirds and pinnipeds rely on terrestrial sites for breeding, and during this period critical aspects of their life history can be monitored. Consequently, these species are often considered to be useful indicators of environmental conditions as their physiological and behavioural responses are likely to reflect the dynamics at lower trophic levels (Boyd, Wanless & Camphuysen 2006; Wanless *et al*. 2007). To date, most phenological studies of marine top predators in the North Sea have focused on seabirds (Frederiksen *et al*. 2004a; Frederiksen *et al*. 2004b; Wanless *et al*. 2007). However, Reijnders, Brasseur & Meesters (2010) recently suggested that harbour seals in the southern North Sea have significantly advanced their timing of pupping over the last 35 years due to an improved forage base. This study lacked direct measures of the timing of pupping, but instead used the date on which the maximum number of pups was counted as a proxy for annual variation in the timing of births. Further work is therefore needed to test whether the maximum pup count does provide a robust proxy of the timing of births. Regardless, individual-based studies are required to explore whether observed phenological changes are due to individual responses to changes in resource availability or whether they result from other factors such as a change in population age-structure. The suggestion that harbour seal foraging conditions in the southern North Sea have improved is of particular interest given that several other key harbour seal populations in the North Sea have suffered long-term declines (Lonergan *et al*. 2007). The causes of these declines are still poorly understood, but it has been argued that their widespread nature suggests that the key drivers involve large scale environmental processes (Lonergan *et al*. 2007).

Whereas the distribution and abundance of harbour seals in the UK is well studied, an understanding of individual-level responses to environmental variation is required to gain insights into their population dynamics. Studies of phenological variation can clearly contribute to this understanding, but obtaining direct estimates of the timing of pupping in harbour seals is extremely challenging as females do not remain ashore throughout the breeding season. Here we use a rare opportunity to study variation in breeding phenology and lactation performance of individual female harbour seals across multiple breeding seasons. First, we test the key assumption underlying Reijnders, Brasseur & Meesters's (2010) study by assessing whether there is a relationship between the timing of pupping and the timing of maximum pup counts. We then describe inter-annual variation in the timing of pupping and investigate the consequences of birth date on lactation duration and offspring survival.

## Methods

### *Species characteristics*

Harbour seals depend on terrestrial haul-out sites, typically inter-tidal sandbanks and skerries, for resting (da Silva & Terhune 1988), giving birth and nursing pups (Thompson 1989). Female harbour seals mature at an age between three and five years old (Ellis *et al*. 2000; Bowen *et al*. 2001a; Bowen *et al.* 2003), after which they generally produce one pup each year. Female harbour seals nurse their pup for a relatively short period of time (15-30 days; Muelbert & Bowen 1993) and due to their small body size often make intermittent foraging trips during the latter part of lactation to sustain the energy demands of the pup (Boness, Bowen & Oftedal 1994). Weaning is abrupt and females mate shortly thereafter (Thompson 1988; Thompson *et al.* 1994). Delayed implantation ensures a highly synchronised pupping season, whereby the fertilised egg enters diapause before implanting in the uterus (Lindenfors, Dalén & Angerbjörn 2003). Changes in photo-period initiate the timing of the blatocyst implantation, and this is therefore assumed to take place at more or less the same time in all females (Mead 1989; Temte 1993).

### *Data collection*

The study was carried out in the Loch Fleet National Nature Reserve in the Moray Firth, NE Scotland (see Chapter II & III). The proximity of the observation point to the main sandbank used by harbour seals allowed individual animals to be recognised using photo-identification (Thompson & Wheeler 2008). Data were collected daily during the pupping season (late May to late July) from 2006 to 2010. Photographs were taken to identify all the seals hauled out on the main sandbank. Typically, seals hauled out soon after the sandbanks were exposed at low tide. Surveys were therefore started an hour after low tide to allow seals to settle, and were continued for two to three hours to ensure that photographs were obtained of all individuals using the sandbank. Photographs were taken of the head and neck region using a digital camera and a telescope (Nikon Coolpix 5100 camera, 20-60x80mm Swarowski HD-ATS 80 telescope). These photographs were matched against a catalogue of the best images (left and right side of the head) of all seals photographed during the study. Photographs were also used to record whether or not individually identified females were seen with or without a pup. On each day, repeated counts of pups present on all sandbanks within the study area were carried out throughout low tide depending on the level of movement and activity (between one and five times).

### *Estimation of the timing of pupping and lactation duration*

Daily sightings and re-sightings of individual seals were recorded in a capture history matrix (Appendix III), which included information on the status of individual females (whether she was seen or not seen and, if seen, whether or not she was with a pup). From this capture history, the pupping date and lactation duration for each female were determined using the method described in Thompson and Wheeler (2008). In short, pupping dates were calculated as the midpoint between the day that the female was last seen alone and the day that she was first seen with pup. If this period was ≤ 3 days the pupping dates was defined as accurate, if the period was longer than three days the pupping date was not included in subsequent analyses. All pupping dates were converted to day of the year (Julian day).

Reproductive investment of female phocid seals may be measured in several different ways including the length of time the pup spends suckling (Bowen *et al*. 2001b), pup growth rates (Bowen, Oftedal & Boness 1992) and variation in milk quality (Lang, Iverson & Bowen 2005). However, it is challenging at most sites to acquire even the simplest measure of reproductive investment in harbour seals as females and pups spend a significant amount of time in the water. I was able to follow recognisable individuals throughout the pupping season which provided the opportunity to use lactation duration as a measure of female investment. Lactation duration was defined as the number of days from the day the pup was born to the day the mother-pup pair was last seen together, after which females typically leave the breeding site for several days to go on long foraging trips (Thompson *et al*. 1994). Lactation durations were therefore only estimated for females with accurate pupping dates. To ensure lactation durations were representative of weaned pups, and not simply movement of mother-pup pairs to other sandbanks, I only used lactation durations where the females were also seen alone shortly after (<10 days) being last seen with their pup.

*The consequences of variation in lactation duration on pup survival*

The potential consequences of variation in lactation duration on pup survival were estimated using data from other studies on pup growth during lactation (Bowen *et al*. 2003) and the relationship between weaning mass and first year survival (Harding *et al*. 2005). First, I used information on average pup birth weight (11kg) and rate of mass gain in pups during lactation (0.6kg/day) obtained from studies on Sable Island, eastern Canada (Bowen *et al*. 2003), to estimate the difference in weaning weight for pups with different lactation durations:

$$pup\ weight = birth\ weight + (lactation\ duration\ \times rate\ of\ mass\ gain)$$

The estimated weights of pups with different lactation durations were then used to compare differences in survival rates using the following equation from Harding *et al*. (2005):

$$S_1^{(j)} = \frac{\exp\left(\alpha + \beta w_j\right)}{1 + \exp\left(\alpha + \beta w_j\right)}$$

where $w$ is the mass of individual j, and $\alpha$ and $\beta$ describe the slope and intercept.

### Statistical analysis

All analyses were carried out in R 2.11.1 (R Development Core Team, 2010). To allow for correlation between observations as a result of repeated sampling of the same individual females, generalised linear mixed modelling with a Poisson distribution was used to analyse the relationship between pupping dates and lactation durations of individual females using the `nlme4` package. Due to potential variation in the timing of pupping between years, pupping dates were centred on the annual median (relative pupping dates). This also allowed for a more meaningful model intercept as pupping dates in Julian day were located far from zero. Despite centring pupping dates, the relationship between pupping dates and year was still confounding, and year was therefore included as a random effect. To account for variation associated with repetitive measures of the same individuals, individual ID was also included as a random effect. To correct for small sample size (97 observations from 35 individual females), $AIC_c$ scores were used to compare models (Bolker *et al.* 2009). The initial model is given below.

$$Lactation\ duration \sim Relative\ pupping\ date + (1|fYear) + (1|fID)$$

**Results**

The frequency distribution of pupping dates was approximately normal but with a slight left tail of premature pups which did not survive (Fig. 1). The overall median pupping date was Julian day 166 (15 June).

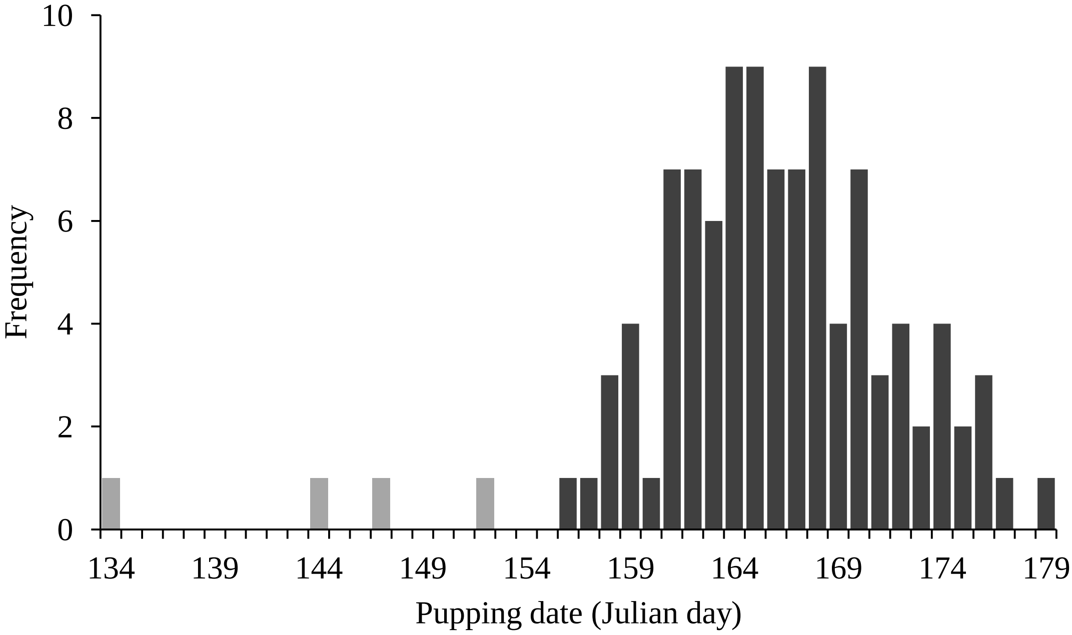

*Figure 1. Frequency histogram of pupping dates (n=166; light grey bars indicate premature pups).*

The frequency distribution of lactation durations revealed large spread, and suggested two separate biological groupings of lactation durations (Fig. 2). The first group of short lactation durations (n=11) represent pups that were either born prematurely (commonly seen with lanugo cover – the white coat shed prior to birth; see Bowen *et al.* 1994; Ellis *et al.* 2000) and died at birth or shortly after, or pups that were separated from their mother shortly after birth, when females were typically seen searching for their pup for several days without finding them. The larger group with longer lactation durations (n=86) represents naturally weaned pups. The overall mean lactation duration for naturally weaned pups was 23 days.

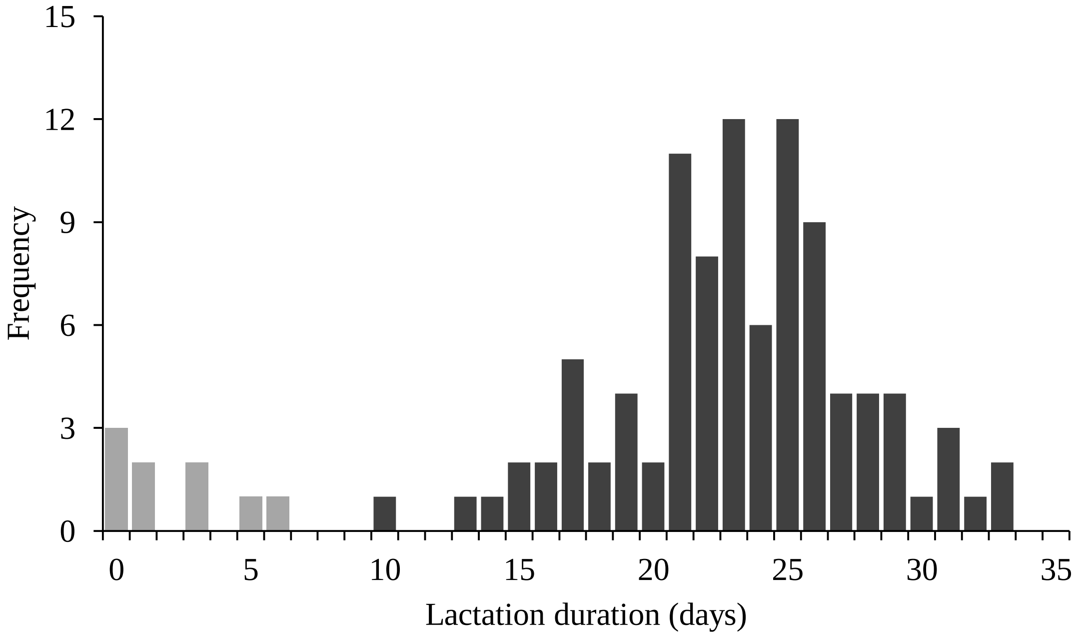

*Figure 2. Frequency histogram of lactation durations (n=97; light grey bars indicate premature pups, pups that died or were separated from the mother at or soon after birth).*

Over the five years of this study, 66 females were recorded to have given birth at least once, and 58 of these females had at least one accurate pupping date. This resulted in a total of 166 pupping dates and 97 lactation durations (Table 1). Of these, 97 pupping dates and lactation durations from 35 females were paired, i.e. obtained from the same female in the same year.

*Table 1. The number of females with between one and five pupping dates (n=58 females) and lactation durations (n=35 females).*

| | **Number of years studied** | | | | |
|---|---|---|---|---|---|
| | One | Two | Three | Four | Five |
| Pupping dates | 14 | 13 | 10 | 9 | 12 |
| Lactation durations | 6 | 12 | 5 | 8 | 4 |

In each year the detailed history of pupping dates was summarised as a pupping curve including the daily maximum pup counts for comparison (Fig. 3; Appendix IV). Towards the end of lactation daily max pup count became more variable, probably due to pups spending more time in the water.

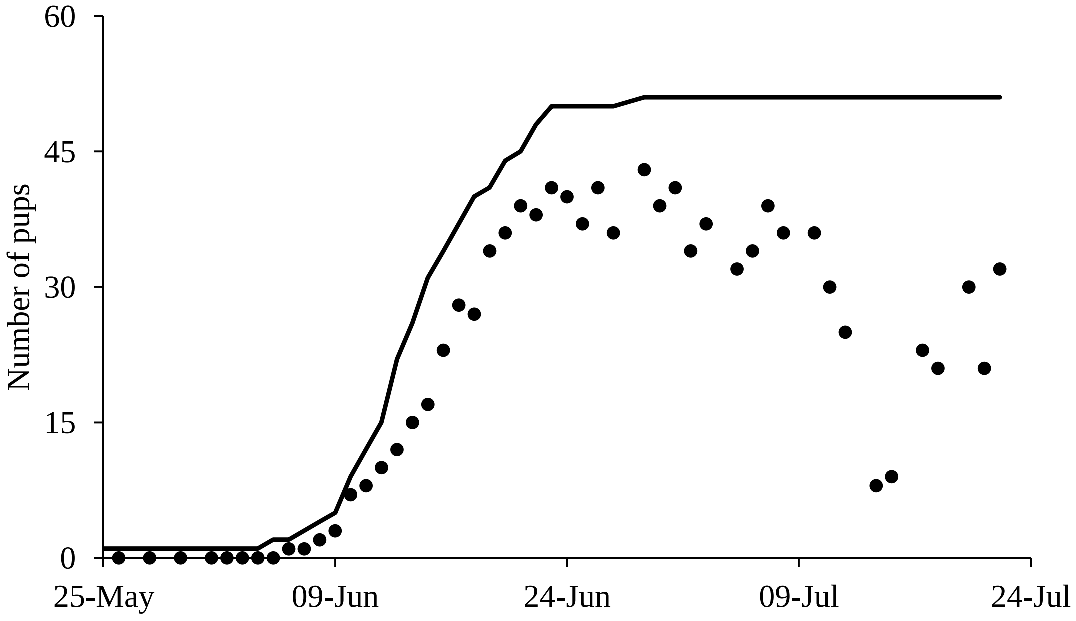

*Figure 3. Pupping curve from 2010 showing cumulative number of pups born (—) and max pup count on each day (●).*

The percentages of the cumulative number of pups born in each year were used to plot pupping curves, portraying relative differences in the timing of pupping between years (Fig. 4).

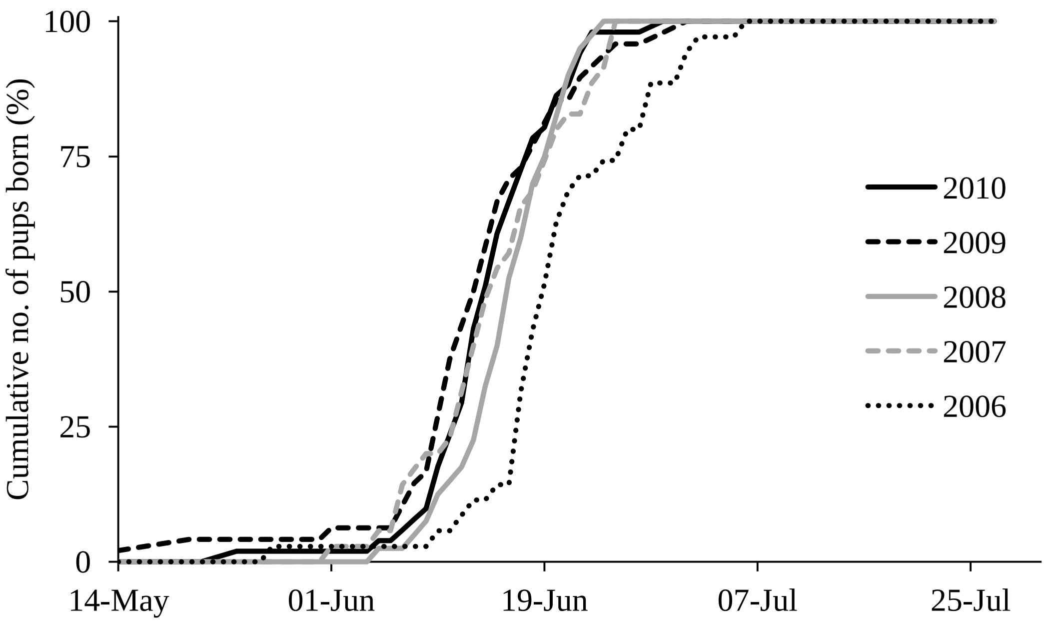

*Figure 4. Cumulative pupping curves signifying the timing of pupping in each year.*

To test the use of ‘day of first pup’, ‘day of max pup count’ and ‘day of 50% max pup count’ as proxies for the actual timing of pupping (Table 2), a Spearman rank order correlation was calculated. The date of first pup was defined as the date of the first pup born in June, as pups born prior to this date were classified as premature. There was a strong positive and significant association between median pupping date and the day of first offspring (Fig. 5; Spearman rank order, $r_s$=0.92, S=1.58, p=0.03).

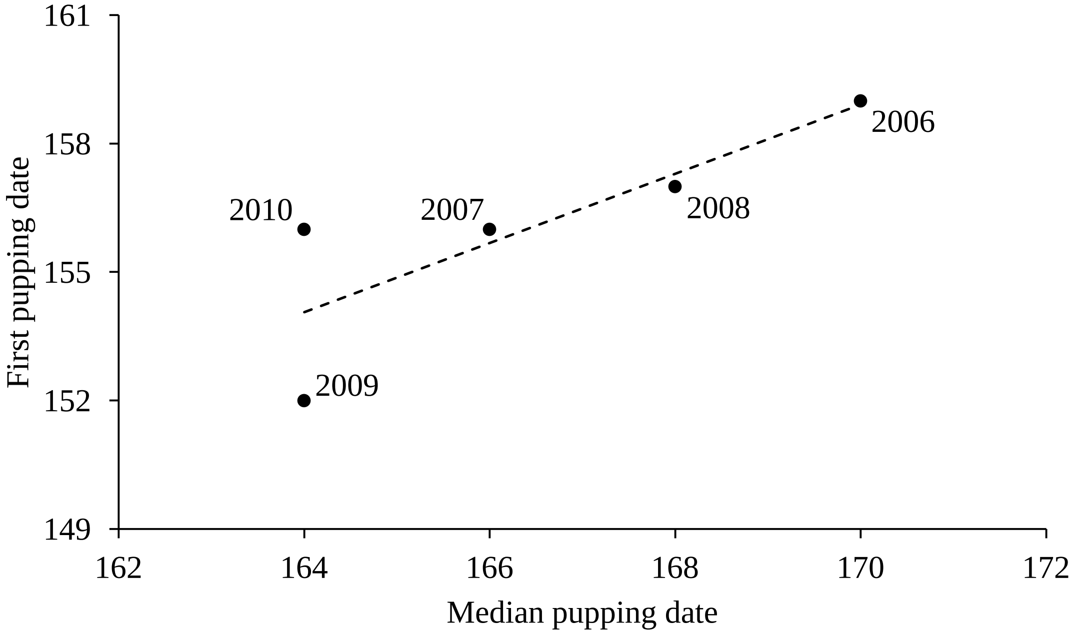

*Figure 5. The relationship between the date of first offspring and the median pupping date.*

In contrast, the correlation between median pupping date and day of max pup count revealed a weak negative association which was not significant (Fig. 6; Spearman rank order, $r_s$=-0.24, S=24.74, p=0.7).

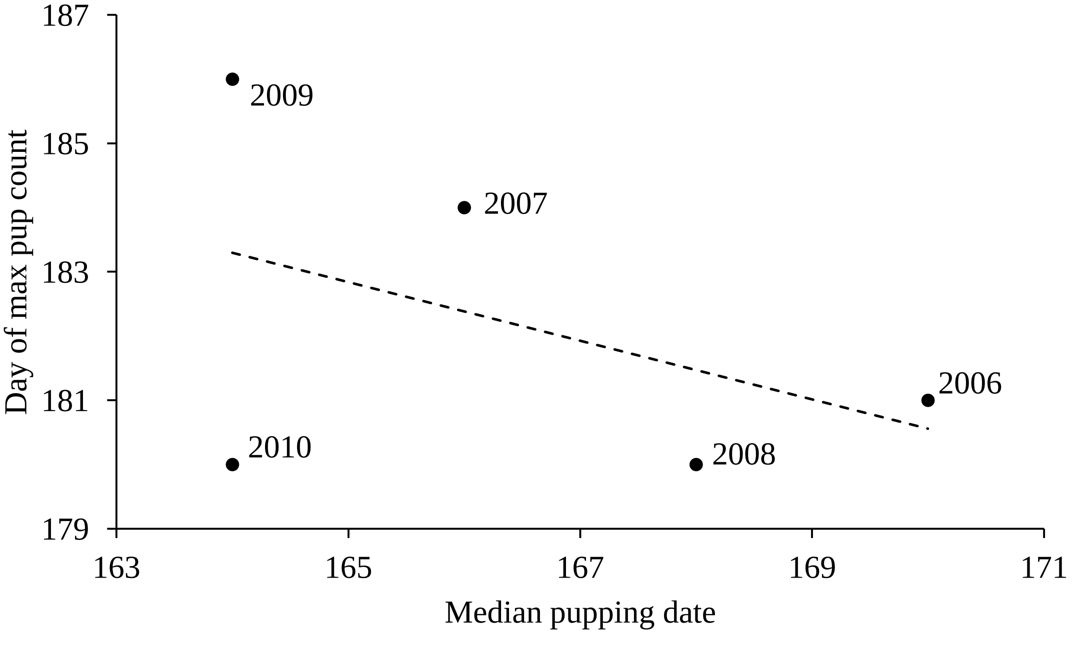

*Figure 6. The relationship between the timing of max pup count and median pupping date.*

There was a positive, although not significant, association between median pupping date and day of 50% max pup count (Fig. 7; Spearman rank order, $r_s$=0.68, S=6.32, p=0.20).

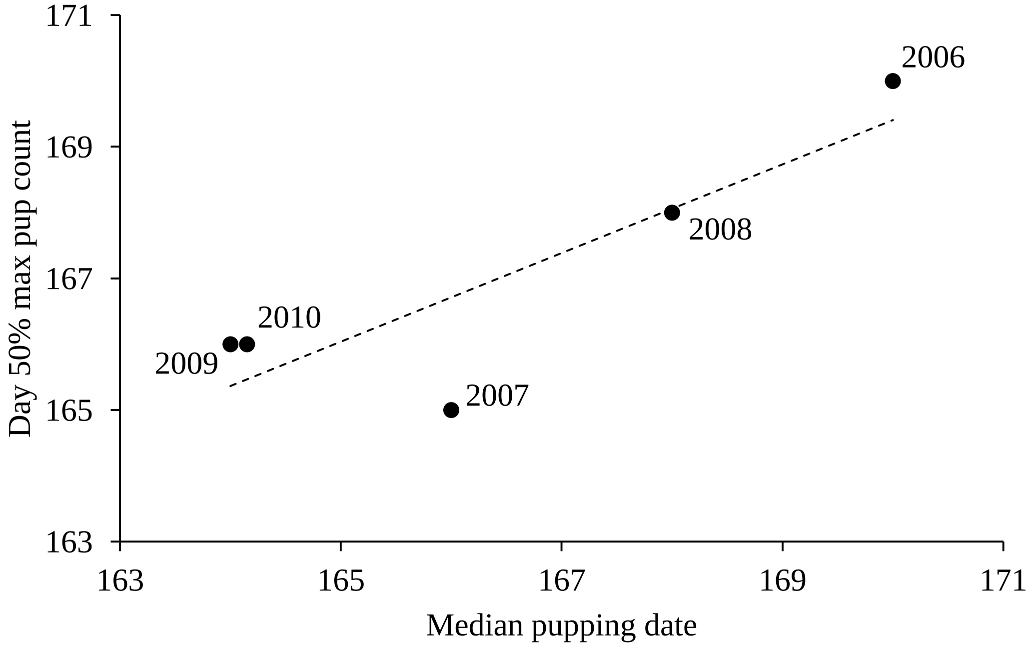

*Figure 7. The relationship between the timing of 50% max pup count and median pupping date.*

The annual median timing of pupping ranged between 13 June and 19 June. The number of pups born in each year increased over the course of the study, and the majority of pups (90%) were typically born within a two week period (Table 2).

*Table 2. Summary data for each year on the number of pups born, number of premature pups in brackets, as well as the median, first and last pupping date, the period in which 90% of pups were born, and the Julian day of max pup count and day of 50% of max pup count. (*2008 was a leap year).*

| Year | Number of pups | Median | First – last birth date | 90% | Day max pup count | Day 50% max pup count |
|---|---|---|---|---|---|---|
| 2006 | 34 *(1)* | 170 (19 June) | 159 – 179 | 17 | 181 | 170 |
| 2007 | 37 *(0)* | 166 (15 June) | 156 – 177 | 17 | 184 | 165 |
| 2008 | 41 *(1)* | 168 (16* June) | 157 – 176 | 13 | 180 | 168 |
| 2009 | 49 *(3)* | 164 (13 June) | 152 – 175 | 15 | 186 | 166 |
| 2010 | 51 *(1)* | 164 (13 June) | 156 - 174 | 13 | 180 | 166 |

Individual females were generally consistent in their relative timing of pupping within the pupping season (Fig. 8). The mean range between relative pupping dates for individual females was seven days, with a minimum range of two days (across four years) and a maximum range of 20 days (across four years).

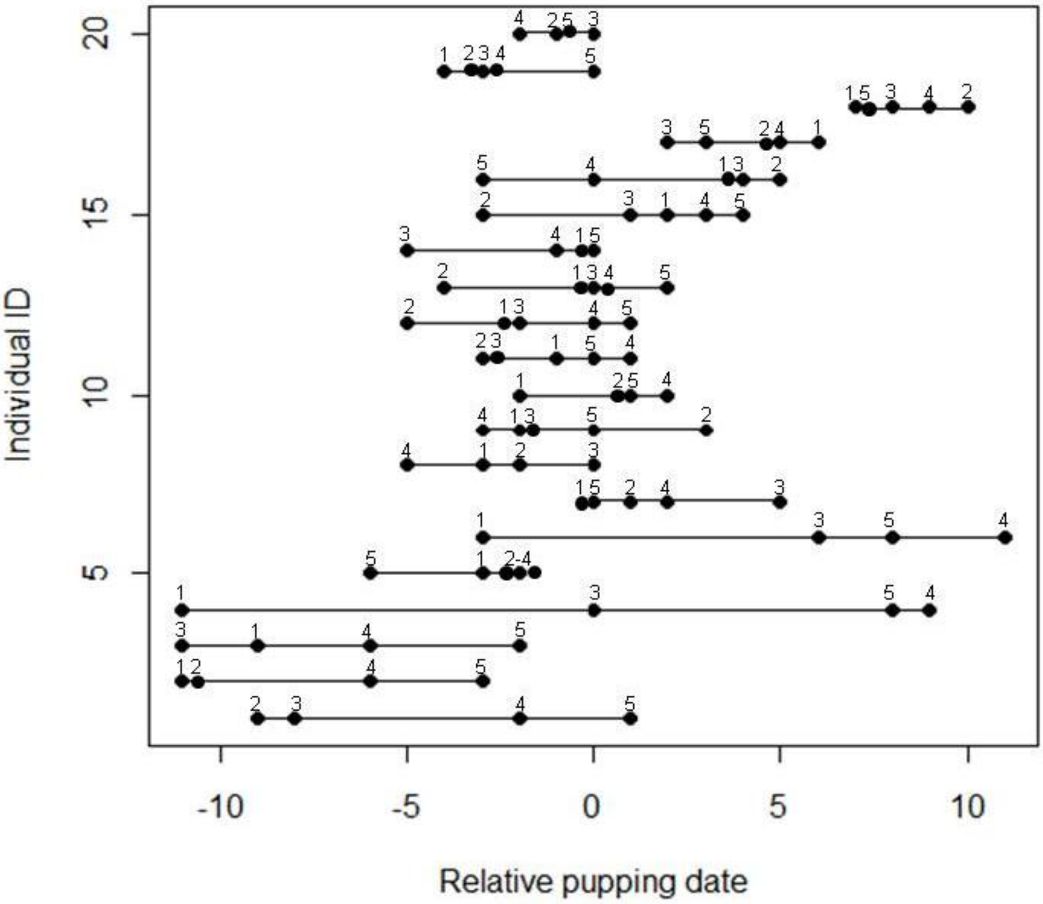

*Figure 8. The consistency of relative pupping dates for individual females (n=20) with ≥ 4 pupping dates (2006=1, 2007=2, 2008=3, 2009=4, 2010=5).*

There were significant differences in the median timing of pupping between years (Kruskall-Wallis (for medians), df=4, Chi-squared = 16.706, $p<0.005$). Post hoc analysis with a Tukey's honest significant difference test showed that the timing of pupping in 2006 was significantly different to both 2009 and 2010, indicating that seals pupped significantly earlier in recent years (Fig. 9).

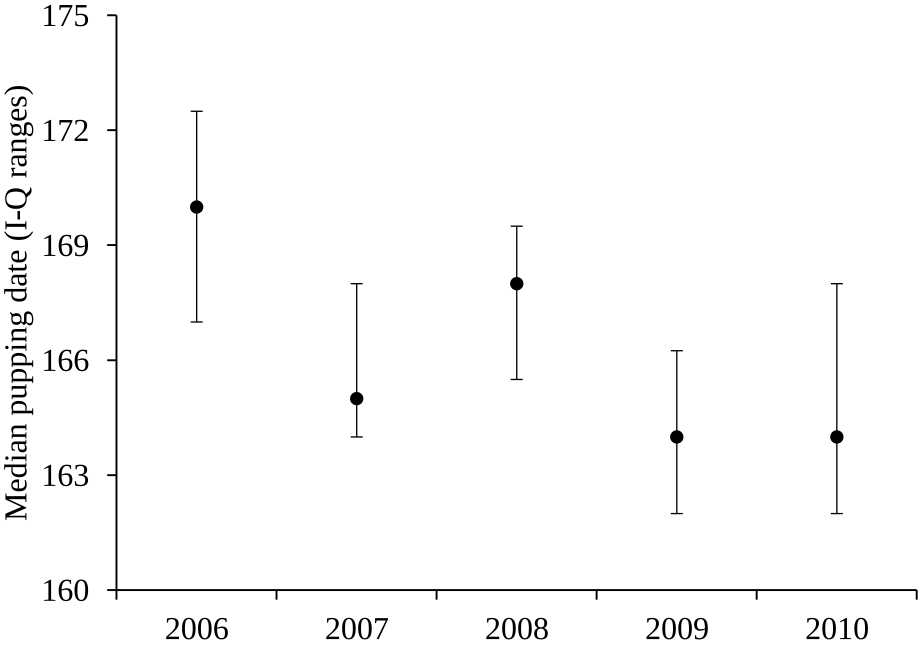

*Figure 9. Annual median pupping dates (Julian day) with inter-quartile ranges.*

There were significant differences in mean lactation durations between years (one-way ANOVA (for means), df=4, F=2.811, $p<0.05$). This was due to differences in mean lactation duration between 2010 and 2006 (Tukey's honest significance difference test), indicating that seals are lactating significantly longer in recent years compared with the beginning of the study (Fig. 10).

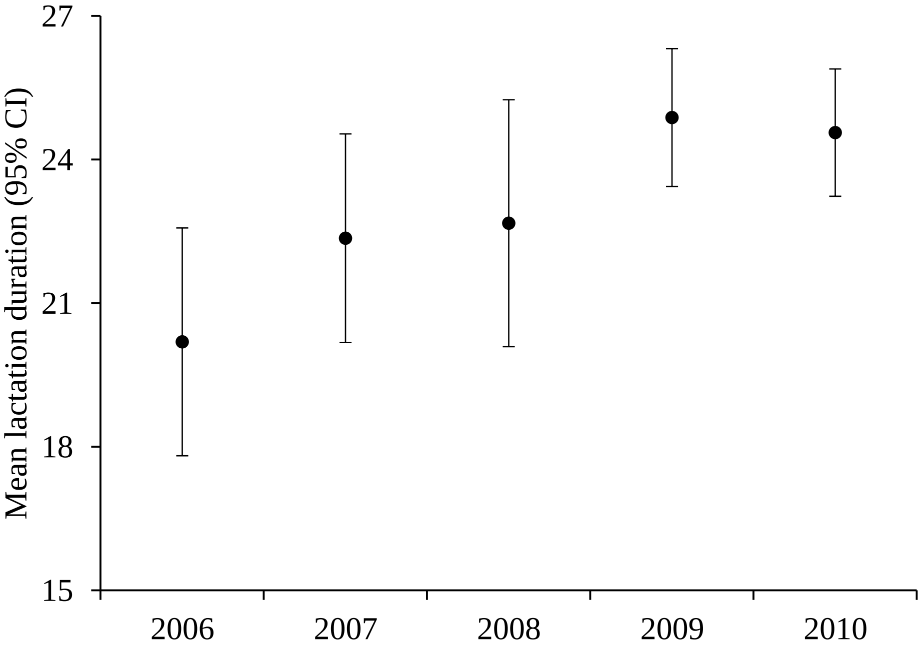

*Figure 10. Mean lactation durations with 95% confidence intervals.*

There was a strong negative association, which was significant, between annual mean lactation duration and median pupping date (Fig. 11; Spearman rank order, $r_s$= -0.87, S=37.44, p=0.05).

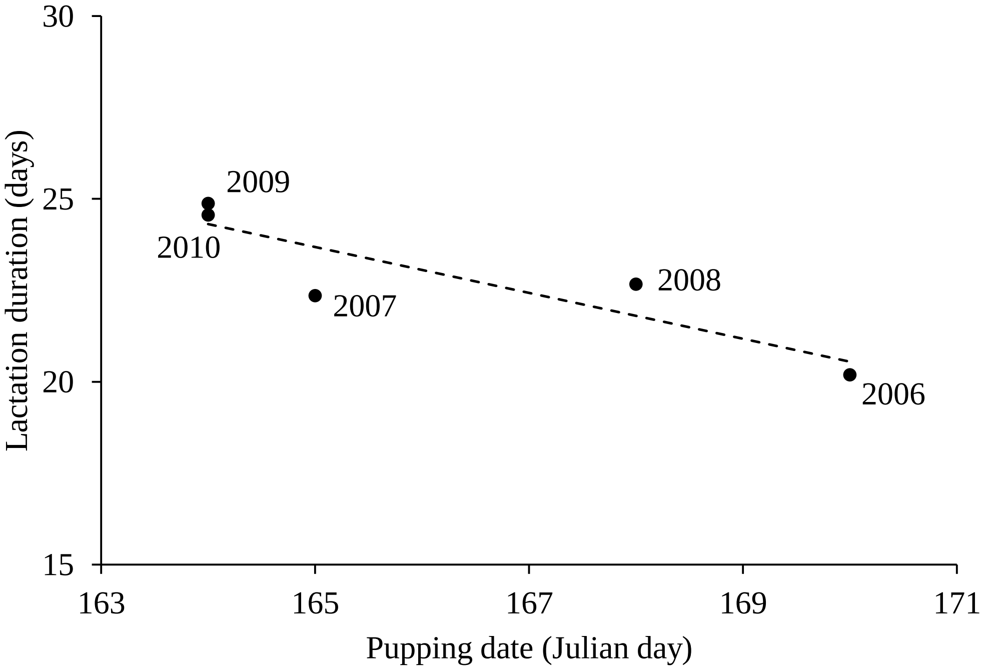

*Figure11. Relationship between median pupping date and mean lactation duration.*

Lactation duration and the number of days the female was seen during lactation showed a strong positive correlation (Pearson product moment, r=0.687, df=95, p<0.0001; Fig. 12).

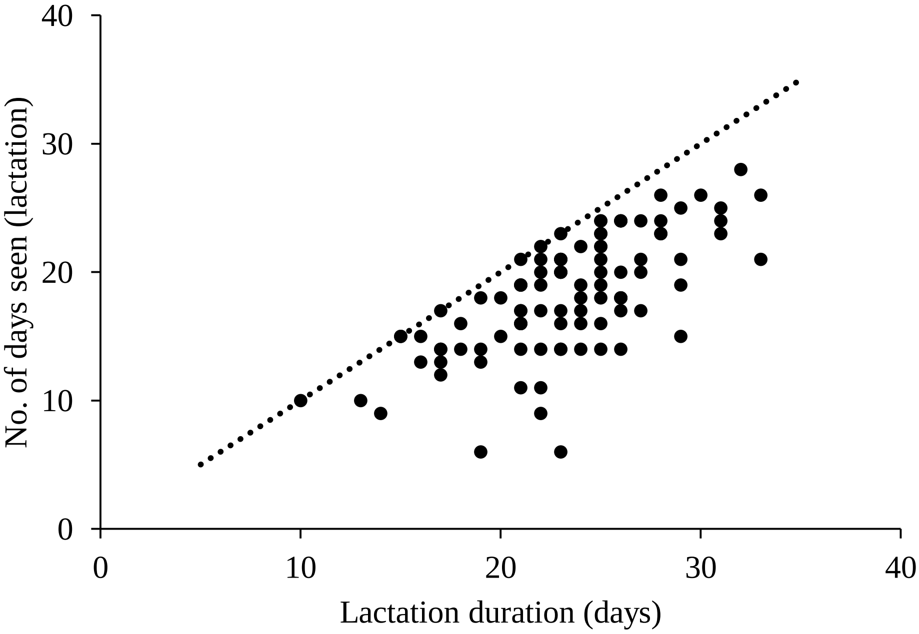

*Figure 12. The relationship between lactation duration and the number of days the females were seen during lactation. Dotted line represents a perfect one to one relationship.*

The generalised linear mixed model showed a significant negative relationship between lactation duration and relative pupping date (Table 3). This indicated that females that pupped early during the breeding season had longer lactation durations (Fig. 13). According to the model output, ID did not explain any of the variation in the data. This is probably due to the model being over-parameterised as around half of the females had just one or two accurate pupping dates. Individual ID was retained, despite the improvement of the model fit by two AICc scores when removing it, because it reflected the study design and may still account for some of the structure in the data. There was a slight indication of underdispersion which is likely due to the limited range of lactation durations. Residuals were plotted against fitted values and all explanatory variables and showed good model fit (Fig. 14).

The optimal model was given by:

$$Lactation\ Duration \sim Relative\ pupping\ date + (1|fYear) + (1|fID)$$

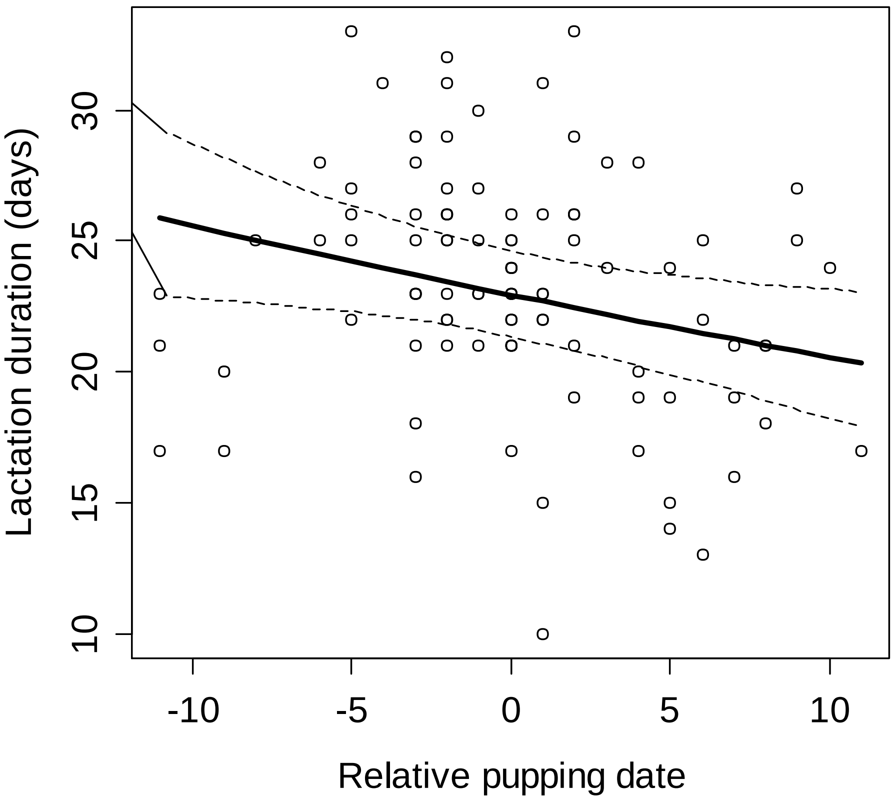

*Figure 13. The predicted relationship between relative pupping dates and lactation duration with 95% CI estimated as the variation for an average individual in an average year.*

*Table 3. Generalised linear mixed modelling results.*

| The influence of pupping date on female investment | | | | |
|---|---|---|---|---|
| Fixed effects | Estimate | Std. Error | z value | p-value |
| Intercept | 3.133 | 0.037 | 85.760 | <0.0001*** |
| Relative pupping date | -0.011 | 0.005 | -2.330 | 0.02* |
| | | | | |
| Random effects | Variance | Std. Dev | | |
| ID | 0.000 | 0.000 | | |
| Year | 0.004 | 0.066 | | |

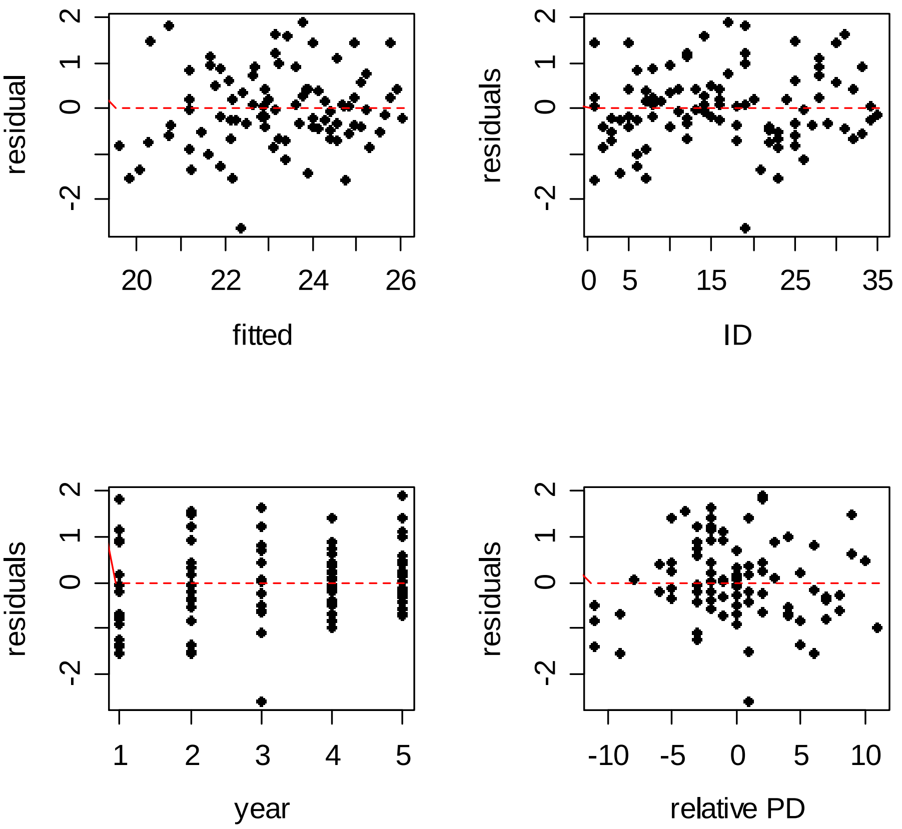

*Figure 14. The fit of the generalised linear mixed model, including plots of residuals versus fitted values, and residuals versus all explanatory variables.*

Based upon the predictions of the GLMM, early born pups were suckled for ~26 days whereas late born pups were suckled for ~21 days. Using rate of mass gain data from Sable Island (Bowen *et al*. 2003), this five day difference in lactation duration equates to a three kilogram difference in weight between early (~27kg) and late born pups (~24kg). Using Harding *et al*.'s (2005) relationship between weaning mass and first year survival, this equates to survival rates of 0.90 and 0.85 for early and late born pups, respectively.

## Discussion

This study provides the first direct estimates of variability in the timing of pupping in European harbour seals, and suggests that between-year and individual differences in pupping phenology influence lactation performance. Median pupping dates varied significantly over the course of the study, with pupping occurring significantly earlier in recent years. Other studies have also documented changes in harbour seal pupping phenology, but these have often been based on count data, which cannot take into account within individual shifts in breeding phenology or potential changes in population age-structure (Jemison & Kelly 2001; Reijnders, Brasseur & Meesters 2010). The mechanism underlying these effects can only be reliably identified through repeated monitoring of the same individuals. Results from this study show that the timing of pupping was highly synchronised and that individual females were generally consistent in their timing of pupping between breeding seasons (Fig. 8). This indicates that the population-level shifts in pupping phenology that we recorded were the result of individuals responding in a consistent manner, as observed in other colonial breeders (Reed *et al*. 2006). Individual consistency in the timing of pupping in harbour seals has previously only been demonstrated on Sable Island (Ellis *et al*. 2000) and in captivity (Temte 1991). Consistency in the timing of pupping can be both a behavioural trait as well as genetically determined, whereby individuals that are born late, breed late when reaching sexual maturity (Le Boeuf and Reiter 1988; Price, Kirkpatrick & Arnold 1988). Ultimately, over multiple generations, climate induced changes in breeding phenology may lead to a selection for earlier or later breeding (Husby, Visser & Kruuk 2011).

The reproductive investment of females can be measured in several different ways, but obtaining even the simplest measure in harbour seals is extremely difficult as females and pups often spend a significant amount of time in the water where they cannot be observed. By using lactation duration as an indication of female investment it was important to ascertain whether females with long lactation durations foraged more frequently and therefore spent less time with the pup, and whether females with short lactation durations only made intermittent foraging trips and so suckled their pup more intensely. Results demonstrated no difference in the proportion of days a female was seen with her pup during lactation regardless of whether lactation duration was long or short (Fig. 12). This confirms that differences in lactation were not simply due to differences in the intensity of time the female spent with the pup and suggests that lactation duration provides a good proxy for female investment.

Lactation durations were significantly longer in recent years compared with the beginning of the study, suggesting that females are experiencing better conditions which may be interpreted as an inter-annual or short-term response to improved environmental conditions (Fig. 10). At the same time there was a strong negative association between annual mean lactation duration and median pupping date (Fig. 11) indicating that shifts in the timing of pupping are due to consequences of energetic constraints. Furthermore, this highlights the use of timing of pupping as an indicator of lactation performance. There are no parallel data available on food availability or foraging effort for this population over this period, but I suggest that variability in the timing of pupping could provide an immediate indicator of prevailing environmental conditions. This hypothesis is consistent with studies of other pinnipeds, deer and birds, where the timing of breeding was typically delayed and offspring survival low during years of low food availability (Clutton-Brock, Albon & Guinness 1988; Lunn, Boyd & Croxall 1994; Boyd 1996; Ratcliffe, Furness & Hamer 1998; Soto, Trites & Arias-Schreiber 2004; Loe *et al*. 2005). The Moray Firth harbour seal population has declined by 2-5% per year since the mid 1990s (Thompson *et al*. 2007) as seen across much of the UK (Lonergan *et al*. 2007). This reduction in density may have resulted in an increase in per capita food availability, thereby reducing intra-specific competition for reproductive females. Intra- and inter-specific competition have also been suggested as the driving forces behind trends in breeding phenology of other harbour seal populations elsewhere in the world (Jemison & Kelly 2001; Bowen *et al*. 2003). In contrast to these other studies, we have observed an advance in the timing of pupping during a period of overall population decline. However, this study took place towards the latter part of the decline when the density of harbour seals was already reduced and where the population may in fact be recovering (Fig. 15; Sea Mammal Research Unit, *Unpublished Data*).

Despite the timing of pupping appearing to have advanced over the five years of this study, care should always be taken in interpreting trends in short-term phenological studies as observed patterns may result purely from inter-annual variation, while trends only become obvious on the decadal scale. Nevertheless, opportunities such as this are rare, and highlight how individual-based studies of breeding performance provide a sensitive indicator of population responses to environmental change.

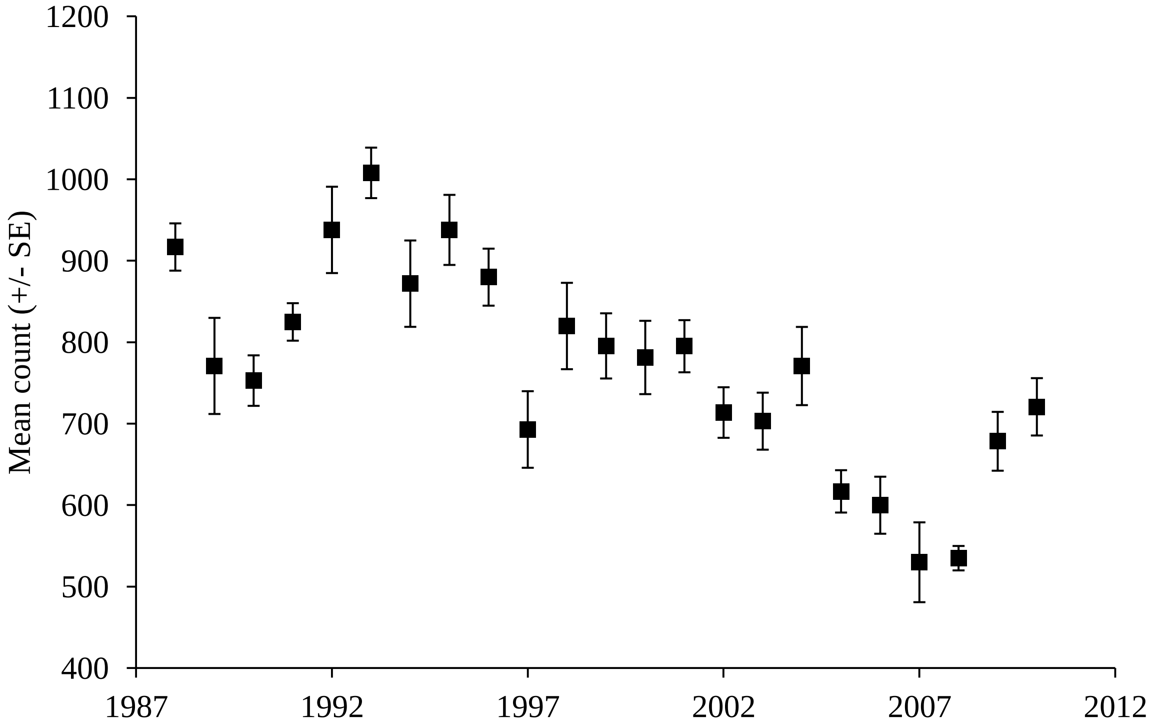

*Figure 15. Trend in mean counts (+/- SE) of harbour seals in the Moray Firth.*

The climate and fisheries driven changes that have taken place within the North Sea over the last few decades (Furness 2002; Edwards & Richardson 2004; Perry *et al.* 2005) could have caused or contributed to the long-term widespread decline of UK harbour seals. However, the current reduction in harbour seal density and intra-specific competition may now be masking these pressures, hence the observed patterns in pupping phenology and lactation performance. These results suggest that the timing of pupping in UK harbour seals may have varied temporally over the last few decades.

The use of marine top predators as indicators of environmental variation has mainly focussed on seabirds whose behavioural responses typically depend upon spring conditions (Frederiksen *et al.* 2004a; Wanless *et al.* 2009; Love *et al.* 2010). Temporal variation in the time of year when conditions are most likely to influence the breeding phenology of marine top predators limits the extent to which inter-species comparisons may be drawn. Although it is difficult to assess the exact time of year food availability is most important for the condition of pregnant harbour seals, studies suggest that autumn and winter conditions play a key role in the fitness of adult seals (Pitcher 1986). Within the Moray Firth, key prey species have shown seasonal as well as inter-annual variation, and harbour seals were shown to suffer reduced body condition following years of low winter prey abundance (Thompson *et al.* 1996).

Analysis confirmed that females who pupped early in the breeding season were able to suckle their pups significantly longer (Fig. 13). Studies of pinnipeds and deer have shown that older or larger females give birth earlier in the season (Clutton-Brock, Albon & Guinness 1988; Le Boeuf and Reiter 1988; Sydeman *et al*. 1991; Lunn, Boyd & Croxall 1994; Pomeroy *et al*. 1999), and that offspring arriving early have higher chances of survival than ones born late (Clutton-Brock, Albon & Guinness 1988; Sydeman *et al.* 1991; Catry *et al*. 1998). The observed difference in lactation duration between early and late born pups equated only to a slight advantage in survival of early born pups (5%). When estimating these survival rates we assumed that all pups were the same size at birth and that all pups gained mass at the same rate during lactation. If, for example, Moray Firth pups were smaller at birth and/or gained mass at a slower rate, the difference in survival between early and late born pups would be much more pronounced (Harding *et al*. 2005). A study from Sable Island showed that harbour seal pups with older or larger mothers were heavier at birth, which may have further survival advantages (Ellis *et al*. 2000). However, there did not appear to be a relationship between birth date and pup mass (Ellis *et al*. 2000).

This individual-based study of harbour seal reproductive ecology was only possible due to an easily accessible observation point being in close proximity to the undisturbed breeding site within Loch Fleet. There are certainly other sites around the world where important comparative work could be conducted. However, most key harbour seal populations of conservation concern lack these individual-level research opportunities, and available data are typically restricted to annual censuses. Instead, Reijnders, Brasseur & Meesters 2010 used data on the timing of peak pup counts from a long-time series of population censuses in the Dutch Wadden Sea as an indicator of phenological change. Nevertheless, there was uncertainty surrounding the use of such a proxy. We found a strong, but negative, association between the timing of max pup count and the median timing of pupping (Fig. 6). Even though this correlation was not significant, we would expect a positive association if the timing of peak pup count was to be used as a reliable proxy for the timing of pupping. The timing of first offspring has been a successful proxy for the timing of breeding in seabirds (Wanless *et al*. 2009). Here, day of first pup and the median timing of pupping showed a strong positive and significant association (Fig. 5). Although, sample sizes were small, day of first offspring seems likely to provide a better proxy for the timing of pupping in harbour seals at locations where individual-based data cannot be collected. However, pupping dates of premature pups were excluded from this analysis as these observations are unlikely to represent healthy breeding attempts and are also greatly influenced by survey effort prior to 1 June. Population-level studies will therefore have to be designed to exclude these premature pups when using day of first pup as a proxy for the timing of pupping. As an alternative I also tested the use of day of 50% max pup count, which revealed a positive association. Although this association was not significant, in the long-term this may provide a simpler, yet still reliable, proxy for the timing of pupping.

Here I have shown that population-level shifts in harbour seal pupping phenology are due to consistent individual-level energetic responses. The patterns observed in the timing of pupping and lactation duration indicate that environmental conditions were favourable for pregnant females during the study period, which is most likely due to the reduction in intra-specific competition following the long-term population decline. This study highlights the significance of harbour seal pupping phenology as an indicator of environmental conditions. Long-term monitoring of pupping phenology as well as identifying relevant environmental variables, such as winter sea surface temperature or chlorophyll, could provide important information on the key drivers of harbour seal population dynamics, particularly as the latest counts may indicate the beginning of a recovery of this population.

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# CHAPTER VI

## BALANCING COSTS AND BENEFITS OF A LONG-TERM INDIVIDUAL-BASED STUDY OF HARBOUR SEALS

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### Introduction

Long-term individual-based studies offer important insights into the ecological and evolutionary processes that drive population dynamics (Clutton-Brock & Sheldon 2010). More specifically, research of this sort provide an understanding of age-related changes in life history parameters, causes of underlying variation in growth, reproductive success and survival, the influence of social relationships on reproductive success and survival, differences in reproductive success between individuals and their offspring, and the influence of environmental variation on cohort performance (see Clutton-Brock & Sheldon 2010 for review). Passerine birds provided the initial focus of individual-based studies (Kluijver 1951; Smith 1988; Grant, Grant & Petren 2001) and this approach was subsequently extended to seabirds (Dunnet, Ollason & Anderson 1979) and other shorebirds (Harris 1970; Scott 1988). Meanwhile, the first long-term studies of mammals involved primates (Goodall 1986), followed by ungulates (Clutton-Brock, Albon & Guinness *et al*. 1988; Festa-Bianchet 1989), carnivores (Packer *et al*. 1988), and later moved on to marine mammals (Mann *et al.* 2000) and other smaller terrestrial mammals (Kerth 2008).

Several methods have been applied to allow individual animals to be followed over time, the majority of which involve an initial capture for tagging (*soay sheep,* Clutton-Brock *et al*. 1996; *weddell seal,* Hadley, Rotella & Garrott 2007), branding (*elephant seal,* Hindell 1991; *grey seal*, Schwarz & Stobo 2000), or ringing (*birds*, Dunnet, Ollason & Anderson 1979; Reed *et al*. 2009). The disadvantage of this type of approach is that the physical capturing of animals can be logistically challenging and costly both economically and in some cases also in terms of the animal's survival (Saraux *et al.* 2011). Furthermore, samples sizes are often limited, which may compromise the consistency and quality of the data obtained. Tags and rings may also be lost over time limiting the possibility for monitoring individual life histories. In contrast, species with natural distinct markings offer unique opportunities for long-term individual-based studies as all the individuals in the study area are immediately available for sightings, and marks are often consistent throughout their lives. For these species, photographic identification techniques have been developed and are now used on a variety of taxa from fish (Arzoumanian, Holmberg & Norman 2005; Marshall, Dudgeon & Bennett 2011) to both terrestrial (Moss 2001; Karanth *et al*. 2006) and marine mammals (Pomeroy *et al*. 1999; Wilson, Hammond & Thompson 1999). Nevertheless, running and maintaining long-term individual-based studies is often challenging (Clutton-Brock & Sheldon 2010). Many study populations of interest occupy remote areas which add logistic challenges in terms of accessibility (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Pomeroy *et al*. 1999). To maintain data quality over time repetitive sampling from a significant number of individual animals is required. In addition, long-term data collection often involves several different people and consistency may vary as a result. Furthermore, long-term studies are often costly and maintaining funding can be difficult when key outputs take several years to produce.

The success of the individual-based research detailed throughout this thesis in estimating key demographic parameters (Chapter IV) and obtaining direct measurements of variation in physiological responses (Chapter V) provides a rare opportunity for developing a new long-term individual-based study of harbour seals. However, this requires an evaluation of the study's strength and limitations. In particular, the intensive survey effort used to date may not be realistic or cost-effective for long-term monitoring of temporal variation in survival and fecundity or developing trends in pupping phenology. I therefore evaluate the effectiveness as well as the costs and benefits of reduced survey regimes for the long-term continuation of this study.

## Methods

### *Study area and full survey regime*

The study was carried out in Loch Fleet National Nature Reserve, a tidal estuary on the north-east coast of Scotland within the Moray Firth (see Chapters II & III). During low tide, harbour seals haul-out on intertidal sandbanks for resting, giving birth and suckling pups. The proximity of the main sandbank within Loch Fleet to an onshore observation point (approximately 130m) allowed individual seals to be recognised using photographic identification of the pelage patterns in the head and neck region. From 2006 to 2010, daily photographic identification surveys were carried out of all harbour seals hauled out on the main sandbank during each pupping season from the end of May to the end of July. Sightings of individuals and females with pups were used to estimate survival and reproductive rates using mark-recapture analyses (Chapter IV). Individual sightings were also used to determine pupping dates of individual females in order to investigate inter-annual variation in pupping phenology (Chapter V). Furthermore, the extension of this comprehensive survey regime into July also allowed the estimation of lactation durations of individual females.

### *Reduced survey regimes*

Whereas this intensive approach was appropriate for a PhD study, it may not be realistic or cost-effective for the long-term continuation of this research. To explore the consequences of reducing survey effort, I used the intensive survey data from 2006-2010 to simulate three alternative survey protocols. The aim of these simulations was to compare both the quality of the data they might produce and the relative costs of these programs. The evaluation of the cost-effectiveness of the three sampling regimes was based on the most costly scenario, i.e. the cost of hiring and running a research vehicle and the employment of temporary field assistants based at the field station, which is one hour drive from the study site.

Firstly, the long-term importance of different life history parameters was evaluated. Over the next decade, assessing the consequences of individual covariates and key environmental variables on individual survival, reproduction and breeding phenology will help to understand temporal variation in population dynamics. Lactation duration was considered a lower priority compared to the monitoring of demographic parameters and pupping phenology, especially as pupping phenology may be used as an indicator of lactation durations (Chapter V). Therefore, as the primary goal during the month of July was to monitor lactation durations (Chapter V), this period of data collection was excluded. From 2006 to 2010 all females gave birth within the month of June, apart from a few premature pups born in May (Chapter V). The peak timing of pupping occurred between the 13-19 June and therefore, to increase the chances of both sighting females with pups and obtaining as many pupping dates as possible, the reduced survey regimes were centred on 16 June, the overall median pupping date. In addition, both males and females showed relatively high haul-out probabilities during June, which maximised the chances of sighting individuals (Chapter III). In each year, all pups (excluding premature pups) were born within 21 days (Chapter V), and survey regime 1 was therefore designed to encompass this period through daily surveys for three weeks from the 6 to the 26 June (Table 1). Ninety percent of pups were born within 14 days (Chapter V), which formed the basis for survey regime 2, encompassing daily surveys for two weeks from the 10 to 23 June (Table 1).

Finally, survey regime 3 was the lowest intensity approach, involving surveying every other day but for an extended period (2 – 28 June) while relaxing the restriction on estimating pupping dates from a three day to a five day window (the period between last seen without a pup and first seen with a pup) (Table 1).

*Table 1. Summary of conditions for reduced survey regimes.*

| | **Period** | **Survey intensity** |
|---|---|---|
| *Regime 1* | 21 days (6 to 26 June) | Daily |
| *Regime 2* | 14 days (10-23 June) | Daily |
| *Regime 3* | 27 days (2-28 June) | Every other day |

### Statistical analysis

To test the efficacy of the three sampling regimes in estimating sex-specific survival rates and fecundity, the multistate model and open robust design multistate model with misclassification were carried out again using the reduced data sets (see Chapter IV for details). These results were then compared to survival and reproductive rates obtained from the full data set (Chapter IV).

In short, multistate analyses for estimating sex-specific survival ($S$) included sightings of individuals based on the state they occupy, male (M), female (F) or individual of unidentified sex (U). Only sightings of individuals within the specified windows of each survey regime were included in each analysis. Until the sex of an individual was identified sightings were recorded as U, whereas after sex had been identified sightings were recorded as either M or F. Transitions between states ($\psi$) were only allowed from U to either M or F ($\psi^{UM}$ and $\psi^{UF}$), whereas all other transitions ($\psi^{MF}$, $\psi^{MU}$ and $\psi^{FU}$) were fixed at 0.

The robust design multistate analyses with misclassification for estimating conditional and unconditional reproductive rates ($\psi^{NB}$, $\omega^{B}$) included sightings of individual females based on their breeding state, breeder (B) or non-breeder (N). Unobservable events could also occur where the female’s breeding state was uncertain and sightings were recorded as “u” (not considered an actual state). The robust design incorporates additional information in that this includes sightings within primary occasions (year or breeding season). Therefore, for each of the reduced survey regimes there were consistently five primary occasions (year or breeding season). However, the number of secondary occasions (surveys) with each primary occasion varied as specified by the design of the reduced survey regime. Due to the intensive survey effort, secondary occasions were summarised per week during the analysis of the full dataset, so six, instead of 42 secondary occasions within each primary occasion (see Chapter IV). Regime 1 therefore had three, instead of 21, secondary occasions within each primary. Regime 2 had two, instead of 14, secondary occasions, and finally, regime 3 had four, instead of 14, secondary occasions within each primary.

## Results

### *Success of reduced survey regimes*

Regime 1 generally performed better than regime 2 & 3, capturing 91% of individuals, 89% of females with pups, and 92% of pupping dates (Fig. 1) in comparison with the full data set from this study.

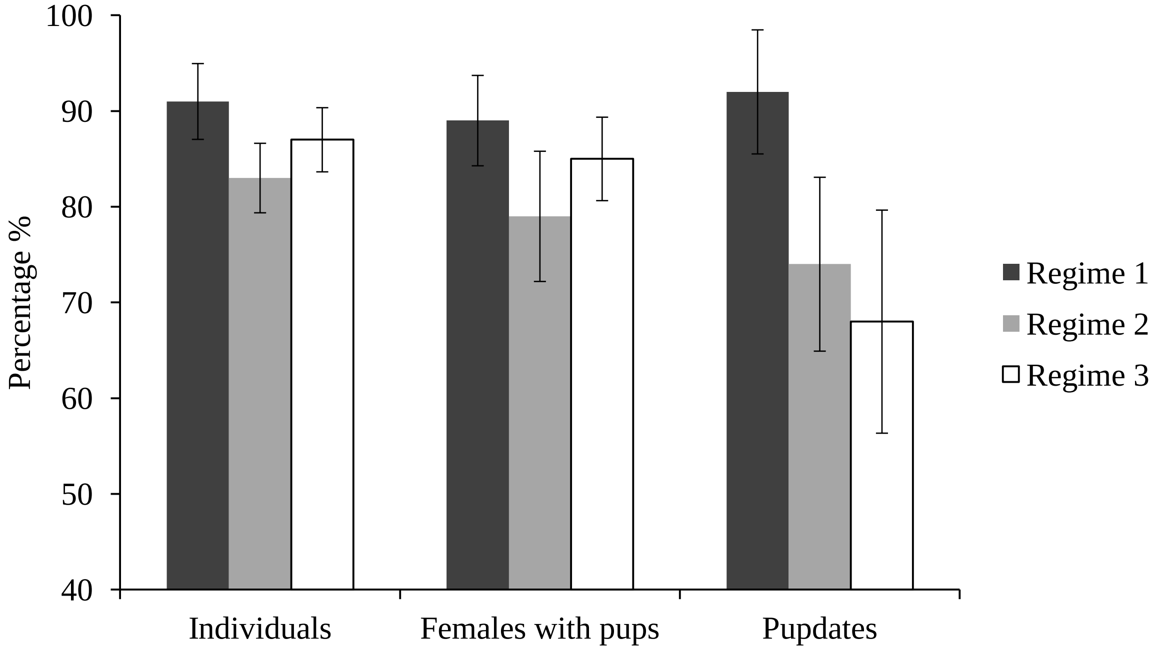

*Figure 1. Percentage of individuals, females with pups, and pupping dates detected by each of the reduced survey regimes, compared to the full data set.*

To test the actual efficacy of the three reduced sampling regimes in obtaining robust estimates of survival, the multistate model was applied to the sightings data from each of the reduced data sets (Table 2). The most general model fit was {S(*g*,*t*), p(*g*,*t*), ψ(*g*,*t*)} which allowed variation in survival (*S*), recapture probability (*p*) and transition probabilities (*ψ*) between states (*g*=male, female and unknown) and across time (*t*).

Goodness of fit was tested in the program U-CARE and revealed a moderate lack of fit within each of the three sampling regimes. The variance adjustment factors (c-hat) were used to adjust the $\mathrm{AIC}_c$ scores and standard errors accordingly.

*Table 2. Comparison of fit for multi-state models estimating sex-specific survival probabilities for each of the three reduced survey regimes.*

| **Regime 1** (*c-hat=1.96*) | *No. Par.* | *$\Delta QAIC_c$* | *$QAIC_c$ Weight* | *Model likelihood* |
|---|---|---|---|---|
| S(.,.) p(g,.) ψ(.,.) | 5 | 0.00 | 0.85 | 1.00 |
| S(g,.) p(g,.) ψ(.,.) | 7 | 3.78 | 0.13 | 0.15 |
| S(.,.) p(.,.) ψ(.,.) | 3 | 7.78 | 0.02 | 0.02 |
| S(.,.) p(.,.) ψ(g,.) | 4 | 9.73 | 0.01 | 0.01 |
| S(g,.) p(.,.) ψ(g,.) | 6 | 12.55 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) | 32 | 37.44 | 0.00 | 0.00 |
| **Regime 2** (*c-hat=2.00*) | No. Par. | $\Delta QAIC_c$ | $QAIC_c$ Weight | Model likelihood |
| S(.,.) p(g,.) ψ(.,.) | 5 | 0.00 | 0.89 | 1.00 |
| S(g,.) p(g,.) ψ(.,.) | 7 | 4.13 | 0.11 | 0.13 |
| S(.,.) p(.,.) ψ(.,.) | 3 | 13.34 | 0.00 | 0.00 |
| S(.,.) p(.,.) ψ(g,.) | 4 | 15.29 | 0.00 | 0.00 |
| S(g,.) p(.,.) ψ(g,.) | 6 | 17.83 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) | 32 | 36.85 | 0.00 | 0.00 |
| **Regime 3** (*c-hat=1.76*) | No. Par. | $\Delta QAIC_c$ | $QAIC_c$ Weight | Model likelihood |
| S(.,.) p(g,.) ψ(.,.) | 5 | 0.00 | 0.82 | 1.00 |
| S(g,.) p(g,.) ψ(.,.) | 7 | 3.15 | 0.17 | 0.21 |
| S(.,.) p(.,.) ψ(.,.) | 3 | 10.36 | 0.00 | 0.01 |
| S(.,.) p(.,.) ψ(g,.) | 4 | 12.36 | 0.00 | 0.00 |
| S(g,.) p(.,.) ψ(g,.) | 6 | 12.55 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) | 32 | 35.41 | 0.00 | 0.00 |

For each of the three survey regimes, $\mathrm{AIC}_c$ consistently showed support for the two top models. The first of the two top models within all sampling regimes was {S(.,.), p(*g*,.), ψ(.,.)} which allowed no variation in survival between states (*g*=male, female, unknown) or across time (*t*), variation in recapture probabilities between states but not across time, and no variation in transition probabilities between states or across time. The second model {S(*g*,.), p(*g*,.), ψ(.,.)}, consistently between regimes allowed variation in survival between states. For all three of the reduced survey regimes, the survival rates with no variation between states were similar (Table 3). However, survival rates including variation between states (sex-specific) were less consistent, particularly as regime 2 seemed to overestimate male survival (Table 3).

*Table 3. Summary of survival estimates from the full and three reduced sampling regimes.*

| | $S^{all}$ | $S^{M}$ | $S^{F}$ | $S^{U}$ |
|---|---|---|---|---|
| **Full regime** | **0.95 (± *0.02*)** | **0.89 (± *0.06*)** | **0.97 (± *0.02*)** | **0.95 (± *0.02*)** |
| Regime 1 | 0.96 (± *0.02*) | 0.92 (± *0.08*) | 0.96 (± *0.02*) | 0.96 (± *0.03*) |
| Regime 2 | 0.97 (± *0.02*) | 0.97 (± *0.10*) | 0.97 (± *0.02*) | 0.96 (± *0.03*) |
| Regime 3 | 0.95 (± *0.02*) | 0.90 (± *0.09*) | 0.96 (± *0.02*) | 0.94 (± *0.03*) |

The open robust design model with misclassification was applied to the sightings from each of the three reduced data sets for estimating reproductive rate (Table 4). The most general model was {S(*g*,*t*), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), p(*g*,*t*), δ(*g*,*t*), pent(*g*,*t*), Φ(*g*,*t*)} which allowed variation in all parameters between states (*g*=breeder, non-breeder) and across time (*t*). Goodness of fit testing of the models revealed a good fit.

*Table 4. Comparison of fit of open robust design multi-state models for estimating reproductive rate using each of the three sampling regimes.*

| **Regime 1** (*c-hat=0.94*) | *No. Par* | *$\Delta QAIC_c$* | *$QAIC_c$ Weight* | *Model Likelihood* |
|---|---|---|---|---|
| S(.,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 44 | 0.00 | 0.55 | 1.00 |
| S(g,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 45 | 1.79 | 0.23 | 0.41 |
| S(.,.) p(g,.) ψ(g,.) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 38 | 3.07 | 0.12 | 0.22 |
| S(g,.) p(g,.) ψ(g,.) π(g,.) ω(g,.) δ(g,.) ϕ(g,.) | 32 | 3.38 | 0.10 | 0.18 |
| S(g,t) p(g,t) ψ(g,t) π(g,t) ω(g,t) δ(g,t) ϕ(g,t) | 125 | 115.10 | 0.00 | 0.00 |
| **Regime 2** (*c-hat=0.87*) | No. Par | $\Delta QAIC_c$ | $QAIC_c$ Weight | Model Likelihood |
| S(g,.) p(g,.) ψ(g,.) π(g,.) ω(g,.) δ(g,.) ϕ(g,.) | 22 | 0.00 | 0.61 | 1.00 |
| S(g,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 35 | 2.07 | 0.22 | 0.35 |
| S(.,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 34 | 2.47 | 0.18 | 0.29 |
| S(.,.) p(g,.) ψ(g,.) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 28 | 37.05 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) π(g,t) ω(g,t) δ(g,t) ϕ(g,t) | 85 | 101.11 | 0.00 | 0.00 |
| **Regime 3** (*c-hat=0.78*) | No. Par | $\Delta QAIC_c$ | $QAIC_c$ Weight | Model Likelihood |
| S(.,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 54 | 0.00 | 0.75 | 1.00 |
| S(g,.) p(g,.) ψ(g,t) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 55 | 2.26 | 0.24 | 0.32 |
| S(g,.) p(g,.) ψ(g,.) π(g,.) ω(g,.) δ(g,.) ϕ(g,.) | 42 | 11.98 | 0.00 | 0.00 |
| S(.,.) p(g,.) ψ(g,.) π(g,t) ω(g,t) δ(g,.) ϕ(g,.) | 47 | 37.69 | 0.00 | 0.00 |
| S(g,t) p(g,t) ψ(g,t) π(g,t) ω(g,t) δ(g,t) ϕ(g,t) | 165 | 81.69 | 0.00 | 0.00 |

The two top models for regimes 1 and 3 were consistently {S(.,.), p(*g*,.), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), δ(*g*,.), ϕ(*g*,.)} and {S(*g*,.), p(*g*,.), ψ(*g*,*t*), π(*g*,*t*), ω(*g*,*t*), δ(*g*,.), ϕ(*g*,.)} both of which allowed variation in conditional ($\psi^{NB}$) and unconditional reproductive rates ($\omega^{B}$) between states and across time. For regime 2, the second top model was the same, but the first was {S(*g*,.), p(*g*,.), ψ(*g*,.), π(*g*,.), ω(*g*,.), δ(*g*,.), ϕ(*g*,.)} which did not allow variation across time in reproductive rates. Only estimates of conditional and unconditional reproductive rates from 2009 and 2010 were presented because by this time all females had given birth to at least one pup, whereas in the earlier years not all females were reproductively mature. This confirmed that all females were of reproductive age which eliminated any bias from immature females. Regimes 1 and 3 produced similar estimates of reproductive rate to that of the full regime (Table 5). However, regime 2 seemed to underestimate reproductive rates in all cases (Table 5).

*Table 5. Summary of unconditional ($\omega^{B}$) and conditional ($\psi^{NB}$) reproductive rates from the three reduced sampling regimes in 2009 and 2010.*

| | $\omega^{B}_{09}$ | $\omega^{B}_{10}$ | $\psi^{NB}_{09}$ | $\psi^{NB}_{10}$ |
|---|---|---|---|---|
| **Full regime** | **0.87 (± *0.04*)** | **0.89 (± *0.04*)** | **0.94 (± *0.06*)** | **0.86 (± *0.13*)** |
| Regime 1 | 0.87 (± *0.04*) | 0.88 (± *0.04*) | 0.94 (± *0.06*) | 0.85 (± *0.13*) |
| Regime 2 | 0.82 (± *0.05*) | 0.82 (± *0.05*) | 0.87 (± *0.07*) | 0.50 (± *0.12*) |
| Regime 3 | 0.87 (± *0.04*) | 0.88 (± *0.04*) | 0.94 (± *0.06*) | 0.83 (± *0.13*) |

Similarly, the annual median pupping dates from the reduced data sets were plotted against the actual median timing of pupping (Fig. 2).

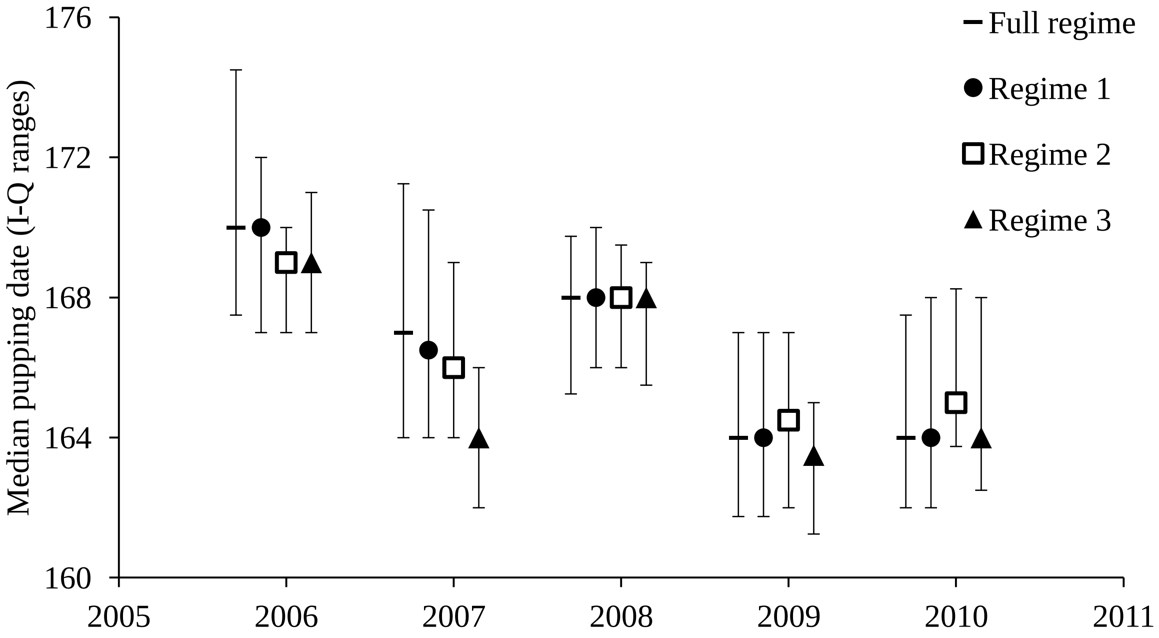

*Figure 2. Annual median pupping dates from each of the reduced sampling regimes compared to the full regime.*

Of the reduced survey regimes, regime 1 was more expensive than the other reduced survey regimes, mainly due to the extended and more intensive use of a field assistant and the research vehicle. More specifically, regime 1 was 50% more costly than regime 2, and 40% more costly than regime 3. However, the cost of regime 1 was only 42% of the cost required for the full survey regime (Table 6).

*Table 6. Costs involved in carrying out the full and reduced survey regimes.*

| | Full | Regime 1 | Regime 2 | Regime 3 |
|---|---|---|---|---|
| No. of surveys | 50 | 21 | 14 | 13 |
| Days of person time | 25 | 11 | 7 | 7 |
| Temporary contract (~£65/day) | 1625 | 715 | 455 | 455 |
| Fuel costs (£20/survey) | 1000 | 420 | 280 | 260 |
| Vehicle rental | 550 | 230 | 155 | 285 |
| Total (£) | **~3175** | **~1365** | **~890** | **~1000** |

## Discussion

Whereas short-term individual-based studies offer unique insights into present population dynamics, long-term studies allow insights into the responses of individuals to the dynamic environment which they occupy. However, the design and planning of long-term individual-based studies require an understanding and assessment of its strengths and limitations as well as its costs and benefits.

Obtaining accurate measures of adult survival is critical for explaining population growth (Caswell 1978; Gaillard, Festa-Bianchet & Yoccoz 1998). Both regime 1 and 3 performed well in estimating accurate overall survival rates as well as sex-specific survival rates, whereas regime 2 overestimated male survival. In addition, changes in fecundity have proved useful in understanding shorter term responses to variation in population density or food availability (Lunn, Boyd & Croxall 1994; Clutton-Brock *et al*. 1996; Coulson *et al*. 2001; Barbraud & Weimerskirch 2005; Hadley, Rotella & Garrott 2007), but obtaining estimates of reproductive rates require annual data collection, as comparisons are based on individual reproductive histories. Regime 1 and 3 performed best in estimating both conditional and unconditional reproductive rates, whereas regime 2 strongly underestimated both conditional and unconditional reproductive rates in both 2009 and 2010.

Obtaining direct estimates of variation in breeding phenology provides more immediate insights into the responses of individuals to the prevailing environmental conditions (Clutton-Brock, Albon & Guinness 1988; Lunn, Boyd & Croxall 1994; Boyd 1996) as well as longer term responses to climate change (Forchhammer, Post & Stenseth 1998; Réale *et al*. 2003; Frederiksen *et al*. 2004; Møller, Flensted-Jensen & Mardal 2006). However, obtaining annual pupping dates of individual females requires consistent and repeated surveys of the same individuals within pupping seasons and between years, and, within the pupping season the females have to be seen without a pup and subsequently with a pup. In the long-term, however, the restriction of a three day window in estimating pupping dates may be relaxed. Despite regime 1 being considerably better at detecting pupping dates of individual females (Fig. 1), all of the reduced regimes performed reasonably well in displaying the patterns in pupping phenology that were observed under the full regime (Fig. 2).

This study overcame many of the usual challenges and costs faced by many individual-based studies. Individual seals were recognised remotely by their natural markings and no costs were therefore involved in “capturing” individuals. There were no logistical challenges in terms of the study site’s accessibility as the onshore observation point was located by a public road. The most costly scenario for the continuation of this study involved a field assistant on a temporary contract based at the field station, and hiring and running a research vehicle for transportation to the study site. Although regime 1 was more expensive than regime 2 and 3, the extra cost seems negligible considering the accuracy of the data acquired. Less expensive scenarios should also be considered such as finding accommodation near the study site to save the costs of the hire vehicle and reduce the study's carbon footprint. Additionally, identifying suitable and interested local volunteers are also a cost saving option.

Furthermore, new statistical approaches are being developed which require less intensive survey regimes. For example, the "open" robust design multistate model with misclassification was developed and programmed over the course of this study, which meant that reproductive rates could be estimated using only data from June and all capture history data from this month could be incorporated in a full robust design. This allowed individuals to arrive and depart at staggered intervals, i.e. females' haul-out behaviour differs pre-parturition and post-weaning compared to during lactation. Prior to the development of the "open" model, the "closed" model could be used and forced to act like an "open" model. However, this required data from both June and July to produce reduced capture histories with only two occasions, one for each month. The "open" model was therefore able to incorporate more detailed data from a shorter survey period in estimating vital rates, compared to the "closed" model.

The initial intensive survey regime of this study provided the unique opportunity to test the efficacy of reduced survey regimes to ensure that time and funds are used most effectively while maintaining data quality. I have shown that the reduced and relatively low cost survey regimes 1 and 3 both would be successful in maintaining consistency and quality of data in the long-term. However, developing trends in the timing of pupping would have to be taken into account over the years and the survey regime adjusted accordingly. The long-term data that this site and these individuals are providing open up unique opportunities for investigating harbour seal life history. More specifically, greater knowledge of temporal variation in key demographic parameters and pupping phenology in relation to individual covariates, population density and environmental processes would improve our understanding of harbour seal population dynamics as well as improve and inform conservation measures. Ideas and directions for future research are developed in Chapter VII.

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# CHAPTER VII

## GENERAL DISCUSSION

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Globally, marine ecosystems are under pressure from climate change and anthropogenic impacts (Walther *et al*. 2002; Heath 2005), which has caused adverse affects on populations of top predators worldwide (Baum *et al*. 2003; Myers & Worm 2003; Österblom *et al*. 2008). Apex predators are a key component of marine as well as terrestrial and freshwater ecosystems and their removal has resulted in cascading effects throughout the food web (Estes *et al*. 2011). Several marine top predators, from seabirds to polar bears and pinnipeds, have proved to be important indicators of ecosystem conditions (Boyd, Wanless & Camphuysen 2006). Harbour seals have the potential to provide a unique bio-indicator amongst these top marine predators, due to their broad temperate distribution, which offers the possibility for worldwide inter-population comparisons. Available data indicate that harbour seal populations around the world are showing varying trends in abundance but the causes of these changes are often uncertain (Reijnders *et al*. 1997; Lucas & Stobo 2000; Jeffries *et al*. 2003; Small, Pendleton & Pitcher 2003; Brown *et al*. 2005; Gilbert *et al*. 2005; Jemison *et al*. 2006; Lonergan *et al*. 2007; Teilman, Rigét & Härkönen 2010). This limited understanding of the drivers causing change is largely due to the lack of individual-based studies of this species, leaving conservation efforts constrained and uninformed. Indeed, individual-based studies of pinnipeds are generally biased towards colonially breeding otariids (Boyd *et al*. 1995; Beauplet *et al*. 2006; Pendleton *et al*. 2006) and large phocids (Pistorius *et al*. 2004; Baker & Thompson 2007; Hadley, Rotella & Garrott 2007). In contrast, studies of smaller phocids are sparse, most likely due to nearly half of the phocid species hauling out in remote inaccessible areas of the Arctic and Antarctic. This study provided critical information on vital rates and reproductive ecology of harbour seals in north-east Scotland, offering a better understanding of the current dynamics of this population.

During the recent harbour seal declines in the UK (Lonergan *et al*. 2007), Loch Fleet was the only monitored site in Scotland where numbers of harbour seals were increasing (Chapter II). Trends at this site were even contrasted with patterns observed just 10km south in the Dornoch Firth and Morrich More Special Area of Conservation (SAC) (Chapter II). This raised the question whether patterns observed in Loch Fleet were representative of the region, or whether different conditions at this site resulted in fine-scale differences in demographic and behavioural patterns. Although local conditions such as structural changes in sandbanks may have changed seals preference for haul-out sites (Chapter II), I was unable to identify any reasons why demographic parameters within the Moray Firth would vary between breeding groups. Variations in growth rates between areas are more likely to result from differences in the behaviour and age and sex-specific composition of the breeding group rather than actual differences in survival and reproductive rates (Härkönen, Harding & Heide-Jørgensen 2002). However, behavioural differences are unlikely to have caused the observed differences in growth rates, particularly as seals in this region have been shown to forage in broadly similar areas (Chapter II; Thompson *et al*. 1996a; Tollit *et al*. 1998). Differences in the age and sex-specific composition of breeding groups due to localised age or sex-specific culling may explain the observed differences in growth rates, as culling due to conflict with fisheries has occurred in most areas outside Loch Fleet. However, these pressures should have decreased after the designation of the Dornoch Firth and Morrich More SAC in 2000, and especially after the implementation of the Moray Firth Seal Management Plan in 2005 (Butler *et al*. 2008). Demographics and behavioural responses observed in Loch Fleet therefore appear to be representative of the wider Moray Firth region over the period of this study (2006 to 2010).

### *Individual-based approaches to understanding population dynamics*

This study presented the first concurrent estimates of survival and reproductive rates of harbour seals within a naturally regulated population (Chapter IV). Apparent adult survival and reproductive rates were high and there was no indication of any costs of reproduction on survival. Survival rate was higher for females compared to males, which is expected in populations that are naturally female biased (Bigg 1969; Boulva & McLaren 1979; Clutton-Brock, Major & Guinness 1985; Härkönen & Heide-Jørgensen 1990; Clutton-Brock & Lonergan 1994; Clutton-Brock *et al*. 2002). Estimates were also comparable to those obtained from dead animals (Härkönen & Heide-Jørgensen 1990; Heide-Jørgensen & Härkönen 1992). Until now reproductive rates have mainly been estimated from analysis of ovaries in dead females (Boulva & McLaren 1979; Härkönen & Heide-Jørgensen 1990; Bjørge 1992). In this study, reproductive rate was estimated based on sightings of females with pups, which does not include information on pregnancy or early abortions which are more likely to be preserved in ovarian scars. As a result, the reproductive rate obtained in this study may better represent a “birth rate”. Despite the difference in methodology, reproductive rates estimated here were only slightly lower than those obtained from dead seals harvested in eastern Canada (Boulva & McLaren 1979) and collected after the 1988 epizootic in the Kattegat and Skagerak (Härkönen & Heide-Jørgensen 1990), highlighting the robustness of estimating reproductive rates based on sightings of females with pups.

The timing of pupping occurred significantly earlier in recent years and females nursed their pups significantly longer (Chapter V), suggesting that prevailing conditions are good. This is consistent with other studies of long-lived mammals where shifts in the timing of breeding were typically associated with variation in female condition and offspring survival (Clutton-Brock, Albon & Guinness 1988; Sydeman *et al.* 1991; Lunn, Boyd & Croxall 1994; Boyd 1996). Nevertheless, care must be taken in interpreting trends in short-term phenological studies as observed patterns may purely result from inter-annual variation while trends only become evident on the decadal scale.

Both the demographic parameters and physiological responses obtained in this study suggest that conditions within this region are currently favourable. However, this may purely be an artefact of the recent population decline resulting in an increase in per capita food availability due to reduced intra-specific competition, rather than an actual improvement in environmental conditions. Population viability analysis, using the estimated vital rates, predicted that the Moray Firth population should currently be growing. Recent increases in counts of harbour seals in the Moray Firth (Chapter IV) appear to support this, but another 5 to 10 years of data are required before any firm conclusions about a potential recovery can be made.

Finally, it is important to highlight that Loch Fleet is a newly developed haul-out site, which has only become an important breeding site post 1995 (Chapter II). If the growth in this area is supported by local recruitment, then the high survival and reproductive rates may simply be a result of individuals being relatively young. Likewise, as older females in species of mammals tend to give birth earlier than younger females (Lunn, Boyd & Croxall 1994; Loe *et al*. 2005), the observed advance in the timing of pupping could be explained by an ageing female population. Although this is a relatively short study, an increase in five years of age is a significant proportion of a female’s reproductive life. However, the reduction in the relative use of the Dornoch Firth and Morrich More SAC, and lack of any other nearby haul-out sites, indicate that some adult seals may have re-located to Loch Fleet over the years (Chapter II), indicating that numbers of harbour seals in Loch Fleet are not purely supported by own recruitment (Chapter II). Additional captures of known individuals will provide a better understanding of the age-structure of this group. Similarly, continued photo-identification studies of new recruits will provide further information on ages of females.

These estimates of contemporary demographic parameters and physiological responses do not give insights into the causes for the past decline. Nevertheless, earlier work within a different area of the Moray Firth, estimated survival rates similar to those in this study (Mackey *et al*. 2008). If survival rates have not varied temporally, the decline may have been caused by yearling/juvenile mortality. Unfortunately the coat characteristics of yearlings and juveniles do not allow for consistent photo-identification, and survival rates could not be estimated for these individuals. Larger scale ecosystem changes have occurred within this region which may have resulted in less favourable conditions for harbour seals. It is well documented that the North Sea ecosystem has undergone dramatic changes over the last few decades through two or more regime shifts since the late 1970s, causing changes in the salinity, temperature and the distribution and abundance of demersal fishes (Beaugrand *et al*. 2003; Perry *et al*. 2005; Weijerman, Lindeboom & Zuur 2005). In other temperate marine regions, regime shifts have altered community structure, introducing an abundance of so-called “junk food”, resulting in top predators suffering nutritional stress, reduced productivity and high juvenile mortality (Trites & Donnelly 2003). There has also been evidence of this “junk food” hypothesis within the Moray Firth, where physiological responses were evident in harbour seals as a result of switching prey (Thompson *et al.* 1997). Seals were in poorer condition when clupeid abundance was low and prey consumption was dominated by gadoids (Thompson *et al*. 1996b). Studies within the North Sea have also documented adverse effects of fisheries altering the abundance and structure of fish populations by fishing down the food web and disrupting the predator-prey balance (Pauly *et al*. 1998). Long-term studies of seabirds along the North Sea coast have provided mixed indications regarding the impacts of fisheries and climate change, largely due to inter-species variation in sensitivity resulting from differences in foraging ranges, costs of foraging, body size and ability to switch prey (Furness & Tasker 2000). Despite the extensive fishing of sandeel in the 1990s (ICES 2003), most studies of seabird breeding success are more concerned over the impacts of warming temperatures and predatory fish on the recruitment and size of sandeel (Furness 2002; Frederiksen *et al*. 2011). Sandeels and clupeids also form an important part of the diet of harbour seals (Thompson *et al.* 1991; Tollit & Thompson 1996; Tollit *et al.*

1998). Studies have shown that variation in the abundance of these key prey species resulted in prey switching and a change in haul-out and foraging distribution. Increased foraging costs and lower quality prey may ultimately have consequences on individual fitness and larger scale population dynamics (Thompson *et al*. 1996b).

*Pupping phenology as an indicator of female investment and environmental conditions*

The apparent relationship between the timing of pupping and lactation duration indicate that shifts in harbour seal pupping phenology are most likely due to the energetic consequences of variation in food availability rather than plastic responses to environmental variation (Chapter V). To date, most studies of breeding phenology as an indicator of environmental conditions within the North Sea are biased towards seabirds (Frederiksen *et al*. 2004a; Frederiksen *et al*. 2004b; Wanless *et al*. 2007). However, the use of seabirds is constrained due to the plastic responses of some species (Grémillet & Charmantier 2010) as well as their sandeel-specific prey preference, which does not give an indication of the overall condition of the ecosystem. Harbour seals are generalist foragers (Härkönen 1987; Hall, Watkins & Hammond 1998) and behavioural responses are therefore more likely to reflect the overall conditions within the environment. Simultaneous phenological studies of seabirds and seals could offer a multi-species approach to understanding temporal variation in ecosystem conditions.

Despite harbour seal pupping phenology appearing to be a useful indicator of environmental conditions and population fitness, its worldwide application remains limited due to the lack of suitable sites where individual-based studies can be carried out. I had the unique opportunity to test the use of the three proxies for determining the timing of pupping in population-level studies, namely the timing of max pup count (as used by Reijnders, Brasseur & Meesters 2010), the timing of 50% max pup count, and date of first offspring (typically used in studies of birds, Wanless *et al*. 2009). There was a poor fit with the timing of max pup count and median pupping date (Chapter V). In contrast, date of first offspring gave the best correlation with median pupping date (Chapter V). However, dates of premature pups were excluded in the analysis of date of first offspring, as these data are highly influenced by survey effort prior to the breeding season. This makes the use of date of first offspring more challenging in population-level studies as these would have to find a way to identify and exclude premature pups. The day of 50% max pup count, although not as good as day of first pup, may provide the simplest proxy for the timing of pupping in population-level studies, although this requires frequent count surveys.

Apart from the individual-based research on Sable Island which has been discontinued due to the dramatic decline of this population in the late 1990s (Lucas & Stobo 2000; Bowen *et al*. 2003), most other studies have used count data to estimate variation in the timing of pupping of harbour seals (Jemison & Kelly 2001; Reijnders, Brasseur & Meesters 2010). However, these population-level studies do not take into account changes in age-structure of the population which influence the timing of pupping as older females tend to breed earlier than younger females (Lunn, Boyd & Croxall 1994; Loe *et al*. 2005). Nevertheless, both individual-based and population-level studies documented delays in the timing of pupping of harbour seals during population decline and advances in the timing of pupping during population growth (Jemison & Kelly 2001; Bowen *et al.* 2003). This study observed an advance in the timing of pupping during, or possibly immediately after a period of overall population decline. Shifts in pupping phenology may therefore provide insights into the drivers of population decline. Delays in the timing of pupping are most likely to occur as a result of nutritional stress, whereas advances in the timing of pupping are likely either to result from per capita increases in food availability, for example following predation or culling, or age-specific mortality.

### *Population structure and management implications*

This study was the first to assess long-term patterns of site-use (Chapter II). Harbour seals appeared to change their preference for sites over the course of two decades, which may have resulted from localised changes in the structure of sandbanks. This highlighted the importance of continued monitoring of harbour seal haul-out sites within and around protected areas when assessing the efficacy of conservation measures over time. Furthermore, whereas breeding season or moult surveys are useful as a standardised approach for monitoring population trends, year-round monitoring is necessary to assess the importance of specific sites throughout the year (Chapter II). Year-round individual-based studies provide even more detailed information on the stability and structure of harbour seal breeding groups. Sightings of adults revealed that a large proportion of animals remained faithful to haul-out sites throughout the year, as well as between years (Chapter III). This indicates a meta-population structure with multiple levels, where the overall population is made up of clustered and relatively discrete subpopulations which in turn are made up of relatively discrete breeding groups, at least regarding the dispersal of adults. Gaining information on site fidelity is crucial for assessing the viability of breeding groups in relation to age or sex-specific mortality through culling or severe disease outbreaks as well as its impacts on genetic fitness.

### *Directions for future research*

One aim of this work was to evaluate the potential for developing a long-term individual-based study of harbour seal life histories. Over the next decade, this could enable a more extensive assessment of temporal variation in survival rates in relation to observed trends in abundance. Furthermore, the influence of density dependent effects and environmental conditions on between-year variation in reproductive rates and costs of reproduction can be investigated in much greater detail. Over the last five years there has been significant inter-annual variation in the timing of pupping, but, a longer time-series will allow us to assess whether there is a clear trend in the timing of breeding as suggested by Reijnders, Brasseur & Meesters (2010). Future work should also work on identifying robust environmental variables to help explain the observed patterns in pupping phenology and demography. These may also allow an examination of the exact periods of the year in which environmental conditions are most important for pregnant females, and which factors are likely to cause shifts in the timing of pupping. The continuation of this work will be particularly valuable if it can be linked with efforts to catch seals in Loch Fleet and investigate individual differences in foraging patterns and their consequences on breeding success, as well as obtaining additional information on age, morphometrics, diet and contaminant burdens to include in demographic and phenological analyses.

There are currently plans for the development of offshore wind farms in Europe, several of which will be located within harbour seal foraging areas. Proposed wind farms for the Moray Firth (Marine Scotland SEA 2010) are located close to the Dornoch Firth and Morrich More SAC and the Loch Fleet NNR, and within a foraging area used by these individuals. Concerns have been raised regarding the population consequences of acoustic disturbance (PCAD) from piling noise during the construction of wind farms, either through direct injury, mortality or displacement (Bailey *et al*. 2010; Lindeboom *et al.* 2011), or indirectly through changes in prey availability and distribution. The high levels of site fidelity revealed in Chapter III, also has implications for the assessment of the environmental impacts of these wind farms. Depending on the duration of their construction there may be fitness or reproductive consequences for the animals if site fidelity is constraining their movement out of the area, or alternatively, if avoidance involves using lower quality sites, increased travel costs or exposure to increased competition (Gill, Norris & Sutherland 2001). The impacts of disturbance may also be overlooked if site fidelity prevents animals moving away from the area (Gill, Norris & Sutherland 2001). However, due to the difficulties in obtaining relevant data, there are uncertainties over the threshold levels at which seals will be affected, as well as how to assess the potential impacts. Displacement of seals is equally challenging to quantify without long time series of count data as well as individual histories of site fidelity. Avoidance of key foraging areas cannot be assessed unless previous work has identified their location. And finally, fitness and reproductive consequences of disturbance may go unnoticed without established individual-based studies monitoring their life histories. The long-term monitoring of harbour seal distribution and abundance within the Moray Firth, in addition to the continuation of the individual-based life history work in Loch Fleet – the closest breeding site to the wind farm site – presents a unique opportunity to achieve a detailed assessment and understanding of the impacts of piling noise and vessel traffic on the use of haul-out sites and foraging areas as well as any consequences on key demographic parameters of harbour seals.

### *Conclusion*

Worldwide populations of harbour seals are showing varying and differing trends, and the causes often remain uncertain (Reijnders *et al*. 1997; Lucas & Stobo 2000; Jeffries *et al*. 2003; Small, Pendleton & Pitcher 2003; Brown *et al*. 2005; Gilbert *et al*. 2005; Jemison *et al*. 2006; Lonergan *et al*. 2007; Teilman, Rigét & Härkönen 2010). Alaskan populations are generally declining which is thought to be linked with nutritional stress from a reduction in food quality or inter-specific competition (Pitcher 1990; Jemison & Kelly 2001; Matthews & Pendleton 2006). In contrast, populations from south-eastern Alaska to California are generally increasing, with some even reaching carrying capacity as a result of the Marine Mammal Protection Act putting a closure to bounty programs (Jeffries *et al.* 2003; Brown *et al.* 2005). This is similar to patterns observed on the east coast of North America (Baraff & Loughlin 2000; Gilbert *et al*. 2005), with the exception of Sable Island where the population has declined dramatically either as a result of shark predation or inter-specific competition with a growing grey seal population (Lucas & Stobo 2000; Bowen *et al.* 2003). In Europe, populations in the Wadden Sea and south and eastern parts of Scandinavia have been increasing since the reduction in hunting pressure (Reijnders & Lankester 1990; Helander & Bignert 1992; Teilman, Rigét & Härkönen 2010), but suffering periodic declines after disease outbreaks (Härkönen *et al.* 2006). In more north-western areas, such as the UK and Iceland, populations have suffered long-term declines either due to culling, inter-specific competition or changes in ecosystem condition (Hauksson *et al*. 2004; Lonergan *et al.* 2007).

The lack of understanding of the dynamics of these populations, particularly the specific drivers of decline, call for new measures for monitoring harbour seal populations. This study has highlighted the current and long-term importance of individual-based data in understanding population dynamics of harbour seals. Accurate measures of survival and fecundity, as well as direct measures of physiological responses, are critical for the production of reliable information of population dynamics and the implementation of effective conservation measures. Wherever possible, selected sentinel sites should be identified in other regions to permit inter-population comparative studies, preferably at sites exhibiting differing trends in abundance. Individual-based work is already being carried out at Tugidak Island in Alaska (Hastings, Hiby & Small 2008), while one or two sites in California may be suitable for the development of individual-based work (e.g. Nicholson 1997; Yochem & Stewart 1998). At Sable Island a long record of individual-based data already exists and the continuation of this study, albeit at a smaller scale, could provide an understanding of the relative role of competition and predation in the recent decline (e.g. Bowen *et al.* 2001 & 2003). Comparative individual-based studies of harbour seal population dynamics at these sentinel sites would provide a global single-species indicator of ecosystem conditions across temperate regions in the northern hemisphere.

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# **APPENDIX I** – *Loch Fleet harbour seal catalogue*

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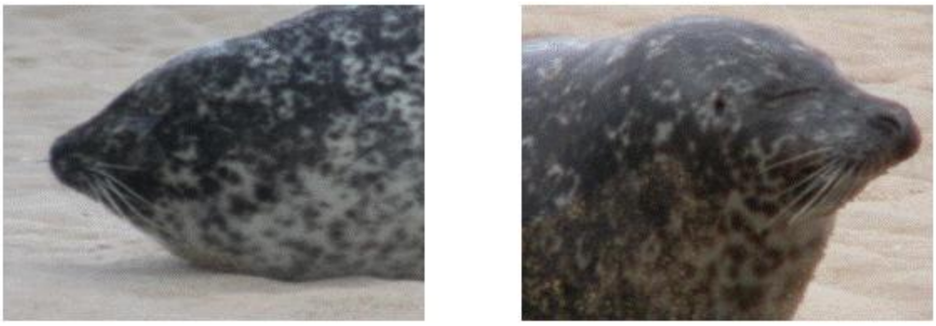

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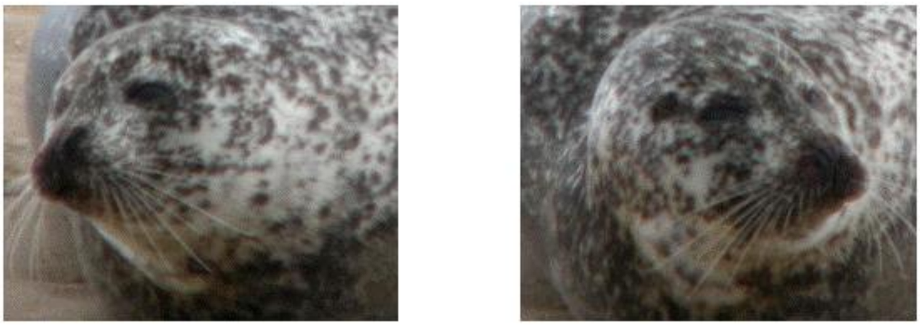

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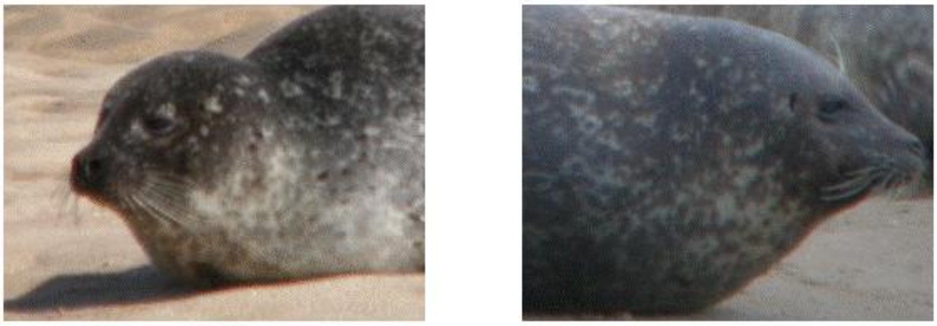

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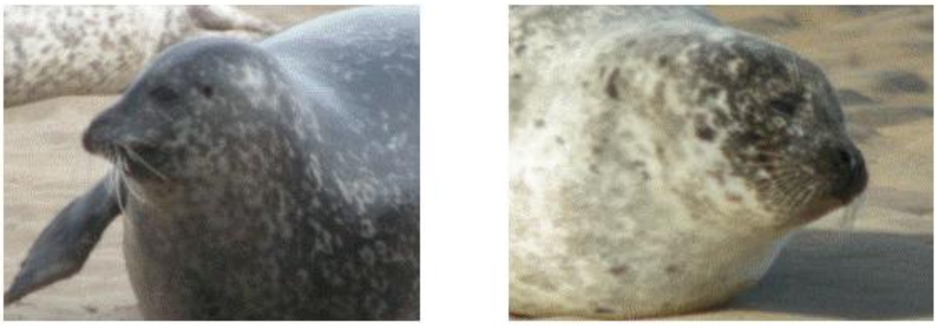

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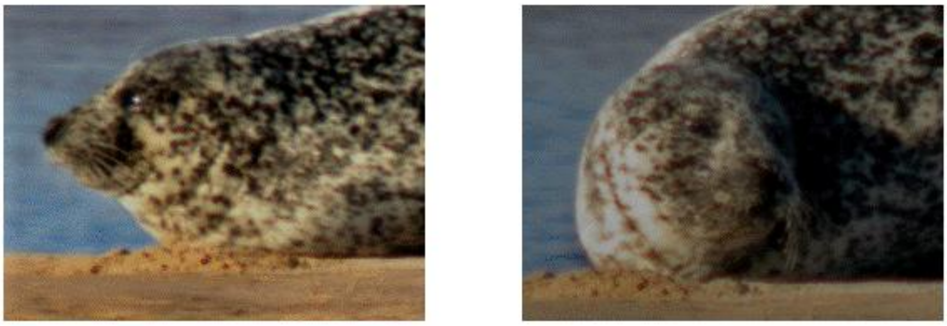

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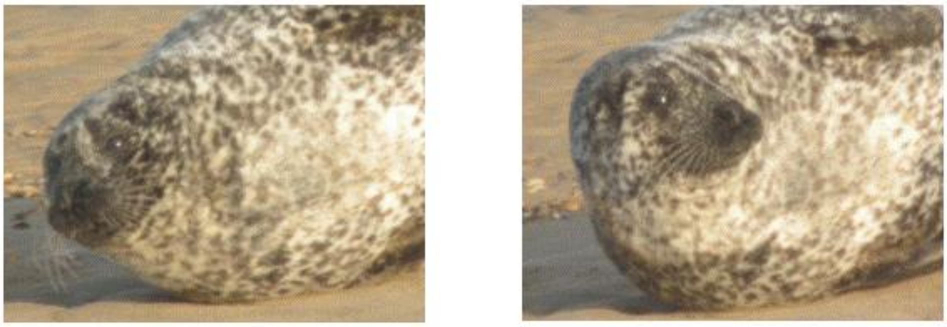

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## **APPENDIX II** – *Estimated ages of caught females from tooth growth rings.*

| ID | SEX | CAUGHT | BIRTH YEAR | AGE IN 2006 |
|---|---|---|---|---|
| 002 | F | 2009 | 2002 – 2004 | 2 – 4 |
| 015 | F | 2008 | 1998 – 2001 | 5 – 8 |
| 030 | F | 2008 | 1995 | 11 |
| 042 | F | 2009 | 1999 | 7 |
| 046 | F | 2009 | 1992 – 1994 | 12 – 14 |
| 054 | F | 2008 | 1996 | 10 |
| 061 | F | 2008 | 2001 – 2002 | 4 – 5 |
| 076 | F | 2008 | 2003 | 3 |
| 149 | F | 2009 | 2003 – 2004 | 2 – 3 |
| 158 | F | 2008 | 2004 | 2 |
| 164 | F | 2009 | 2005 – 2006 | 0 – 1 |

# **APPENDIX III –** *Example section of a capture history*

| ID | 31-May | 01-Jun | 02-Jun | 03-Jun | 04-Jun | 05-Jun | 06-Jun | 07-Jun | 08-Jun | 09-Jun | 10-Jun | 11-Jun | 12-Jun | 13-Jun | 14-Jun | 15-Jun | 16-Jun | 17-Jun | 18-Jun | 19-Jun | 20-Jun | 21-Jun | 22-Jun | 23-Jun | 24-Jun | 25-Jun | 26-Jun | 27-Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 |  |  |  | 1 |  |  | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 2 |  |  | 1 |  |  |  | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |  |  |  |  | 1 | 1 | 1 | 1 | 1 | 1 |
| 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 4 |  | 1 |  |  | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | ? | 1 |  | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 5 |  |  |  |  | 1 | 1 |  |  |  |  |  |  |  | 1 | 1 | 1 |  |  |  |  |  | 1 | 2 | 2 | 2 | 2 | 2 | 2 |
| 6 |  | 1 |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  | 1 |  | 1 |  | 1 |  | 1 | 1 | 1 |  |
| 7 | 1 | 1 | 1 |  | 1 |  |  | 1 |  |  | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | ? | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 2 |
| 8 | 1 |  | 1 | 1 | 1 |  |  |  |  |  |  | 1 |  |  |  |  | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 | 2 | 2 | 2 | 2 |
| 9 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 10 |  |  |  |  | 1 |  | 1 | 1 |  |  | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 11 |  |  | 1 |  |  | 1 |  | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 |  | 2 | 1 | 1 | S | 2 | 2 | 2 | 2 | 2 | 2 |
| 12 |  |  |  |  |  |  |  |  |  | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 13 |  |  | 1 | 1 |  |  |  | 1 | 1 |  |  |  | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 |  | 2 | 2 | 1 | 2 | 2 | 2 |
| 14 | 1 |  | 1 | 1 |  |  |  |  | 1 |  | 1 |  | 1 | 1 |  | 2 | 2 | 2 |  | 1 | 2 |  | 2 | 2 |  | 2 | 1 | 2 |
| 15 |  | 1 | 1 | 1 |  |  | 1 |  | 1 |  | 1 | 1 |  | 1 | 2 |  | 2 |  |  |  |  | 2 | 2 |  | 2 | 2 | 2 | 2 |
| 16 |  |  |  | 1 |  |  |  |  |  |  | 1 |  | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 |
| 17 |  |  | 1 | 1 |  | 1 |  |  |  | 1 | 1 | 1 |  | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 |  |  | 2 |  | 2 |
| 20 |  | 1 |  |  | 1 | 1 |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |  | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 21 | 1 |  |  |  |  |  |  |  | 1 | 1 | 1 | 1 |  | 1 |  | 1 | 1 |  | 1 | 2 |  |  |  | 2 | 1 | 2 | 2 |  |
| 23 | 1 |  |  |  | 1 |  | 1 |  |  |  |  | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| 24 |  |  |  | 1 |  |  |  |  |  |  | 1 | 2 | 2 | 2 | 2 |  | 2 | 2 |  |  | 2 | 2 | 2 | 2 | 2 | 2 |  |  |
| 27 |  | 1 |  |  | 1 |  |  | 1 |  |  | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 2 |  | 2 | 1 | 1 | 2 | 2 |
| 28 | 1 | 1 |  |  |  |  | 1 |  |  |  | 1 | 1 |  |  |  | 1 | 2 |  | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 30 |  | 1 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 31 |  |  |  |  | 1 |  |  |  |  | 1 | 1 |  | 1 |  |  | 1 | 1 |  |  |  |  |  | 1 | 1 | 1 | 1 |  |  |
| 33 |  |  | 1 | 1 | 1 | 1 | 1 |  |  |  |  |  |  |  |  |  | 1 | 1 |  | 1 |  |  |  |  |  |  |  |  |
| 35 |  | 1 |  | 1 |  |  | 1 | 1 |  |  |  |  | 1 | 2 | 2 |  | 2 | 2 |  |  |  | 2 |  | 2 | 2 | 2 |  |  |
| 42 |  |  |  | 1 | 1 |  |  |  |  | 1 | 1 | 1 |  |  |  | 1 | 1 | 1 |  | 2 |  |  |  | 2 | 2 | 2 | 2 | 2 |
| 46 |  | 1 | 1 | 1 | 1 |  | 1 |  |  |  | 1 |  |  |  | 1 |  |  |  |  |  |  |  | 1 |  |  |  |  |  |
| 47 | 1 | X | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 48 |  |  | 1 |  |  |  |  | 1 |  |  |  | 1 |  |  |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 |
| 52 |  | 1 |  |  |  |  |  | 1 | 1 |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 53 |  |  |  | 1 | 1 |  |  |  | 1 | 1 |  |  |  |  | 1 | 1 |  |  |  |  | 1 |  |  |  | 1 | 1 | 1 |  |
| 54 |  | 1 |  |  | 1 |  | 1 |  |  | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 56 |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 |
| 59 |  |  |  |  |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 61 |  |  |  | 1 | 1 |  |  |  |  | 1 |  |  |  |  |  |  | 2 |  |  |  |  |  | 2 |  | 2 |  |  |  |
| 62 |  |  | 1 | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 | 1 | 1 |  | 1 |  | 2 | 1 |  |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 63 |  |  |  |  | 1 |  | 1 | 1 |  |  | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 2 |
| 65 | 1 | 1 | 1 | 1 |  |  | 1 | 1 |  |  |  | 1 |  |  | 1 | 1 |  |  |  | 1 | 2 |  | 1 | 1 | 2 | 2 | 1 | 1 |
| 66 |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  | 1 |  |  |  | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 67 |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 70 | 1 |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 71 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 72 | 1 | 1 | 1 | 1 | 1 |  | 1 |  |  | 1 | 1 |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 73 |  | 1 |  | 1 | 1 | 1 |  | 1 |  |  | 1 |  | 1 | 1 |  | 1 |  |  |  |  |  | 1 |  | 1 |  |  | 1 |  |
| 74 |  | 1 |  |  |  |  |  |  | 1 | 1 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 75 | 1 | 1 | 1 |  |  |  |  | 1 |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  | 1 |  |  |  |
| 76 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |  |  |  | 1 | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 | 1 |  | 1 | 1 | 1 | 1 | 1 |  |
| 77 | 1 | 1 | 1 | 1 |  |  |  |  |  | 1 |  | 2 | 2 | 2 | 2 |  |  | 2 |  |  | 2 | 2 | 2 |  | 2 | 2 | 2 | 2 |
| 78 |  | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |  | 2 | 2 | S | 2 | 2 |
| 79 |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  | 1 |  |  |  |  |  |
| 80 | 1 |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 81 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  | 2 |  | 2 |
| 82 |  | 1 | 1 |  |  |  |  |  | 1 |  | 1 | 1 | 1 |  | 1 | 1 | 1 | 1 | 1 |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 83 |  |  |  |  | 1 |  |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 84 |  |  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 85 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 86 | 1 | 1 | 1 |  |  |  |  | 1 | 1 | 1 | 1 |  | 1 |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |
| 87 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 90 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |
| 92 |  |  | 1 | 1 |  |  |  | 1 | 1 |  |  |  |  | 1 |  |  | 1 |  |  |  |  |  |  | 1 | 1 |  |  |  |
| 93 |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 |  |  |  | 1 | 1 | 1 |  |  | 1 |  |  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
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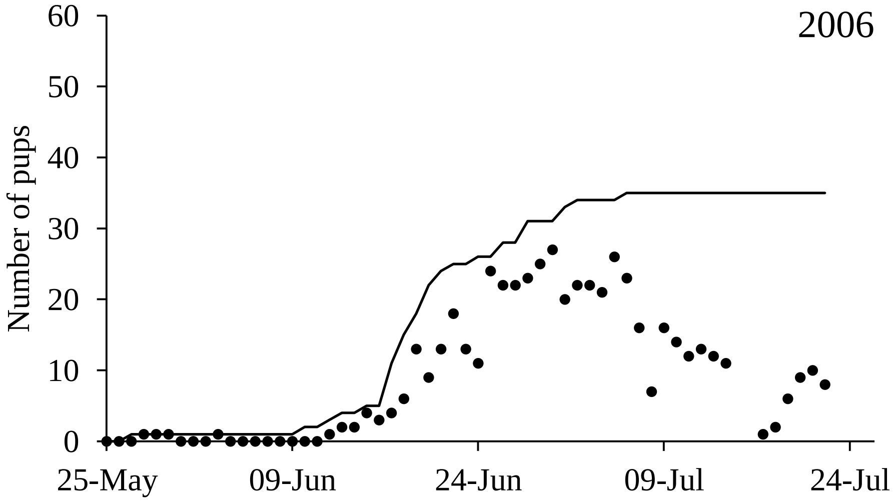
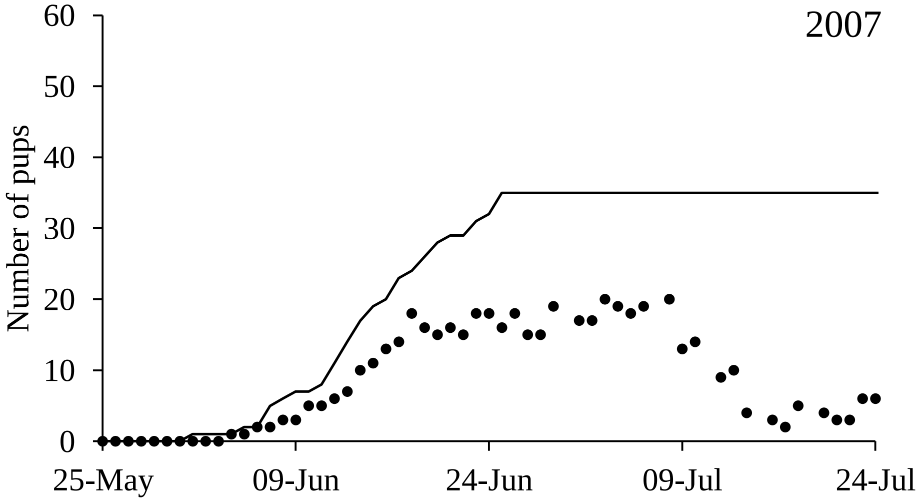
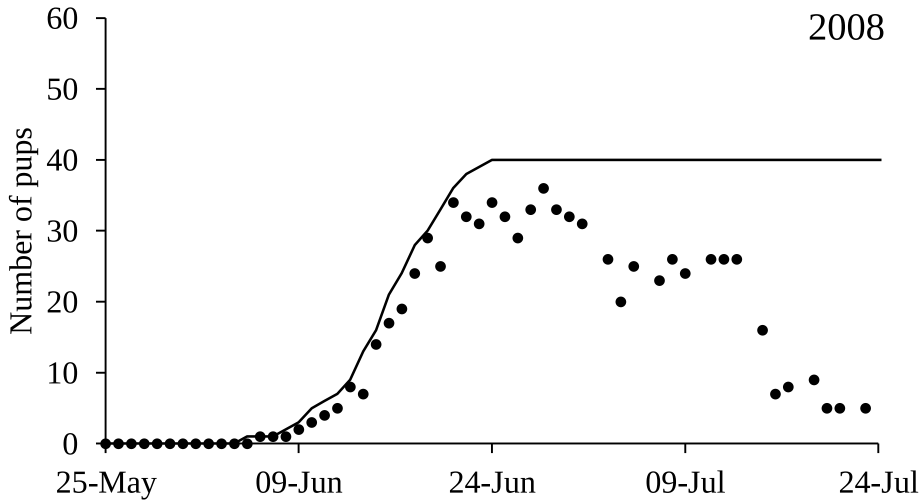
| 95 |  |  |  | 1 |  | 1 | 1 |  |  |  |  |  |  | 1 |  |  | 1 |  |  |  | 1 |  |  |  |  |  | 1 |  |
| 96 |  | 1 | 1 |  | 1 |  | 1 |  |  | 1 |  |  |  | 1 | 1 | 1 | 1 |  | 1 |  |  | 1 | 1 |  |  |  |  | 1 |

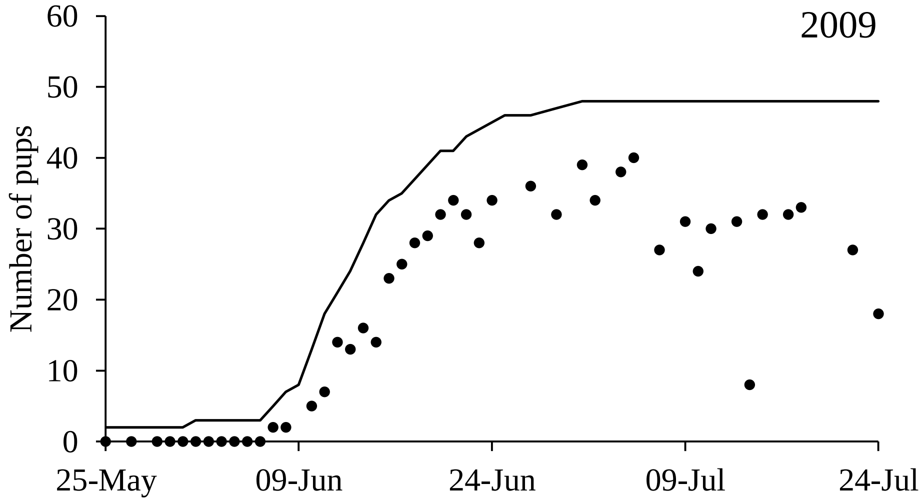
(1=seen, 2=seen with pup, x=stillbirth)

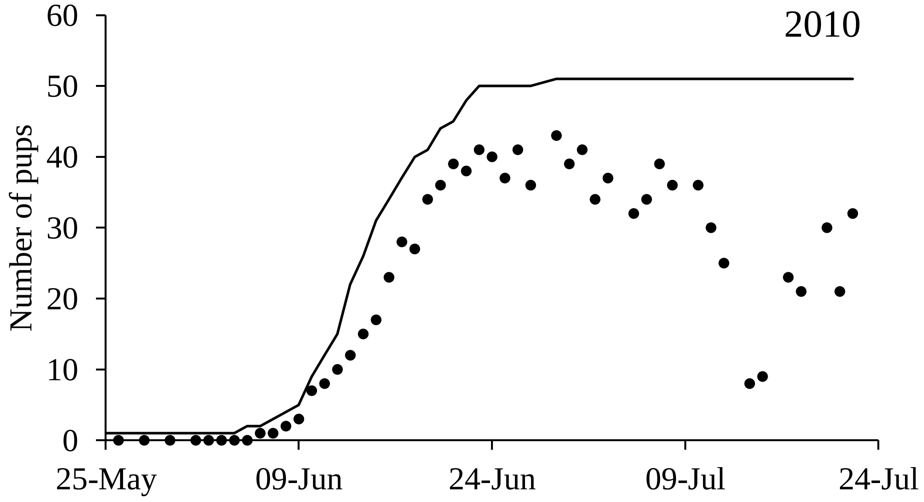
## **APPENDIX IV** – *Annual pupping curves including daily max pup count (•) and the cumulative number of pups born (-).*






2008
Number of pups
60
50
40
30
20
10
0
25-May
09-Jun
24-Jun
09-Jul
24-Jul


2009
Number of pups
60
50
40
30
20
10
0
25-May
09-Jun
24-Jun
09-Jul
24-Jul


2010
Number of pups
60
50
40
30
20
10
0
25-May
09-Jun
24-Jun
09-Jul
24-Jul