Long-term human impacts on sub-Antarctic ecosystems and mesopredator abundance

A Dissertation Presented

by

Catherine M. Foley

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

May 2019

Stony Brook University

The Graduate School

Catherine M. Foley

We, the dissertation committee for the above candidate for the
Doctor of Philosophy degree, hereby recommend
acceptance of this dissertation.

Dr. Heather J. Lynch – Dissertation Advisor
Associate Professor, Department of Ecology and Evolution, Stony Brook University

Dr. Resit Akçakaya – Chairperson of Defense
Professor, Department of Ecology and Evolution, Stony Brook University

Dr. Lesley Thorne – Committee Member
Assistant Professor, School of Marine and Atmospheric Sciences, Stony Brook University

Dr. Ian Stirling – Committee Member
Research Scientist Emeritus, Wildlife Research Division, Environment Canada

This dissertation is accepted by the Graduate School

Dean of the Graduate School

Abstract of the Dissertation

Long-term human impacts on sub-Antarctic ecosystems and mesopredator abundance

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2019

While many conservation biologists have focused on the need to prevent biodiversity loss, it is equally important to promote the recovery of impacted species and understand recovery dynamics. Recent studies have highlighted the need to identify appropriate baseline states against which to compare current populations. However, this is made difficult due to the ever-present threat of "shifting baseline syndrome", whereby an arbitrary (and often degraded) environmental baseline is used to measure subsequent ecological change. It is thus of critical importance to identify appropriate metrics against which to evaluate population change. Often the challenges of assessing recovery are compounded by logistical difficulties associated with surveying large and inaccessible populations, and the development of novel tools and technologies to survey such populations is therefore necessary. Using a combination of historical archival research, new remote-sensing techniques, and population models to correct census data for within-season phenological dynamics, I explore the recovery dynamics of two historically harvested species on the sub-Antarctic island of South Georgia: Antarctic fur seals (*Arctocephalus gazella*) and king penguins (*Aptenodytes patagonicus*). By reconstructing historical population data and estimating current abundance, I assess the current state of these two species' populations in reference to their historical baselines. Results suggest that both king penguins and Antarctic fur seals experienced substantial population growth upon release from harvesting. Completing the first-ever island-wide survey of king penguins, I estimate the current population as 405,425 (95% CI: 102,624 - 2,375,061) breeding pairs and find evidence that, in addition to release from harvest, both glacial retreat and climate forcing likely contribute to population growth. While fur seals also experienced substantial population growth, I demonstrate that the current population of Antarctic fur seals represent only ~20% of the historical, pre-harvest, population. Despite the similarities in the historical ecology of these species, results suggest that while South Georgia king penguins have likely recovered and are thriving, the South Georgia Antarctic fur seal population is far from recovered. With the expected increase in environmental variability associated with climate change and the negative demographic consequences on fur seals, the full recovery of this population may be impossible under current 'no-analog' environmental conditions.

Dedication Page

To Mom and Dad

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Acknowledgments

I would like to thank Heather Lynch and all the members of the Lynch Lab for their support, feedback, ideas, and assistance. Thank you to my collaborators T. Hart and W. Fagan for their support and assistance. Thank you to C. Black, A. Borowicz, G. Clucas, G. Humphries, M. Lynch, B. Goncalves, C. O'Leary, M. Schrimpf, and C. Youngflesh for help with data collection. Thank you to the team of undergraduate and high school student assistants who dedicated countless hours to helping digitize king penguin panoramas: C. Bell, R. Biondo, L. Caliguri, K. Gregory, V. Kennelly, S. Vincent, A. West, and T. Wong. Thank you to everyone at Oceanites, One Ocean Expeditions, Cheeseman's Ecological Safaris, Quark Expeditions, and Golden Fleece Expeditions for their field support. Thank you to S. Poncet and contributors to the South Georgia GIS platform, from which some data here is adapted. Thank you to S. Bewick, J. Calabrese, C. Che-Castaldo, N. Friedenberg, L. Ginzburg, and E. Talis for comments and discussion about population and mathematical models and to Y. El-Laham and Z. Krayem for help improving sampling efficiency of ABC models. Thank you to the research teams at the New Bedford Whaling Museum, G.W. Blunt White Library at the Mystic Seaport, British Library, and the Scott Polar Research Institute for help with archival research.

Thank you to the organizations that provided funding support: US National Science Foundation Office of Polar Programs (Award No. NSF/OPP-1255058), the Ecological Society of America's E.C. Pielou Award in Statistical Ecology, Explorer's Club Mamot Award, Stony Brook University Sokal Awards for Statistical Ecology, and Stony Brook University Cost of Education Awards and travel grants from the Institute for Advanced Computational Sciences (IACS) at Stony Brook University, Scientific Committee for Antarctic Research, the Ecological Society of America, and the Ecological Forecasting Initiative. Thank you to everyone at IACS

and the SeaWulf computing cluster for high performance computing support. Thank you to the National Outdoor Leadership School for providing a course scholarship for field training and to the Stony Brook Science Training & Research to Inform Decisions (STRIDE) Program, National Socio-Environmental Synthesis Center, IEEE Earthzine Writing Club, Antarctic Circumpolar Expedition Maritime University, and Polar Geospatial Center for additional training.

A very special thanks goes to my committee of Ian Stirling, Resit Akçakaya, and Lesley Thorne for their advice and mentoring.

And finally thank you to my family, friends, Murray, and Bailey for their endless support throughout this process.

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1. Introduction

1.1. SHIFTING BASELINES AND SPECIES RECOVERY

The loss of biodiversity is a major challenge facing conservation biologists in the Anthropocene. The impact of the human footprint is profound and lasting. Human societies alter the natural landscapes they inhabit through direct exploitation and indirect modification of natural features and assemblages (Crosby 2000; Jackson et al. 2001; Reynolds et al. 2001; Pinnegar and Engelhard 2008). The long history of human alteration of natural systems creates a quandary for modern ecologists and environmental managers: what is 'natural' for any given ecosystem? Indeed, recent work by Akçakaya et al. (2018) argues that historical baselines are essential in assessing the recovery status of threatened species and should be implemented in the forthcoming International Union of Conservation of Nature (IUCN) Green List of Species, which was mandated by a 2012 resolution of IUCN members.

It is well documented, however, that identifying appropriate baselines is challenging. In his seminal essay, Pauly (1995) drew attention to the “shifting baseline syndrome” in fisheries science. He argues that as each new generation of scientist assesses the environment around them, they impose a baseline standard of the state of the environment at the beginning of their careers to which all subsequent changes will be compared. But as each successive generation uses this metric, the baselines shift resulting in “a gradual accommodation of the creeping disappearance of resource species, and inappropriate reference points for evaluating economic losses resulting from overfishing, or for identifying targets for rehabilitation measures” (Pauly 1995). Studies have demonstrated shifting baseline syndrome in a variety of ecological systems, ranging from African bushmeat hunters (Papworth et al. 2009), California oak savannas (Whipple et al. 2011), British bird populations (Papworth et al. 2009), and Chinese tropical forests (Kai et al. 2014). While it is often possible to identify shifting baselines over the short term, identifying changes occurring over long time scales is much more difficult, especially in places with limited human habitation and a sparse historical record. As noted by Pauly (1995), the only method to overcome shifting baseline syndrome is to incorporate historical data into frameworks of environmental management. It is thus of critical importance to identify appropriate metrics against which to evaluate environmental change. In many cases, this requires the reconstruction of any history of exploitation and management of populations.

Several studies have focused on the recovery potential of species from persistent exploitation (Hutchings 2000; Jennings 2001; Fortune, et al. 2013) and found that recovery is determined by the population size, intrinsic rate of population growth, and the rate of recruitment into the breeding population. In practice, this makes the study of population recovery from harvesting complex and studies of collapsed marine fish stocks have suggested that recovery from overexploitation is unlikely, even in these r-selected species (Hutchings 2000). Riedman (1991) noted that recovery from harvesting by K-selected marine mammal species tends to be slow and arduous, though some pinniped species, including the Northern elephant seal, have revealed remarkable resilience (Stewart et al. 1994). Importantly, the ecosystems in which these organisms currently live may be fundamentally different from historical analogues. Many studies have suggested that this return to a no-analog state may explain failures in fishery recovery of Northwest Atlantic fish stocks (Richardson et al. 2011; Steneck et al. 2013). Overall, the dynamics of species recovery from persistent harvesting are complex and often poorly understood.

1.2. DECLINE AND RECOVERY OF KING PENGUINS AND ANTARCTIC FUR SEALS AT SOUTH GEORGIA

To assess recovery dynamics, I reconstruct the historical population data and estimated current abundance of two species: king penguins (*Aptenodytes patagonicus*) and Antarctic fur seals (*Arctocephalus gazella*) (Figure 1.1). These are considered sub-Antarctic species, favoring the warmer, ice-free waters to the north of the Antarctic continent, and their current distribution closely tracks the maximum sea ice extent. Both species were historically harvested and currently maintain large breeding populations on the sub-Antarctic island of South Georgia. This 170 km long crescent-shaped island lies in the Atlantic sector of the Southern Ocean, 1,450 km away and across the Antarctic Front from the closest point of land (Figure 1.2). Due to its location in the midst of the Polar Front region, South Georgia is geographically and ecologically isolated from nearby land masses. Upon its discovery and exploration in the late eighteenth century, South Georgia became a hub for the exploitation of seals, whales, and, to a lesser extent, penguins. In fact, throughout the nineteenth and twentieth century, South Georgia was considered the primary location for all land-based whaling in the Southern Ocean (Headland 1984) and hosted six permanent shore-based whaling stations (Bannister 1964). Because of its complex geography and oceanography, the species inhabiting and breeding on South Georgia are quite isolated. South Georgia is the second largest of the sub-Antarctic islands with over half of its total 3,755 km^2 surface area covered with permanent snow and ice. The highest of the sub-Antarctic islands, two mountain chains, the Allardyce and Salvesen Ranges form a ridge running the entire length of the island, effectively isolating the southern and northern coasts and offering the northern side of the island protection from the prevailing southwest winds. Because of this, the regional climate of the northern coast tends to be much milder and less glaciated than that of the south and is home to a greater diversity of wildlife. South Georgia's close proximity to the productive foraging grounds of the Polar Front, located only 350 km to the north, has led some researchers to identify the island as a hotspot for potential range limits (Boyd et al. 1998; Guinet et al. 2001; Biuw et al. 2009; Scheffer et al. 2010). Furthermore, under recent oceanographic models, climate change is expected to shift the Polar Front closer to South Georgia. Recent studies have suggested that South Georgia is one of the only sub-Antarctic islands expected to experience this convergent shift of the Front and thus may be an important refugium for sub-Antarctic species in the coming centuries (Cristofari et al. 2018).

The king penguins of South Georgia have experienced dramatic increases in their populations over the last 100 years, and recent observations suggest a forthcoming range expansion (Petry et al. 2013; Juares et al. 2014; Juares et al. 2017) with migrants likely originating from the South Georgia population (Juáres et al. 2014; Clucas et a. 2016). The king penguin is the second-largest species of penguin, consisting of two subspecies defined by their range. *A. p. patagonicus* is found in the Atlantic sector of the Southern Ocean, while *A. p. halli* are found in all other sectors. This central place forager's diet consists mostly of small lanternfish of the family *Myctophidae* and various species of squid. Of the *A. p. patagonicus* populations, South Georgia is home to the largest number of breeding individuals. Furthermore, recent research has suggested that the South Georgia population of king penguins is one of only two extant populations expected to experience this convergent shift of the Front, where foraging grounds will move closer to breeding colonies and thus may be an important refugium allowing the species to persist under current models of climate change (Cristofari et al. 2018). In identifying these potential future population trends, however, it becomes necessary to consider the historical ecology of the species, as well. King penguins likely experienced significant harvesting pressure throughout the 18th and 19th centuries. Several historical accounts have cited the use of king penguin skins to fuel the tripots used to process elephant seal oil, feathers to decorate shoes, and eggs for food and decoration (Debenham 1945; Murphy 1915; Headland 1984; Headland pers. com. 2015). While the number of penguins harvested likely pales in comparison with the contemporaneous whaling and sealing industries, historic reports also suggest that there were fewer penguins on the island, so any harvest from these populations may have had an enormous effect on the population as a whole.

The life cycle of king penguins is unusually complex which poses difficulties for modelling their population dynamics. This is the only penguin species whose breeding cycle lasts more than a full calendar year and, consequently, there is a much lower rate of inter-annual monogamy. Stonehouse (1956) observed a single colony of king penguins at Ample Bay on South Georgia and suggested that their breeding cycle lasts approximately 14 months from egg laying to chick fledging. He proposed that chick fledging success was highest when adults bred early, with egg laying in December and hatching in late January, because first-year chicks are left at the colony over the austral winter and receive only sporadic parental care and feeding during this period. Consequently, chicks born to late-breeding adults enter the overwintering period with a lower body mass than earlier hatched chicks and thus are prone to starvation and insufficient thermoregulation (Stier et al. 2014). King penguins are also likely subject to substantial Allee effects. The combined effect of aerial predators and extreme overwinter weather leave chicks extremely vulnerable outside of the crèche. LeBohec et al. (2005) demonstrated the importance of crèche size and concluded that “crèching behavior in king penguins is a strategy that protects chicks from adult aggression, predation, and severe weather.” Due to this staggered breeding, individuals are present at the colony throughout the year, with different “waves” of chicks residing at the colony contemporaneously.

While records clearly indicate the growth of king penguin populations across their range (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009), estimates of abundance and hence analyses of trends are complicated by this unusual breeding phenology. Since the number of chicks and attending adults varies over the course of the year, it is difficult to directly compare population estimates. Moreover, count data derived from infrequent survey opportunities, as in the case of South Georgia, will often differ with respect to their alignment with the colony's breeding phenology. While the challenge of establishing a precise trend in king penguin abundance at South Georgia remains an issue, anecdotal evidence (Clarke et al. 2012) suggests significant increases in abundance with potential consequences for the health of terrestrial vegetation and interspecific competition for habitat and resources (Bried and Jouventin 2002; Ellis 2005).

South Georgia is also the breeding grounds of the Antarctic fur seal. These are eared seals of the family Otariidae. They are largely a pelagic species, spending the majority of the year almost entirely at sea, but are considered highly philopatric and form large, dense colonies on land during the breeding season (Hoffman and Forcada 2012). All fur seal species are polygynous, breeding in a harem system with a single dominant male guarding several females for the duration of the breeding season. In the southern hemisphere fur seals, dominant males guard a spatially explicit patch, and maintain sole breeding rights to the females within their defended territory (Bonner 1968). Named for their dense fur coat, these seals were heavily exploited throughout the 19th century, and their large breeding aggregations made them relatively easy to hunt and particularly enticing for fur traders.

The Antarctic fur seal was harvested in particularly high numbers by British and American sealers, to the point where the species was considered by many to be ecologically and commercially extinct by the turn of the 20th century, with records of only the occasional observation of individuals. By the late 1930s, however, small breeding colonies were observed on South Georgia, and since that time the population has expanded rapidly. Currently, experts estimate that the South Georgia population consists of approximately 95% of all Antarctic fur seals. This dramatic recovery, however, has led to interesting consequences for the island's other key species. As early as 1985, the apparent population explosion of fur seals on South Georgia has caused concern. Bonner (1985) noted the substantial damage breeding fur seals cause to terrestrial vegetation, degrading the breeding habitat for ground-nesting birds native to the island. This concern has been renewed in recent years, following the 2018 completion of a multimillion dollar invasive rat and reindeer eradication program aimed at restoring habitat for native birds.

Additionally, the krill surplus hypothesis, proposed by Sladen (1964) and expanded by Laws (1977; 1985), posits that historic depletion of krill-eating whales in the Southern Ocean during the 20th century led to a surplus of unconsumed krill for other predators. It was during this time that fur seal populations began to recover, leading some to suggest that their continued population growth could be inhibiting the recovery of large whales (Hucke-Gaete et al. 2004) and causing a decline in some species of penguins (Trathan et al. 2012). Despite uncertainty surrounding the impact of the overexploitation of seals and whales, and recent scrutiny of the krill surplus hypothesis, it remains clear that the entire Southern Ocean ecosystem likely shifted in response to the depletion of whales in the Southern Ocean (Ballance et al. 2006; Ainley et al. 2007; Surma et al. 2014). Lastly, the current ubiquity of fur seals on South Georgia, and the growing number of tourists to the island (9,000 visitors in the 2016/17 austral summer; Waugh 2017), has set the stage for negative seal-human interactions. In the 2014/15 and 2015/16 austral summers, four tourists were bitten by fur seals, one of which required immediate medical evacuation

(Browning 2015; Browning 2016). The Government of South Georgia and the South Sandwich Islands, recognizing that increasing fur seal density presents a safety hazard, is currently working to establish protocols for visitor-seal interactions (McKee 2017).

Due to the substantial difficulty in surveying this species, because of the remoteness of South Georgia, large colony sizes, and highly aggressive nature of the adults, few studies of the current population on South Georgia exist. However, researchers and environmental managers have noted an increase in population and in recent years, they have increasingly been discussed as a nuisance species. As early as 1985, concern has been raised over the impact of fur seals on terrestrial vegetation, important breeding habitat for several flying bird species (Bonner 1985). Norton et al. (1997) further suggested that seal trampling may cause significant damage to vegetation and a 2013 study found that fur seals can act as ecosystem engineers, negatively impacting the native tussock grass and increasing the establishment of exotic vascular plants.

1.3. SATELLITE IMAGERY FOR MONITORING WILDLIFE POPULATIONS

While remote sensing technologies have been available to address environmental research questions for more than 40 years, the spatial and temporal resolution has often prohibited its use to address research questions in population monitoring. Schwaller et al. (1984) pioneered the use of satellite imagery to monitor populations, demonstrating that 15 meter resolution Landsat satellite imagery could be used to assess Adélie penguin (*Pygoscelis adeliae*) colonies. Since that time, technological advances increasing the spatial resolution of satellite imagery allow for the detection of species which was previously impossible. Currently, commercially available high-resolution satellite imagery can have a sub-meter spatial resolution and the use of such very high resolution (VHR) imagery has been used to assess populations of penguins (Fretwell et al. 2012;

Naveen et al. 2012; Lynch and LaRue 2014), albatross (Fretwell et al. 2017), wombats (Swinbourne et al. 2018), polar bears (Stapleton et al. 2014), African megafauna (Yang et al. 2014), and whales (Fretwell et al. 2014), among other species. While the use of VHR satellite imagery has expanded in the last decade, the technology is still underutilized but has the potential to be a revolutionary new technology in wildlife monitoring, particularly for populations that are remote, inaccessible, large, and aggressive, and thus would be logistically difficult to survey using traditional *in situ* methods.

Figure 1.1. (a) King penguins and (b) Antarctic fur seals on South Georgia.

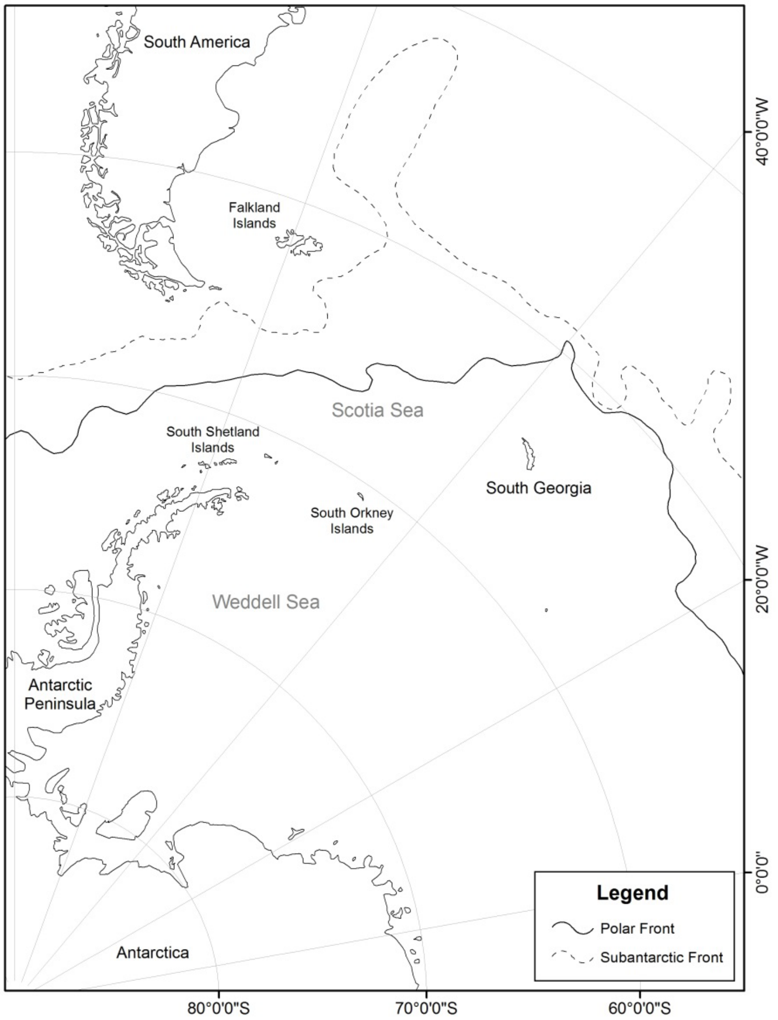

Figure 1.2. Map of Atlantic Sector of Southern Ocean.

2. King penguin populations increase on South Georgia but explanations remain elusive

2.1. ABSTRACT

While dramatic increases in populations of king penguins (*Aptenodytes patagonicus*) have been documented throughout their range, population changes on the island of South Georgia have not been assessed. I reconstructed time series of population size for six major colonies across South Georgia using historical data stretching back to 1883 and new population estimates derived from direct on-the-ground censuses and oblique, high-resolution digital photographs. I find evidence for a significant increase in the population of king penguins at all colonies examined over the 124 years of available survey data. I discuss my findings in the context of four established hypotheses explaining king penguin population growth: (1) favorable changes in the pelagic food web; (2) climate forcing; (3) greater availability of breeding habitat; and (4) the cessation of harvesting. While I do find evidence that glacial retreat may have increased suitable breeding habitat at some colonies and facilitated population expansion, glacial retreat is not associated with all of South Georgia's growing populations. Local anomalies in sea surface temperature have increased in parallel with king penguin population growth rate, suggesting that climate forcing may contribute to colony growth, but a complete explanation for the island's rapidly growing king penguin population remains unclear.

2.2. INTRODUCTION

Since the cessation of most whaling and sealing operations, the sub-Antarctic islands have seen dramatic changes in ecosystem structure and composition. King penguin (*Aptenodytes patagonicus*) populations have received substantial attention because they were harvested in great numbers for their oil (Bost et al. 2013) during the sealing epoch of the nineteenth and twentieth centuries. Populations on some islands, notably Heard and Macquarie Islands in the Indian and Pacific Ocean sector of the Southern Ocean, respectively, suffered substantial declines and even local extirpation (Budd 2000; van den Hoff et al. 2009; Bost et al. 2013), but relatively little is known about the historic abundance, dynamics, or demographics of king penguin colonies in the Atlantic sector of the Southern Ocean, notably South Georgia, the centroid of king penguin abundance within the region.

While island-wide king penguin surveys are not regularly conducted at South Georgia, the island is thought to possess the largest breeding colony of the *A. patagonicus patagonicus* subspecies of king penguin. Trathan et al. (1996) estimated there could be as many as 650,000 breeding pairs assuming a constant growth rate since 1976. In a more recent attempt, the IUCN estimates that the current breeding population consists of 450,000 pairs (BirdLife International 2017). This, however, is only a rough estimate, as an island-wide survey of king penguins has never been conducted. Our understanding of their population dynamics is complicated by the fact that recovery from historic exploitation is now occurring alongside environmental fluctuations due to climate change (Jacka and Budd 1998; Gille 2002; Curran et al. 2003; Trathan et al. 2007). Additionally, while records clearly indicate the growth of king penguin populations across their range (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009), estimates of abundance and hence analyses of trends are complicated by their unusual breeding phenology. Since the number of chicks and attending adults varies over the course of the year, it is difficult to directly compare population estimates. Moreover, count data derived from infrequent logistical survey opportunities, as in the case of South Georgia, will often differ with respect to their alignment with the colony's breeding phenology. While the challenge of establishing a precise trend in king penguin abundance at South Georgia remains an issue, anecdotal evidence (Clarke et al. 2012) suggests significant increases in abundance however closer examination of those trends is necessary.

On other islands in the sub-Antarctic, four hypotheses have been proposed to explain population increases of king penguins (Conroy and White 1973). The first hypothesis suggests that changes in the pelagic food web have led to favorable conditions for king penguins (Sladen 1964; Laws 1973). Second, climate forcing has been suggested as a potential driver of population increases. Third, it has been proposed that king penguin colonies are limited by the availability of breeding habitat, as discussed by Delord et al. (2004) based on observations at Crozet archipelago. Lastly, the cessation of penguin harvesting has been proposed as an explanation for population increases on other sub-Antarctic islands, though there is little evidence to suggest a substantial industry in hunting king penguins on South Georgia.

While some work has been conducted to understand how the population of king penguins has changed on South Georgia (Poncet and Crosbie 2005), there are no published reports of population trend or abundance from within the last 10 years. Additionally, because many of the king penguin colonies on South Georgia are so large, direct ground counting of individuals, which had been the method used for previous surveys, is no longer feasible for much of the population. In response to these issues, I sought to: (1) develop the appropriate methods and best practices to census king penguin populations; and (2) identify population trends of king penguin colonies on South Georgia and explore their potential drivers. Better identifying the important drivers of change for king penguins will facilitate our understanding of their dynamics under climate change and their likely impact on the ecological community of South Georgia.

2.3. METHODS

2.3.1. Estimation of abundance

King penguin breeding populations on South Georgia have been surveyed intermittently since the late 1800s. However, due to their inaccessibility and the unusual breeding phenology of the species, creating a coherent time series from these previous censuses is difficult. I used a two-pronged approach to develop time series of abundance at six of South Georgia's king penguin colonies: (1) ground-based digital photographic counts were conducted for recently visited colonies and (2) historical data were collected from available scientific reports and expedition notes. Where known, the timing of each census was defined as either "optimal" or "suboptimal". Optimal nest and chick censuses were conducted January 15th–February 15th and October 1st–November 15th, respectively. Photographs and ground counts were collected opportunistically at these six colonies between October 2014 and February 2017. Direct in situ counts were conducted and, where feasible, replicated three times by one or more trained observers. Larger colonies (> 5000 pairs; see Online Resource) required counts to be made from photographs. Digital photographs used for counting were taken from multiple viewpoints at higher elevation locations surrounding the colony. For the largest colonies, a GigaPan EpicPro robotic camera head was used to automate and assemble panoramas of the entire colony, which were then stitched using Microsoft Research's Image Composite Editor software.

Abundance was calculated by identifying nesting and loafing adults and chicks in each panorama. Nesting penguins were defined as those actively incubating eggs or chicks. Loafing penguins were defined as any penguin in adult plumage at the colony which was not actively incubating eggs or chicks. Incubating penguins can be easily identified by their posture (Figure 2.1), as incubating penguins maintain a "c-shaped" body position, observable from any angle, and a folded brood patch. At least one panorama from each site was counted independently by two or more trained observers. Observers conducted all counts manually labeling each individual using ArcMap software. Wherever possible, panoramas captured from different vantage points were used to estimate the error associated with obstructed views of penguins within the colony. Taken together, this information was used to estimate the overall precision of population estimates derived using photographs.

Historic data were collected from scientific reports and expedition notes (Conroy and White 1973; Lewis Smith and Tallowin 1979; Clark 1984, 1985; Trathan et al. 1996; Poncet and Crosbie 2005; Poncet Unpublished). Only data with estimates associated with individual colonies were used in the present analysis. Count data were classified according to the type of count (individual, adult, chick, pair, etc.) and, when known, the timing of the count.

2.3.2. Population models

Only historic counts that included breeding season, location, and information on count type (individuals, adults, breeding adults, or chicks) were included in the time series. Given the scarcity of existing data even for the six relatively well-surveyed colonies examined (Gold Harbour, Right Whale Bay, Brisbane Point at Royal Bay, Salisbury Plain, St. Andrew's Bay, and Whistle Cove at Fortuna Bay; Figure 2.2), I fit simple log-linear models to the abundance data available. This approach allowed us to estimate the average population growth rate for the site, though it did not allow us to investigate nonlinear or cyclic dynamics that may capture fluctuations in abundance over shorter time scales (Woehler et al. 2001; Delord et al. 2004).

2.3.3. Drivers of population change

To determine whether glacial retreat might explain why king penguin colonies on South Georgia were growing, I used data on glacial front locations from Cook et al. (2010) to quantify the change in glacial area between 1958 and 2003–2008 to determine if there was a correlation between glacial retreat and colony growth. Colonies were identified as being in close proximity to a glacier if they were within 1 km from a glacial front in 1958, and distant from a glacier if they were more than 1 km from a glacial front in 1958. For this analysis, I included three colonies (Ample Bay, Cooper Bay, and Elsehul) in addition to the six for which I were able to construct reasonably complete time series, as they provide additional information on trends at colonies proximal (Ample Bay) and distant (Cooper Bay and Elsehul) from glaciers.

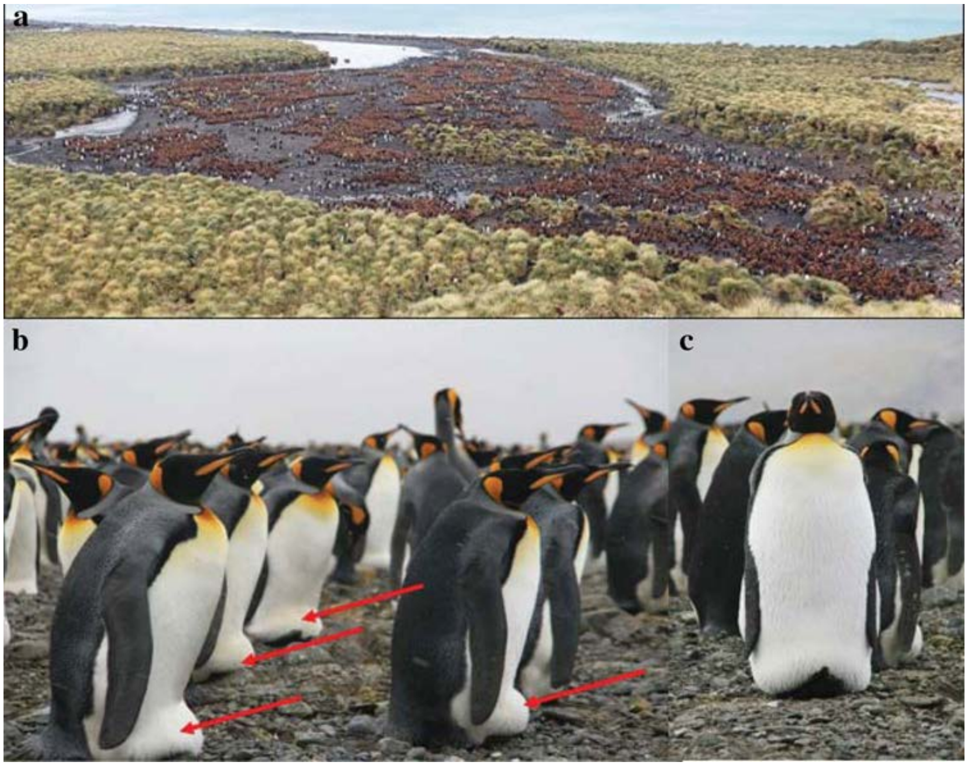

Figure 2.1. King penguin high-resolution digital photography survey methods. High-resolution photographs were used to create panoramas of breeding colonies (a) which were used to quantify chicks and nesting adults. Nesting (b) and loafing (c) king penguins are distinguished by their posture. The brood patch of nesting penguins is folded over the egg, resting on the feet (arrows), as penguins lean forward. Loafing penguins frequently rest leaning back on the heels of the feet with the metatarsals exposed.

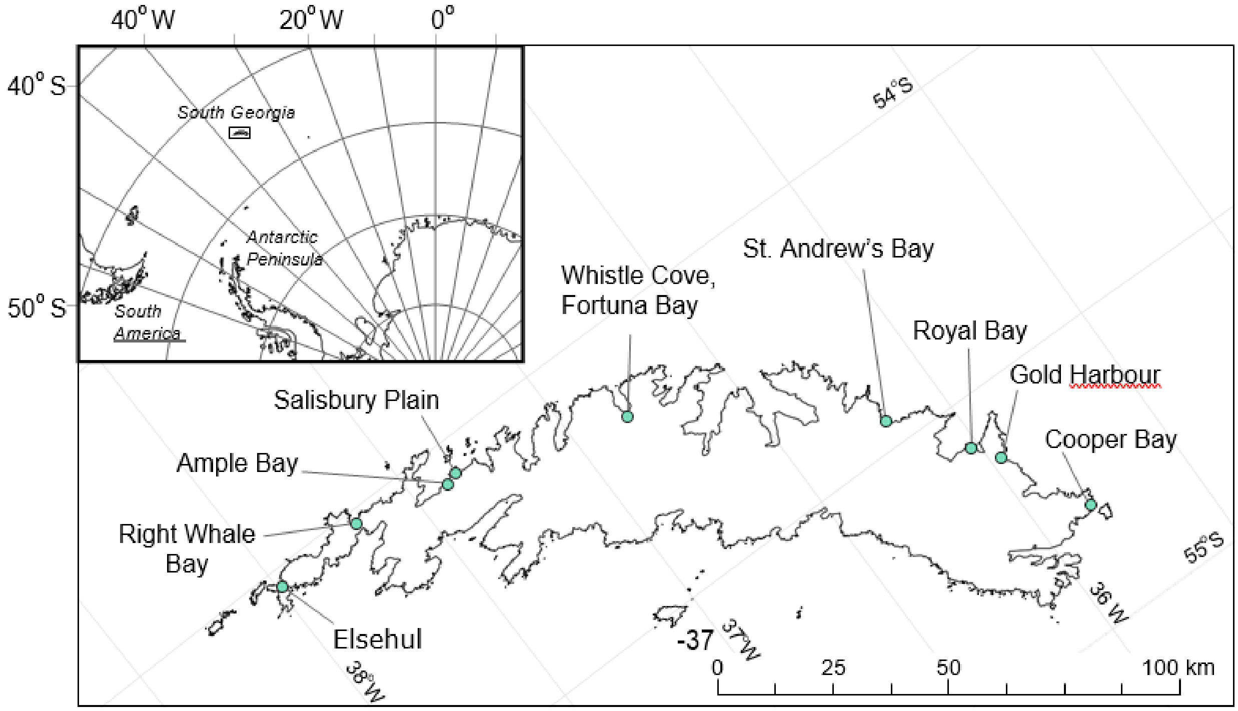

Figure 2.2. South Georgia is located in the Atlantic Sector of the Southern Ocean. Reference colony locations described in this chapter are highlighted

2.5. RESULTS

2.5.1. Population models

The longest time series obtained was from St. Andrew's Bay, where the 19 available census counts stretch back to 1883. The earliest records from Whistle Cove at Fortuna Bay were from 1905, creating a data set spanning 110 years. At three colonies, Right Whale Bay, Brisbane Point at Royal Bay, and Salisbury Plain, the earliest observations were recorded from 1914, creating a 100-year data set (n = 4, 9, 14, respectively). Lastly, the earliest reports from Gold Harbour were from 1936, creating a 79-year data set (n = 22).

Of the 33 duplicate colony counts (same panoramic, different observers), interobserver error rates ranged from 3 to 10%. Errors associated with different vantage points ranged from 0 to 47%. Larger errors associated with different vantage points were due to obstructed views in some photographs. In these instances, the census derived from the larger estimate was used. Across the six colonies evaluated, dramatic population increases were apparent, despite considerable interannual variation (Figure 2.3). The rate of increase predicted by the log-linear models varied across colonies (Table 2.1) with the fastest rate of increase observed at Whistle Cove (4.3% per year) and the slowest rate of increase at Royal Bay (0.7% per year). The mean rate of increase was 1.6% per year (SD 1.4%).

2.5.2. Glacial retreat as a driver of population change

Six colonies in close proximity to glaciers were identified (Ample Bay, Whistle Cove, Gold Harbour, Brisbane Point at Royal Bay, Salisbury Plain, and St. Andrew's Bay). Retreat of the glacial front was prevalent across all of these sites, and in some cases, the present king penguin colony extent was completely within areas covered by the glacier for much of the time series (Figure 2.4). While there is a weak, positive correlation between net annual glacial retreat and king penguin growth rate (slope = 0.43, R2 = 0.12), this relationship is not statistically significant (p = 0.28) and the degree of causality is ambiguous (Figure 2.5a). Cooper Bay, Elsehul, and Right Whale Bay are three colonies that are not within 1 km of a glacier but have grown in size nonetheless over the available time series (Figure 2.5b).

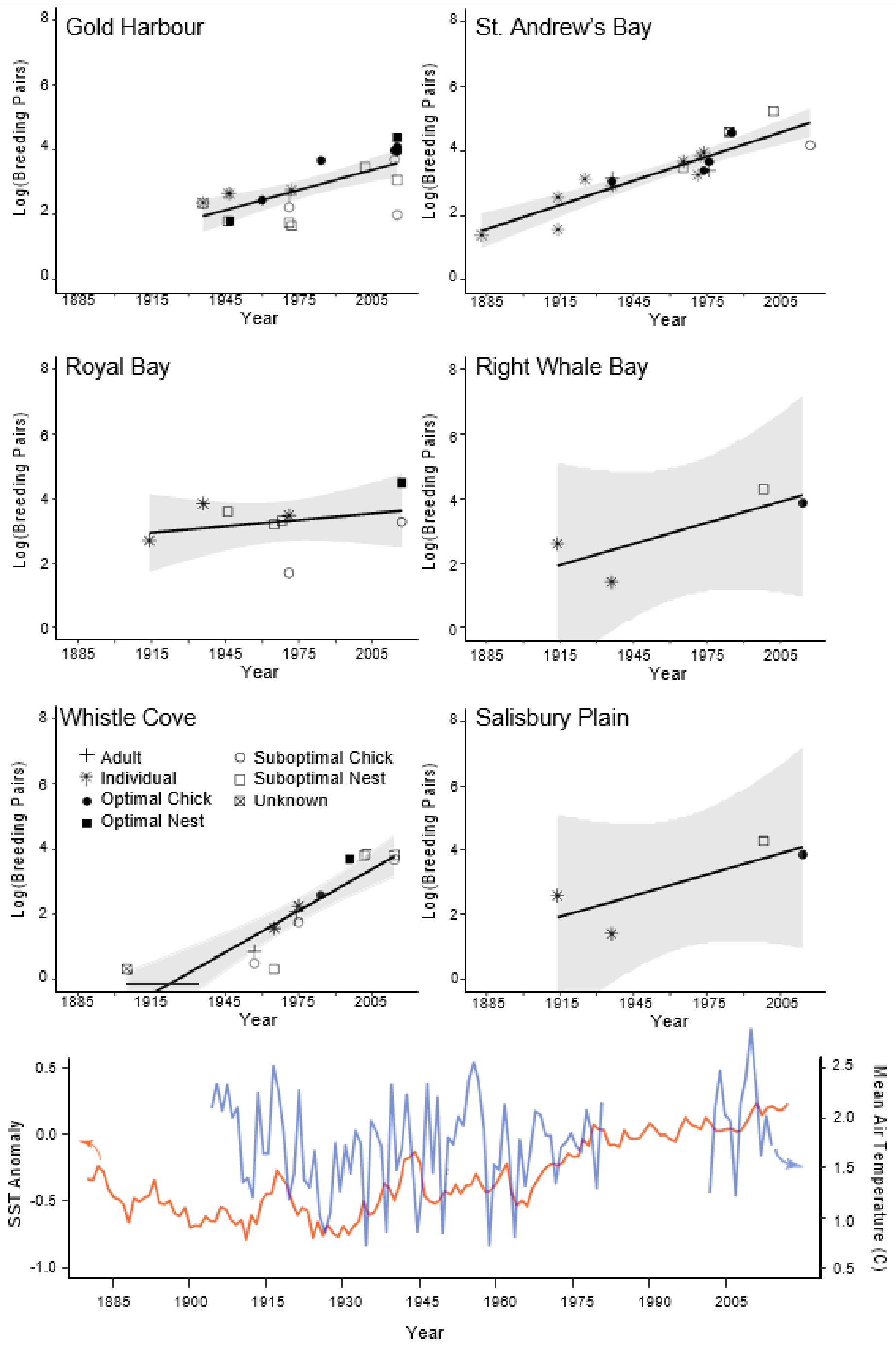

Figure 2.3. King penguin breeding colony population change at Gold Harbour, St. Andrew's Bay, Royal Bay, Right Whale Bay, Whistle Cove, and Salisbury Plain (top) and regional air temperature (blue; Turner et al. 2004) and ocean temperature anomalies (red; Boyin et al. 2015) over the same period (bottom). Symbols denote count type: Adults (X); individuals (∗); chicks (○); and nests (□) or unknown (⊕). Filled symbols indicate the optimal timing of the census. Open symbols denote censuses with suboptimal or unknown timing.

Table 2.1. Model description for the population growth at six colonies across South Georgia.

Colony	Latitude	Longitude	Model	R^2
Gold Harbour	−54.6188	−35.9457	0.007	0.508
Royal Bay	−54.5764	−36.0128	0.007	0.086
St. Andrew’s Bay	−54.4473	−36.1810	0.026	0.792
Whistle Cove, Fortuna Bay	−54.1402	−36.8218	0.043	0.774
Right Whale Bay	−54.0158	−37.6814	0.022	0.651
Salisbury Plain	−54.0544	−37.3402	0.014	0.600

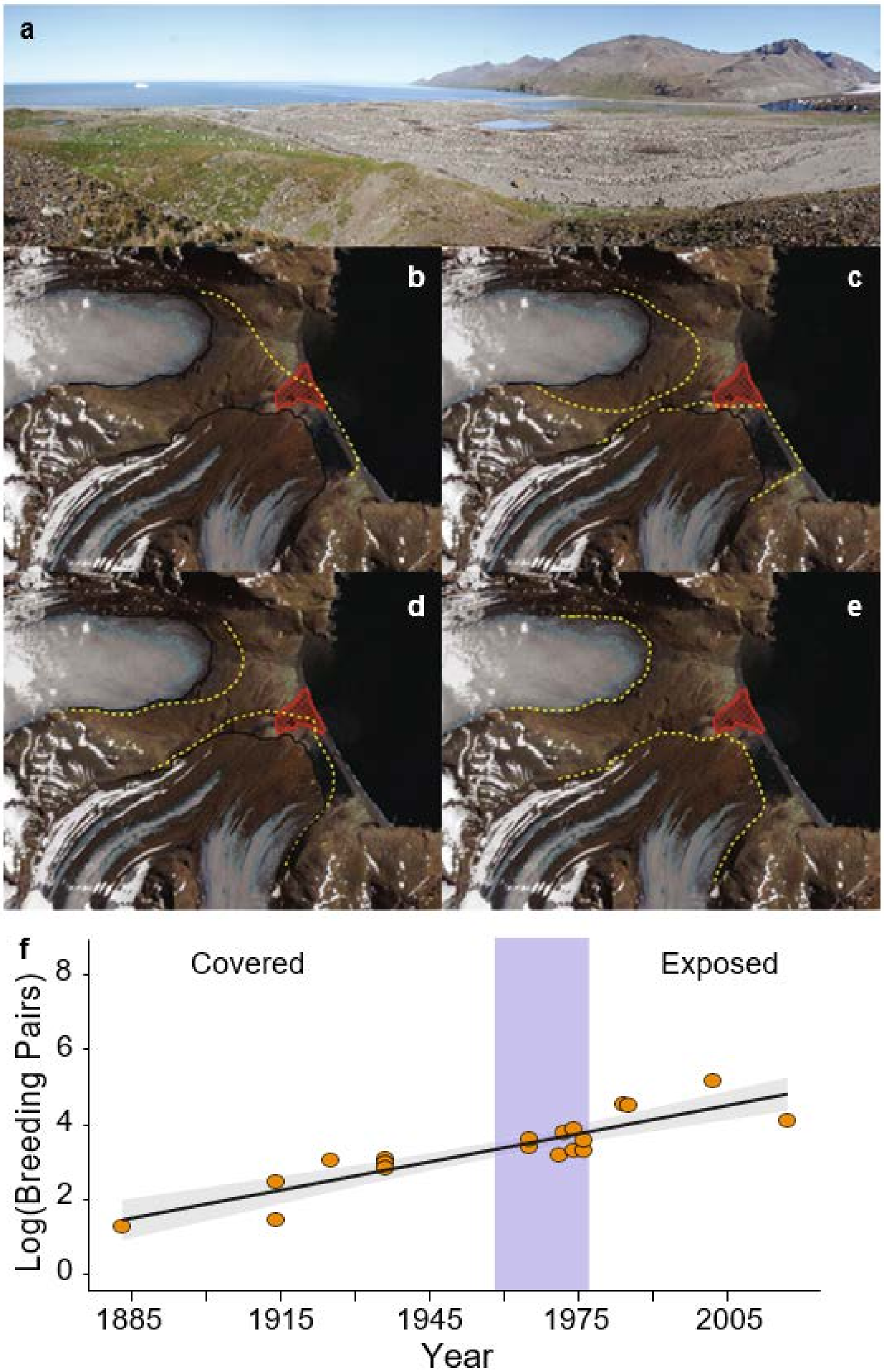

Figure 2.4. Glacial retreat on South Georgia has been implicated as a potential driver for king penguin population growth. Sites such as St. Andrew's Bay have experienced substantial glacial retreat exposing the (a) current extent of the expanded breeding colony. The glacial front [yellow dashed line; background image: Landsat 2002/03 image mosaic (British Antarctic Survey 2018)] has consistently receded since observations in 1958 (b), 1977 (c) and 1993 (d). Red hatched area indicates current colony extent. The last reported glacial front location was recorded in 2003 (e), and leaves the entire current colony exposed. Population data (f) collected during the window of rapid glacial retreat which left the modern colony exposed (blue shaded region) indicates that this was likely a period of rapid population growth.

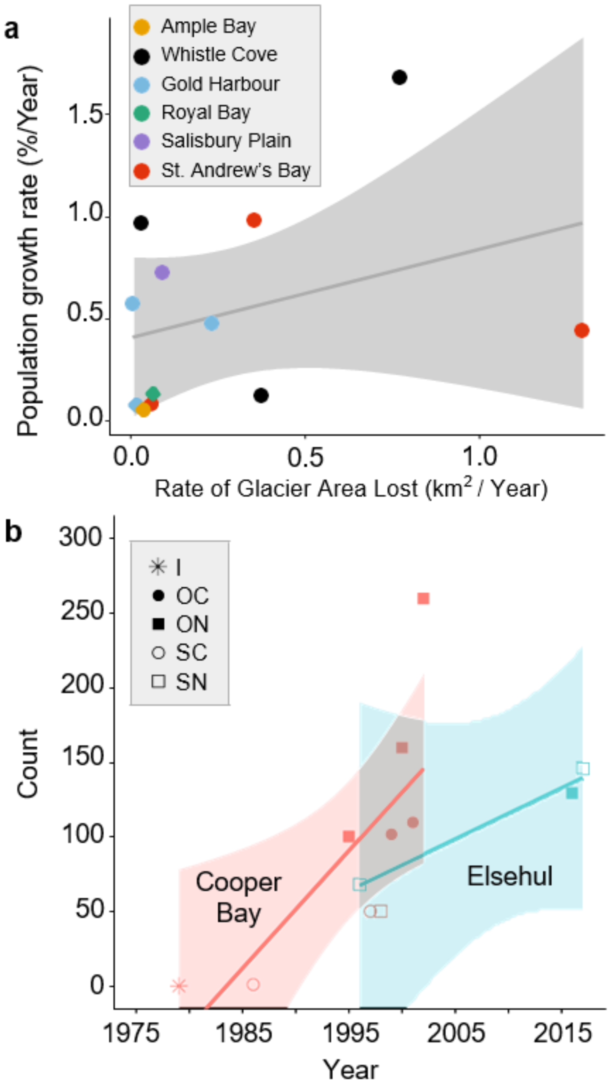

Figure 2.5. While there is a weak, positive relationship between annual population growth rate and net glacial retreat (a), the causality is ambiguous. At other colonies (b), such as Cooper Bay and Elsehul, there is no evidence of recent glacial retreat, however, the populations have experienced consistent growth. Symbols denote count type: Individuals (∗); chicks (○); and nests (☐) or unknown (⟐). Filled symbols indicate the optimal timing of the census. Open symbols denote censuses with suboptimal or unknown timing.

2.6. DISCUSSION

Despite limitations imposed by poor historical data and a complex breeding phenology, king penguin populations on South Georgia have unambiguously increased over the last century (Figure 2.3). This is consistent with observations of king penguin populations on other sub-Antarctic islands, which have also increased in abundance over the last century (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009). Conroy and White (1973) proposed four primary hypotheses to explain the increases observed in king penguin populations. First, scientists have proposed that the removal of large whales and seals have allowed for a surplus of food—namely Antarctic krill (*Euphausia superba*)—for marine mesopredators (Sladen 1964; Laws 1973). This Krill Surplus Hypothesis is often cited as a potential driver for rapid increases in seal and penguin populations throughout the Antarctic. These effects become more complex in the case of king penguins, whose diet consists primarily of myctophid fish throughout much of their range (Olsson and North 1997; Raclot et al. 1998). The degree to which these fish use krill resources is unclear (Williams 1985; Lancraft et al. 1989; Pakhomov et al. 1996; Pusch et al. 2004). Saunders et al. (2015) noted that the larger myctophid species consistently consumed Antarctic krill and estimated that myctophid predation could account for approximately 2% of the daily krill productivity in the Scotia Sea, amounting to nearly 17 million tons per year. In fact, it has been proposed that large myctophids could be the main consumer of krill in the Scotia Sea (Lancraft et al. 1989; Pusch et al. 2004; Hill et al. 2007), consistent with an apparent link between myctophid and krill abundance (Chamaillé-James et al. 2000). In contrast, Murphy et al. (2007) noted the importance of the mesopelagic myctophid pathway in the Atlantic Sector of the Southern Ocean while omitting the krill-myctophid link. Further complicating our understanding of the key trophic interactions, commercial fishing operations harvest Southern Ocean myctophids. An estimated 200,000 tons of myctophid biomass were extracted from the South Georgia region of the Southern Ocean between 1979 and 1992 (Collins et al. 2008). The link between the Krill Surplus Hypothesis and increasing king penguin populations is thus indirect. While the causal pathways remain unclear, several studies have implicated increased near-shore food availability with increases in king penguin populations (Crozet Islands: Weimerskirch et al. 1992; LeBohec et al. 2008; Trucchi et al. 2014; Heard Island: Budd 2000; South Georgia: Woehler and Croxall 1997).

The second hypothesis for king penguin population expansion focuses on the effect of climate forcing. There are two primary mechanisms through which climate might affect king penguin populations. Studies have found correlations between breeding success and the Southern Oscillation Index and associated changes in near-shore food availability (Delord et al. 2004; LeBohec et al. 2008). Indeed, Trucchi et al. (2014) suggested that recolonization of king penguins on the sub-Antarctic islands following the Last Glacial Maxima was likely due to climate forcing affecting food availability. Differences in the pelagic community between these sites may have important consequences in foraging dynamics across summer and winter seasons. Studies have demonstrated a link between king penguin foraging habitat and oceanographic conditions (Jouventin et al. 1994), however, the relationship may be complicated by behavioral differences across the breeding cycle. Jouventin et al. (1994) noted a preference for foraging near the 5 °C isotherm, which is associated with the Polar Front (Jouventin et al. 1994), but during brooding, they preferentially forage at the Southern Antarctic Circumpolar Current, located much closer to breeding colonies (Trathan et al. 2008). Additionally, recent studies have suggested that a shift in the Polar Front's location, which is expected under most current climate models (Turner et al. 2014; Gutt et al. 2015) and has already been observed (Sokolov and

Rintoul 2009), will likely have profound negative impacts on king penguin populations (LeBohec et al. 2008).

Impacts of increasing sea surface (SST) and air temperature may have more direct impacts on breeding colonies. Studies have demonstrated regional increases in mean SST across the sub-Antarctic (Boyin et al. 2015), and more fine-scale analyses have demonstrated significant warming of the waters around South Georgia over the twentieth century (Figure 2.3; Whitehouse et al. 2008). Such changes in ocean conditions within the region have been linked to declining habitat suitability for lower trophic level species in the sub-Antarctic (Whitehouse et al. 2008). Changes in mean air temperature could also have important implications for king penguin population dynamics (Figure 2.3; Turner et al. 2004). Increases in winter air temperature have been linked to wetter winter conditions in the region (Summerhayes 2009; Constable et al. 2014; Gutt et al. 2015). Because chicks over-winter at breeding colonies in their downy plumage, they are more sensitive to changes in precipitation, particularly during colder weather (Boersma 2008; Chapman et al. 2011; Ropert-Courdert et al. 2014).

The third hypothesis proposes that king penguin populations are limited by the availability of breeding habitat. Indeed, this was proposed as a possible mechanism regulating the population size of king penguins on the Crozet archipelago, where the rate of population growth declined in association with a lack of suitable, flat, vegetation-free areas for nesting (Delord et al. 2004). On South Georgia, 50% of the island is glaciated and a large proportion of the remaining area is highly vegetated (Cook et al. 2010), which raises the possibility that habitat for incubation and crèching may be a limiting factor. At the same time, however, there are many coastal areas free of permanent snow and ice that might provide breeding habitat. At present it is difficult to determine whether king penguins are habitat limited because I lack a fine-grained suitability model and suitable breeding habitat requirements are often difficult to determine in seabirds because they frequently congregate in small areas, leaving apparently suitable habitat space unoccupied (Bried and Jouventin 2002). Regardless of its potential role as a limiting factor island-wide, recent analyses have indicated that 97% of the 103 coastal glaciers on the island have retreated over the last 70 years (Cook et al. 2010) and, in doing so, may have exposed additional suitable habitat for king penguin breeding colonies near the glacier margins.

Our analysis suggests that glacial retreat may function as one mechanism for king penguin population regulation, however, there are likely other mechanisms involved as well. The Heaney and Cook Glaciers at St. Andrew's Bay have experienced a combined loss of nearly 6.5 km2 since 1958, and the current extent of the penguin colony is contained entirely within this recently exposed terrain (Figure 2.4). At other colonies, such as Cooper Bay, Elsehul, and Right Whale Bay, no substantial glacial retreat has been observed near the penguin colonies and other factors, separate from deglaciation, must be driving the increase in king penguin populations (Figure 2.3 & Figure 2.5). It is worth noting in this context that some king penguin colonies located in the Falkland Islands, which are not glaciated, have also experienced substantial population growth (Bingham 1998).

Lastly, and perhaps most obviously, the cessation of harvesting has been proposed as a primary driver of king penguin population increases. While this is certainly a plausible explanation for much of their distribution (Budd 1970; Rounsevell and Copson 1982), it fails to account for populations located on South Georgia, where it is unlikely a large-scale king penguin harvesting operation existed (Clarke et al. 2012). There is evidence, however, to suggest that small-scale harvesting almost certainly occurred and may have affected populations from small breeding colonies. Upon returning from his 1912–1913 trip to South Georgia, Robert Cushman

Murphy noted, “As an example of incidental vandalism, I saw many of the magnificent and rapidly disappearing king penguin (*Aptenodytes*) of the island destroyed in order that their gold-collared skins might be used as shoes by New Bedford sealers.” (Murphy 1915). Additionally, the Russian explorer Bellingshausen reported observing the use of king penguin skins to fuel sealing tripot fires during his 1819 trip to South Georgia (Debenham 1945). Despite little evidence supporting a large-scale king penguin harvest, the historical record suggests that some harvest did occur. If penguin populations during this time were already limited by other ecological factors, even small-scale harvesting would have the potential to inhibit already-depressed populations. Release from such harvest, especially if it co-occurred with release from other inhibiting factors, may have allowed for rapid population expansion.

2.6.1. Challenges of monitoring king penguin populations

Much interest has been focused on the issue of bias in wildlife survey methods (Pollock and Kendall 1987; Bart et al. 2004), however, most studies have focused only on the estimation of error associated with the counting of individuals present at the study site rather than the availability of individuals to be counted. In many populations, particularly asynchronous breeders like the king penguin, it cannot be assumed that all individuals are present at the time of surveying (Frederick et al. 2006). Indeed, studies have found substantial error associated with estimating population sizes of phenologically asynchronous bird species [47% in wading birds (Frederick et al. 2006) and 69–79% in shorebird populations (Farmer and Durbain 2006)], because there is no single time when all breeding individuals will be present at the colony. Future studies on king penguin populations should consider the impact of poorly timed surveys and should seek to minimize biases associated with incomplete colony attendance at the time of surveying. To best account for these biases, I propose a suite of best practices for the estimation of king penguin abundance on South Georgia that are easily tailored for populations elsewhere in their range. (1) Chick counts should be completed in early spring, between October 1st and November 15th. This will allow for the quantification of chicks that have successfully overwintered, but prior to fledging. (2) Nesting adult counts should be completed at peak nesting, between January 15th and February 15th. This will allow for the survey of both early and late breeding individuals at a single point in time, as this is when you would expect all breeding adults to be present and nesting at the colony. Explicit mathematical models of colony attendance and breeding phenology may be required to separate the underlying (but unknown) abundance of breeding pairs and the flux of individuals into and out of the population available for counting on any given day (e.g., Condit et al. 2007). In the meantime, only large changes occurring over long time scales are probably interpretable from simple census counts. Additionally, it is important to consider the impact of dispersal on the population dynamics across their range. While it is possible that such metapopulation dynamics could play a role, Clucas et al. (2016) noted that while most other king penguin populations appear to be genetically homogenous, the South Georgia population of king penguins is significantly differentiated from all other sub-Antarctic populations. Thus, it seems that metapopulation dynamics could be important in other king penguin populations, but are likely less substantial in South Georgia.

2.6.2. Looking ahead

Surprisingly, the drivers allowing for dramatic growth in population remain elusive. Due to the lack of evidence for consistent harvesting of king penguins on South Georgia, release from harvesting pressure is unlikely to explain these increases. Additionally, while there does appear to be a relationship between glacial retreat and colony growth in some areas, glacial decline is not a necessary condition for king penguin population increases. Climate change may actually play a more direct role in the complex life cycle of the king penguin by controlling the extent to which king penguin chicks need to crèche. Studies have demonstrated that king penguin crèching behavior increases in colder and wetter weather (LeBohec et al. 2005) presumably because large breeding aggregations allow chicks to stay warm through the austral winter. Climate change in this region is predicted to cause warmer (though wetter) winters (Summerhayes 2009; Constable et al. 2014; Gutt et al. 2015), which may reduce the required crèche size and facilitate more successful colonization of new colonies. By highlighting past trends, underlying dynamics will help us understand their documented and likely continuing southward expansion to the Antarctic Peninsula region (Petry et al. 2013; Juáres et al. 2014; Juáres et al. 2017).

Notwithstanding the inherent challenges of assessing king penguin population abundance, populations at South Georgia appear to have followed similar trajectories of other sub-Antarctic island populations (Gales and Pemberton 1988; Budd 2000; Delord et al. 2004; van den Hoff et al. 2009). Historical and current survey methodologies, however, have failed to account for the demographic and population implications of the king penguin breeding cycle, leading to high errors associated with population estimates, and correction factors should be developed to account for temporal differences in monitoring efforts across breeding seasons. Moreover, while remote sensing methodologies may facilitate more regular monitoring of the abundance of South Georgia’s king penguin population, mark-recapture of individuals is likely required if I are to understand the demographic drivers of these observed population increases.

3. Correcting for within-season demographic turnover to estimate the island-wide population of king penguins on South Georgia

3.1. ABSTRACT

King penguins (*Aptenodytes patagonicus*) live in remote locations, in large colonies with asynchronous breeding. These three factors hinder the design and conduct of king penguin censuses, and assessments of trend often require piecing together mis-matched surveys of different demographic components. This study introduces a new method to remotely census these populations year-round and correct population estimates for the king penguin's unique breeding phenology. I combined *in situ* ground counts with estimates based on high-resolution satellite imagery to catalog the distribution of breeding colonies and estimate population abundance across the island of South Georgia, in the south Atlantic. While most king penguin populations are forecast to decline significantly over the next century, South Georgia is expected to experience more favorable conditions and represents an important refugium for the species, though the challenges of surveying king penguins have precluded a comprehensive census. Due to the variable timing of both *in situ* and remote counts, I developed a discrete time age- and stage-structured population model that provides stage- and day-specific correction factors for standardization of census counts. I estimate the current population of king penguins on South Georgia as 405,425 (95% CI: 102,624 - 2,375,061) breeding pairs and find that population trends that do not account for phenological biases persistently underestimate the population growth rate. Correction factors are highly sensitive to annual egg mortality and the total breeding population is best estimated using nest counts of early-breeding pairs. While asynchronously breeding species present a unique challenge to population monitoring, careful accounting of within-season dynamics can be used to assemble a self-consistent time series from heterogeneous survey data.

3.2. INTRODUCTION

Asynchronously breeding species present unique challenges to population monitoring, because there is no single point in the season where all potential breeders (or offspring) are available to be counted (Frederick et al. 2006; Williams et al. 2011). One striking example of this phenomenon can be found among king penguins (*Aptenodytes patagonicus*), which attempt to breed on an annual cycle even though successfully raising a chick to fledging requires more than a single year (Figure 3.1). This asynchrony has proven to be a persistent problem in population studies of this species, and, to date, has not been addressed in the literature. Furthermore, it has long been recognized, that penguin abundance estimates are sensitive to the timing of the survey relative to the breeding phenology of the species (Lynch et al. 2009; Southwell et al. 2010; McKinlay et al. 2010; Southwell et al. 2013), and that correction factors can be used to minimize bias stemming from mis-timed surveys. While it is difficult to estimate the total population size of asynchronously breeding species like the king penguin, doing so is a prerequisite for understanding how populations may be changing over time. This has become a pressing issue because king penguins, which act as central place foragers during the breeding season, live within a narrow latitudinal band near the polar front and north of the maximum sea ice extent, both of which will be impacted by future climate change (Cristofari et al. 2018). The proximity of the polar front to breeding colonies is of critical importance to the health of these populations, and dramatic shifts in the position of the polar front have been predicted (Cristofari et al. 2018). In association with these changes, population declines have been observed in breeding colonies located farther from the new polar front locations (Le Bohec 2008; Peron et al. 2012; Weimerskirch et al. 2018).

While Chapter 2 documented that king penguin populations have increased across the island over the last century, there are no recent estimates of the island-wide breeding population of king penguins. This is partially due to the remote location of South Georgia and to the difficulty in censusing large colonies. Trathan et al. (1996), having assumed populations had grown consistently since 1976, estimated as many as 650,000 breeding pairs on South Georgia in 1996, while the IUCN estimates a current breeding population of 450,000 pairs (BirdLife International 2017). This population represents a critical knowledge gap for these penguins, as South Georgia is home to what is thought to be the largest breeding colony of the *A. patagonicus patagonicus* subspecies, has been implicated as an important refugium from climate change, and is likely acting as a source population for emergent colonies further south in the South Shetland Islands (Petry et al. 2013; Juares et al. 2014; Juares et al. 2017).

While direct manual counting of individuals has been the method of surveying king penguin populations for nearly a century, high-resolution (sub-meter) satellite imagery has become increasingly valuable as a mechanism for studying wildlife in remote areas. Penguins provide an ideal target for remote survey due to their polar habitat, contrasting coloration, and relatively large body size, and previous studies have demonstrated the feasibility of satellite imagery to assess penguin populations (Fretwell et al. 2012; Naveen et al. 2012; Lynch et al. 2012; Lynch and LaRue 2014). Satellite imagery was identified as a possible mechanism for surveying king penguins as early as 1996 (Guinet et al. 1996), and a satellite census was recently published at Ile aux Cochons in the Crozet archipelago (Weimerskirch et al. 2018). Weimerskirch et al. (2018) noted a massive decline in the area occupied by the king penguin population, however they cautioned that estimating population size required an estimate of penguin density, which may be variable.

I use data from panoramic photographs and direct count surveys, supplemented with high-resolution satellite imagery to estimate the total population of king penguins breeding on South Georgia. Furthermore, I correct for differences in the timing of censuses by constructing a phenological model of the king penguin breeding cycle, from which I constructed daily correction factors. These correction factors are appropriate for application to both the satellite estimates I make herein, and to historical counts of king penguin populations. Combining these methods allows for the construction of a complete time series of king penguin populations and, for the first time, an estimate of the population at South Georgia based on direct observation of nearly all known colonies.

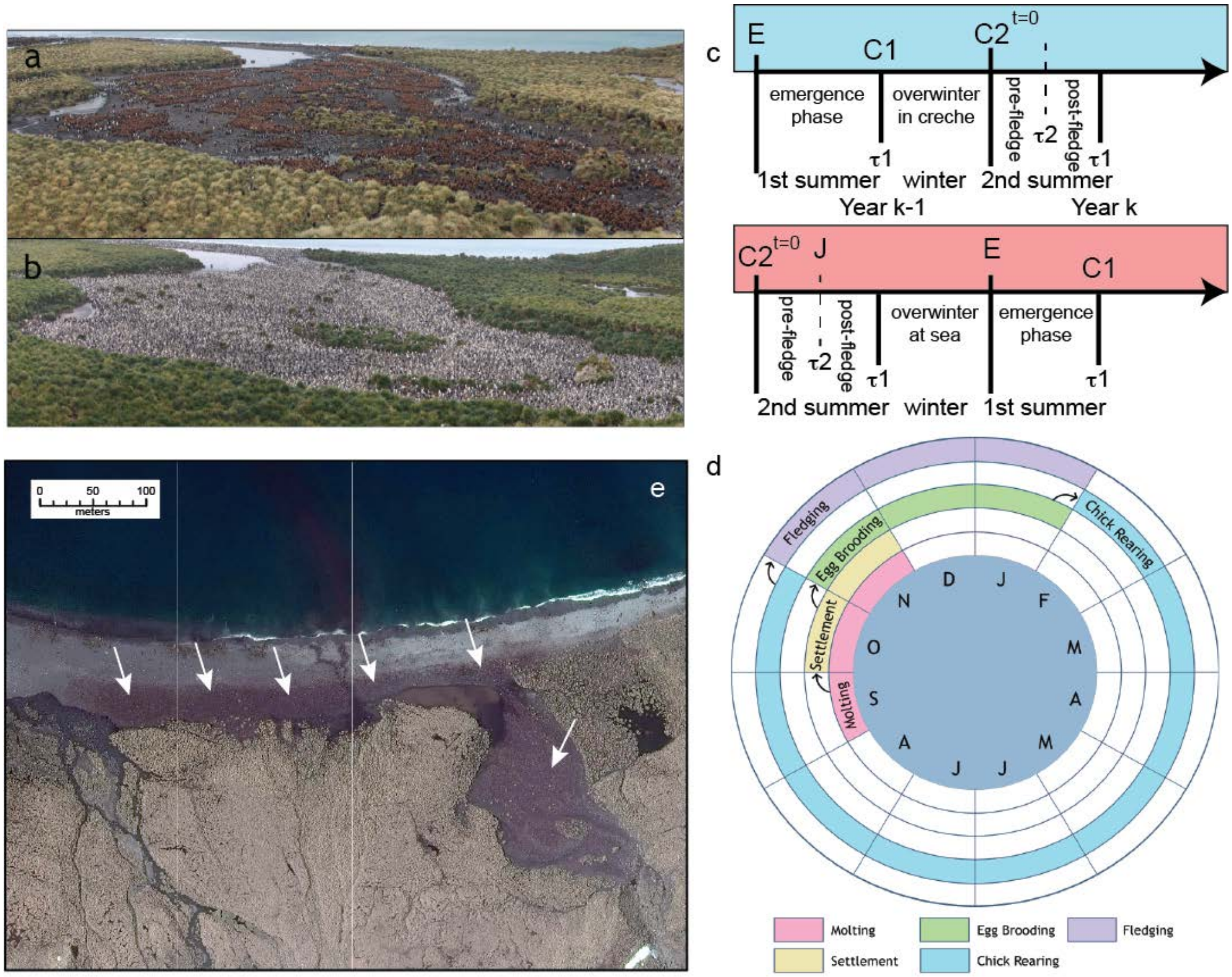

Figure 3.1. The king penguin colony at Gold Harbour, South Georgia, looks dramatically different depending upon the timing of visitation: (a) the colony is composed of mostly fledging chicks in early November, and (b) breeding adults in January. These temporal differences are due to the complex breeding cycle of king penguins (c), which is parameterized in the phenology model (d). (e) WorldView-3 satellite image of king penguin colony at Gold Harbour, South Georgia on November 15, 2015. The brownish-red areas (indicated by white arrows) are the king penguin colony. Image © 2015 DigitalGlobe, Inc.

3.3. METHODS

3.3.1. Survey of king penguin abundance

Commercially available, high-resolution satellite imagery (0.31-0.6 m resolution; DigitalGlobe, Longmont, Colorado, USA) was used to assess the presence and abundance of king penguin colonies on South Georgia. As a proof-of-concept, two independent reviewers digitized the colony area of three satellite images using ArcGIS (Figure A1.1). Total colony area was compared between reviewers and compared to ground counts of the total colony size that occurred within 15 days of satellite image acquisition. By pairing ground counts with satellite imagery, I estimated the apparent density of king penguins within the observed breeding colony.

After confirming that satellite imagery could be used to estimate king penguin populations, an island-wide search of the imagery was conducted. All records of king penguin breeding locations were obtained from the South Georgia GIS platform, maintained by the British Antarctic Survey. For each colony within the database, commercially available high-resolution satellite imagery was used to assess the likelihood for presence of breeding king penguin aggregations (Figure 3.1e). For any record where a penguin colony was not identified within the satellite imagery, the historical accounts of penguin presence were consulted to determine if the record accounted for presence or breeding. For all colonies where breeding was observable in the imagery, the colony perimeter was manually digitized in ArcGIS in at least one cloud-free satellite image. I constructed a comprehensive time-series of king penguin population growth by combining these estimates of abundance with historical time series identified by Foley et al. (2018) and additional previously unpublished ground counts of king penguin colonies using the methods described therein.

3.3.2. Phenology model

Due to the complex breeding cycle of king penguins, and the variable timing of previous surveys of abundance and image acquisition, I constructed a phenological model of king penguin population dynamics that focused on those portions of the life cycle that are routinely censused on shore: eggs, first-year chicks, second-year chicks, and reproductive adults. Due to the 14-month breeding cycle, the timing of egg-laying is determined, in part, according to the success or mortality of the breeding pair's last chick. To accommodate this two-phased breeding structure, I separate the production of eggs into early (I use the letter I for this 'initial' cohort to avoid confusion) and late (L) cohorts, yielding

$$E_k^I = \alpha_{E,k} B_k^I \quad \text{and} \quad E_k^L = \alpha_{E,k} B_k^L \tag{3.1}$$

where E_k and B_k are the number of eggs produced and the number of breeding pairs, respectively, in year k, and $\alpha_{E,k}$ is survivorship through the egg incubation stage to the point at which chicks are first visible in year k. Note that king penguins only lay a single egg at a time. Due to the variability in egg survivorship rates reported in the literature, survivorship was modeled as a stochastic process described by a Beta distribution consistent with previously published estimates by Weimerskirch et al. (1992), Williams (1995), and Schweizer (2016),

$$\alpha_{E,k} \sim Beta(\alpha = 2, \beta = 3)$$

where new estimates of egg survival were drawn independently in each year k (Figure 3.2a).

As chicks hatch, I follow two cohorts of first-year chicks (*C1*) which change on a daily basis according to:

$$C1_k^I(0) = C1_k^L(0) = 0 \tag{3.2a}$$

$$C1_k^I(t) = (1 - m_{C1}^I)^t * C1_k^I(t-1) + E_k^I g^I(t,\theta), \quad for \ \ 1 \le t \ \le \tau_1 \tag{3.2b}$$

$$C1_k^L(t) = (1 - m_{C1}^L)^t * C1_k^L(t-1) + E_k^L g^L(t,\theta), \quad for \ \ 1 \le t \ \le \tau_1 \tag{3.2c}$$

where $C1_k(t)$ is the number of first-year chicks on day *t* (Figure 3.1c) from either the Early ($C1_k^I(\tau_1)$) or Late cohorts ($C1_k^L(\tau_1)$), $g(t, \theta)$ is a probability mass function describing the Poisson process of chicks hatching from eggs as a function of time (Figure 3.2b), m_{C1} is the daily probability of mortality of first-year chicks, and τ_1 is the last day of the summer growing season. Note that $g^L(t, \theta)$ occurs later in the growing season than does $g^I(t, \theta)$, and therefore $C1_k^L(t) = 0$ for an extended period of time. Note further that the daily mortality risk differs between Early and Late cohort chicks during the growing season. This time-dependent model allows the estimation of day-specific correction factors that can be used to adjust chick counts recorded at a given census (Figure 3.2c).

As with mortality risks during the growing season, chicks in the two cohorts face different overwinter survivorship. Thus, the number of second-year chicks (*C2*) is governed by:

$$C2_k(t) = (1 - m_{C2})^t * [\alpha_{ow}^I C1_{k-1}^I(\tau_1) + \alpha_{ow}^L C1_{k-1}^L(\tau_1)] \ \ for \ \ 1 \le t \le \tau_2 \tag{3.3}$$

where α_{ow} is the overwintering survivorship of first-year chicks, and m_{C2} is the daily probability of mortality of second-year chicks from the start of the growing season through the day of fledging (τ_2). Note that $\alpha_{ow}^I C1_{k-1}^I(\tau_1) = C2_k^I(0)$, $\alpha_{ow}^L C1_{k-1}^L(\tau_1) = C2_k^L(0)$, $C2_k(0) = C2_k^I(0) + C2_k^L(0)$, and $C2_k(\tau_2)$ is the number of chicks that successfully fledge in their second year. While chicks produced by the Early and Late waves of hatching suffer differential overwinter mortality, I assume that by the beginning of their second year they are no longer distinguishable, and thus I combine them into a single category for all subsequent years.

The total abundance of adults in year *k* consists of the sum of first-year breeders and returning adults, which can be written:

$$A_k = \overbrace{\sum_{i=k-1}^{k-9} \gamma_{k-i} * (\alpha_P)_{k-i} * C2_i(\tau_2)}^{\substack{first\ year\ breeders \\ returning\ after\ 1\ to\ 9\ years\ at\ sea}} + \overbrace{\alpha_A * A_{k-1}}^{\substack{returning \\ adults}} \tag{3.4}$$

where γ_{k-i} is the proportion of penguins ($\sum \gamma = 1$) that return to breed for the first time after being at sea for a period that ranges from 1 to 9 years, and α_P and α_A are the annual survivorship of pre-breeding adults and returning adults, respectively.

The breeding population in year k consists of two parts, one of which breeds early, B_k^I, and the other of which breeds late, B_k^L. Early breeders are all those birds not caring for a second-year chick at the beginning of the growing season,

$$B_k^I = A_k - C2_k(0). \tag{3.5}$$

Late breeders are those birds that are caring for a second-year chick at the beginning of the growing season, regardless of the fate of that chick,

$$B_k^L = C2_k(0). \tag{3.6}$$

The model described in Equations 1-6 can be used to calculate phenological correction factors that link the number of animals counted in each stage to a standardized abundance of breeding pairs. This model is required because the historical data are a heterogeneous patchwork of counts of breeding individuals, nests, chicks, adults, and total individuals, and because the time dependence of egg hatching and chick mortality causes the number of animals within each age group to vary throughout the year. Specific correction factors for each stage are applied as follows.

- The number of breeding individuals was assumed to be twice the number of incubating breeders. The correction factor for the number of incubating breeders was applied to all ground counts conducted on nests and *all* satellite counts occurring between the mean fledging date (January 28; Williams 1995) and the mean creching date (March 10; Weimerskirsch et al. 1992; Bost et al. 2013). Corrections for incubating breeders accounted for egg mortality prior to chick emergence.

- First-year chick count correction factors were applied to all chick counts occurring after the mean creching date (March 10; Weimerskirsch et al. 1992; Bost et al. 2013) until the end of the model year (October 31) in a given year. These factors corrected counts upward to estimate the number of pairs attempting to breed in a given year.
- Second-year chick count correction factors were applied to all ground counts of chicks occurring prior to the mean creching date (November 1 – March 10) in a given year, the time period where new chicks would not be expected to hatch nor stray from brooding.
- Individual count correction factors were applied to all counts ground counts of individuals and all satellite counts occurring before the mean fledging date (November 1 – January 28). It was assumed that in these satellite images, it is impossible to distinguish between second-year chicks and molting adults, both of which would likely be in residence at the breeding colony. Due to the inherently imprecise nature of these counts, I assume that all counts of individuals reflect the breeding population within 50%.

These correction factors were retrospectively applied to historical counts of king penguin abundance, as listed in Foley et al. (2018), as well as new satellite imagery-derived counts to create a corrected time series of king penguin abundance on South Georgia. Due to the variability in timing of censuses, ground counts and satellite censuses were adjusted according to phenological correction factors, accounting for expected variation due to their complex breeding cycle and observation error. Due to the paucity of data for many breeding colonies, the median population estimate for all counts occurring since 2010 was used to estimate the current breeding population size of king penguins on South Georgia.

3.4. RESULTS

King penguin populations have been noted at 47 South Georgia locations. Of these, no penguin colony was visible at 13 sites in the available satellite imagery where the record of presence cannot be confirmed and one, Schlieper Bay, for which no cloud-free satellite imagery was available. Among the remaining 33 sites, 23 were surveyed using direct survey methods, and 10 were surveyed using an analysis of high-resolution satellite imagery at least once since 2010. Multiple satellite images were available for some sites and I estimated abundance in each available image to assemble a more complete time series.

Satellite images were acquired throughout the breeding season and the count category (individuals, incubating adults, chicks) was determined according to the timing of image acquisition. The identification of colony area in satellite images was determined to be a reliable and repeatable measure. For the three satellite images where two independent reviewers digitized the colony area, variability in identified colony area was less than 6%. When compared to ground counts occurring within 15 days of satellite image acquisition, apparent nesting density was estimated to be 0.41-0.54 incubating adults per square meter. Satellite imagery-derived apparent incubating density was substantially lower than nesting density as measured *in situ*, 2.48 incubating adults/m^2 (n = 63, SD = 1.28). A total of 70 satellite censuses across 31 breeding colonies were conducted using the satellite imagery to supplement ground count data.

Simulations from the phenology model demonstrated that breeding success was highly sensitive to egg survival parameters (Figure 3.2), however daily breeding success from hatching through fledging followed a similar annual pattern (Figure 3.2). Across the 100-year simulation, the adult king penguin population in the model grew exponentially (Figure 3.3a). While all other age classes demonstrated dramatic population growth, there was variation between age classes in the estimated trend as well as substantial interannual variability within the time series for each age class. The population of early breeders is most reflective of the adult breeding population and follows a similar trend. All other age classes do not accurately capture the overall population trend across the simulated time series. To determine the best censusing strategy, population trends were compared across age classes with sampling windows of 2-50 years (Figure 3.3b). Early breeders were consistently the least biased age class, yielding a substantially better estimate of population trend than any other age class. Furthermore, while bias in determining population trend from early breeders decreased with longer sampling windows, the accuracy of the trend estimate increased little after a 4-year sampling window.

Correction factors were applied to all available satellite and ground counts. Overall, uncertainty in phenologically-corrected abundance estimates was predominantly driven by the correction factors rather than observation errors. On average, count data represented an underestimate of population size. Mean abundance correction was an increase of 8,542 breeding pairs (Range: -949 – 309,363). Uncertainty in phenological correction factors, themselves, was largely driven by variability in modeled egg survival. There was a substantial difference in the estimated population growth rate, with phenologically-corrected time series demonstrating a persistently higher population growth rate across colonies with trend data (Figure 3.3c-h). After correcting for observation error and phenological variability, the current population of breeding king penguins on South Georgia was estimated to be 405,425 pairs (95% CI: 102,624-2,375,061 pairs) (Table 3.1).

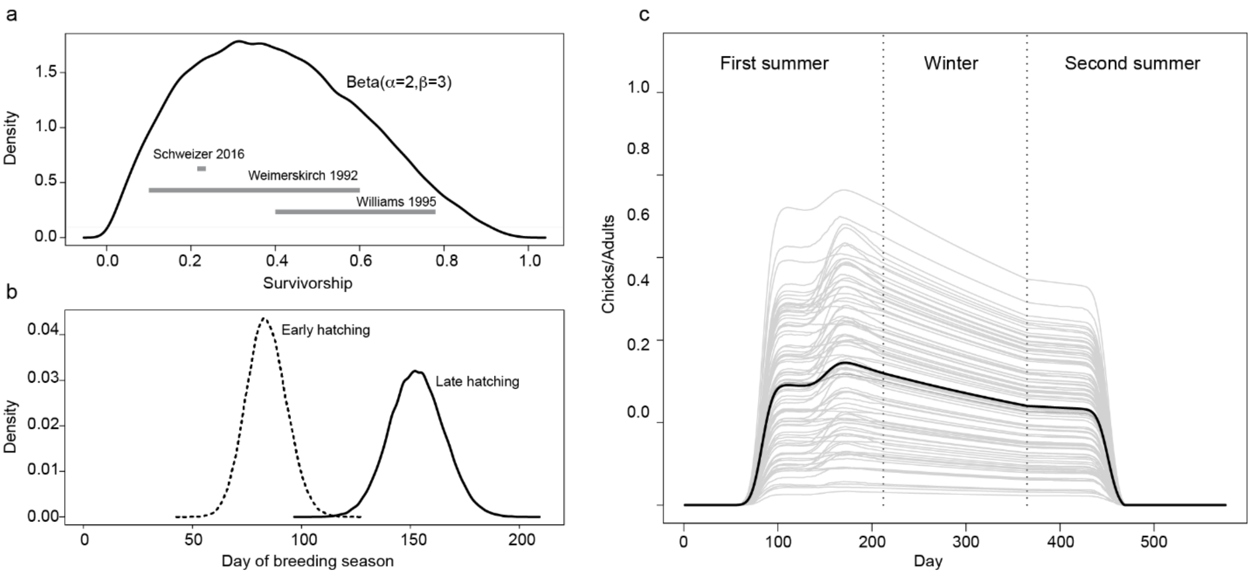

Figure 3.2. Distribution of modeled egg survivorship (a) and egg hatching (b) for early (dashed) and late (solid) breeding adults over the course of the breeding season. (c) Modeled proportion of chicks in attendance each day at the breeding colonies relative to the number of adults breeding each year.

Table 3.1. Island-wide abundance of king penguins on South Georgia. Current abundance is based on the median of the distribution formed by propagating the errors involved (see text) and averaged over all counts (N=number available) from 2010-2017. The 95% LL and 95% UL form the 95th percentile confidence intervals for abundance. Data Source: C=Count, S=Satellite.

Site	N	Median	95% LL	95% UL	Data Source
Ample Bay	2	3792	1479	23622	S
Anchorage Bay	0	0	0	0	
Antarctic Bay	3	647	217	4387	S
Cape Best	5	1333	299	40576	S
Beckmann Fjord	1	488	210	2519	S
Cheapman Bay East	3	2256	389	7326	S
Cheapman Bay West	3	1799	640	3621	S
Cooper Bay	1	348	151	1955	S
Doris Bay	1	3485	1446	17813	S
Elephant Cove	2	258	102	851	S
Fortuna Glacier East	3	3484	936	16353	S
Fortuna Glacier West	2	115	23	1445	S
Gold Harbour	10	25586	4390	131083	S, C
Holmsstrand	1	361	149	1614	S
Hope Bay	0	0	0	0	
Horten	1	264	111	1478	S
Hound Bay	1	244	232	257	C
Iris Bay	4	3051	1168	19042	S
Jason Harbour	2	41	37	387	S, C
Joke Cove, Elsehul	6	235	196	358	C

Site	N	Median	95% LL	95% UL	Data Source
Low Rock Point	1	1455	776	2768	S
MacKay Bay	1	3993	2535	6308	S
Miles Bay	1	4059	1671	25584	S
Morsa Cove	1	5386	2761	10444	S
Narval Bay West	0	0	0	0	
Nilse Hullet	2	581	112	1209	S
Olsen Valley	1	92	56	142	C
Peggoty Bluff	0	NA	NA	NA	Absent
Possession Bay	1	1735	721	10420	S
Queen Maud Bay	0	0	0	0	
Right Whale Bay	3	12934	2513	101011	S, C
Right Whale Bay, Bluff Point	0	0	0	0	
Royal Bay	4	21081	7496	93042	S, C
Rocky Bay	0	0	0	0	
Salisbury Plain	5	44684	8875	231674	S, C
Sandwich Bay	0	0	0	0	
Schlieper Bay	0	0	0	0	
Sea Leopard Fjord	1	3928	1772	18518	S
Sorn & Bernt	0	0	0	0	
St. Andrew’s Bay	3	250565	58871	1502848	S, C
Trendall Crag	4	1547	600	7051	S
Trollhul	1	1081	478	5660	S

Site	N	Median	95% LL	95% UL	Data Source
Undine Harbour	0	0	0	0	
Wales Head	0	0	0	0	
Whistle Cove, Fortuna Bay	5	4517	1212	83695	S, C
Wirik Bay	0	0	0	0	
TOTAL	85	405425	102624	2375061	S, C

3.5. DISCUSSION

To date, king penguins on South Georgia have been highly understudied, in part due to difficulties in accessing breeding colonies. The use of satellite imagery to census king penguin populations was proposed as a feasible method over twenty years ago (Guinet et al. 1995), however limited resolution and scarce cloud-free images prevented successful application of the technology. Recent efforts by Weimerskirch et al. (2018) demonstrated the use of modern high-resolution satellite images (WorldView-3 pan-sharpened to 31cm resolution) to quantify population changes in king penguin colonies on the Crozet Islands by monitoring the change in area of king penguin colonies. The authors note that while the detection of king penguin colonies is relatively easy, “obtaining population estimates remains challenging and requires making a series of assumptions and ground truthing” (Weimerskirch et al. 2018). While Weimerskirch et al. (2018) provided an initial methodology to extrapolate population size from satellite images, they posited that the variability associated with their method was too great to offer reliable population estimates. This study serves to build upon this foundation by ground-truthing satellite imagery derived estimates of abundance and nesting density and correcting for poor phenological timing of censuses.

Previous studies of king penguin breeding dynamics reported a nesting density of 1.3-2.2 penguins/m^2 (Williams 1995), however reported densities were variable across month, region, and location within the colony. Weimerskirch et al. (2018) assumed a nesting density of 1.6 penguins per square meter, a figure well-aligned with both published observations (Gerum et al. 2018) and my *in situ* observations (Foley Unpublished data). This nesting density, however, was substantially higher than the nesting density I observed by comparing satellite imagery with concurrent ground surveys. This is consistent with earlier observations that the ‘apparent’ density of penguins in satellite imagery may be different from the density of penguins as observed on the ground (LaRue et al. 2014; Lynch and Schwaller 2014), which means that the density used for estimating abundance must come from direct comparisons of ground counts with approximately coincident satellite imagery. It should be noted that these packing densities assumed the presence of nesting adults. During the overwintering period of first-year chicks, packing densities are much higher to aid in successful thermoregulation. The present study allowed no estimation of chick packing density in the overwintering period, so population estimates derived from winter satellite imagery likely underestimate true abundance. Future efforts to refine phenological corrections of satellite data should account for these differences in penguin density.

Additionally, previous efforts to monitor king penguin populations failed to account for variability in the timing of surveys. Population trends across the 100-year simulation varied across age classes, and only early-breeding adults correlated with the population trend (Figure 3.3). Furthermore, differences in timing of censuses are critical: relatively small differences in survey timing may correspond to large differences in population estimates, thereby resulting in substantial error (Figure 3.3c-h). Without correcting for these timing issues due to the unusual phenology of king penguins, biased estimates of population abundance are inevitable. This was particularly true at the larger breeding colonies such as St. Andrew’s Bay, Salisbury Plain, Royal Bay, and Gold Harbour, where uncorrected abundances underestimated population size by as much as 300,000 breeding pairs. Notably, Weimerskirch et al. (2018) commented on this issue, noting an 8% difference in colony area occupied between their satellite surveys in January and August. As compared to uncorrected abundance estimates, phenologically-corrected censuses revealed consistently higher growth rates across colonies (Figure 3.3), further demonstrating the importance of correcting for phenology. This study, in accounting for phenological error, minimizes the expected error associated with population estimates. This method accounts for observation and phenological errors associated with survey timing in ground counts. In satellite counts, I account for errors associated with estimating colony area, estimating nesting density, and phenological errors associated with survey timing. These results indicate that in both ground counts and satellite estimates, most error can be attributed to phenological variability.

While other studies have documented an increasing trend in this population, they have noted the difficulty in identifying specific trends due to the imprecision of censusing methods and complicated phenology of the species (Woehler and Croxal 1997; Foley et al. 2018). This study provides a method to adjust historical estimates of abundance based on phenological correction factors and demonstrates the use of high-resolution satellite imagery to estimate king penguin abundance. This population estimate of 405,425 breeding pairs is remarkably close to the IUCN's most recent estimate of 450,000 breeding pairs (Birdlife International 2017), which was largely based on expert elicitation and opportunistic surveys. Furthermore, these results serve to reinforce the hypothesis that the South Georgia population of king penguins is healthy and South Georgia will serve as an important refugium in coming decades under the expected impacts of climate change. Cristofari et al. (2018) argued that king penguin breeding colonies will not be successful should foraging grounds shift to more than 700 km from breeding grounds (Cristofari et al. 2018). South Georgia appears to be one of the few sites where king penguin foraging grounds are anticipated to shift closer to the breeding colonies, suggesting that this region may play a critical role in sustaining the species. My compilation of active king penguin breeding colonies and the island-wide population estimate of 405,425 breeding pairs provides a key benchmark for assessing future change.

In addition to developing novel methods to monitor king penguin populations, this model provides important guidance about best practices of king penguin surveys. Model results indicate that early breeding adults offer the most accurate estimate of large-scale population dynamics. The timing of both egg laying and hatching would suggest that these surveys are best conducted between November 1st and the mean early hatching date of January 23rd (Bost 2013). Model results also highlight the importance of accurate egg survivorship estimates. For best parameterization of the phenological correction factor, annual egg survivorship estimates should be used, as variability in this parameter account for the majority of modeled phenological variability. These estimates are notoriously difficult to capture and require substantial *in situ* time investment; however, recent success with time-lapse photography (Hinke et al. 2018) shows promise. Lastly, results of the simulation offer guidance regarding the minimum number of years a king penguin population should be censused to provide accurate estimation of population trends (Figure 3.3). The results indicate that only four years of early-breeding adult census data is required to substantially minimize bias associated with accurately estimating population trends. While bias continues to decline with more years of data, the marginal decline is minimal after four years of data collection. As such, I recommend that future efforts to monitor king penguin populations focus on quantifying early-breeding adults between peak egg-laying and peak hatching, and monitoring efforts should be sustained for at least four consecutive breeding seasons.

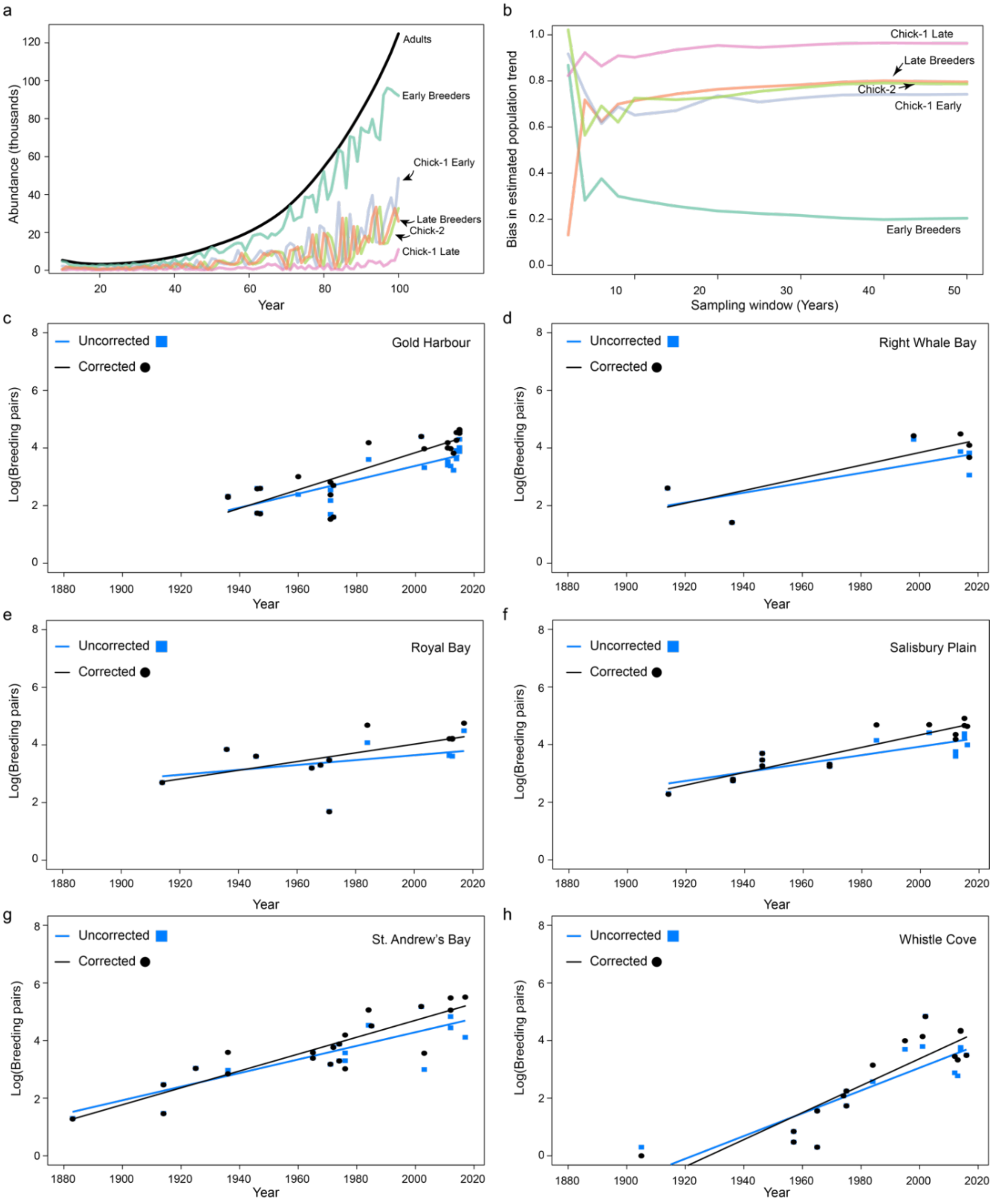

Figure 3.3. (a) Time series of king penguin abundance by age class for a theoretical population demonstrating the relationship among the age classes over time and the interannual variability expected. (b) Number of sampling years was related to the bias in the estimated population trend. Bias was variable across all age classes, with trends estimated from the population of early breeders generally exhibiting the least bias. (c-h) Uncorrected (blue) and phenologically-corrected (black) king penguin colony population changes at Gold Harbour; St. Andrew's Bay; Royal Bay; Right Whale Bay; Whistle Cove, Fortuna Bay; and Salisbury Plain.

4. Estimating the pre-exploitation abundance of a historically harvested marine mammal

4.1. ABSTRACT

Antarctic fur seals (*Arctocephalus gazella*) were commercially exploited on the sub-Antarctic island of South Georgia for over 100 years and driven to near-extinction. Since the cessation of harvesting, however, their populations have rebounded, and they are now often considered a nuisance species whose impact on the terrestrial landscape should be mitigated. Any evaluation of their current population requires the context provided by their historic, pre-exploitation abundance, lest we prey to “shifting baseline syndrome” in which our perspective on current abundance is compared only to an altered state resulting from past anthropogenic disturbance. This context is critical to defining species recovery and setting recovery targets, both of which are needed for the International Union for the Conservation of Nature’s (IUCN) recent efforts to develop a Green List of recovering species. To address this issue, I reconstructed the South Georgia fur seal harvest between 1786 and 1908 from ship logbooks and other historical records, interpolating missing harvest data as necessary using a generalized linear model fit to the historical record. Using an Approximate Bayesian Computation framework, harvest data, and a stochastic age-structured population model, I estimate the pre-exploitation abundance of Antarctic fur seals on South Georgia to be 2.5 million females (95% credible interval: 1.5– 3.5 million). This estimate is similar to estimates of recent abundance, and suggests that current populations, and the ecological consequences of so many fur seals on the island, may be similar to conditions prior to human harvest. While the historic archive on the fur sealing era is unavoidably patchy, the use of archival records is essential for reconstructing the past and, correspondingly, to understanding the present.

4.2. INTRODUCTION

As a physical refuge for ships and crew, the subantarctic islands were a critical logistical hub for whaling and sealing operations and, as a result, were heavily impacted both by the direct loss of wildlife and disturbance relating to harvesting activities. As such, they present a textbook example of the challenges faced by modern-day ecologists trying to define ‘natural’ in a system long ago modified by human activities. The influence of such operations was particularly strong on South Georgia (Figure 4.1a). Shortly following the island’s discovery and subsequent reports of the region’s abundant natural resources, exploitation commenced. Throughout the 19th century, fur sealing continued across South Georgia, decimating the breeding population. The last harvest was reported in 1908 by the US brig Daisy (Figure 4.1b). In the following years, expeditions to find potential locations for whaling stations and an inspection of the island by island magistrate James Ines Wilson reported sighting no fur seals during their circumnavigation of the island.

South Georgia was generally considered devoid of fur seals for a 20-year period, however by the 1930s, a small number of breeding individuals were reported on Bird Island off the northwestern tip of South Georgia (Bonner 1968). Since that time, the fur seal population has experienced massive population growth (Figure 4.1c), with breeding groups progressively recolonizing the northern coastline from the initial recolonized breeding on an outlying island in the northwest (Boyd 1993). Payne (1977) reported that between the 1957/58 and 1972/73 breeding seasons, the annual rate of population growth was 16.8% and Croxall and Prince (1979) reported an annual population growth rate of 11.5% between the 1972/73 and 1976/77 breeding seasons. Currently, it is estimated that South Georgia supports 95% of the global population of Antarctic fur seals (Hofmeyr 2016). The most recent effort to estimate the island-wide abundance of fur seals arrived at an estimate of 1.55 million breeding female fur seals in the 1990/1991 breeding season (Boyd 1993). More recently, the Scientific Committee on Antarctic Research (SCAR) Expert Group on Seals (EGS) estimated 4.5-6.2 million fur seals in the 1999/00 breeding season (SCAR 2008). Both of these estimates stand in sharp contrast to the much lower estimate of 550,000 females determined using quantitative genetic methods (Forcada and Hoffmann 2014), though subsequent criticism of this estimate (Boyd 2014) suggests caution. Regardless of the controversy surrounding their current abundance, it is indisputable that Antarctic fur seals have recovered from the brink of extinction and now represent a significant component of the South Georgia ecosystem.

The question now facing ecologists then becomes: How many fur seals were on South Georgia before human exploitation, and does the current population reflect simply a recovery to pre-exploitation levels or has the ecosystem been altered in such a way that fur seals have overshot what would have been considered ‘normal’? Without an understanding of historic conditions, it is difficult to answer this question. To address this, I use an age-structured population model coupled with a comprehensive survey of the sealing archives to estimate the abundance of fur seals on South Georgia prior to human exploitation through an approximate Bayesian computation (ABC) framework. Methodologically, the use of ABC allows us to reverse engineer the initial population estimate from the approximate date of economic extinction. ABC has frequently been used in the genetic literature (including, for example, in Hoffman et al.’s (2011) estimate of the effective population size of fur seals during their population bottleneck), however the approach is arguably underutilized in population biology. Several notable applications of Bayesian methods in similar contexts include a study on bowhead whale populations in the Bering-Chukchi-Beaufort Seas (Givens 1999), in which the authors used nearly complete historical record of catches to construct a time series of whale abundance. To my knowledge, however, this study represents one of the first to use a patchy historical harvest record to reconstruct a timeseries of abundance and baseline population size. Such an estimate provides crucial context for the current debate surrounding fur seal populations on South Georgia and their relationship to ecosystem-wide changes in the regional food web. Furthermore, ABC may be useful for understanding the historic abundances of other harvested species and represents a valuable tool for historical ecology.

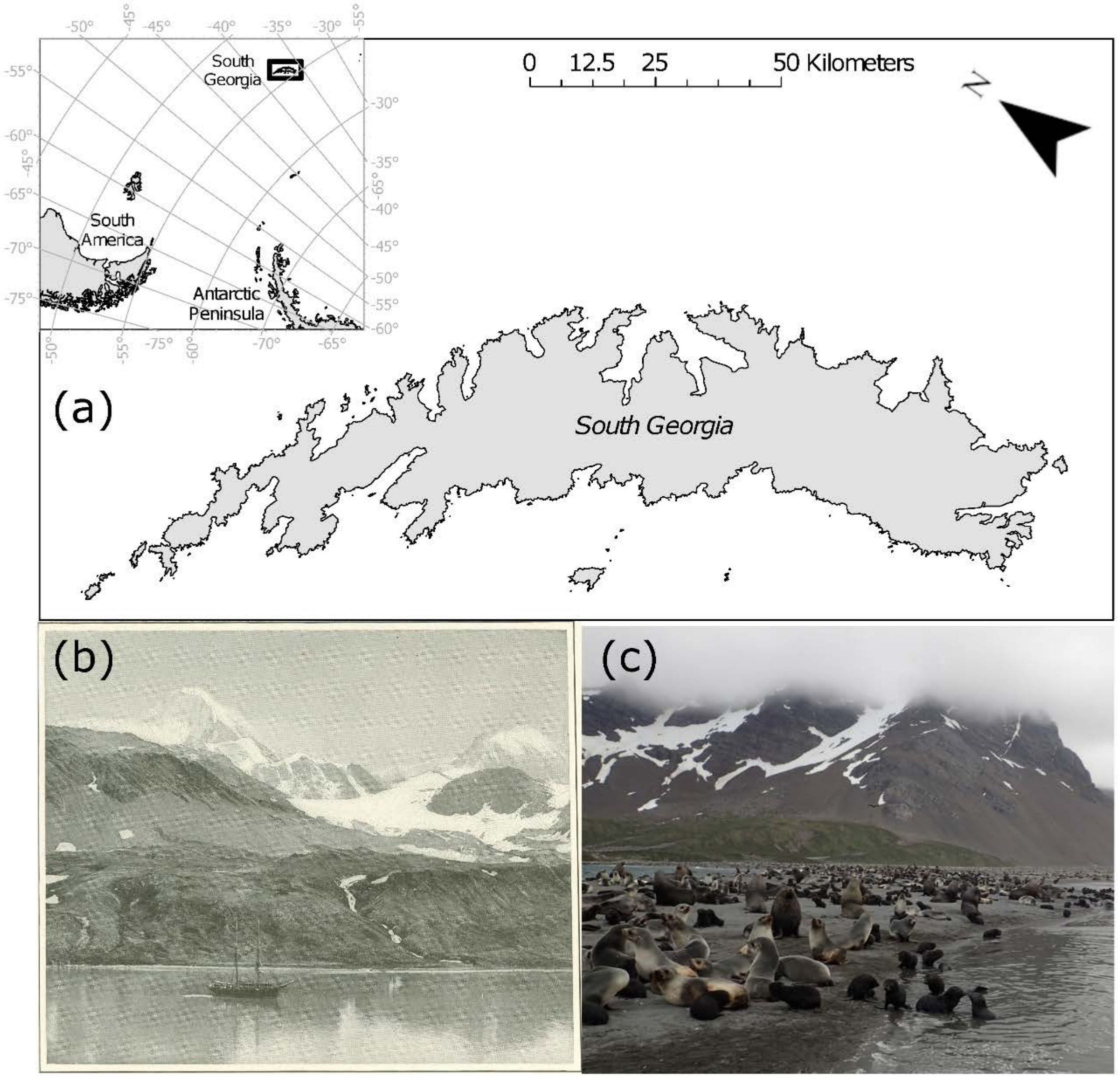

Figure 4.1. (a) South Georgia is an isolated, crescent-shaped island in the Atlantic sector of the Southern Ocean (b) Sealing ship, Daisy, in King Edward Cove, South Georgia. Photo: Robert Cushman Murphy (1913), courtesy of Mystic Seaport Museum. (c) Despite being historically heavily harvested, currently populations of Antarctic fur seals on South Georgia appear to have recovered. Breeding colony of fur seals at Right Whale Bay, South Georgia. Photo: C. Foley (2014).

4.3. METHODS

4.3.1. Historic sealing data

To assemble a comprehensive list of sealing expeditions thought to have visited South Georgia, I conducted an extensive archival search of exploration and sealing expeditions to the region using existing databases and published literature (Goode 1887; Headland 1984; Headland 1989; Dickinson 2007; Clayton 2014; Jones et al. 2017). I investigated each known sealing expedition to confirm the likelihood of both visiting and sealing in South Georgia. Detailed data on the pelt takes associated with each voyage were available for 89 of the 171 voyages known to have harvested seals in South Georgia between 1786 and 1908 (Appendix 2). Unless otherwise specified, I assumed that all pelts taken during these voyages were harvested from South Georgia. Where harvests were reported only in aggregate across a fleet of vessels, I divided the total harvest equally among those ships in the fleet lacking ship-specific harvesting data.

I used the voyages with pelt harvest data to fit a Generalized Linear Model that included departure year and ship tonnage as covariates, and then used that model to predict pelt harvest for the remaining 82 voyages missing pelt harvest data (Appendix 2). For ships where tonnage was not available in the historical record, tonnage was estimated as the mean tonnage of all vessels within the fleet with the same rigging (e.g., bark, brig, schooner, ship, sloop).

4.3.2. Harvesting model

To estimate initial (pre-exploitation) fur seal abundance, I constructed a female-only, age-structured population model for the period between 1776 and 1920 (Figure 4.2). Annual estimates of age-specific population size were conducted assuming a post-breeding census. The number of pups ($N_{0,t}$) was modelled as the sum of all births:

$$N_{0,t} \sim \sum_{a=1}^{16} Binom(N_{a,t-1}, F_a) \tag{4.1}$$

where $N_{a,t-1}$ is the number of seals of age class a at time t-1 and F_a is the fecundity at age a. I assumed that density dependence (modulated by the parameter κ) affects pup survival rather than adult survival or fecundity, as pregnancy rate is unaffected by food availability and female survival is unrelated to population size (Boyd et al. 1993). Accordingly, the number of second-year seals (N_1) is modelled as

$$N_1 = Binom\left(N_{1,t-1}, S_a * \left(1 - \left(\frac{\sum_{a=1}^{16} N_{a,t-1}}{\kappa}\right)\right)\right) \tag{4.2}$$

where S_a is the survival at age a. Note that κ, being defined as the point at which pup survival is zero, is not the population’s carrying capacity. The number in each subsequent age class (age class a) was modelled as the number surviving from in that cohort from the previous year (t-1) minus the number harvested ($H_{a,t}$):

$$N_{a,t} \sim Binom\big(N_{a,t-1}, S_a\big) - H_{a,t}. \tag{4.3}$$

The model was parameterized using age- and sex-specific estimates of fecundity (female birth rate) and survival measured from a tagged population at the Bird Island, South Georgia (Payne 1979; Boyd et al. 1993). Demographic stochasticity was modeled using the mu-phi parameterization of the beta distribution as follows:

$$F_{a,t} \sim Beta(F_a * \phi_F, (1 - F_a) * \phi_F) \tag{4.4a}$$

$$\phi_F \sim Gamma(100, 1) \tag{4.4b}$$

$$S_{a,t} \sim Beta(S_a * \phi_S, (1 - S_a) * \phi_S) \tag{4.4c}$$

$$\phi_S \sim Gamma(100, 1) \tag{4.4d}$$

Note that in this parameterization, $\boldsymbol{E}[\boldsymbol{F}_{\boldsymbol{a},\boldsymbol{t}}] = \boldsymbol{F}_{\boldsymbol{a}}$, and $\boldsymbol{E}[\boldsymbol{S}_{\boldsymbol{a},\boldsymbol{t}}] = \boldsymbol{S}_{\boldsymbol{a}}$.

Initial population size in 1776 was distributed across age classes in the proportions predicted by the Stable Age Distribution. The model was run for 10 years (~1 generation) as a burn-in prior to first harvesting. The total annual harvest was distributed proportionally across age classes, with the exception of first-year pups, which were assumed to be excluded from harvest. In the case where mothers of first-year pups were harvested, both the mother and pup were assumed dead. In this model, harvesting occurs annually, immediately following the breeding season and after the annual census.

4.3.3. Approximate Bayesian Computation

To estimate the initial population size, I used an ABC rejection algorithm (Beaumont 2010). Parameter values for the initial population size and the density dependence parameter κ were drawn from prior distributions for use in the population model described above. A flat prior, bounded by the density dependent parameter (κ), was used for initial baseline population size, Init ~ Unif(5e4,κ). A moderately informative prior κ ~ 1e5+Gamma(4,1e6) was used for the density dependent parameter. Simulated time series that did not match pre-defined criteria were rejected, and parameter combinations that generated time series that did meet the criteria were retained in the posterior. The criteria for acceptance of simulated time series was that the population had to go ‘functionally extinct’, defined as an island-wide population of less than 200 individuals, between 1878 and 1910. This criterion was selected in accordance with both the historical record and Hoffman et al.'s (2011) modeled estimate of the bottlenecked effective population size, which they estimated occurred in 1894, however the historical records indicate that no catches greater than this population size were recorded after 1878.

To increase the acceptance rate of test parameter values, I used an adaptive sampling technique in which new test parameter values were drawn from Gaussian distributions centered upon the accepted parameters (Smith and Gelfand 1992). Sampling ended when the shape of the posterior no longer changed with additional accepted parameter values. In total, 5.5 million simulations were run.

4.3.4. Error propagation and sensitivity analysis

To test the sensitivity of the model to the interpolated harvest data, a sensitivity analysis was performed by propagating the error associated with interpolated data points. Sensitivity analyses were conducted using the 5% and 95% confidence intervals of each interpolated data point to assess the impact on posterior estimates of initial population size and the density dependent term. Additional sensitivity analyses were performed on the demographic rates used within the model by using the upper and lower limits of the 95% confidence interval reported in the original studies. Lastly, a sensitivity analysis on the test statistic (< 200 females between 1878 and 1910) was performed using the upper and lower limit of the 95% credible interval of the effective female population size reported by Hoffman et al. (2011). A complete description of all model runs, including those completed to assess model sensitivity, are included in Appendix 2.

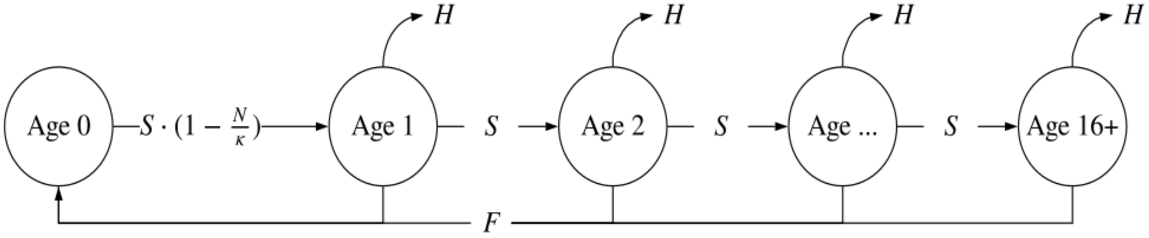

Figure 4.2. Population model framework for Age 0 through Age 16+ seals. N is the total seal population, S is age-specific survival, F is age-specific fecundity, κ is a density dependent term affecting first-year survival, and H is harvest, which is allocated proportionally across ages 1 through 16+.

4.4. RESULTS

A total of 171 sealing voyages to South Georgia were identified between 1786 and 1908 (Figure 4.3). Within this period, three pulses of harvesting voyages are evident: (1) the initial exploration of the island by British sealers and whalers (1786-1804); (2) primary British exploitation period (1806-1850); and (3) the expansion of American sealing (1870-1910). Harvest data suggests very high but variable levels of exploitation through the turn of the 19th century, likely due to the low effort but very high catches of individual vessels (Figure 4.3a). A second, smaller peak in catch occurred between 1815 and 1825, although this peak is substantially lower than landings occurring at the industry's inception. Furthermore, there is a clear exponential decline in the catches per vessel throughout the harvesting period (Figure 4.3b). For 89 of the voyages, direct records of pelts harvested were available, totaling 520,678 pelts. For the remaining 82 voyages, the number of pelts harvested was not recorded (at least among the records I had uncovered) and I estimated the number harvested using a Poisson regression model involving voyage year and ship tonnage (β_0 = 166.2 [SE=0.4]; β_{year} = -0.0875 [SE=0.0002]; $\beta_{tonnage}$ = 0.00159 [SE= 0.00001]; $p < 2e-16$).

The acceptance rate of parameter values was 0.00012% under basic ABC rejection sampling and 0.06% under the adaptive sampling framework. Prior-posterior overlap of initial population size (N_{init}) and the density dependent parameter (κ) were 40.7% and 26.6%, respectively (Figure 4.4), indicating that both parameters are identifiable and the priors not overly informative (Giminez et al. 2009). The posterior mean for initial population size N_{init} was 2.5 (95% credible interval: 1.5– 3.5) million females and the posterior mean for the density dependent parameter was 3.9 (95% credible interval: 3.6 - 4.8) million females.

Model results are robust to changes in fecundity rates (Figure A2.1 - Figure A2.4) and to changes in the test statistic (Figure A2.13 - Figure A2.16), however changes in survival parameters, particularly lower survival parameters have a large effect on estimated initial population size (Figure A2.5 - Figure A2.8). Similarly, interpolated estimates of harvest are differentially sensitive, with higher estimates of harvest having a large effect on estimates of initial population size (Figure A2.9 - Figure A2.12).

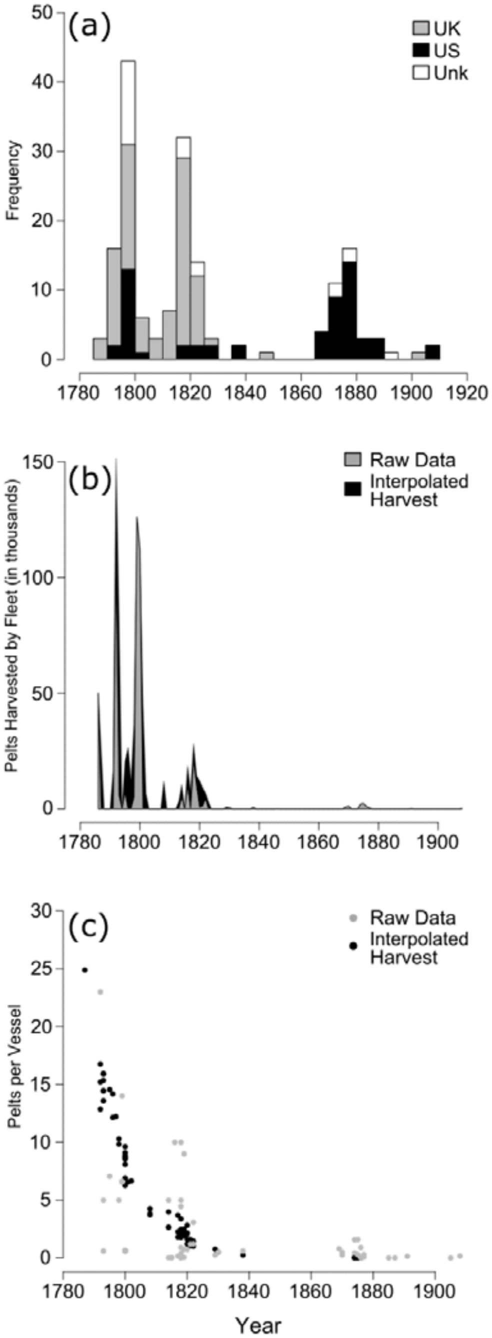

Figure 4.3. (a) Reconstructed record of fur sealing voyages to South Georgia by the vessel flagging: United Kingdom (gray), United States (black), or Unknown (white). (b) Original (gray) and reconstructed (black) record of fur seal takes in South Georgia. Reconstructed harvests were estimated using a Generalized Linear Model that included departure year and ship tonnage as covariates: Harvest ~ Pois(λ) and Log(λ) = β_0 + Departure Year + Ship Tonnage. (c) Original (gray) and reconstructed (black) record of seal harvest by vessel. Total seal harvest by vessel (1786-1908) declined across the duration of the fur sealing industry.

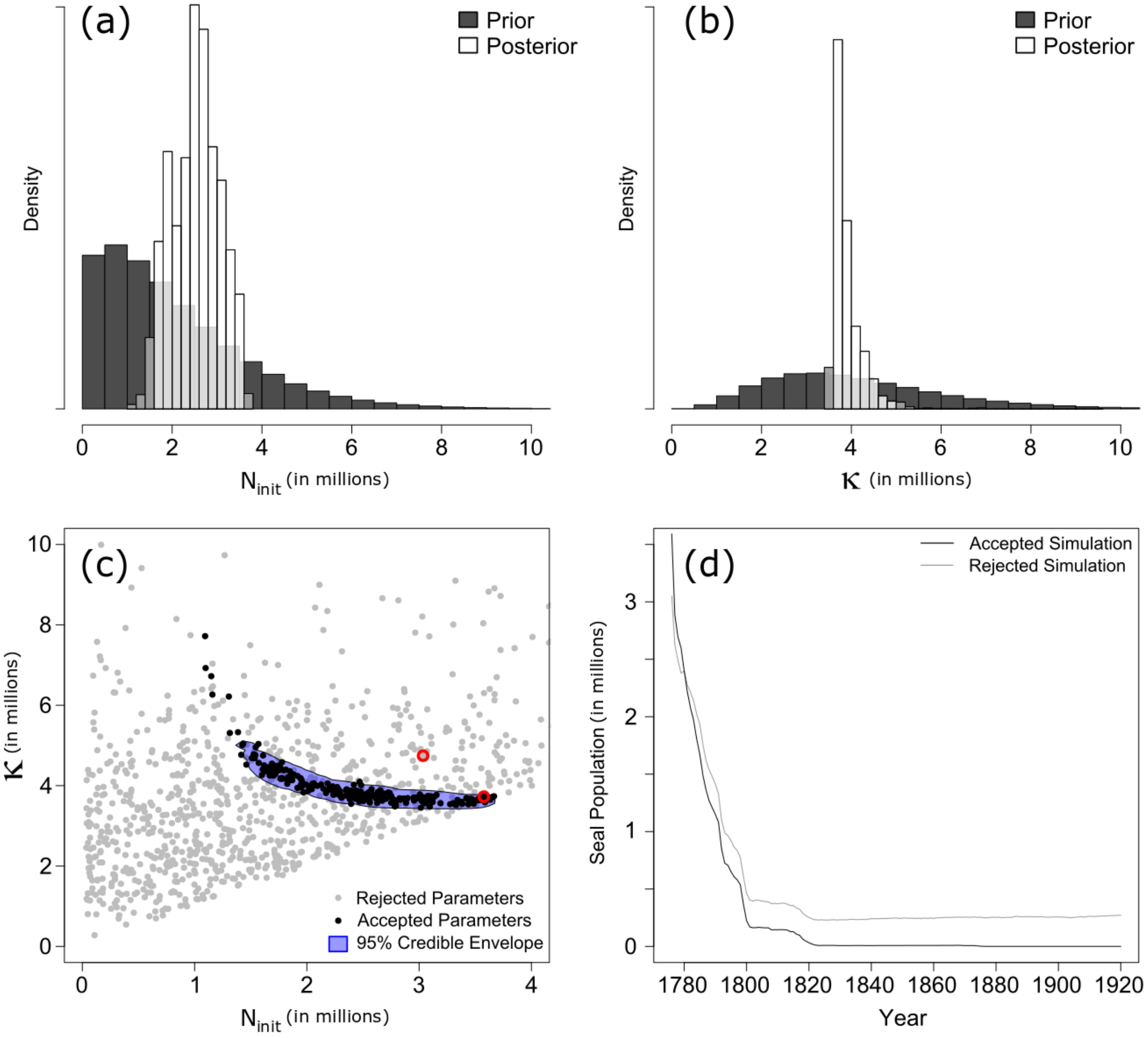

Figure 4.4. ABC model estimates and simulated population trajectories. (a) Prior (dark gray) and posterior (white) with 95% credible interval (light gray) estimate of initial population size. (b) Prior (dark gray) and posterior (white) with 95% credible interval (light gray) estimate of the density dependent parameter (κ). (c) Initial population size and density dependent parameters of a subset of rejected (gray) and accepted (black) simulations. Population trajectories of the parameter combinations circled in red are displayed in (d), where the population trajectory of the accepted parameter combination is traced in black and rejected parameter combinations are traced in gray.

4.5. DISCUSSION

Our estimate of a population size 2.5 million fur seal females prior to human exploitation closely aligns with an estimate proposed by Hoffman et al. (2011) of 770,000 – 2.41 million females. Hoffman et al. used an ABC approach to simulate mitochondrial DNA and microsatellite sequences of Antarctic fur seals on South Georgia. The authors of this study noted that their primary intention was to determine if a population bottleneck had occurred, and although they modeled several additional parameters, including historical effective population size, they were unable to find informative posteriors for the year associated with their preharvest population size. Nevertheless, the close correspondence between their estimate and ours is notable, particularly because the methods used are so different.

Interestingly, my estimate of pre-harvest population size also aligns closely with the SCAR's Expert Group on Seals estimate of current (as of 1999/2000) fur seal abundance, suggesting that the pre-exploitation abundance of Antarctic fur seals was likely similar to the abundance in 1999. Unfortunately, there have been no direct censuses of Antarctic fur seals on South Georgia since the 1990/91 austral summer, so while this analysis provides an estimate of pre-exploitation abundance, it is not yet possible to determine conclusively whether fur seals have recovered or overshot historic norms. That said, even if fur seal populations on South Georgia had continued to grow from the 1990/91 census at the 9.8% per annum rate estimated by Boyd (1993) in 1976/77, it is unlikely that the population has far exceeded historical abundances. Thus, the environmental impacts observed in association with fur seal breeding colonies, such as the degradation of terrestrial vegetation, may be on par with conditions prior to the seal harvest period.

Given the nature of using the historic records to fit a population dynamics model, I must consider the impact of the known uncertainties on the final pre-exploitation abundance estimate. The most obvious ‘known unknown’ is the possibility that some expeditions to the region were not recorded. While I cannot exclude the possibility that additional voyages visited the island, I are confident that the vast majority of sealing expeditions are represented in this data set. Perhaps more seriously, I know that the seal harvest was wasteful and that teams of sealers working on the beaches would often harvest more seals than could ultimately be stored on board the ship (Busch 1985). As a result, the number of seals killed by the known expeditions is likely underestimated. Secondly, I have made several assumptions regarding the behavior of sealers. The first assumption is that sealers would harvest all individuals on the beach, with the exception of seal pups, whose pelts were, per capita, too costly to skin and preserve. This assumption, however, likely underestimates the sealing-related mortality of pups since fur sealers may have killed pups indiscriminately in the quest to harvest as many pelts as quickly as possible (Busch 1985). I also assumed that, when specific data was unavailable, all catch from these vessels could be attributed to the South Georgia population. While this is certainly reasonable in the early period, when ships were able to easily fill their holds with seals from South Georgia, in the latter period ships going on to markets in China may have stopped at other islands on the return journey (Busch 1985).

While the current state of knowledge regarding the historic interplay among the biotic and abiotic components of the Southern Ocean is incomplete, methods to infer the true baseline state of the system allow us to better understand the true impact of human activities. In fact, recent work by the IUCN (Akçakaya et al. 2018) has suggested that a complete understanding of the historical, baseline state of systems is necessary to assess a species’ conservation status. To this end, they have suggested the development of a Green List of Species to complement and expand on the IUCN's well-established Red List. Conservation practitioners should place current populations and demographic data in the proper historical context, and it has been recently argued that "for recovery objectives to be ambitious and aspirational and to avoid shifting baselines, this [baseline] date should be as early as feasible…" (Akçakaya et al. 2018). Doing so, however, has proved challenging in many systems, as historical data regarding abundance and demography is frequently unavailable. My approach of using historical records of harvest and abundance to recreate a population time series through an Approximate Bayesian Computation framework is computationally expensive but requires data and statistical tools already in the 'ecological toolkit'. As such, it can be applied to a wide range of conservation applications and should be considered when establishing baseline conditions for species being considered for IUCN's Green List.

Our data suggests that the present population of Antarctic fur seals on South Georgia is likely similar to its pre-harvesting state, however, we must also consider that the ecosystem as a whole has shifted from this baseline as evidenced by the changing abundance of macaroni penguins (Trathan et al. 2012), king penguins (Foley et al. 2018), and baleen whales (Branch et al. 2006) in addition to the recovery of fur seals (Boyd 1993). Thus, while it is critical to know the baseline state of the system, it is important to keep in mind that this may no longer be 'natural', and that we may have to manage species that recover into an ecosystem that looks nothing like what it once did (Jachowski et al. 2015).

5. Estimating the population size of Antarctic fur seals on South Georgia

5.1. ABSTRACT

Antarctic fur seals (*Arctocephalus gazella*) were heavily harvested throughout their range in the 19th and 20th centuries. In South Georgia, a sub-Antarctic island in the Atlantic sector of the Southern Ocean, the breeding population was considered functionally extinct by 1910. However, in the mid-1930s the presence of breeding populations at isolated beaches was confirmed. Since that time, the population has grown substantially, and most recent population estimates suggest that the breeding population may be somewhere in the range of 550,000-3 million breeding females. The large uncertainty associated with current population estimates stem from challenges in surveying fur seals, which are distributed over remote beaches and can be aggressive and dangerous to survey by direct counting. We develop a new methodology to census the Antarctic fur seal population using commercially-available high-resolution satellite imagery. To correct for variation in image acquisition timing and sex bias in rookery attendance, we use hourly and daily time lapse photographs to develop phenological correction factors accounting for availability bias associated with adult and female haul-out patterns and attendance. We estimate the total adult population of Antarctic fur seals at South Georgia to be 740,513 individuals (242,924 - 1,730,128 95% CI) and the population of breeding females to be 489,647 individuals (206,555 - 973,118 95% CI), suggesting that the current population is likely smaller than previously estimated. Critically, our population estimate suggests that, despite concerns of high fur seals densities which may be damaging terrestrial and marine ecosystems, the current population represents only ~20% of the historical, pre-harvest, population.

5.2. INTRODUCTION

Monitoring long-term changes in populations and understanding the mechanisms underlying these fluctuations is a basic tenet of ecology and forms the foundation of many conservation efforts. Monitoring changes in populations of marine predators has been demonstrated to be especially crucial in understanding changing ecosystem dynamics and providing tools to establish rapid assessment and adaptive monitoring frameworks for management (Boyd et al. 2006). In the Southern Ocean, this approach has been adopted by the primary managing body, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which focuses on understanding population-level impacts of fisheries on upper trophic level “dependent species” (Agnew 1997). Indeed, studies in the Southern Ocean have found that the ecological performance of upper trophic level predators correlates with ecosystem changes. Boyd and Murray (2001) found that subtle changes in the biotic and abiotic environment were amplified in the responses of upper trophic level predators, including the Antarctic fur seal (*Arctocephalus gazella*).

Currently, it is estimated that the sub-Antarctic island of South Georgia supports 95% of the global population of Antarctic fur seals (Hofmeyr 2016). South Georgia is a 170 km long island, located in the Atlantic sector of the Southern Ocean and was once an epicenter of Southern Ocean sealing and whaling operations (Bonner 1968; Headland 1984). Between the beginning of the fur sealing industry on the island in 1786 until the last reported harvest in 1908, human hunting drove the population to functional extinction (Bonner 1968). In the early 1930s, however, a small number of breeding individuals were reported at the northwestern tip of the island (Marr 1936). Since that time, the fur seal population has experienced massive growth, with breeding populations progressively recolonizing the coastline in a west-to-east pattern

(Boyd 1993). Historical records of fur seal catches were recently used to reconstruct the baseline, pre-exploitation abundance of Antarctic fur seals, which was estimated to have been 2.5 million (95% credible interval: 1.5– 3.5 million) breeding females (Foley and Lynch, In review). To accurately assess whether this population has recovered, however, we need an estimate of current abundance at South Georgia and a means for monitoring population changes in the future.

Conducting a complete census of Antarctic fur seals is complicated by the difficulty associated with directly surveying them, particularly in South Georgia where much of the coastline is inaccessible. During the breeding season, seals are extremely aggressive, with males defending territories and harems, making direct ground counts dangerous and often impossible. Additionally, the density of breeding seals and harems can be very high and topography and vegetation limit the viewshed for ground surveys. Furthermore, timing surveys to capture the entire breeding population is challenging. Pregnant females return to the rookery within a few days of pupping and shortly thereafter begin making frequent foraging trips (Boyd 1993). Therefore, surveys must be conducted within a small temporal window during the pupping period, when the majority of the breeding population is in attendance. Boyd (1993) noted that while the absolute abundance of seals in attendance was variable across years, the daily attendance pattern across the breeding season at the rookery was consistent, with the first females arriving at the rookeries on November 13 and the maximum number of seals in attendance on December 8-9, after which attendance declines exponentially. This leaves only two days in which to conduct population surveys where the entire population is available to be counted at one time.

There have been several attempts over the last 50 years to estimate the total abundance of fur seals on South Georgia, using both direct surveys of individuals as well as a variety of alternative methods. These studies, however, have generated wildly inconsistent population estimates. The earliest methodical surveys were conducted by direct manual counting of individuals (Bonner 1968), possible only because the population size was so low at the time and there were relatively few active breeding locations. Later surveys relied upon mark-recapture methods at study sites (Payne 1977) and yacht-based estimates of abundance (Boyd 1993). In the 1990/1991 breeding season, Boyd (1993) calculated a breeding population of 1.55 million females using a mark-recapture approach (Table 5.1).

In recent years, the density of seals at breeding beaches has made direct survey methods impossible, and no in situ survey of the island has been completed since 1991. The Scientific Committee on Antarctic Research (SCAR) Expert Group on Seals (EGS) relied upon an expert elicitation approach to estimate 4.5-6.2 million adult fur seals in the 1999/00 breeding season (SCAR 2008). More recent attempts at quantifying the population have relied upon genetic methods. Hoffman et al. (2011) estimated a population of 770,000-2.41 million females using an analysis of mitochondrial DNA. Forcada and Hoffman (2014) estimated a breeding population size of 550,000 females through integrated quantitative genetic and mark-recapture methods, although criticism of their sampling methods has yielded skepticism of their estimate’s accuracy (Boyd 2014; Hofmeyr 2016).

Fortunately, recent advances in the use of high-resolution (sub-meter) satellite imagery for studying wildlife in remote areas allows for an island-wide census of Antarctic fur seals on South Georgia, and previous studies in other regions have demonstrated the feasibility of satellite imagery to assess seal populations (LaRue et al. 2011; McMahon et al. 2014; Moxley et al. 2017). This study uses commercially-available high-resolution satellite imagery to estimate the total breeding population of Antarctic fur seals on South Georgia. We develop a new methodology to survey this population accounting for daily adult attendance and haul-out patterns. By correcting for phenological differences in colony attendance, we account for availability bias due to differences in the timing of census, sex-biases in haul-out behavior, and rookery attendance – all of which are required to use the opportunistically-collected data available. Furthermore, we construct a model to estimate abundance on unsurveyed beaches using beach length and expert classification of regions into density categories. These methods allow us to construct an island-wide population estimate of Antarctic fur seals and demonstrate the feasibility of using high-resolution satellite imagery for monitoring fur seal population dynamics.

Table 5.1. Antarctic fur seal population estimates.

Year	Population Estimate	Source
2017/2018	745,021 (439,496-1,223,897 95% CI) adults 493,435 (322,448- 731,530 95% CI) females	This study
2012	550,000 females	Forcada and Hoffman (2014); Hofmeyr (2016)
2003/2004	770,000-2.41 million females	Hoffman et al. (2011)
1990/1991	1.55 million females	Boyd (1993)
1999/2000	4.5-6.2 million adults	SCAR 2008

5.3. METHODS

5.3.1. Satellite survey of Antarctic fur seal abundance

Commercially available, high-resolution satellite imagery (0.31-0.6 m resolution; DigitalGlobe, Longmont, Colorado, USA) was used to assess the presence and abundance of Antarctic fur seals on South Georgia (Figure 5.1). As a proof-of-concept, reviewers digitized the seals observable on breeding beaches of three satellite images using ArcGIS and satellite abundance was compared to breeding density estimates collected during field surveys. Colony attendance and breeding densities were estimated during field surveys in 2019, however because pupping date is highly conserved between years (Boyd 1993), these densities were compared to satellite densities in other years. After confirming that satellite imagery could be used to estimate Antarctic fur seal abundance, an island-wide search of the imagery was conducted.

Locations of all beaches with suitable breeding habitat were digitized from high-resolution imagery and the length of each beach was measured by digitizing the length of the coastline adjacent to suitable breeding habitat. To estimate total population, the island was divided into four quadrants, and coastlines were categorized by their relative density of fur seals (None, Trace, Low, Medium, High) according to survey data from the British Antarctic Survey's South Georgia GIS platform (SG GIS 2019). Approximately fifteen beaches from each quadrant were randomly selected to be counted, for a total of 55 beaches counted. For each sampled beach, a high-resolution satellite image acquired between December 1st and January 31st was identified for digitization. Cloud-free WorldView-3 imagery was preferentially selected for digitizing seals, due to its higher spatial resolution, and imagery acquired between December 15th and January 15th was preferentially selected due to its close alignment with the peak Antarctic fur seal breeding season. For each subsampled beach, all identified seals were digitized and the linear density of breeding adult fur seals was calculated.

5.3.2. Phenology corrections

Reconyx Hyperfire trail cameras were installed at three seal breeding beaches along the northern coast of the island under Regulated Activity Permits from the Government of South Georgia and South Sandwich Islands (GSGSSI): Fortuna Bay (2016-17), Right Whale Bay (2014-15), and Elsehul (2015-16). Hourly photos of beaches were captured between sunrise and sunset for the duration of the fur seal breeding season (Figure 5.1). To assess variation in hourly seal attendance, all photos from two days in the early season (December 17-18) and late-season (January 15-16) were digitized to assess differences in adult attendance by time of day. Hourly seal attendance did not differ substantially over the course of the day (Appendix 3). Thus, it was assumed that a single image from each day of the breeding season was sufficient to assess adult attendance.

To correct for survey error associated with phenological differences in the date of satellite acquisition, the best image acquired between 11:00 am and 1:00 pm each day was selected for all days between November 15 and January 31. Two correction factors were calculated from these data: (1) total number of breeding seals and (2) total number of breeding females. To correct for the total number of breeding seals, the mean proportion of adult seals visible in each frame was divided by the maximum number of adult seals observed at a site during the breeding season. To correct for the number of breeding female seals, the mean proportion of adult females in attendance was divided by the maximum number of pups observed at a site within the breeding season.

5.3.3. *Estimating Antarctic fur seal abundance*

Phenological correction factors were applied to all 55 seal counts from digitized beaches to estimate the total number of breeding adults and breeding females expected on each beach. We used the phenologically-corrected counts ($Count_i$ for beach i) to fit a Poisson Generalized Linear Model that included beach length L_i as an offset and beach type (None, Trace, Low, Medium, or High as reported by South Georgia's GIS platform; SG GIS 2019) as a random effect,

$$Count_i \sim Pois(\lambda_i L_i) \tag{5.1a}$$

$$\log(\lambda_i L_i) = \log(\lambda_i) + \log(L_i) = \beta_0 + \beta_1 I[BeachType] + \log(L_i) \tag{5.1b}$$

where I[] is the indicator function, β_0 reflects average linear density, and $\beta_1$captures the change in linear density associated with each beach type ($\overline{\beta_i} = 0$). Note that λ_i is a linear density and represents the number of seals per meter of beach coastline. We used this model to predict peak abundance for the remaining unsurveyed beaches on South Georgia. Beach area was not included as a covariate because the beach edges are ambiguous, particularly along the inland boundary where sand gradually gives way to denser stands of tussock.

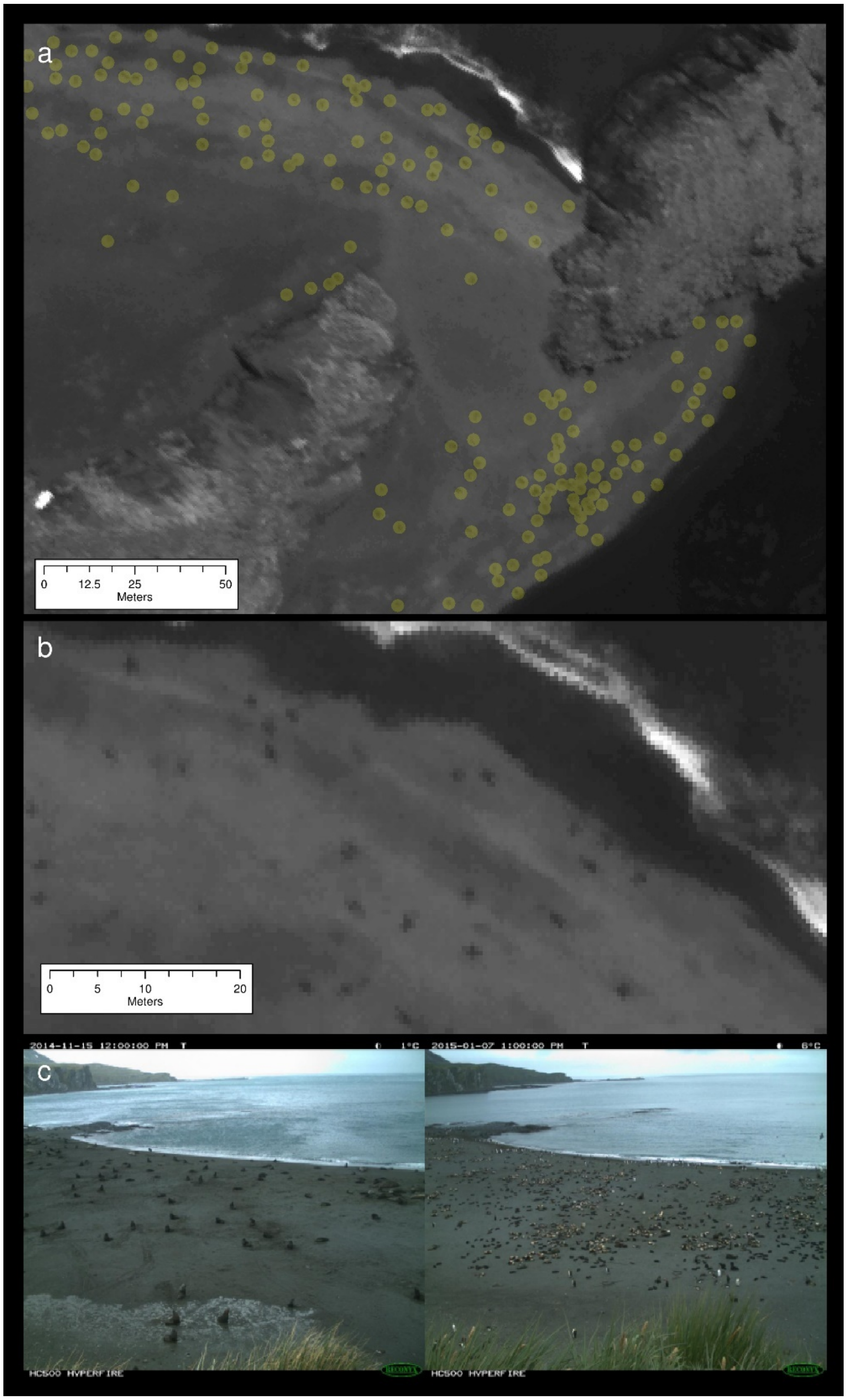

Figure 5.1. (a-b) WorldView-3 satellite image of an Antarctic fur seal breeding beach on November 21, 2016. Image © 2015 DigitalGlobe, Inc. (b) Time-lapse photographs of an Antarctic fur seal breeding beach at Right Whale Bay, South Georgia on (c) November 15, 2014, when the rookery is mostly attended by males and (d) January 7, 2015, when the rookery is dominated by harems of females and pups.

5.4. RESULTS

5.4.1. Antarctic Fur Seal Breeding Phenology

Hourly attendance of Antarctic fur seal adults and pups were similar and did not vary significantly over the course of each day (Appendix 3). Furthermore, Antarctic fur seal breeding phenology was consistent across all measured sites (Appendix 3). Male attendance at breeding beaches remains consistent during the early breeding season before steadily declining around December 24. Female seals begin arriving at the breeding beach between November 21-23 with a maximum attendance between November 30 - December 11. The first pups are identified in the period November 27 - December 1 with a maximum abundance from December 17 – January 5. The phenological correction factors demonstrated that surveys of seal abundance are most accurate when conducted during the middle of the breeding season, December 4 – January 13, with larger correction factors necessary in early- and late-season surveys (Fig 5.3b).

5.4.2. Estimating Antarctic Fur Seal Abundance

A total of 1,416 beaches were identified along the coast of South Georgia, ranging in length from approximately 20 meters to 2,700 meters. The identification of individual seals within high-resolution, cloud-free satellite imagery was determined to be a reliable and repeatable measure, as estimates of breeding density derived from satellite digitization were comparable to *in situ* density estimates. Of the 55 beaches that were counted, there was a minimum of seven seals and a maximum of 1,500 seals observed, with a mean linear density 0.609 ± 0.556 SD seals per linear meter of beachline (range: 0.070 – 3.230 seals/meter; Figure 5.2). After applying phenological correction factors to correct for adult attendance at the beaches, mean seal linear density was 1.731 ± 2.032 SD seals per meter (range: 0.099 – 9.989 seals/meter; Figure 5.3).

Observed seal linear densities closely corresponded to estimates of seal density from the South Georgia GIS system (Figure 5.2). Total number of breeding adults across all beaches was estimated to be 740,513 (242,924 -1,730,128 95% CI) individuals and the total number of breeding females was estimated to be 489,647 (206,555 - 973,118 95% CI) individuals (Figure 5.4).

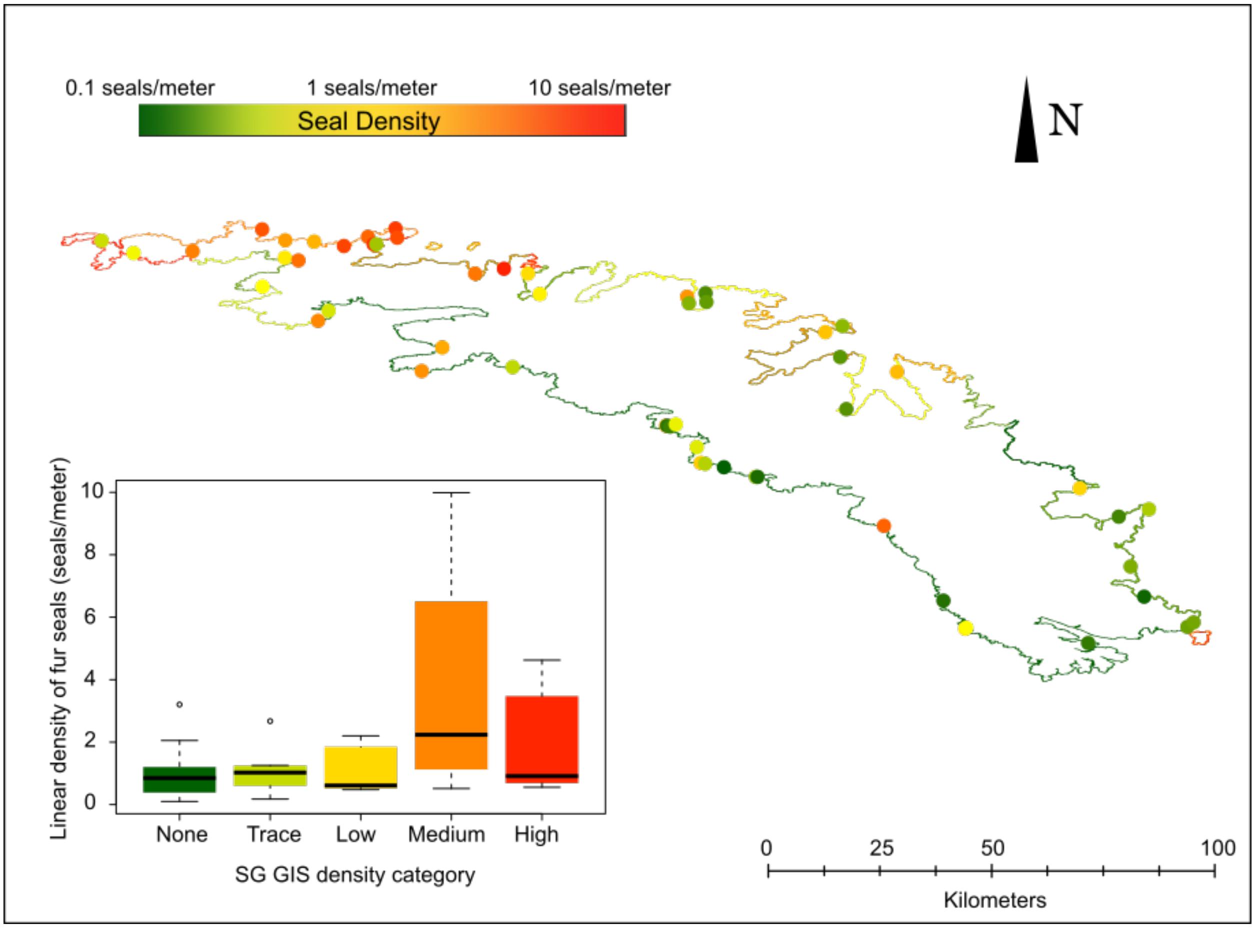

Figure 5.2. Measured linear density of Antarctic fur seal rookeries (colored points corresponding to measured density) correspond well with the 1991 and 2001 estimates from the South Georgia GIS database (coastline coloration). Boxplot indicates the categorization of each measured beach.

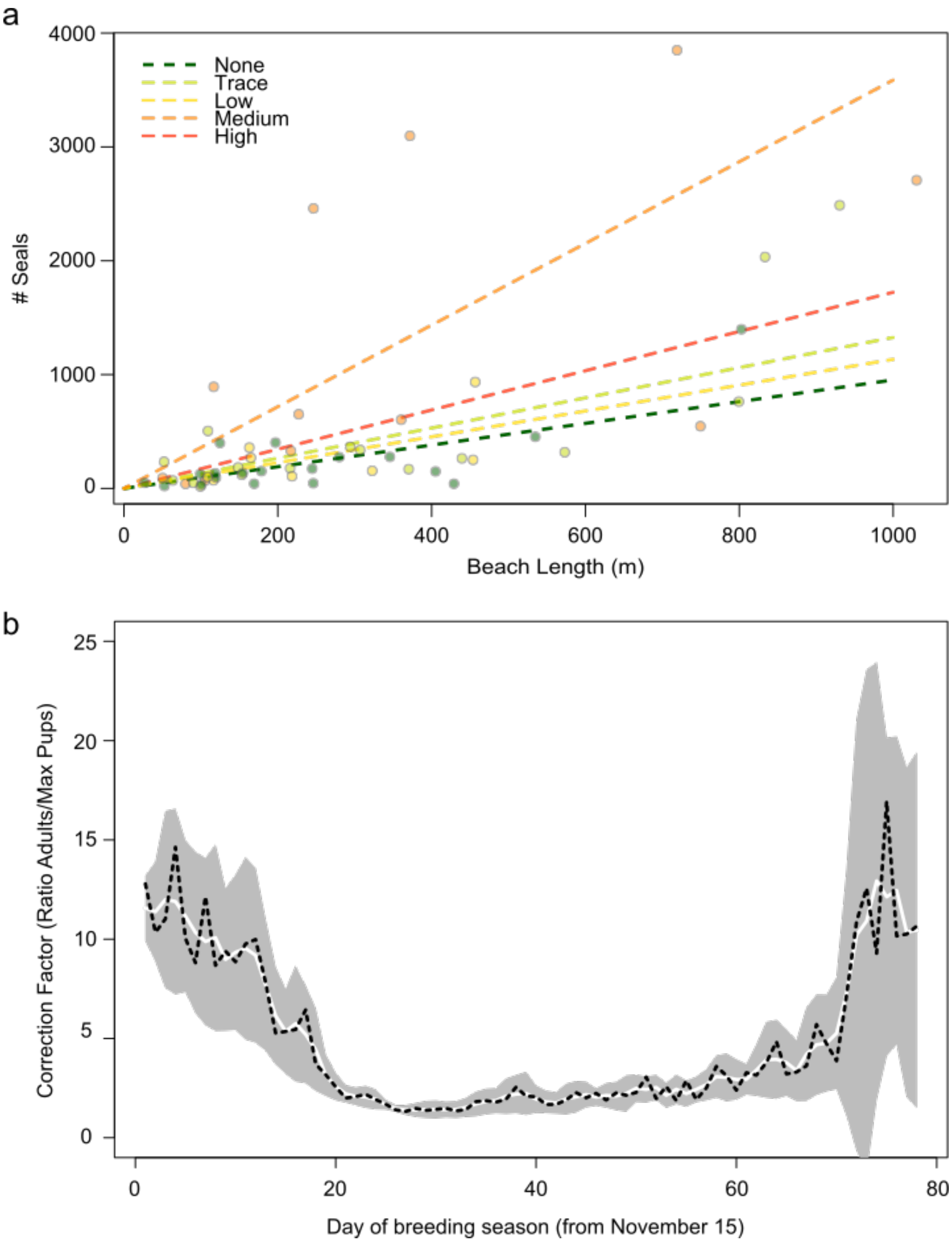

Figure 5.3. (a) A Poisson Generalized Linear Model was constructed to predict the number of seals breeding on all identified beaches by the length of beach. The model accounted for random effects of seal density, as identified by the 1991 and 2001 estimates from the South Georgia GIS database. Best fit lines, accounting for random effects of seal density (None, Trace, Low, Medium, High Density) are plotted. (b) Phenological correction factors were created for each day of the breeding season to estimate the total breeding population size.

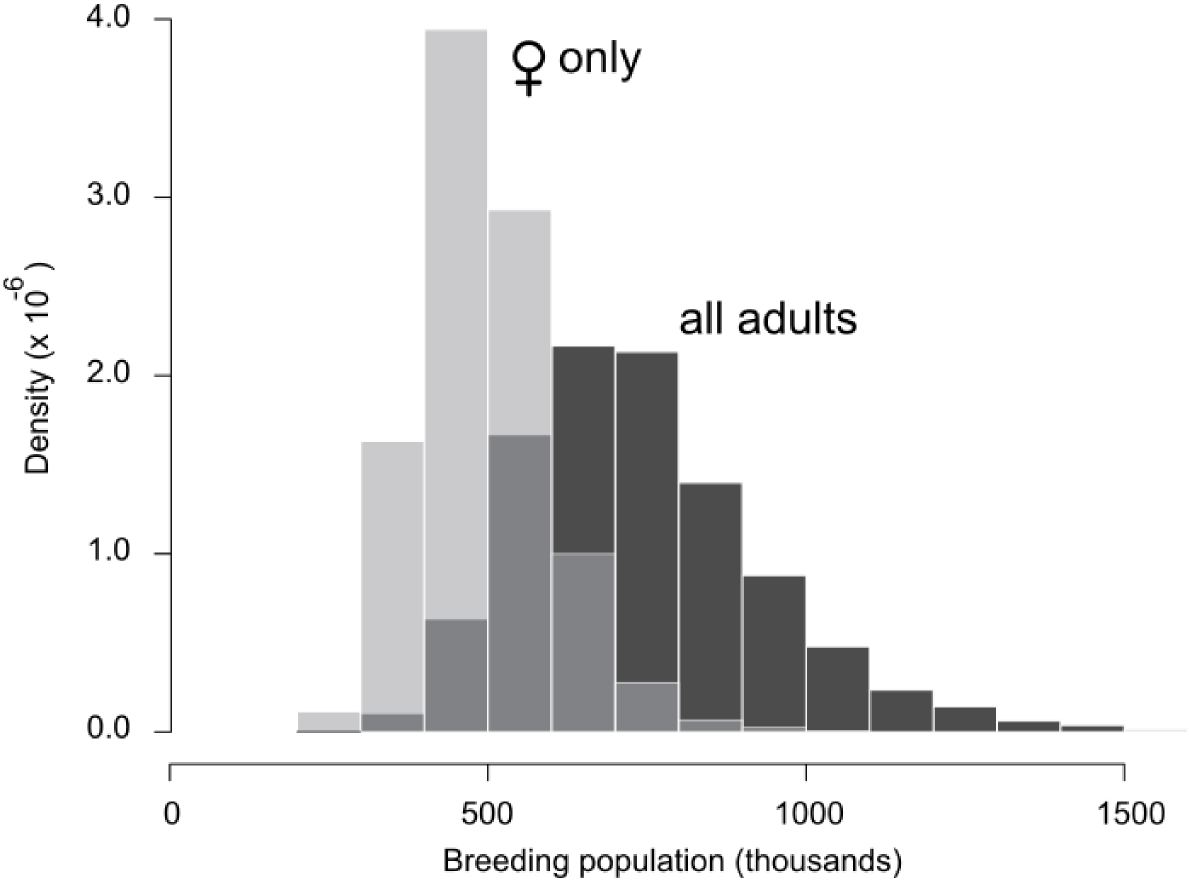

Figure 5.4. Modeled total breeding population of Antarctic fur seals (dark gray) and breeding female abundance (light gray) on South Georgia.

5.5. DISCUSSION

We estimate that the current population of Antarctic fur seals on South Georgia consists of nearly 500,000 breeding females. This estimate is lower than other estimates of abundance (Table 5.1), however it is similar to the most recent estimate of population size of 550,000 females (Forcada and Hoffman 2014; Hofmeyr 2016). While the population of Antarctic fur seals at South Georgia is generally considered healthy (Hofmeyr 2016), studies have indicated substantial declines over the last 30 years (Forcada and Hoffman 2014), which may explain our low estimate of abundance. Forcada and Hoffman (2014) described a population decline at Bird Island, South Georgia of 24% between 1982 and 2012, with the most drastic decline occurring between 2003 and 2012. Increases in climate variability and anomalies in sea surface temperature have been implicated as the primary driver for this decline (Forcada et al. 2005; Forcada et al. 2008). However, these reported trends have been questioned, with critics citing limitations in sampling, increases in density dependence, and a still-expanding population on the rest of the island (Boyd 2014; Hofmeyr 2016).

Despite the uncertainty in recent population estimates and trend, our results combined with previous analyses of pre-harvest abundance suggest that the population of Antarctic fur seals on South Georgia is far from recovered. Recent studies suggest that prior to human harvesting, South Georgia supported approximately 2.5 million breeding females (Foley and Lynch, in review). By 1910, however, the population was considered functionally extinct due to intense exploitation (Bonner 1968). Following the demise of the fur sealing industry at South Georgia, breeding aggregations began to reappear in the late 1930s (Marr 1936; Bonner 1968), and by the 1980s, populations appeared healthy and steadily increasing (Boyd 1993). The fur seal population recovered so quickly, in fact, that in recent years, they have increasingly been discussed as a nuisance species. However, the current population on South Georgia, though many orders of magnitude larger than at the turn of the 20th century, represents less than 20% of the historical population size.

The population trends of Antarctic fur seals in South Georgia appear to represent a prime example of “shifting baseline syndrome”. In his landmark essay, Pauly (1995) drew attention to the problem of shifting baselines in fisheries science, where each successive generation imposes an artificial baseline to assess environmental changes occurring within their lifetime. However, as successive generations of biologists impose this standard, the result is a “a gradual accommodation of the creeping disappearance of resource species, and inappropriate reference points for evaluating economic losses resulting from overfishing, or for identifying targets for rehabilitation measures” (Pauly 1995). In South Georgia, the complex history of human exploitation has created a unique example where, over a handful of generations, the human memory of the “baseline” environmental state has changed dramatically, which has made it difficult to assess whether the current densities of fur seals are ‘normal’ or cause for concern.

As early as 1985, concerns were raised regarding the impact of growing fur seal rookeries on terrestrial vegetation (Bonner 1985). Additionally, as the Southern Ocean ecotourism industry has grown, concerns have been raised regarding negative seal-human interactions. In the 2014/15 and 2015/16 austral summers, four tourists were bitten by fur seals, one of which requiring immediate medical evacuation (Browning 2015; Browning 2016). The Government of South Georgia and the South Sandwich Islands, recognizing that increasing fur seal density presents a safety hazard, is currently working to establish protocols for visitor-seal interactions (McKee 2017) and have identified the need for an Antarctic fur seal population estimate as a research priority (Grant et al. 2018). The methodology we have developed provides a relatively straightforward mechanism by which to monitor South Georgia’s fur seals and map areas of particularly high density where guidelines for visitors may be required.

Lastly, concerns have been raised regarding the impact of expanding fur seal populations on other recovering marine mammals and seabird populations. The krill surplus hypothesis, proposed by Sladen (1964) and expanded by Laws (1977; 1985), suggests that historic exploitation and depletion of krill-predators in the Southern Ocean led to a surplus of unconsumed krill for other predators. The hypothesis proposes that due to the decline of marine mammal populations through whaling and sealing, a niche was expanded for other krill predators (Laws 1977) and substantial evidence supports this idea (Emslie and Patterson 2007; Emslie et al. 2013; Surma et al. 2014). It was during this period that fur seals were released from exploitation, leading some to suggest that their continued population growth could be inhibiting the recovery of large whales (Hucke-Gaete et al. 2004) and causing a decline in some species of penguins (Trathan et al. 2012). While the specific mechanisms underlying the krill surplus hypothesis have recently come under scrutiny (Lavery et al. 2014), there remains speculation that a large increasing population of fur seals could be inhibiting or slowing the recovery of other species (Ballance et al. 2006; Ainley et al. 2007; Surma et al. 2014). Our results suggest that these concerns regarding a fast-growing seal population may be unwarranted. Prior to human intervention, there were likely five times more seals breeding in the region. Indeed, if we assume the maximum seal density observed in this study of 9.89 seals/meter were maintained across all beaches on South Georgia, we would expect a total population size of approximately 4.2 million seals. While changes in oceanographic habitat and increases in climate variability likely prevent this from being a sustainable carrying capacity, a population of that size may have been sustainable in the past.

While we demonstrate a method to census fur seals and extrapolate total abundance for remaining unsurveyed beaches, it is technically feasible to count all of South Georgia’s beaches on a regular basis if we can make data collection in this region a priority. While 93% of the South Georgia coastline has already been captured by high resolution satellite imagery, 90 km of the coastline has no available WorldView-3 imagery and imagery in other areas is contaminated by clouds. While our methodology to monitor fur seals provides an avenue forward in the continued monitoring of these populations, it should be noted that manually digitizing seals in satellite imagery, as was done for this pilot study, is extremely time- and labor-intensive. Recent advances in the use of machine learning algorithms, however, may provide a useful tool for sustained monitoring efforts. Goncalves et al. (In Review) demonstrated the use of such algorithms in the identification of pack ice seals in the Antarctic. In addition to developing automated survey techniques, additional research on habitat suitability and colonization dynamics would better inform our understanding of how seal density varies spatially along South Georgia’s coastline. Seal density appears to be highly variable even between neighboring beaches, likely due to historical artifacts associated with the recolonization process and as-yet unidentified habitat covariates that may include both marine and terrestrial characteristics conducive to pup rearing. Further research to account for this variation would allow for more precise estimates of seal density and abundance where cloud cover or image scarcity makes a complete annual census impossible.

6. Conclusions

This body of work represents my efforts to better understand the recovery dynamics of species which have been historically exploited. I reconstructed a time series of king penguin abundance on South Georgia, demonstrating their dramatic population growth over the last century. In an effort to extend this time series, I developed new methods to census king penguin populations using remote sensing technologies including high-resolution panoramic photography and high-resolution (sub-meter) satellite imagery. To account for the complex breeding cycle of king penguins, I used a discrete-time age- and stage-structured population model to provides stage- and day-specific correction factors for phenological standardization of census counts. Results indicate that the current population of king penguins on South Georgia is 405,425 (95% CI: 102,624 - 2,375,061) breeding pairs and found that population trends that do not account for phenological biases persistently underestimate the population growth rate. Furthermore, I explored the established hypotheses explaining king penguin population growth and found evidence that glacial retreat may have increased suitable breeding habitat at some colonies and facilitated population expansion, however glacial retreat is not associated with all of South Georgia's growing populations. Additionally, anomalies in sea surface temperature have increased in parallel with king penguin population growth rate, suggesting that climate forcing may contribute to colony growth, but a complete explanation for the island's rapidly growing king penguin population remains unclear.

Similar to the king penguins, Antarctic fur seals experienced massive population growth following the cessation of harvesting. However, no historical records of abundance during or prior to harvesting were available. To estimate their pre-harvesting baseline population, I reconstructed the South Georgia fur seal harvest between 1786 and 1908 from ship logbooks and other historical records, interpolating missing harvest data as necessary using a generalized linear model fit to the historical record. Using an Approximate Bayesian Computation framework, harvest data, and a stochastic age-structured population model, I estimated the pre-exploitation abundance of Antarctic fur seals on South Georgia to be 2.5 million females (95% credible interval: 1.5– 3.5 million). To assess the current state of the Antarctic fur seal population on South Georgia, I developed a new methodology to census the Antarctic fur seal population using high-resolution (sub-meter) satellite imagery. I used time-lapse photography to develop phenological correction factors which correct for availability bias associated with adult and female haul-out patterns, attendance, and variation in image acquisition timing. I estimated the total adult population of Antarctic fur seals at South Georgia to be 740,513 individuals (242,924 -1,730,128 95% CI) and the population of breeding females to be 489,647 individuals (206,555 - 973,118 95% CI), suggesting that the current population is likely dramatically smaller than previously estimated and may represent only ~20% of the historical, pre-harvest, population.

In conjunction, these findings present a divergent story of the recovery dynamics of two historically harvested species. King penguin populations on South Georgia currently exceed all known historical baselines and are expected to continue to increase under current climate change predictions (Cristofari et al. 2018). Antarctic fur seals have also experienced dramatic increases in abundance since being released from harvesting pressure. However, my estimates of historical and current abundance suggest that this population is far from recovered. With the expected increase in environmental variability associated with climate change and the negative demographic consequences on fur seals, it is possible that the full recovery of this population may be impossible in the current no-analog environmental conditions.

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Appendix 1

This appendix contains supplemental information for work presented in Chapter 3.

SATELLITE IMAGERY SURVEY PROOF-OF-CONCEPT

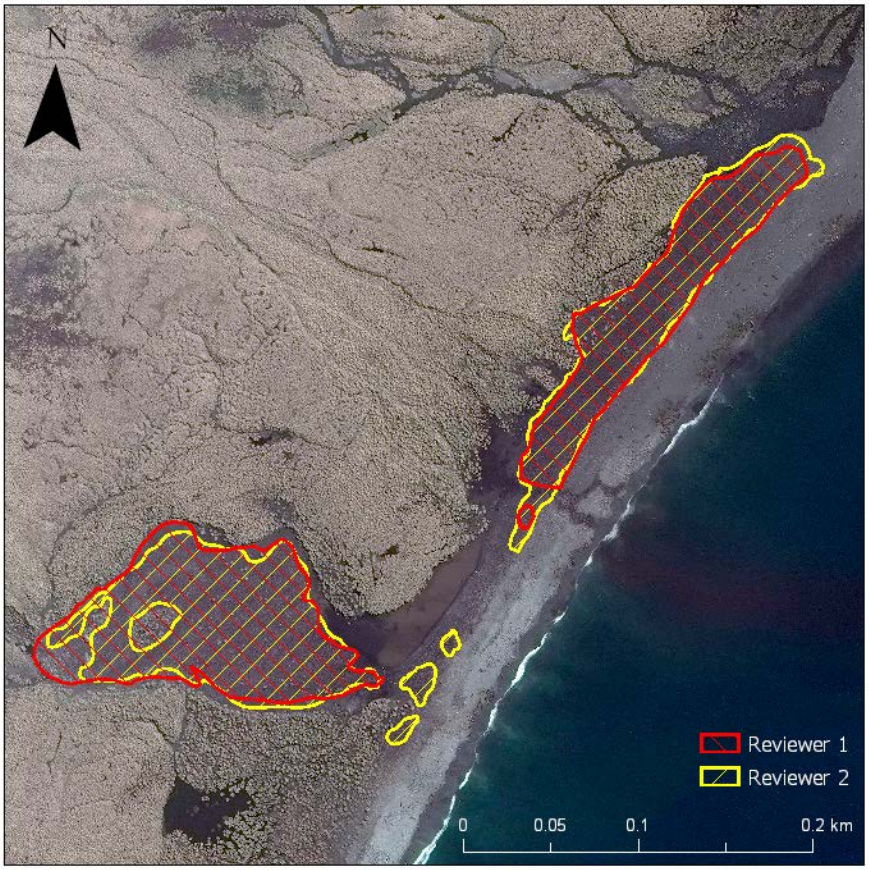

Figure A1.1. WorldView-3 image of the king penguin colony at Gold Harbour, South Georgia on 15 November 2015. Colony perimeter was digitized by two expert reviewers (red & yellow). Difference between reviewer estimates of colony area were less than 2%. Image © 2015

Appendix 2

This appendix contains supplemental information for work presented in Chapter 4.

SENSITIVITY ANALYSIS RESULTS FOR PARAMETER: FECUNDITY

Sensitivity analyses were conducted using the upper and lower limit (95% confidence intervals) of estimated fecundity rates reported in Boyd et al. (1995) and Payne (1979).

Table A2.1. Values of upper and lower limits of fecundity used in sensitivity analyses.

Age	Fecundity	95% LL	95% UL
0	0.000	0.000	0.000
1	0.000	0.000	0.000
2	0.032	0.000	0.075
3	0.386	0.312	0.460
4	0.645	0.569	0.721
5	0.747	0.682	0.812
6	0.843	0.788	0.898
7	0.852	0.798	0.906
8	0.878	0.824	0.931
9	0.839	0.773	0.904
10	0.796	0.721	0.871
11	0.811	0.729	0.993
12	0.835	0.746	0.925
13	0.787	0.665	0.906
14	0.706	0.546	0.861
15	0.810	0.631	0.979
16 +	0.458	0.178	0.629

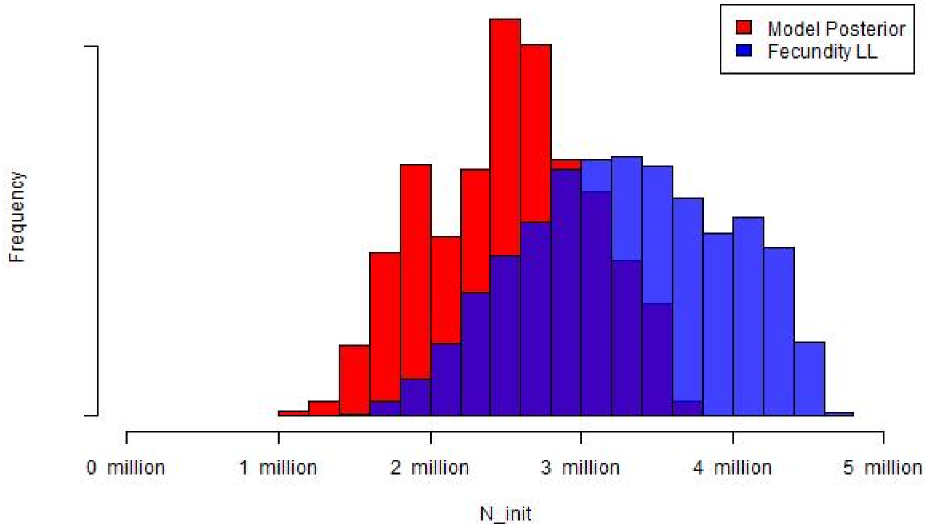

Figure A2.1. Posterior estimates of initial population size for model (red) and lower limit estimates of fecundity (blue).

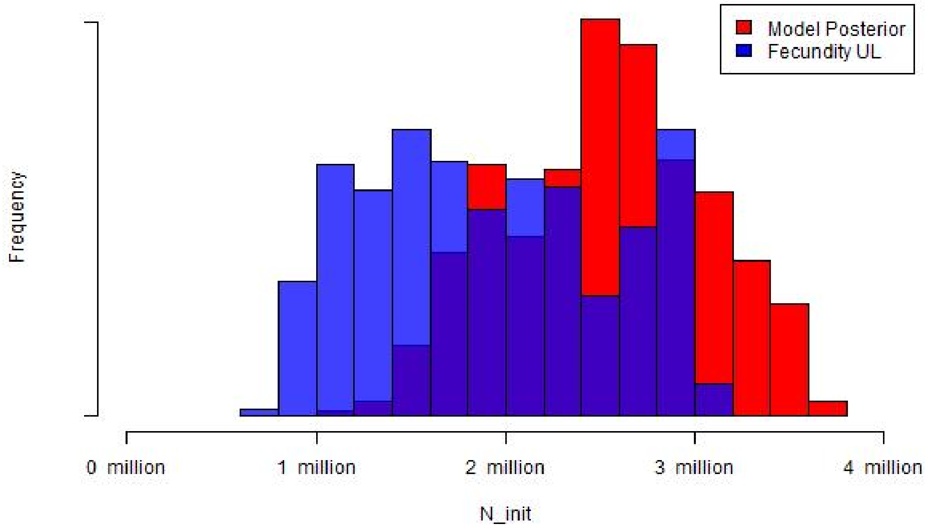

Figure A2.2. Posterior estimates of initial population size for model (red) and upper limit estimates of fecundity (blue).

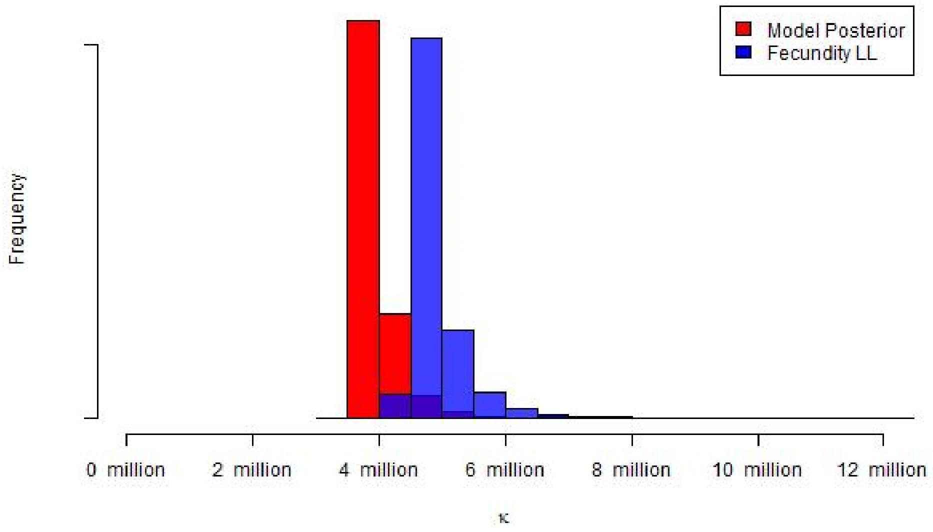

Figure A2.3. Posterior estimates of density dependent parameter (κ) for model (red) and lower limit estimates of fecundity (blue).

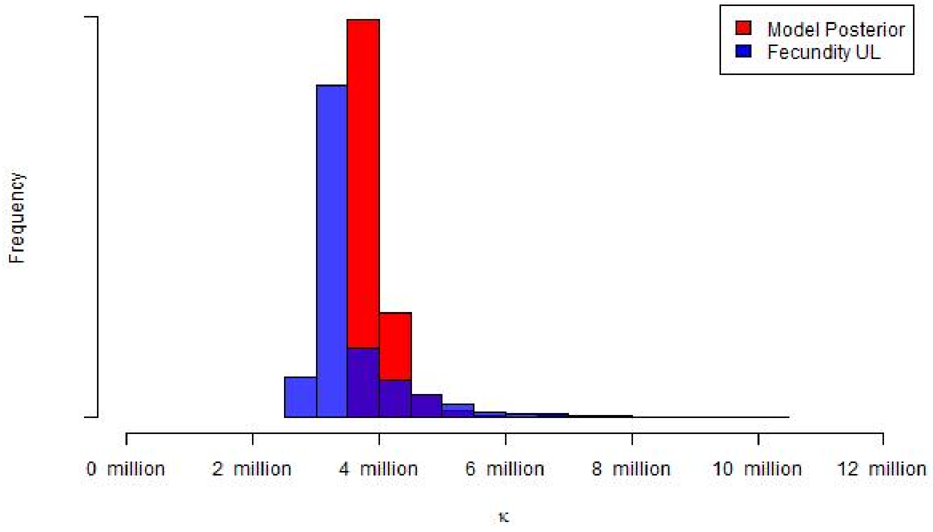

Figure A2.4. Posterior estimates of density dependent parameter (κ) for model (red) and upper limit estimates of fecundity (blue).

SENSITIVITY ANALYSIS RESULTS FOR PARAMETER: SURVIVAL

Sensitivity analyses were conducted using the upper and lower limit (95% confidence intervals) of estimated survival rates reported in Boyd et al. (1995) and Payne (1979).

Table A2.2. Values of upper and lower limits of survival used in sensitivity analyses.

Age	Survival	95% LL	95% UL
0	0.649	0.613	0.835
1	0.954	0.920	1.000
2	0.959	0.920	1.000
3	0.801	0.717	0.887
4	0.872	0.809	0.936
5	0.878	0.822	0.935
6	0.885	0.827	0.942
7	0.896	0.841	0.951
8	0.869	0.703	0.935
9	0.835	0.758	0.911
10	0.846	0.767	0.924
11	0.777	0.677	0.877
12	0.719	0.591	0.843
13	0.839	0.703	0.971
14	0.682	0.493	0.863
15	0.679	0.424	0.914
16 +	0.629	0.433	1.000

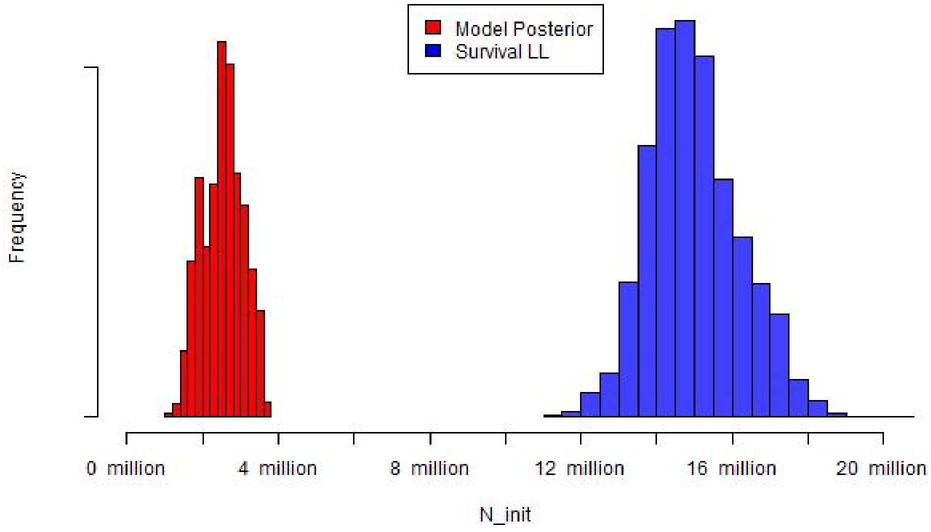

Figure A2.5. Posterior estimates of initial population size for model (red) and lower limit estimates of survival (blue).

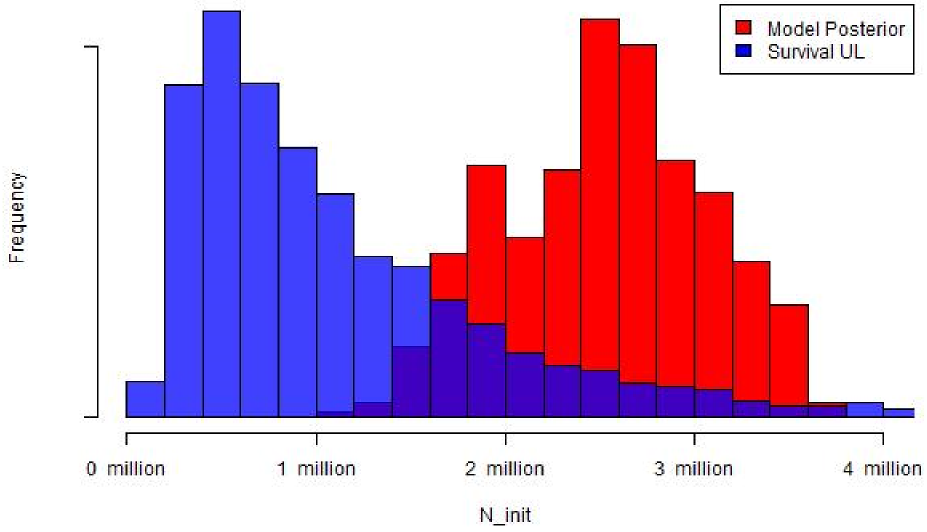

Figure A2.6. Posterior estimates of initial population size for model (red) and upper limit estimates of survival (blue).

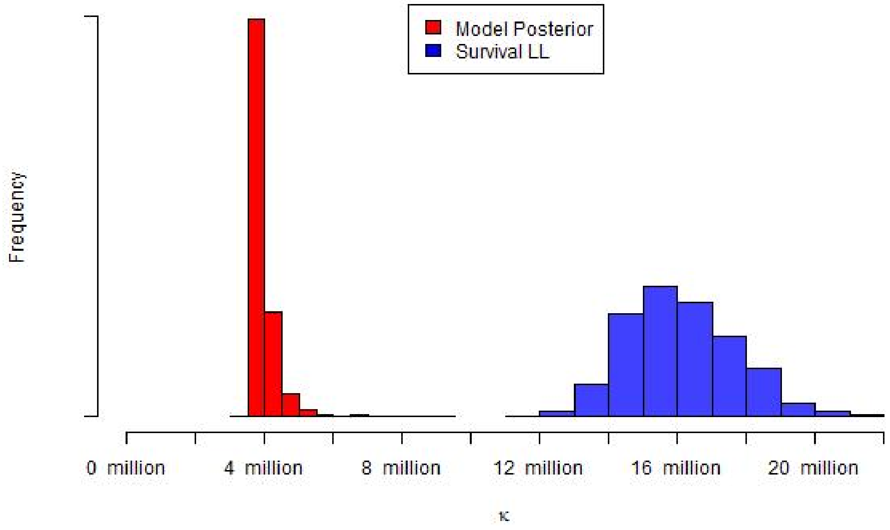

Figure A2.7. Posterior estimates of density dependent parameter (κ) for model (red) and lower limit estimates of survival (blue).

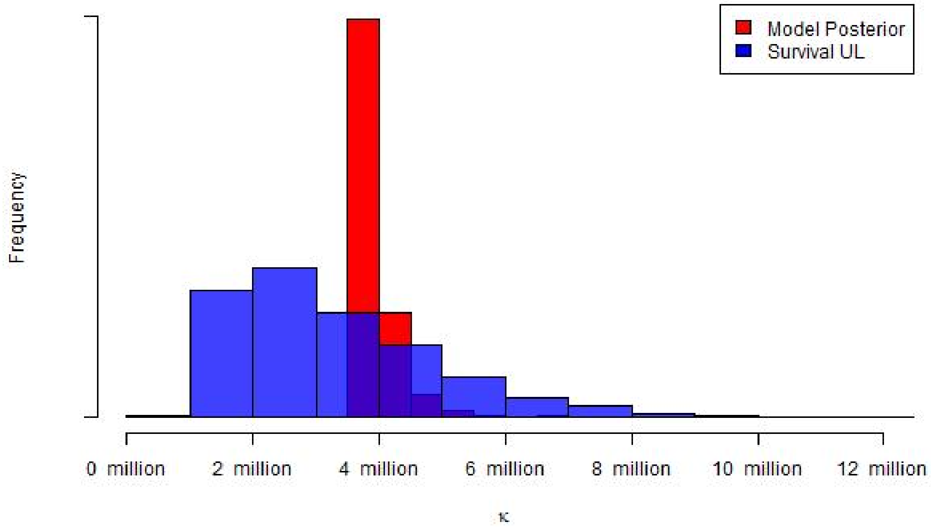

Figure A2.8. Posterior estimates of density dependent parameter (κ) for model (red) and upper limit estimates of survival (blue).

SENSITIVITY ANALYSIS RESULTS FOR INTERPOLATED HARVEST VALUES

Sensitivity analyses were conducted using the upper and lower limit (95% prediction intervals) of interpolated harvest for each missing data point. At the upper limit of GLM estimates, the acceptance rate of model parameters was extremely low, and posterior estimates are constructed with very low sample size (n=29).

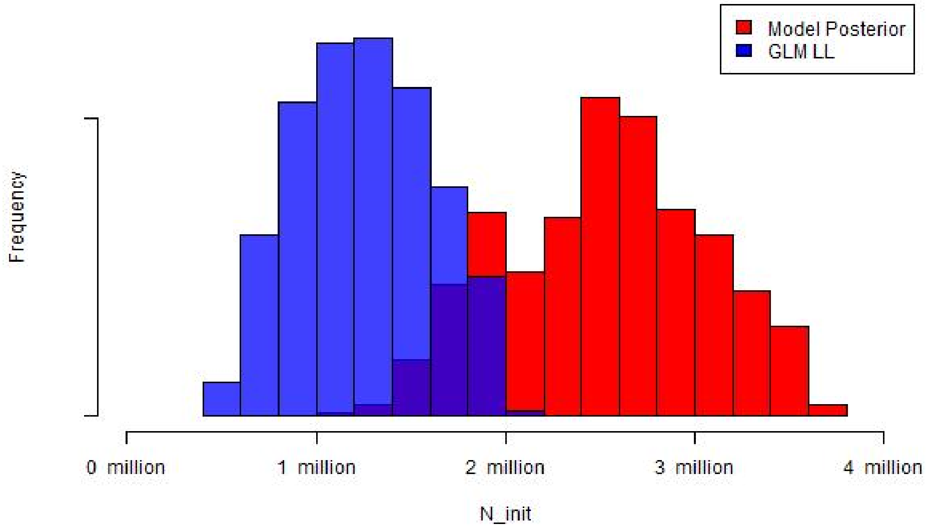

Figure A2.9. Posterior estimates of initial population size for model (red) and lower limit estimates interpolated harvest (blue).

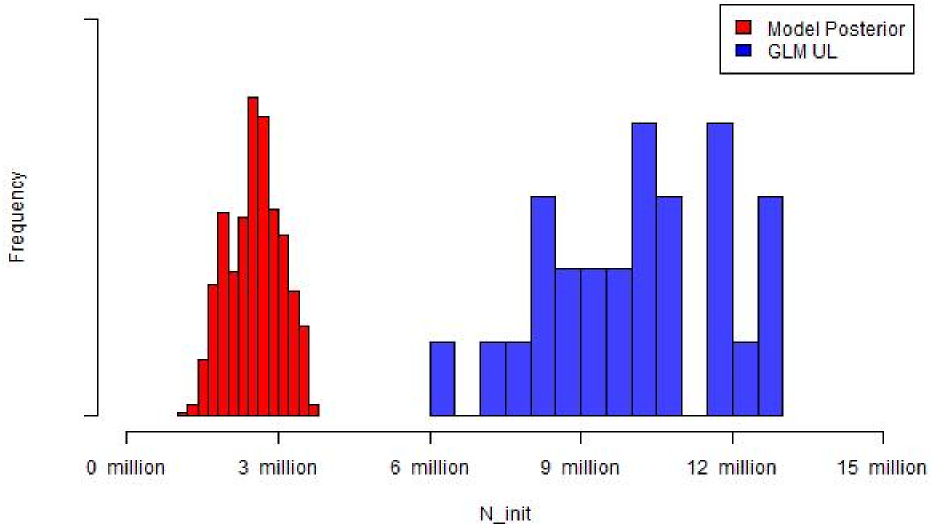

Figure A2.10. Posterior estimates of initial population size for model (red) and upper limit estimates interpolated harvest (blue).

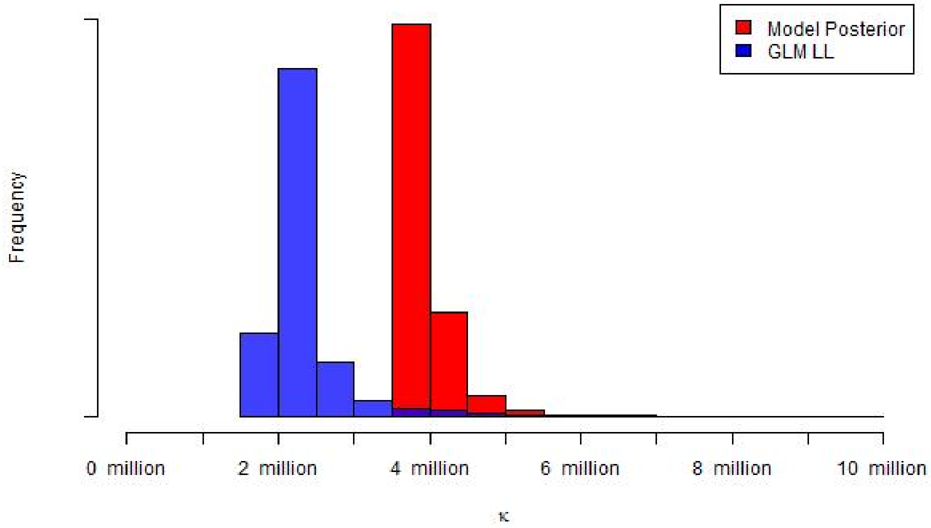

Figure A2.11. Posterior estimates of density dependent parameter (κ) for model (red) and lower limit estimates interpolated harvest (blue).

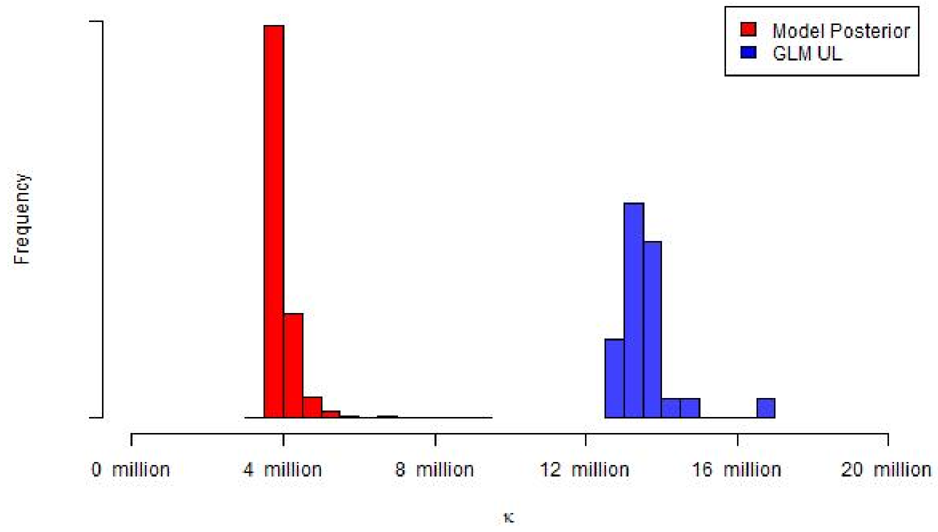

Figure A2.12. Posterior estimates of density dependent parameter (κ) for model (red) and upper limit estimates interpolated harvest (blue).

SENSITIVITY ANALYSIS RESULTS FOR TEST STATISTIC

Sensitivity analyses on the test statistic were conducted using the upper and lower limit (95% credible intervals) of the bottleneck population size reported by Hoffman and Forcada (2011).

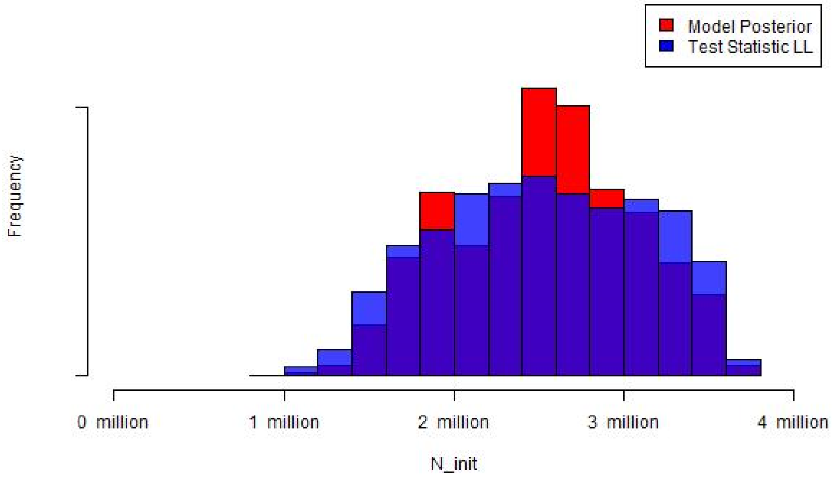

Figure A2.13. Posterior estimates of initial population size for model (red) and model using lower limit estimates of bottleneck population size (blue).

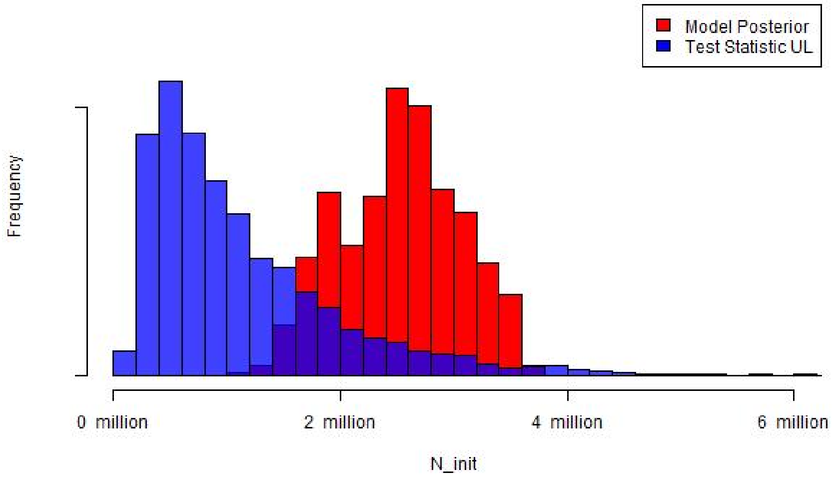

Figure A2.14. Posterior estimates of initial population size for model (red) and model using upper limit estimates of bottleneck population size (blue).

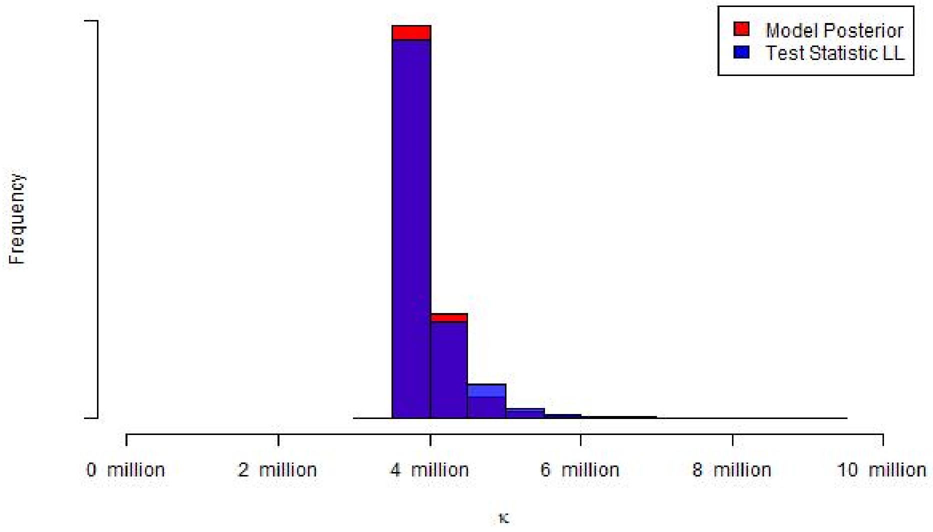

Figure A2.15. Posterior estimates of density dependent parameter (κ) for model (red) and model using lower limit estimates of bottleneck population size (blue).

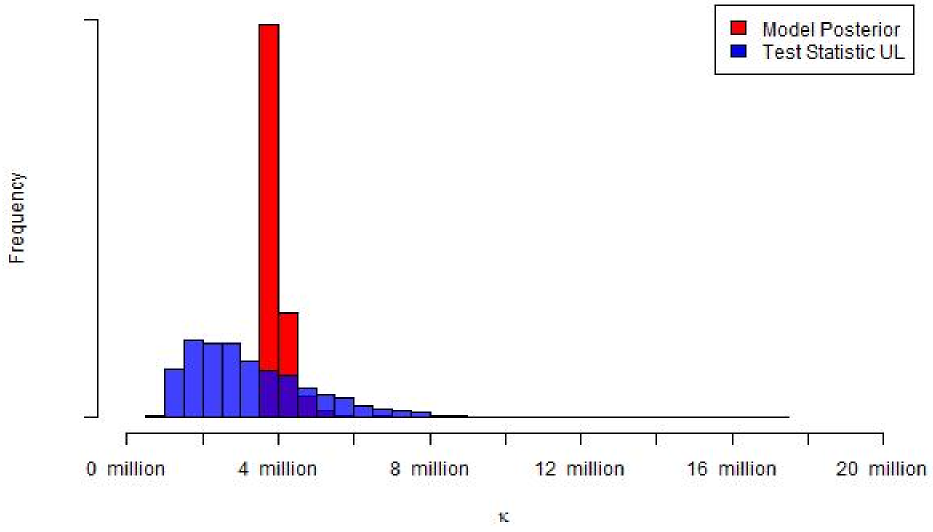

Figure A2.16. Posterior estimates of density dependent parameter (κ) for model (red) and model using upper limit estimates of bottleneck population size (blue).

MODELLING OF DEMOGRAPHIC STOCHASTICITY IN ANTARCTIC FUR SEAL POPULATION MODEL

Demographic stochasticity was incorporated into our model by using random draws from a beta distribution to generate stochastic annual fecundity and survival rates as follows:

$$F_{a,t} \sim Beta(F_a * \phi_F, (1 - F_a) * \phi_F)$$

$$\phi_F \sim Gamma(100, 1)$$

$$S_{a,t} \sim Beta(S_a * \phi_S, (1 - S_a) * \phi_S)$$

$$\phi_S \sim Gamma(100, 1)$$

where $F_{a,t}$ and $S_{a,t}$ signify a year-specific stochastic draw for fecundity and survival, respectively. We have used a parameterization of the beta distribution that includes the expected values F_a (mean fecundity) and S_a (mean survival) as explicit parameters, since these values are available from the literature. The ϕ parameter, which is related to both the mean and the variance, was drawn from a gamma distribution tuned to generate distributions whose variances were consistent with our understanding of fur seal life history and previously published data (Payne 1979; Boyd et al. 1993). The resulting age-specific beta distributions for survival and fecundity are illustrated in Figure S1.

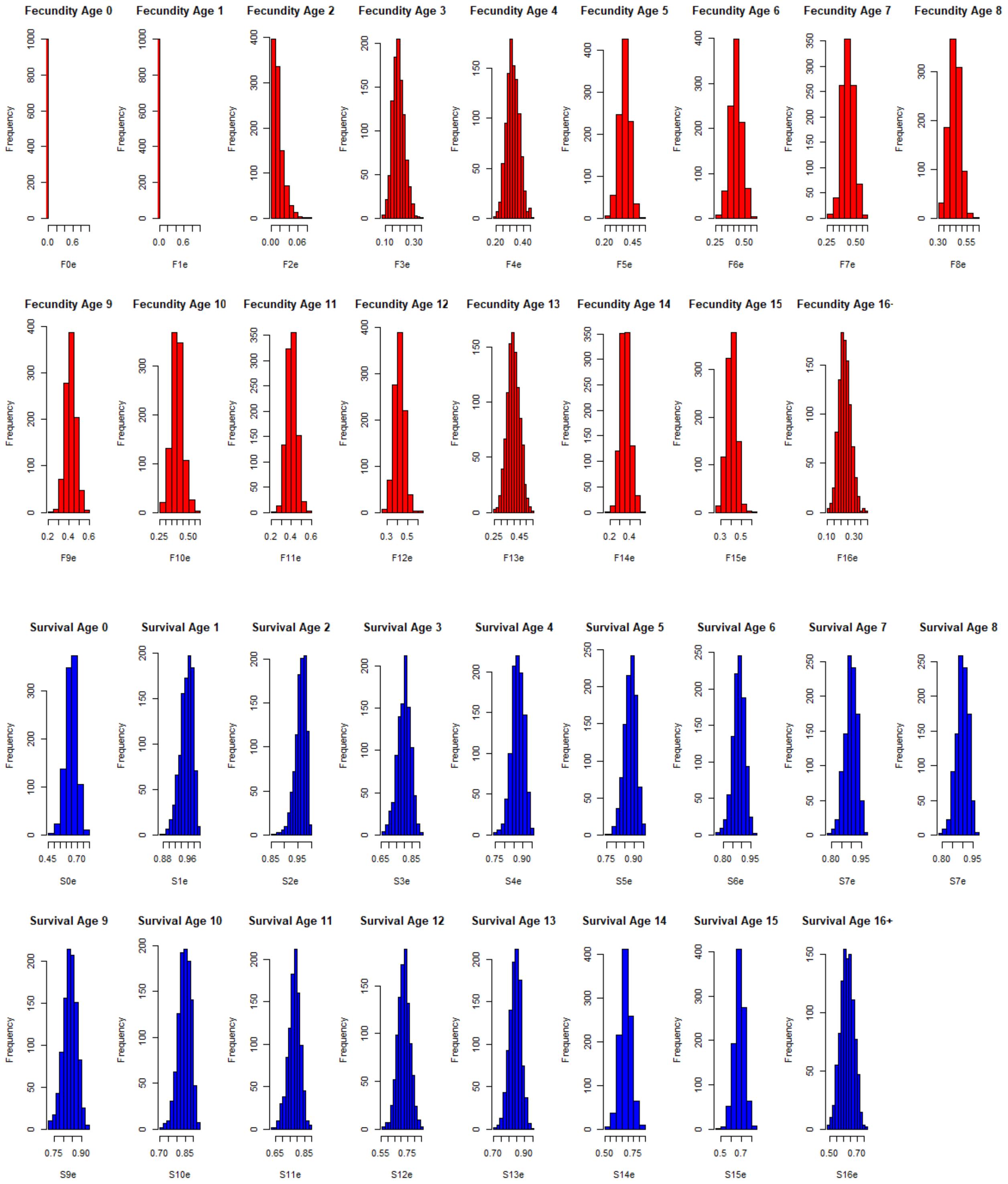

Figure A2.17. Age-specific beta distributions for fecundity (red) and survival (blue).

Appendix 3

This appendix contains supplemental information for work presented in Chapter 5.

ANTARCTIC FUR SEAL BREEDING PHENOLOGY & ATTENDANCE BEHAVIOR

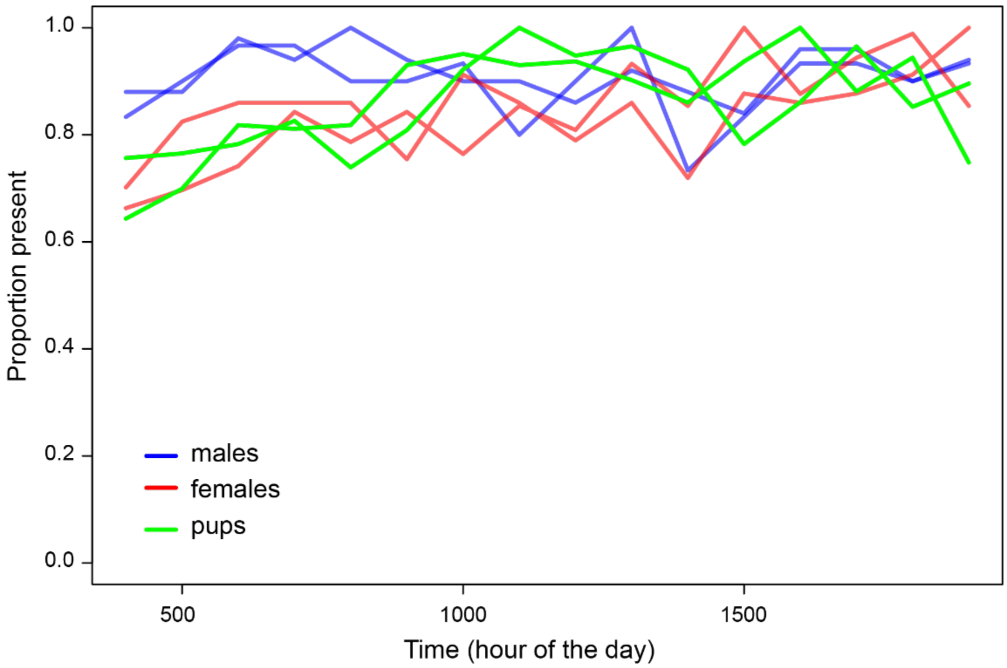

Figure A3.1. Attendance of males (blue), females (red), and pups (green) at the breeding beach was not highly variable across time of day.

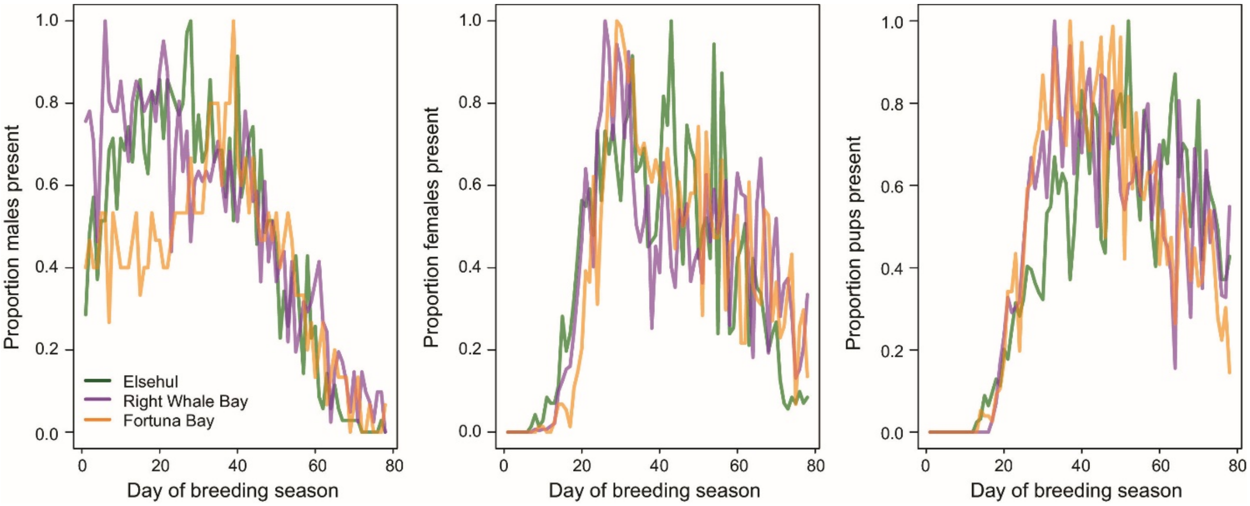

Figure A3.2. Attendance male, female, and pups was consistent across breeding beaches, as measured by the proportion present on each day of the breeding season relative to the maximum observed during the season.

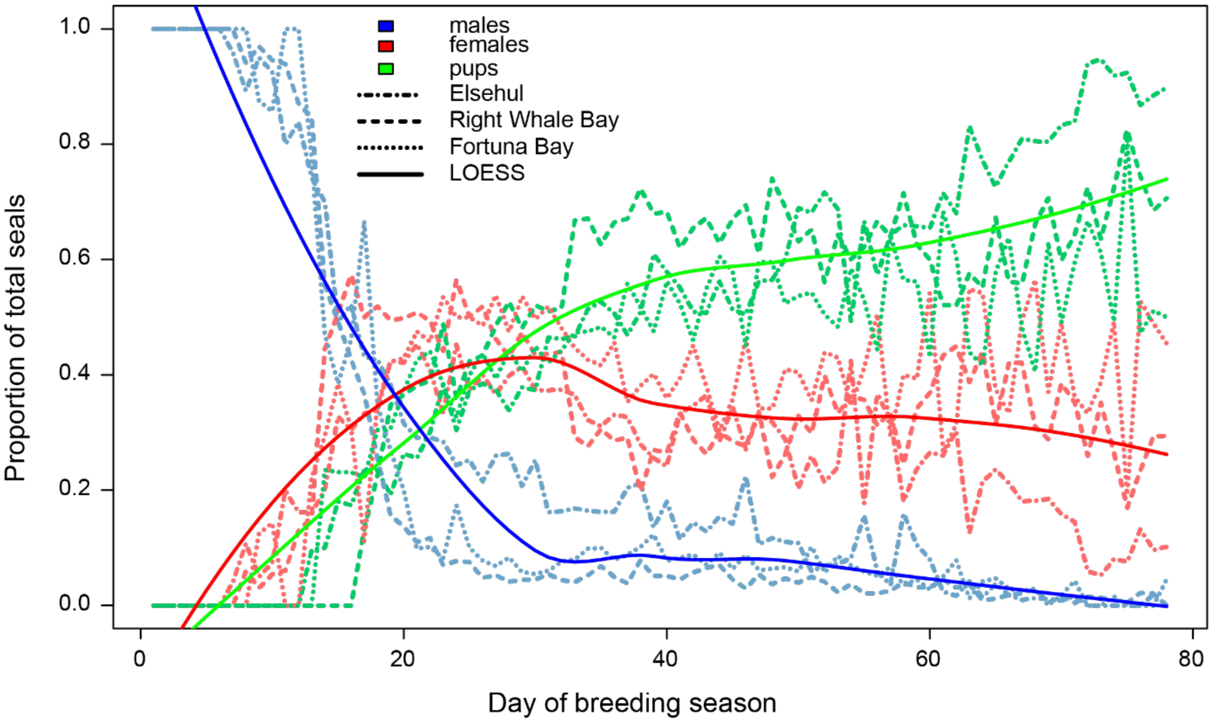

Figure A3.3. Attendance male, female, and pups was consistent across breeding beaches, as measured by the proportion present on each day of the breeding season relative to the maximum total number of seals observed during the season.