

Influence of climate and fisheries on the demography of giant petrels

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ABSTRACT

Understanding how populations and communities will respond to global changes is a major focus of modern ecology, and demographic studies are crucial for understanding the dynamic of wild populations and their responses to change. Here, I first conducted an analytically robust literature to demonstrate that seabird mortality in global fisheries (bycatch) tends to be biased by sex and age, mainly related to differential at-sea distributions, underpinning the population level effect bycatch on the most threatened group of birds. Next I performed a comprehensive longitudinal study, to address effects of fisheries, environmental variability and climate oscillation on population dynamics of northern (NGP, *Macronectes halli*) and southern giant petrel (SGP, *M. giganteus*) at Bird Island, South Georgia. I showed that annual survival and breeding success of NGP and SGP was influenced mainly by climatic oscillation and oceanographic conditions, including fisheries, and that the responses varied by sex and age. Giant petrels survived and reproduced better in warmer years, contrasting with the negative effects of warmer conditions on a range of marine land-based vertebrates in the same ecosystem. Differential accessibility to food resources during chick-rearing due to allochryony have contributed for the NGP breeding success and delayed reproductive senescence compared to SGP, supporting empirical evidence for role of allochryony on their divergent population trajectories. Finally, the findings in this thesis sheds a new light on how phenological mismatch can influence demographic process and on the role of environmental conditions on reproductive senescence, which are among the poorest understood processes in population ecology.

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Strategic workshops during the PhD course

Interdisciplinary Conservation Network Workshop, University of Oxford, Merton College, Oxford, 26-28 June 2016.

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Oral presentations

Same place, different time: interspecific effects of environmental variability on giant petrel demography. *British Ecological Society Annual Meeting*. Liverpool, 11-14 December 2016.

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Influence of allochryony on the population trajectories of northern and southern giant petrels. *13th International Seabird Conference*. Edinburgh. 6-9 September 2016.

Global patterns of sex- and age-specific variation in seabird bycatch. *2nd World Seabird Conference*. Cape Town. 26-30 October 2015.

Peer review for journals

Marine Ecology Progress Series

CHAPTER 1. General Introduction



1.1. Demographic studies in a changing world

Demography is the statistical study of populations based on the observation of individual life histories, a mathematical science with origins in ancient Greece (Srivastava 2005), and an approach vital in the modern world to explore and understand many processes. Demographic studies are crucial for understanding the dynamics of wild populations and their responses to change, both natural or anthropogenic, and are important tools in revealing the ecological consequences of global climate change and other human impacts across the Planet (Parmesan 2006; Halpern *et al.* 2008; Waters *et al.* 2016; Watson & Marco 2016). Hence, understanding how populations and communities will respond to global changes is a major focus of modern ecology (Thomas *et al.* 2004; Poloczanska *et al.* 2016).

In the oceans, biodiversity and ecosystem functioning are threatened by changing temperatures, acidification, harvesting by fisheries, and habitat degradation (Halpern *et al.* 2008; Hoegh-Guldberg & Bruno 2010; Wassmann *et al.* 2011; Lewison *et al.* 2014; Poloczanska *et al.* 2016). The cumulative and interactive impacts of changing climate and fisheries, for instance, have resulted in widespread ecological disruptions of marine ecosystems, with direct and indirect effects on population dynamics of across a wide diversity of taxa, and throughout the world's oceans. Marine megafauna (e.g. marine mammals, seabirds, turtles), have been especially severely impacted by these two stressors. Their vulnerability stems from their naturally slow reproductive rates and high trophic position in the food web (Trathan *et al.* 2007; Barbraud *et al.* 2012; Lewison *et al.* 2014; Sydeman *et al.* 2015). Globally, 28% of the 346 recognized seabird species are threatened (Croxall *et al.* 2012), and the biomass

of predatory fish reduced by 90% in relation to pre-industrial fisheries (Myers & Worm 2003), while steep declines of turtles and marine mammals have been recorded worldwide (Weimerskirch *et al.* 2003; Lewison *et al.* 2004, 2014; Estes *et al.* 2009).

Broadly, climate-driven fluctuations in food availability and effects of unfavourable abiotic conditions on foraging and thermoregulation represent the main impacts of climate change on marine megafauna, involving direct, and complex indirect effects via trophic links (Sydeman *et al.* 2015). Fluctuations in prey quality and availability associated with warm sea temperature anomalies have been linked to declines in marine megafauna populations in several regions. Population trends in seabirds and seals in polar regions have responded to climate-driven shifts in the community structure of forage fish and pelagic/planktonic crustaceans (Weimerskirch *et al.* 2003; Atkinson *et al.* 2004; Murphy *et al.* 2007a; Sydeman *et al.* 2015; Poloczanska *et al.* 2016). Reductions in forage fish availability due to ocean stratification in warm conditions is responsible for catastrophic breeding failure and mortality of seals and seabirds in Humboldt current system (Duffy; Triumich & Limberger 1985).

Fisheries can have positive or negative effects on marine megafauna, either direct or indirect (Montevecchi 2002). Positive effects include direct benefits of extra food provisioning in the form of discards, offal and depredation of fish trapped in the fishing gear (Furness 2003; Votier *et al.* 2004); or indirect effects of removal of certain large carnivorous fish and consequently reduced competition for marine prey (Montevecchi 2002). However, competition between fisheries and marine megafauna for forage fish and crustaceans have been responsible for indirect negative effects of fisheries on a range of marine

vertebrates (Reid *et al.* 2010; Sherley *et al.* 2015; Sydeman *et al.* 2017), which is aggravated by fisheries-driven ecosystem disruption. However, the most pervasive negative impact of fisheries on marine vertebrates is direct mortality in fishing gear, also called bycatch (Lewison *et al.* 2004, 2014; Phillips *et al.* 2016). Populations of medium to large seabirds are particularly susceptible to bycatch because of a combination of their attraction to fishery bait and discards, and their K-selected life histories, which render them sensitive to even small increases in mortality (Lewison *et al.* 2004). The impacts are so extensive that the recent declines of many large marine vertebrates resulting from bycatch have been compared to the historical extirpations and extinctions of terrestrial megafauna by human hunting (Lewison *et al.* 2004, 2014).

Demographic response of marine megafauna to fisheries and climate changes have been subject to great attention, but determining the impacts of change is challenging because of the complexity of anthropogenic perturbations and because top predators integrate processes across multiple trophic levels (Sydeman *et al.* 2015; Poloczanska *et al.* 2016). Moreover, such complex effects are predicted to vary among different components of their populations. For instance response to environmental change may vary according to sex (Lewis *et al.* 2016), age (Oro *et al.* 2014), stage of reproduction (Votier *et al.* 2008) or individual 'personality' (Patrick & Weimerskirch 2015; Tuck *et al.* 2015), making it challenging to understand population-level responses. In this context, detailed, empirical, longitudinal studies on wild populations are critical for forecasting population responses of wild populations to change, and fundamental for advancing the study of life-histories.

1.2. Giant petrels as a study system

The sibling species, northern giant petrel (*Macronectes halli*; hereafter NGP) and southern giant petrel (*M. giganteus*; hereafter SGP) are ecologically-similar congeners breeding on sub-Antarctic and Antarctic islands and with a wide-ranging marine distribution, from the ice edge to the subtropics. Both species forage at sea on Antarctic krill *Euphausia superba* and other marine prey by surface-seizing (Figure 1.1a), on fishing discards (Figure 1.1b), and also extensively on land, mostly scavenging on dead and moribund penguins and pinnipeds (Figure 1.1c), and, to a lesser extent, depredating smaller birds (Hunter 1984, 1985; Patterson *et al.* 2008). Giant petrels also consume penguins killed by pinnipeds close inshore (Bonner & Hunter 1982, Figure 1.1d), and are frequent and dominant scavengers around fishing vessels from sub-polar to subtropical waters, where they are considered to benefit from this food subsidy (Bugoni, McGill & Furness 2010; Copello *et al.* 2011; Krüger *et al.* 2017a). However, the population-level consequences of this association is not known. Giant petrels have also been recorded as bycatch in pelagic and demersal logline, and in trawl fisheries, across their range (Figure 1.2), although the demographic consequence of this mortality has not been quantified. Populations of both NGP and SGP have shown contrasting trends across their breeding range, and factors underlying differing trajectories between species and populations are unknown (ACAP 2010a; b). Both giant petrel species are listed as Least Concern by the IUCN. However, because of the declines in some populations, their high vulnerability to disturbance at breeding sites, and high level of interaction with fisheries, they are listed under the Agreement for the Conservation of Albatrosses and Petrels (ACAP). Therefore, it is perhaps unsurprising that empirical studies

assessing the effects of fisheries on their population dynamics have been identified as a research priority (ACAP 2010a; b).

Giant petrels are the most sexually size-dimorphic of all seabirds, with males up to 30% heavier and 15% larger than females (Table 1.1, Marchant & Higgins 1990; González-Solís 2004). This strong sexual size-dimorphism results in marked sexual segregation during incubation; males monopolise scavenging opportunities on land, forcing females to forage at sea (González-Solís, Croxall & Wood 2000; González-Solís 2004; Forero *et al.* 2005). Later in the breeding season (when carrion availability has declined), and during winter, both sexes forage predominantly at sea (González-Solís, Croxall & Afanasyev 2008; Thiers *et al.* 2014). This results in greater overlap between sexes at a broad spatial scale for much of the year, exposing them to broadly similar environmental drivers and impacts; however, given their high sexual-size dimorphism and correlated ecological traits, males and females are expected to respond differently, at least to some extent, to environmental changes and fisheries, offering an ideal system for studying sex-specific responses to environmental change.

Table 1.1. Morphological measurements of males and females northern and southern giant petrels. Table shows mean \pm SD (min-max).

	Males	Females
Northern giant petrel		
Wing	539.0 \pm 9.3 (521-562)	506 \pm 8.6 (482-522)
Bill	103.3 \pm 3.0 (96-110)	89.4 \pm 2.5 (85-96)
Weight	4902 \pm 391 (4150-5800)	3724 \pm 313 (3050-4500)
Southern giant petrel		
Wing	533.0 \pm 14.1 (492-555)	495.0 \pm 23.9 (460-522)
Bill	104.7 \pm 4.0 (97-111)	89.1 \pm 3.3 (84-94)
Weight	4930 \pm 340 (4200-5500)	3950 \pm 170 (3300-4700)



Figure 1.1. (a) A northern giant petrel surface-seizing in pelagic waters off southern Brazil; (b) giant petrels following a trawler alongside albatrosses on the Patagonian Shelf; (c) northern giant petrels scavenging on a dead elephant seal *Mirounga leonina* pup at South Georgia; and (d) southern giant petrels foraging on a gentoo penguin *Pigoscelys papua* killed by a southern sea lion *Otaria flavescens* at New Island, Falklands.

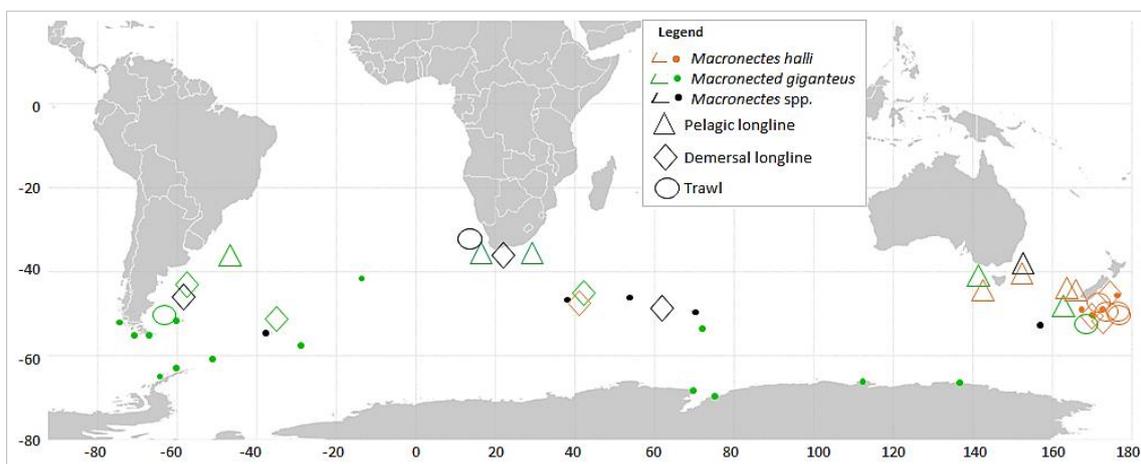


Figure 1.2. Global map of giant petrel bycatch, showing the distribution of the breeding sites (dots), and of bycatch records according to fishery type (symbols). Orange and green dots indicate northern and southern giant petrel colonies, respectively, and black dots indicate sites where both species breed sympatrically. Bycatch records for each species are indicated by the corresponding colours. See details in Table S1.1.

NGP and SGP are sibling species recently split and that conserve virtually identical morphology (Table 1.1), as well ecological and life history traits, apart from timing of breeding (Table 1.2). NGP breed around six weeks earlier than SGP (Marchant & Higgins 1990). This difference in timing of breeding is the key factor in maintaining reproductive isolation between these sympatric species, although hybridization can still occur (Brown *et al.* 2015). This phenological mismatch (allochryony) between the two species also plays a major role in resource partitioning, mainly through differential access to carrion during critical stages of the reproduction (Gonzalez-Solís, Croxall & Wood 2000). At South Georgia, the only site in the Atlantic where both species breed in sympatry (Hunter 1984), because NGP breed earlier, they are better able to exploit Antarctic fur seal (*Arctocephalus gazella*) carrion (pups and dead bulls), which peaks during the early to mid-chick rearing period of NGP. At this time, SGP are still incubating (Hunter 1984; Gonzalez-Solís *et al.* 2000). From the early 1960s to mid-1990s, the population of Antarctic fur seals rapidly recovered at South Georgia, after hunted close to extinction during the first half of the nineteenth century (Payne 1977; Boyd 1993; Forcada & Hoffman 2014). Over the same period, the NGP population also increased, whereas the SGP population was stable or has declined (Hunter 1985; González-Solís *et al.* 2000), suggesting that because of allochryony, bottom-up effects of increasing carrion availability affected species differentially. Furthermore, both species face different conditions according to reproductive stage, hence environmental variability will potentially result in species-specific responses to changing climate (Atkinson *et al.* 2004; Meredith & King 2005; Whitehouse *et al.* 2008).

Table 1.2. Life history traits of northern and southern giant petrels. With the exception of ‘clutch size’ and ‘maximum age’, table shows mean \pm Standard Deviation and, for age ‘at first breeding’ (min-max) when applied. Maximum age refers to the oldest known age individual in the dataset. References (Ref.) for the estimates are presented, and when estimates from two different sources are provided, the reference numbers appears superscripted.

	Northern giant petrel	Southern giant petrel	Ref
Adult survival	0.90 \pm 0.03 ¹ ; 0.91 \pm 0.03 ²	0.90 \pm 0.03 ¹ ; 0.92 \pm 0.05 ²	1; 2
Clutch size (n)	1	1	1
Incubation (days)	60 \pm 1	61 \pm 1	1
Age at fledging (days)	M: 114 \pm 3; F: 110 \pm 2	M: 123 \pm 5; F: 117 \pm 6	1
Age at first breeding (years)	7.5 \pm 0.8 (6-8) ¹ ; 9.4 \pm 0.4 (7-14) ³	7.5 \pm 0.8 (6-9) ¹ ; 9.2 \pm 0.6 (7-12) ³	1; 3
Juvenile survival	0.88 \pm 0.02 ¹ ; 0.85 \pm 0.07 ²	0.88 \pm 0.02 ¹ ; 0.90 \pm 0.07 ²	1; 3
Maximum age (years)	37	38	3

*Reference: 1 – This thesis, Chapter 3; 2 – Hunter 1984; 3 - This thesis, Chapter 5

Our study populations of giant petrels were located at South Georgia, one of the fastest-warming regions on Earth (Meredith & King 2005). Here oceanographic and atmospheric changes have produced a range of ecosystem-level disturbances, affecting a diversity of marine megafauna (Atkinson *et al.* 2004; Murphy *et al.* 2007a; Trathan *et al.* 2007; Forcada, Trathan & Murphy 2008; Louise Allan *et al.* 2013; Forcada & Hoffman 2014). This region, and subtropical waters to the north, have also been exploited by large-scale commercial fisheries, causing unsustainable levels of bycatch and ecological change (Croxall & Nicol 2004; Sullivan, Reid & Bugoni 2006; Tuck *et al.* 2011; Yeh *et al.* 2013; Jiménez *et al.* 2014). Several studies have investigated the effects of climate change and fisheries on life history traits of land-based marine vertebrates in the Southern Ocean (Forcada *et al.* 2005, 2008, Barbraud *et al.* 2011, 2012; Descamps *et al.* 2016); however, very few have examined sex-specific responses or compared allochronic populations.

Unlike other well-monitored land-based marine vertebrates (e.g. albatrosses, penguins and seals), the population ecology of giant petrels is poorly understood, despite their key role in the Southern Ocean ecosystem. Accordingly, I analysed data from a long term study of these two sympatric long-lived marine vertebrates to address the effects of fisheries, environmental variability and climatic oscillation on their population dynamics, advancing knowledge of their life-histories, and providing valuable insights into the environmental and anthropogenic factors driving population changes of marine predators in the Southern Ocean.

1.3. Thesis outline

The broader focus of this thesis is to unravel the complexities of potential demographic responses of marine megafauna to climate change and anthropogenic impacts across different components of their populations.

In **Chapter 2**, I provide the first global assessment of how fisheries bycatch, which is possibly the most pervasive threat to seabirds worldwide, varies by sex and age, and used Generalised Linear Mixed models (GLMMs) to investigate the effects of region and fishing method on bycatch proportions. This study contributed towards a better understanding of the frequency and magnitude of sex- and age-biased bycatch across taxa, regions and fishery gear-type, as well as the implications for demography, management and conservation.

Subsequently, in **Chapters 3, 4 and 5**, I analysed data from longitudinal studies using capture-mark-recapture (CMR) and Population Projection Matrix Models (PPMs), combined with detailed information on at-sea distributions, environmental data and fisheries effort, to reveal the array of factors underlying

demographic responses of these two congeneric and sympatric species, and their divergent population trajectories.

In **Chapter 3**, I test for sex-specific effects of climate cycles, oceanographic conditions, and fisheries on the survival and demography of these two highly sexual size-dimorphic species, and modelled the influence of sex-specific effects of environmental drivers on population growth rate.

In **Chapter 4**, I focused on the potential role of allochryony in driving divergent population trajectories between the two species. I provide the first robust comparison of the influence of annual changes in carrion availability on land, and other potential environmental drivers at sea, on reproduction and population growth rate of these two sympatric species.

In **Chapter 5**, I compared reproductive ageing patterns in the two giant petrel species and also examine age-specific survival and variation in reproductive traits between inexperienced and experienced breeders in early adulthood.

Finally, in **chapter 6**, I integrate the results of each chapter to reveal the complex population dynamics of giant petrels and their response to changes, and discuss the implications of the findings in the broader context of conservation, ecology and life-history theory.

CHAPTER 2. Global patterns of sex- and age-specific variation in seabird bycatch



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ABSTRACT

Fisheries bycatch is a major threat to seabird populations, and understanding sex- and age-biases in bycatch rates is important for assessing population-level impacts. We analysed 44 studies to provide the first global assessment of seabird bycatch by sex and age, and used generalised models to investigate the effects of region and fishing method. Bycatch was highly biased by sex (65% of 123 samples) and age (92% of 114 samples), with the majority of samples skewed toward males and adults. Bycatch of adults and males was higher in subpolar regions, whereas there was a tendency for more immatures and females to be killed in subtropical waters. Fishing method influenced sex- and age-ratios only in subpolar regions. Sex- and age-biases are therefore common features of seabird bycatch in global fisheries that appear to be associated largely with differences in at-sea distributions. This unbalanced mortality influences the extent to which populations are impacted by fisheries, which is a key consideration for at-risk species. We recommend that researchers track individuals of different sex and age classes to improve knowledge of their distribution, relative overlap with vessels, and hence susceptibility to bycatch. This information should then be incorporated in ecological risk assessments of effects of fisheries on vulnerable species. Additionally, data on sex, age and provenance of bycaught birds should be collected by fisheries observers in order to identify regions and fleets where bycatch is more likely to result in population-level impacts, and to improve targeting of bycatch mitigation and monitoring of compliance.

2.1. Introduction

Fisheries are one of the primary threats to marine biodiversity, impacting ecosystems from the open ocean to the coast, and from the poles to the tropics (Jackson *et al.* 2001; Halpern *et al.* 2008). Commercial fishing has resulted in severe and widespread ecosystem disruption primarily as a result of over-harvesting, habitat degradation and the mortality of non-target species, also called bycatch (Hall, Alverson & Metuzals 2000; Jackson *et al.* 2001; Halpern *et al.* 2008). Populations of large marine vertebrates, such as sea turtles, sharks, marine mammals, and seabirds, are particularly susceptible to bycatch because of a combination of their attraction to fishery bait and discards, and their naturally slow reproductive rates rendering them sensitive to even small increases in mortality (Hall *et al.* 2000; Lewison *et al.* 2004), 2004). The impacts are so extensive that the recent declines of many large marine vertebrates resulting from bycatch have been compared to the historical extirpations and extinctions of terrestrial megafauna by human hunting (Lewison *et al.* 2004, 2014). Seabirds are particularly at risk from fisheries, as they are bycaught in a wide range of gear types (Montevecchi 2002; Croxall *et al.* 2012; Phillips *et al.* 2016). For example, drift nets set by Japanese, Korean and Taiwanese vessels are estimated to have killed up to 40 million sooty (*Ardenna grisea*) and short-tailed (*A. tenuirostris*) shearwaters in the North Pacific between 1952 and 2001 (Uhlmann, Fletcher & Moller 2005). Coastal gillnet fisheries are also a major source of mortality, with >400,000 seabirds killed annually, worldwide (Žydelis, Small & French 2013). Global longline fisheries are estimated to have killed at least 160,000, and potentially 320,000 seabirds annually, mainly albatrosses, petrels and shearwaters (Anderson *et al.* 2011). Trawl fisheries are also a threat, with about 9,300 birds, mostly albatrosses, estimated to be killed annually just in the waters

off South Africa by wet fish trawls (Sullivan *et al.* 2006; Waugh, MacKenzie & Fletcher D. 2008; Maree *et al.* 2014). These levels of mortality have led to severe declines in many populations and are clearly unsustainable (Piatt & Gould 1994; Croxall *et al.* 1998; Cuthbert *et al.* 2005; Delord *et al.* 2008; Rolland, Weimerskirch & Barbraud 2010; Żydelis *et al.* 2013; Phillips *et al.* 2016).

The impact of bycatch depends not only on the number of individuals killed, but also on the components of the population that are impacted (Bugoni, Griffiths & Furness 2011; Lewison *et al.* 2014). For example, because seabird life histories are characterised by delayed maturation, high survival and low rates of reproduction, mortality of adults will have greater population-level impacts than mortality of immatures (Lewison *et al.* 2014). Moreover, because seabirds are monogamous, with obligate bi-parental care, sex-biased mortality in fisheries can reduce the effective population size (Mills & Ryan 2005; Weimerskirch, Lallemand & Martin 2005). Sex- and age-biases in seabird bycatch are reported in a number of fisheries (Stempniewicz 1994; Gales, Brothers & Reid 1998; Ryan & Boix-hinzen 1999; Awkerman *et al.* 2006), and there has been a review of adult sex-ratios (ASR) in bycatch of albatrosses and petrels (Bugoni *et al.*, 2011). However, there has been no comprehensive review of sex- and age-biases in bycatch of seabirds in general, even though a better understanding of their nature and extent is required to determine the full impact of bycatch on populations and communities. Indeed, this has been identified as one of the highest priority research questions in the field of seabird ecology and conservation (Lewison *et al.* 2012; Phillips *et al.* 2016).

Accordingly, the aim of the current study is to provide the first global review of age- and sex-specific bycatch in seabirds. This will contribute towards a better

understanding of the frequency and magnitude of these effects across taxa, regions and fishery gear-type, as well as the implications for management and conservation. We predict that larger and more dominant individuals, usually adult males, will have higher bycatch rates than adult females, or younger birds of either sex, because they are better able to compete for discards and baits while attending fishing boats (Croxall & Prince 1990; Montevecchi 2002; Bregnballe & Frederiksen 2006; Awkerman, Hobson & Anderson 2007a). However, bycatch rates will also be influenced by region. Many studies have shown that females and immatures tend to travel further from their breeding sites, or to lower latitudes, compared with males and adults (Phillips *et al.* 2004, 2005; Hedd *et al.* 2014). Therefore, because the majority of seabirds breed at high latitudes (Schreiber & Burger 2002) we broadly predict that bycatch in subpolar (sub-Arctic and sub-Antarctic) areas will tend to be skewed towards males and adults, whereas in subtropical regions, bycatch will be biased towards females and immatures.

2.2. Methods

2.2.1. Literature review

We reviewed the literature for studies reporting sex and age composition of seabird bycatch in fisheries from around the world. We searched Thomson Reuters Web of Science and Google Scholar using the following search terms: Topic = (seabird* OR albatross* OR petrel* OR penguin* OR shearwater*) AND (sex OR age OR female OR male OR adult OR juvenile) AND (fishery* OR bycatch OR mortality) AND (bias); Timespan = All Years. To ensure the best possible coverage of the bycatch literature, we supplemented this with grey

literature and contacted a number of experts directly to alert us to any missing references and to access unpublished studies. Only the studies reporting sex or age composition from samples of more than 10 individuals per species were included. We used the term 'immature' to refer to birds of any age below age of first breeding.

Authors utilized different methods for sexing including examination of gonads through necropsies (Petersen *et al.* 2010; Thompson 2010a; b), molecular sexing (Bugoni *et al.* 2011; Jiménez *et al.* 2015b) and ring recoveries of known-sex individuals (e.g.(Jiménez *et al.* 2015a). Birds were aged on the basis of plumage and bill morphology (Neves & Olmos 1997; Cardoso *et al.* 2011), or ring details for known-age individuals (Österblom, Fransson & Olsson 2002; Awkerman *et al.* 2006; Jiménez *et al.* 2015a). To aid interpretation, we classified each sample of seabird bycatch according to the magnitude of sex- and age-bias: highly biased ($\geq 80\%$ belonging to one sex or age class); biased (60% - 79%) and not biased (40% - 59%). The sampling unit for bycatch data refers to the information for each taxon caught in a particular gear type in each study. When possible, bycatch rates were separated by region and season (summer/winter).

To aid comparison across regions, the global oceans were initially divided into five major zones: sub-Antarctic, subtropical southern hemisphere, tropical, subtropical northern hemisphere and sub-Arctic. For the purpose of this study, sub-Arctic and sub-Antarctic zones also included the adjacent temperate waters. Thus, sub-Antarctic and sub-Arctic regions mostly comprise waters between 60° and 40° of latitude (average sea surface temperature (SST) 0°–18° C), subtropical in both hemispheres between 40° and 20° of latitude (average SST

18°-24° C), and tropical between 20° S and 20° N (average SST >25° C). The exception was in the southern hemisphere, where cold water masses extend as far north as 30° S off the west coast of South America and to the south and south-west of Australia, which were included in sub-Antarctic waters (Figure 2.1). In modelling the regional effects on the sex- and age-ratios of seabird bycatch, sub-Antarctic and sub-Arctic areas were combined in “subpolar”, and subtropical waters of both hemispheres combined in “subtropical”.

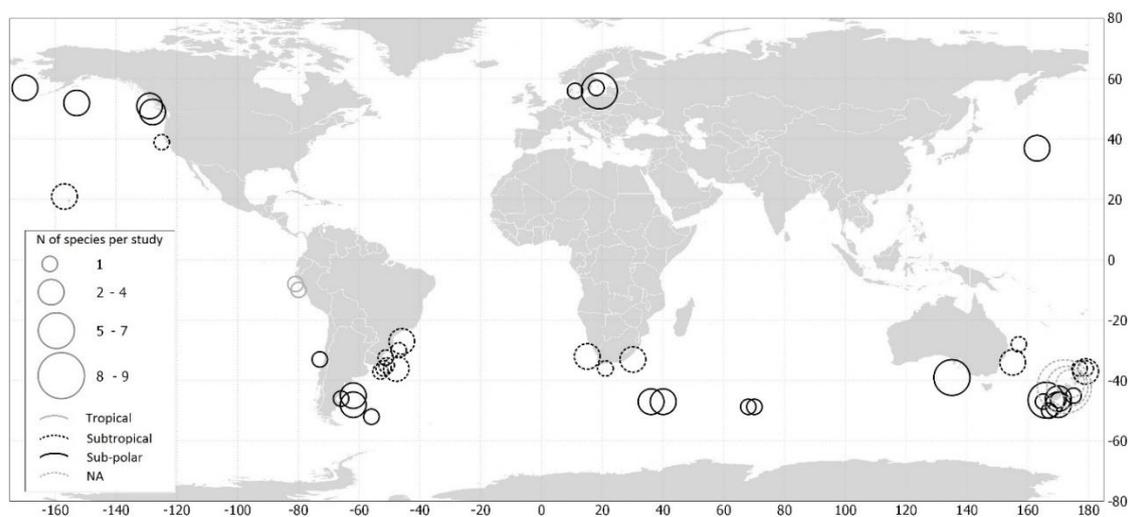


Figure 2.1. Spatial distribution of seabird bycatch studies with data on sex and age composition. The size of the circles indicates the number of species per study. Black solid and dotted circles indicate subpolar and subtropical regions, respectively. Light grey solid circles show studies in the tropics (Peru), and light grey dotted circles correspond to studies from New Zealand without detailed information on region (NA), which were therefore excluded from the analysis of regional effects.

We obtained data from a diverse range of fisheries, including pelagic and demersal longline, gillnet, trawl and pound net (shallow water nets attached to poles to create a funnel). Our sample, however, was dominated by two main gear types and variations therein: longline (pelagic and demersal) and gillnet. Longlines primarily kill surface-feeding birds attracted to baited hooks near the

surface, while gillnets mainly entrap pursuit divers and bottom feeders (Anderson *et al.* 2011; Žydelis *et al.* 2013).

2.2.2. Data analysis

We first compared the number of biased with non-biased (sex and age, respectively) bycatch samples for each fishery type, region and category using contingency tables. We specifically used chi-squared tests with Yates's correction for continuity where there was only one degree of freedom. We then tested for the effects of region (subpolar vs subtropical) and fishery type (longline [demersal and pelagic combined] vs gillnet) on the age and sex ratios of seabird bycatch using linear models followed by analyse of variance (ANOVA). We first ran linear mixed models using the *lmer* function of the *lme4* package in R (Zuur *et al.* 2009; R Development Core Team 2011), including species as a random effect to account for inclusion in multiple datasets. Then, after verifying that the random-effect was not significant, it was dropped and linear models applied instead, using the function *lm* of the same package in R. The proportion of males or adults was used as the response variable for sex and age-bias respectively, using a Gaussian error distribution. Due to the unbalanced geographical distribution of bycatch samples by fishery type, we also tested the effect of the four major gear types (pelagic longline, demersal longline, gillnet and trawl) within the subpolar region. This was the only region with sufficient datasets. All models were weighted by the sample size, which, for the purpose of this analysis, was the number of birds of each taxon caught in a particular gear type in each study. We tested the effect of region and fisheries on sex and age proportions separately. Models were compared using second-order Akaike Information Criterion (AICc), where the best model is taken to be that with the lowest AICc value. AICc

differences of <2 are not considered to be meaningfully different (Zuur *et al.* 2009).

2.3. Results

We found 44 studies, published between 1990 and 2016, that reported sex and age composition of seabird bycatch in fisheries, of which 35 (79%) were in the southern hemisphere and 9 (21%) in the northern hemisphere (Figure 2.1, Table 1.1). Data were available from four main types of fishery: 14 studies for pelagic longline (32%), nine for demersal longline (20%), nine for gillnet (20%), two for trawl (5%). Seven (16%) studies reported data for more than one fishery, separated according to gear type. In addition, two studies combined data from intentional catch, and bycatch in gillnet and longline (5%), and a single study (2%) reported data from pound nets.

Availability of data from each fishery type was not equally distributed, geographically. For example, 82% ($n = 16$) of the samples from demersal longline and 100% ($n = 8$) of those from trawl fisheries came from the sub-Antarctic region, 52% ($n = 27$) of the pelagic longline samples from subtropical waters of the southern hemisphere, and 84% ($n = 15$) of the gillnet samples from sub-Arctic and adjacent subtropical waters combined (Figure 2.2).

The bycatch data with information on sex and age composition comprised 18,389 individuals of 41 seabird taxa, including 15 which are globally threatened: 16 albatrosses (Diomedidae), nine petrels and shearwaters (Procellariidae), six sea ducks (Merginae), three penguins (Spheniscidae), two gulls (Laridae), two alcids (Alcidae), one grebe (Podicipedidae) and two cormorant/shags (Phalacrocoracidae) (Table S2.1).

Table 2.1. List of the studies (n = 44) reporting sex and age composition of seabird bycaught in fisheries, with information on the number of taxa with data (N), type of fishery (PLL, pelagic longline; DLL, demersal longline; TRA, trawl; GIL, gillnet; PND, pound net; INT, intentional), region (SUBANT: sub-Antarctic; SUBARC: sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; TROPIC, tropical), area, and year of the bycatch.

Reference	N species	N sexed	N aged	Fishery	Region	Area	Bycatch year
Jiménez et al., 2016	2	128	0	PLL	SUBTRS	Uruguay	2004-2012
Jiménez et al., 2015a	1	49	116	PLL	SUBTRS	Uruguay	1999-2012
Jiménez et al., 2015b	1	28	28	PLL	SUBTRS	Uruguay	2008-2011
Beck et al., 2013	4	822	694	DLL, PLL	SUBARC, SUBTRN	Hawaii, Alaska	2007-2013
Trebilco et al., 2011	1	233	89	PLL	SUBTRS	Australia	2001-2006
Cardoso et al., 2011	1	0	20	GIL	SUBTRS	Brazil	2009
Phillips et al., 2010	4	365	348	DLL	SUBARC	Alaska	2005
Petersen et al., 2010	3	935	1175	PLL	SUBTRS	South Africa	1998-2005
Delord et al., 2010	1	5189	0	DLL	SUBANT	Kerguelen	2003-2006
Thompson, 2010a	7	312	327	PLL, TRA	SUBANT, SUBTRS	New Zealand	2006-2007
Thompson, 2010b*	7	361	367	PLL, TRA	SUBANT, SUBTRS	New Zealand	2008-2009
Thompson et al., 2009	4	308	311	DLL, PLL, TRA	SUBANT	New Zealand	2005-2006
Roma, 2009	1	100	67	PLL	SUBTRS	Brazil	2006-2008
Burg, 2008	1	27	0	PLL	SUBANT, SUBTRS	New Zealand	1997
Seco-Pon et al., 2007	2	74	18	DLL	SUBANT	Argentina	2005
Gandini and Frere, 2006	2	31	0	DLL	SUBANT	Argentina	200-2001
Awkerman et al., 2006	1	33	0	PLL, GIL, INT	TROPIC	Peru	2005
Bregnballe & Frederiksen, 2006	1	0	289	PND	SUBARC	North Sea	1983-1992
Jiménez-Uzcátegui et al., 2006	1	0	40	PLL, GIL, INT	TROPIC	Peru	1998-2006
Delord et al., 2005	1	379	0	DLL	SUBANT	Kerguelen	2001-2003
Smith & Morgan, 2005	2	205	205	GIL	SUBARC	NE Pacific	1995-2001
Nevins, 2004	1	785	785	GIL	SUBTRN	California	1999-2000
Robertson et al., 2004*	5	643	646	DLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	2001-2002
Robertson et al., 2003*	9	898	1033	DLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	2000-2001
Reid et al., 2004	1	17	0	DLL	SUBANT	Falklands	2001-2002
Ryan et al., 2002	2	0	50	PLL	SUBTRS	South Africa	1998-2000
Nel et al., 2002a	4	962	241	DLL	SUBANT	Prince Edward	1996-2000
Osterblom et al., 2002	1	0	765	GIL	SUBARC	Baltic Sea	1972-1999
Darby and Dawson, 2000	1	42	42	GIL	SUBANT	New Zealand	1979-1997
Robertson, 2000*	4	161	161	PLL, TRA	SUBANT, SUBTRS	New Zealand	1998
Robertson & Bell, 2002	4	150	153	BLL, PLL, TRA	SUBANT, SUBTRS	New Zealand	1998-1999
Ryan and Box-Hinzen, 1999	4	388	367	DLL	SUBANT	Prince Edward	1996-1997
Gandini et al., 1999	1	31	0	TRA	SUBANT	Argentina	1995-1997
Simeone et al., 1999	1	0	663	GIL	SUBANT	Chile	1991-1996
Thompson et al., 1998	2	322	322	GIL	SUBARC	NE Pacific	1994-1994
Gales et al., 1998	8	407	407	PLL	SUBANT, SUBTRS	Australia	1988-1995
Barnes et al., 1997	1	33	0	DLL	SUBTRS	South Africa	1994
Neves & Olmos, 1997	2	50	50	PLL	SUBTRS	Brazil	1994-1995
Langston & Rohwer, 1995	2	308	308	GIL	SUBTRN	North Pacific	1990-1991

Stempniewicz, 1994	7	1149	1149	GIL	SUBARC	Baltic Sea	1972-76, 86-90
Murray et al., 1993	4	100	105	PLL	SUBANT, SUBTRS	New Zealand	1988-1992
Bartle, 1991	1	35	35	TRA	SUBANT	New Zealand	1990
Bartle, 1990	1	16	16	PLL	SUBANT	New Zealand	1989
Croxal & Prince, 1990	1	12	12	PLL	SUBTRS	N Argentina, Uruguay, Brazil	1984-1986

* Bycatch in subtropical and sub-Antarctic areas of New Zealand was pooled.

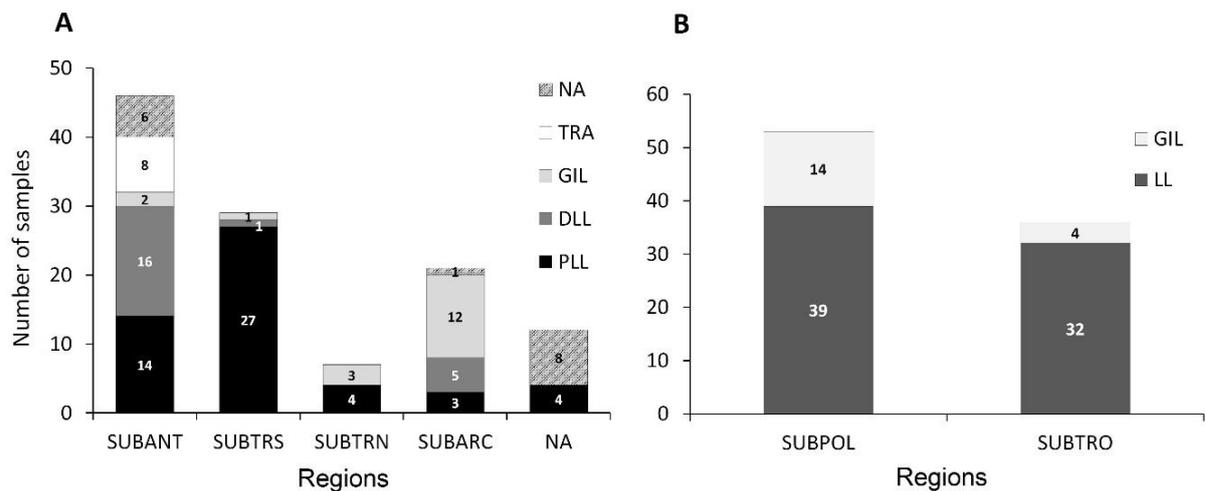


Figure 2.2. Number of bycatch samples by main fishery type and regions, reflecting (A) the original data, and (B) fisheries categories collapsed for the purposes of modelling. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar; SUBTRO, subtropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl; LL, longline; NA, detailed data per fishery type or region was not available.

2.3.1. Sex-specific bycatch

Of 123 samples of sex ratios in seabird bycatch, 43 (35%) were unbiased, 56 (46%) were male-biased (including 20 that were highly biased), and 24 (19%) were female-biased (including five that were highly biased) (Figure 2.3-A, Table S2.2). The number of sex-biased bycatch samples was significantly higher than the number of non-biased ($\chi^2_{Yates} = 10.537$, $P = 0.001$), and the number of samples skewed towards males was significantly higher than that skewed towards females ($\chi^2_{Yates} = 12.013$, $P < 0.001$).

The geographical distribution of the highly sex-biased bycatch samples ($\geq 80\%$ of one sex) is presented in Figure 2.4. There was a significant effect of the interaction between region and fishery type on the sex ratios of seabirds killed in fisheries, with the regional effect influencing the sex ratio of seabird bycaught in longlines but not in gillnets (Figure 2.5, Table 2.2). There was a higher proportion of males bycaught in fisheries in subpolar areas, whereas a trend towards female bycatch in subtropical waters ($F = 38.464$, $P < 0.001$) (Figure 2.6-A, Table 2.3). There was no significant difference in sex-ratios of seabird bycatch between gillnets and longlines (Figure 6-B, Table 3). However, when modelling the effect of the four major fishery gear-types within the subpolar region a significant effect was found ($F = 10.556$, $P < 0.01$), with a higher mortality of males in trawl fisheries (Figure 7-A, Table 4).

2.3.2. Age-specific bycatch

Of 114 samples reporting age composition of seabird bycatch, nine (8%) were unbiased, 78 (68%) were skewed towards adults (62 were highly biased) and 27 (24%) were biased towards immatures (12 were highly biased) (Figure 2.3-B, Table S2.1). Age-biased bycatch was therefore widespread across global fisheries, accounting for 92% of reports ($\chi^2_{\text{Yates}} = 79.167$, $P < 0.001$), with the frequency of adult-biased samples significantly larger than immature-biased ($\chi^2_{\text{Yates}} = 23.810$, $P < 0.001$).

The geographical distribution of the highly age-biased bycatch samples ($\geq 80\%$ of one age class) is presented in Figure 2.8. There was a significant effect of the interaction between region and fishery type on the age ratios of seabirds killed in fisheries, with the regional effect influencing the age ratio of seabird bycaught in longlines but not in gillnets (Figure 2.5, Table 2.2). A higher

proportion of adults was bycaught in subpolar regions whereas no difference was found in age-ratio of seabirds killed in subtropical areas ($F = 6.262$, $P < 0.05$) (Figure 2.6-C, Table 3). More adults than immatures were bycaught in longline, but there was no age bias for seabirds bycaught in gillnets ($F = 13.578$, $P < 0.001$) (Figure 2.6-D, Table 2.3). Fishery type has a significant influence on the age ratio of seabirds bycaught in subpolar regions ($F = 17.175$, $P < 0.001$) (Table 2.4). Mortality of adults was significantly higher than of immatures in demersal longline and trawl fisheries than in other fishery types in these regions (Figure 2.7-B).

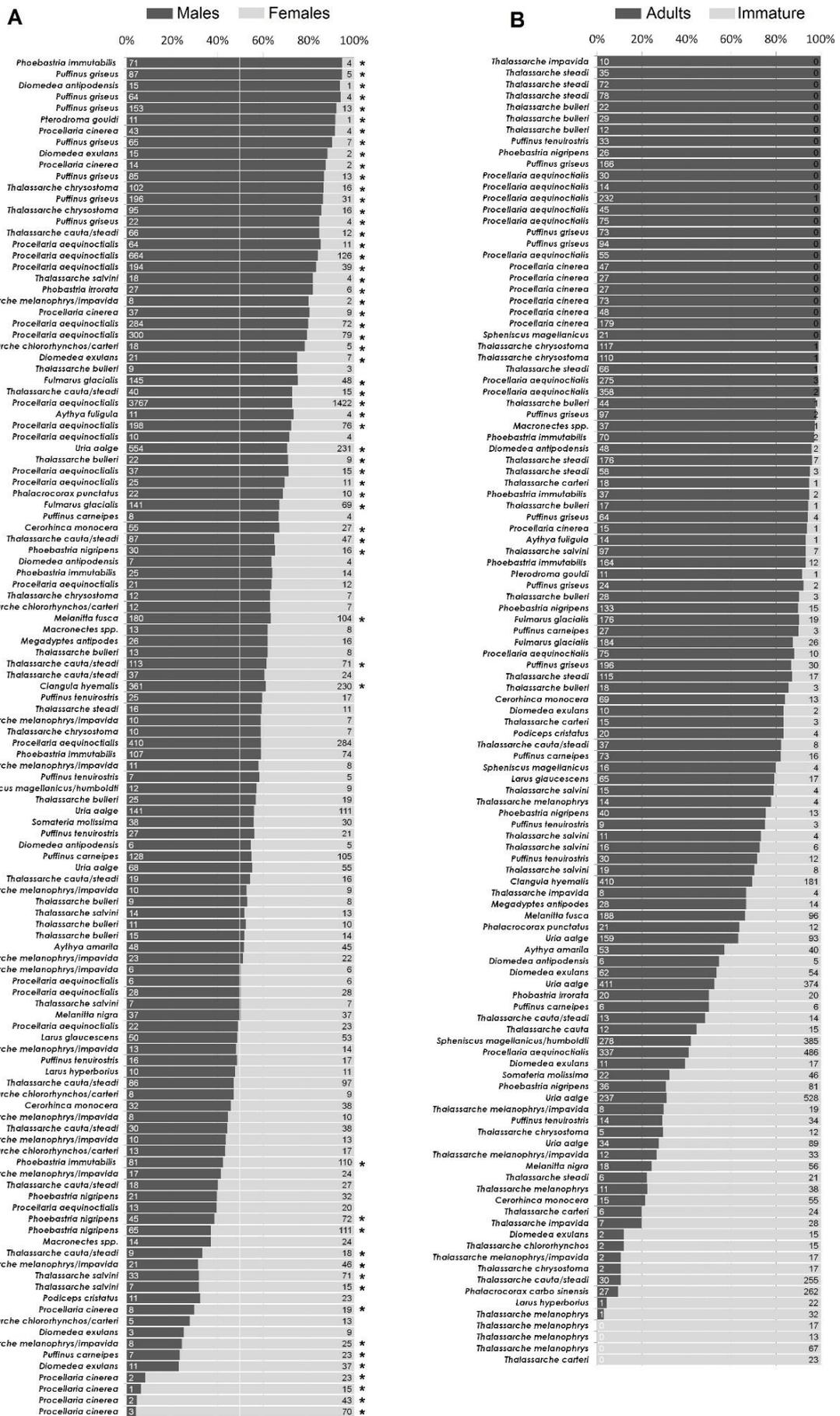


Figure 2.3. Legend next page.

Figure 2.3. Sex (A) and age ratios (B) of seabird species reported as bycatch in global fisheries. The number of individuals in each sample is shown inside the bars, and asterisks indicate sex compositions that deviated statistically from the expected sex ratio of 1:1 ($\chi^2_{Yates}, P < 0.05$). Deviation from a 1:1 ratio age ratios were not tested because equal proportions of adults and immatures are not expected in wild populations.

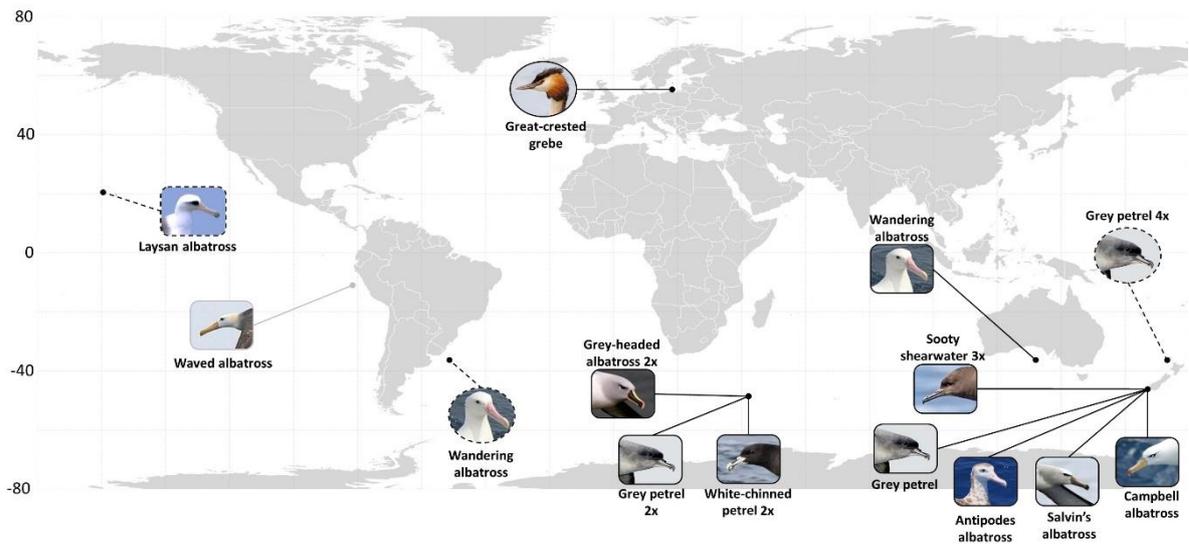


Figure 2.4. Geographical distribution of the highly sex-biased bycatch samples ($\geq 80\%$ of one sex). Squared figures refer to male and circled figures refer to female-biased samples. Black solid, black dotted and grey lines denote bycatch events in subpolar, subtropical and tropical regions respectively. Highly sex-biased samples from studies that subtropical and sub-Antarctic areas of New Zealand were pooled are not shown. The numbers follow common names indicate the number of sex-biased samples for that taxon in the given location.

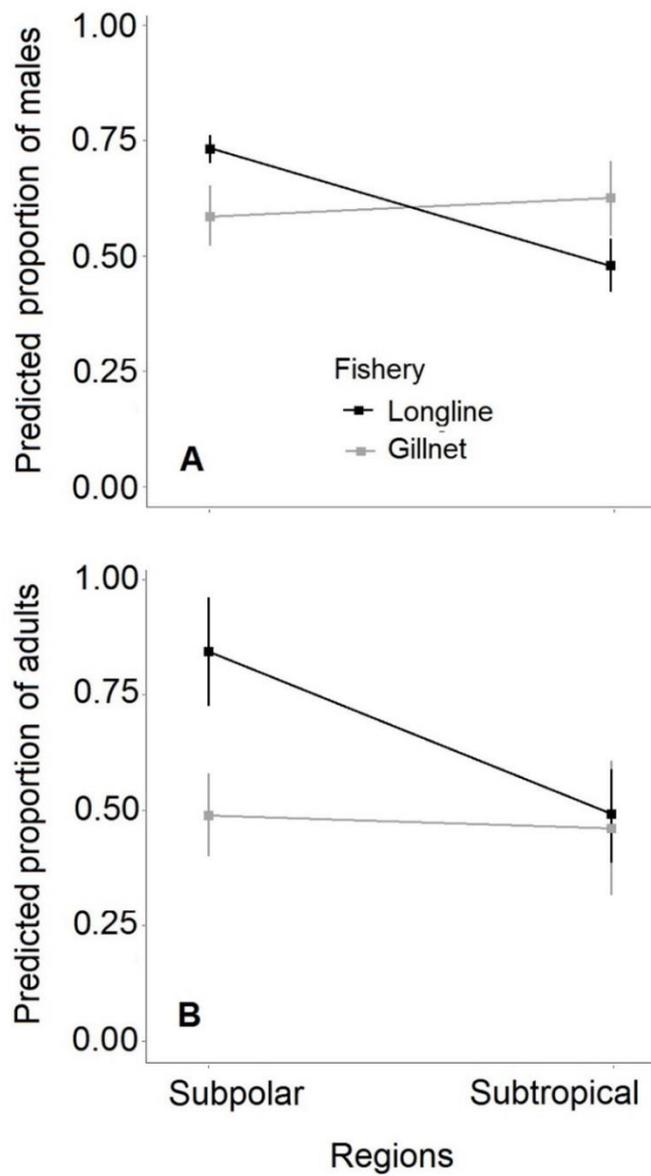


Figure 2.5. Interaction effect of region (subpolar vs subtropical) and fishery type (longline [demersal and pelagic combined] vs gillnet) on the proportion of males (A) and adults (B) in seabird bycatch.

Table 2.2. Candidate mixed effect models for proportion of males, and proportion of adults in seabird bycatch composition as influenced by region and type of fishery. All models included species as a random effect. Best models are highlighted in bold.

Model	df	AICc	Δ AICc	Deviance	Resid df
<i>Sex (y <- proportion of males)</i>					
y ~ Region * Fishery	5	-37.17	0	142.2	79
Y ~ Region	3	-22.37	14.8	211.98	95
y ~ 1	2	-18.27	18.9	183.5	80
y ~ Region + Fishery	4	12.17	49.34	381.34	122
y ~ Fishery	3	18.65	55.82	310.4	90
<i>Age (y <- Proportion of adults)</i>					
y ~ Region * Fishery	5	48.4	0.0	35.1	68
y ~ Region + Fishery	4	55.5	7.1	44.6	69
y ~ Fishery	3	72.1	23.7	63.3	79
Y ~ Region	3	83.3	34.9	74.8	85
y ~ 1	2	109.9	61.5	103.7	112

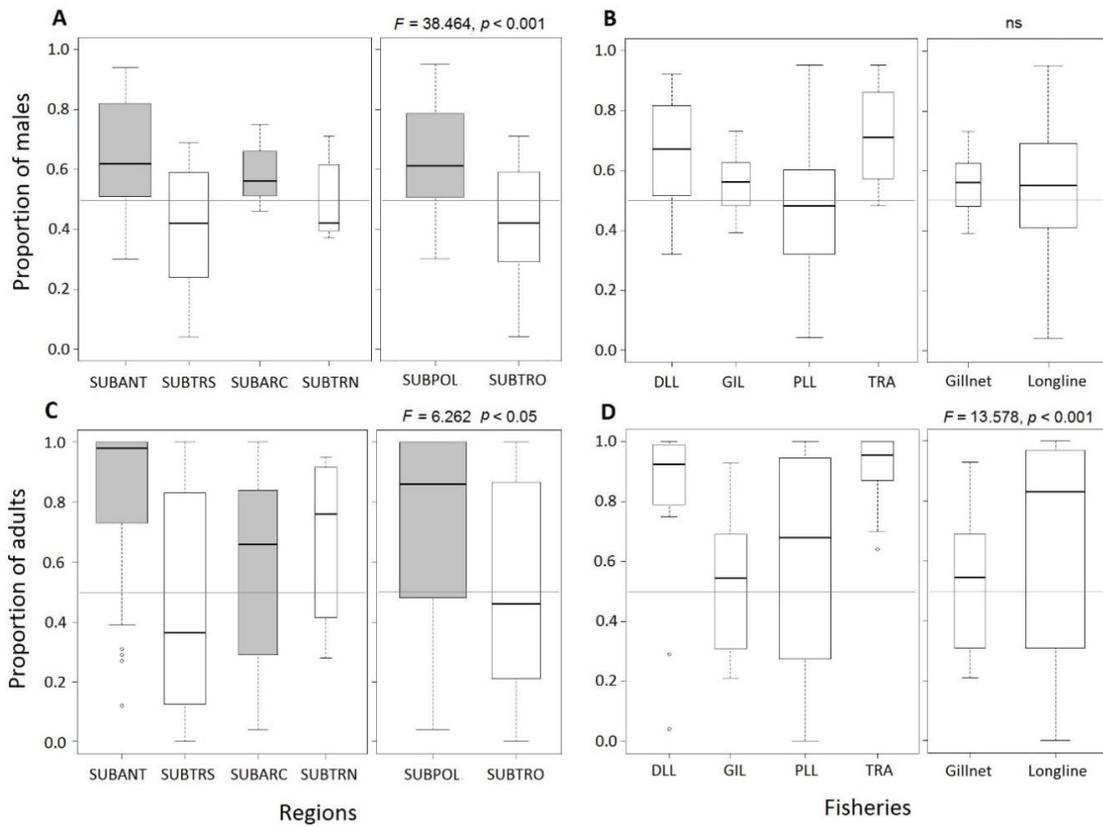


Figure 2.6. Proportion of males (top) and of adults (bottom) in seabird bycatch samples by region (left) and fishery type (right). Box plots show the median and the 25th and 75th percentiles, whiskers indicate values within 1.5 times of the interquartile range, circles represent outliers, and box plot width varies with the sample size, and the horizontal grey line indicates the 0.5 mark. Abbreviations: SUBANT, sub-Antarctic; SUBARC, sub-Arctic; SUBTRS, subtropical southern; SUBTRN, subtropical northern; SUBPOL, subpolar; SUBTRO, subtropical; PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl. Grey boxes in A and C indicate subpolar regions. *F*-statistic and *P*-value from ANOVA comparing the effect of region (subtropical vs subpolar) and fishery type (longline [demersal and pelagic combined] vs gillnet) are shown inside the graph are.

Table 2.3. Frequency of bycatch samples per fishery type and region not skewed and skewed toward males (M) or females (F), and toward adults (A) or immatures (I); per fishery type and regions.

	Sex				Age			p (χ^2_{Yates}): A vs I ^a
	Not skewed	M	F	p (χ^2)	Not skewed	A	I	
<i>Fishery</i>								
Pelagic longline	18	14	16	0.779	5	27	15	0.090
Demersal longline	9	15	2	0.008	0	14	4	0.034
Gillnet	7	6	2	na ^b	3	8	7	1.000
Trawl	5	12	1	0.006	0	17	0	<0.001
Longlines combined	27	29	18	0.249	5	41	19	0.007
<i>Region</i>								
Sub-Antarctic	18	26	3	<0.001	2	29	7	<0.001
Sub-Arctic	8	8	1	0.056	1	11	7	0.479
Subtropical South	8	5	12	0.228	3	10	10	1.000
Subtropical North	2	2	3	na	1	4	2	na
Sub-polar	26	34	4	<0.001	3	41	15	<0.001
Subtropical	10	7	13	0.407	4	14	12	0.844

^a Comparisons were made only between the frequency of adult- and immature-skewed samples since unbalanced age ratios are expected in wild populations; ^b “na” (not available) refers to frequencies not compared due to small sample sizes.

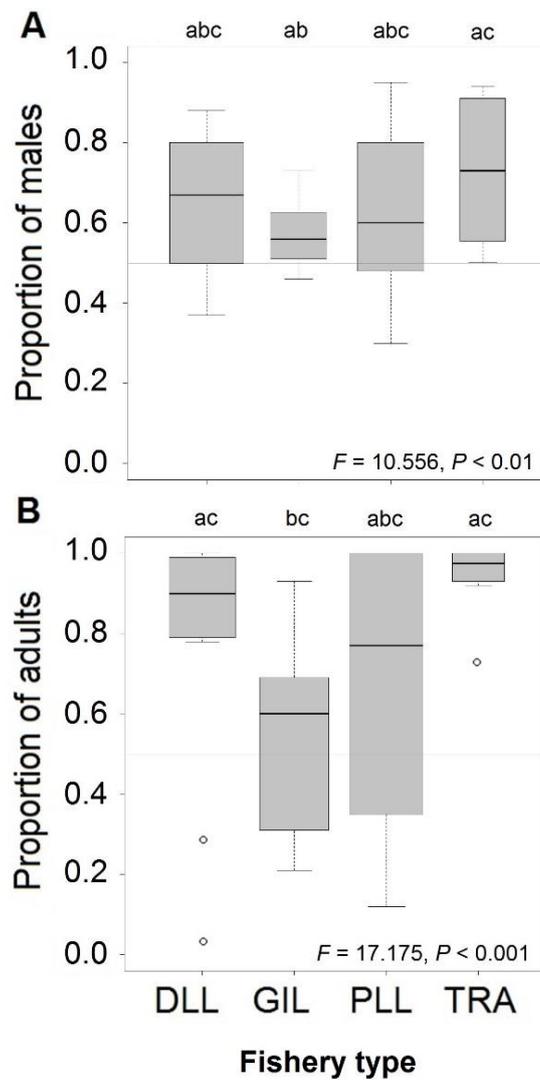


Figure 2.7. Proportion of males (A) and of adults (B) in seabird bycatch samples compared among the four major gear types using only data from subpolar regions. Box plots show the median and the 25th and 75th percentiles, whiskers indicate values within 1.5 times of the interquartile range, circles represent outliers, box plot width varies with the sample size, and the horizontal grey line indicates the 0.5 mark. Abbreviations: PLL, pelagic longline; DLL, demersal longline; GIL, gillnet; TRA, trawl. *F*-statistic and *P*-value from ANOVA comparing the effect of fishery type are shown inside the graph area. Box-plots not sharing the same lower case letters are statistically distinct ($P < 0.05$) according to Tukey post-hoc test.

Table 2.4. Candidate mixed effect models for proportion of males, and proportion of adults in seabird bycatch composition as influenced by fishery gear-type consider fisheries in the subpolar region only, which was the region with comparable sample sizes among fisheries. All models included species as a random effect. Best models are highlighted in bold.

Model	df	AICc	Δ AICc	Deviance	Resid df
Sex (y <- proportion of males)					
y ~ Fishery, subpolar only	4	-40.1	0.0	75.9	54
y ~ 1	1	12.17	5.2	381.3	122
Age (y <- Proportion of adults)					
y ~ Fishery, subpolar only	4	14.4	0.0	188.4	47
y ~ 1	1	95.6	81.2	1033.9	114

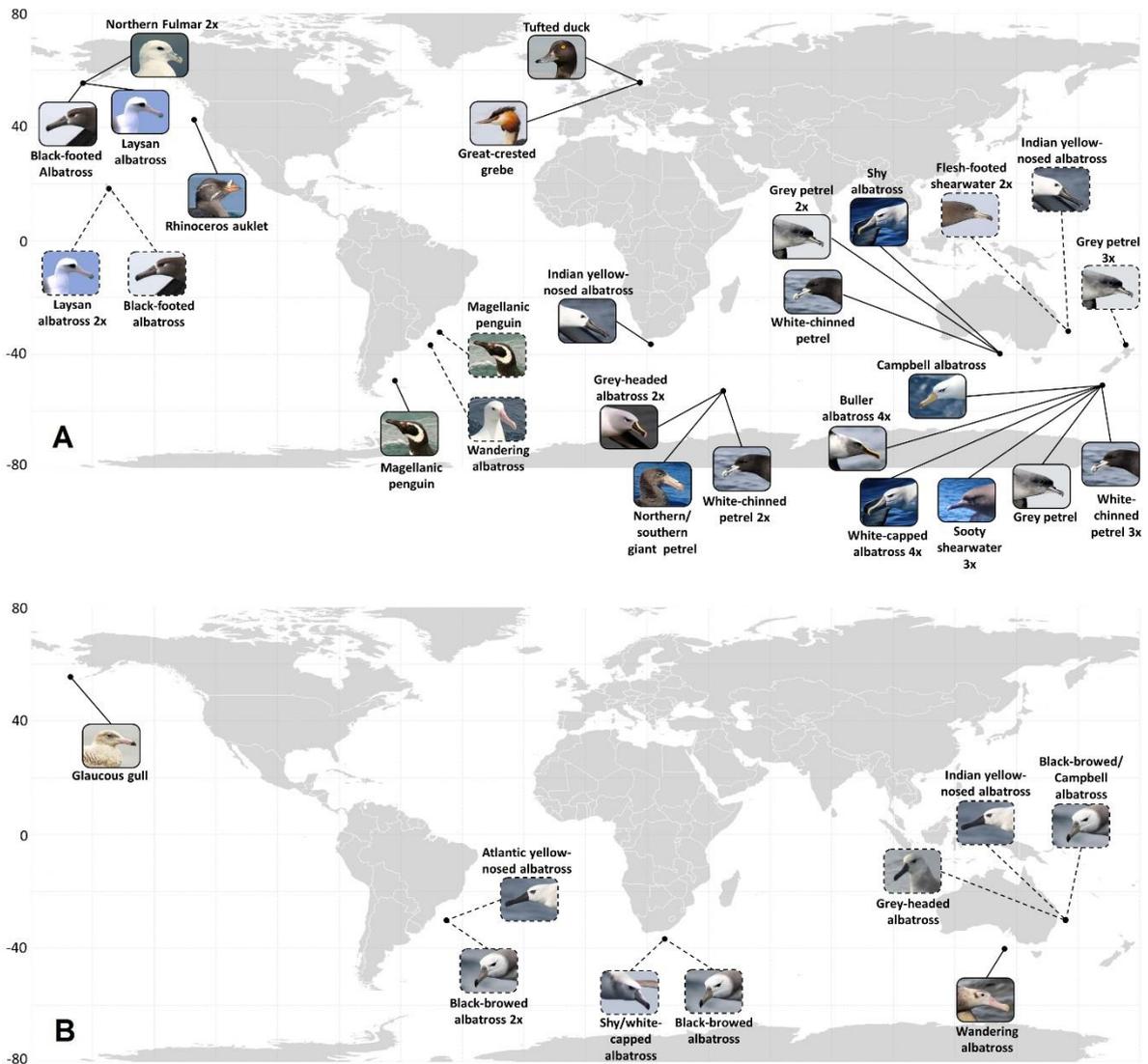


Figure 2.8. Geographical distribution of bycatch samples highly skewed towards adult (A) or towards immature (B) ($\geq 80\%$ of one age class). Solid and dotted lines denote bycatch events in subpolar and subtropical regions respectively. The numbers following common names indicate the number of highly age-biased samples for that taxon in the given location.

2.4. Discussion

Sex- and age-biases in seabird bycatch have been reported in a number of fisheries (Gales *et al.* 1998; Ryan & Boix-hinzen 1999; Nel, Ryan & Watkins 2002b; Delord *et al.* 2005; Phillips *et al.* 2010), and there is growing interest in

both the underlying mechanisms and the potential demographic consequences (Bugoni *et al.* 2011; Lewison *et al.* 2012). Here we provide the first global synthesis of both sex and age-specific variation in seabird bycatch rates by different fisheries and in diverse regions. Overall, our study shows substantial variation in the sex and age ratios of bycaught seabirds, and that unbalanced sex and age proportions are the most common pattern. Additionally, we demonstrate that sex- and age-biases vary by region and, to a lesser extent by fishery type. Globally, male-biased bycatch was significantly more frequent (47%) than female-biased bycatch (18%), and adult-biased (68%) significantly more frequent than immature-biased (24%). These results are consistent with our a priori prediction that the dominance of males and adults foraging behind fishing vessels will lead to higher bycatch. However, there are regional differences in the patterns of age- and sex-biased bycatch, as well as a disproportionately high number of studies from sub-polar waters (68%), indicating that foraging despotism alone does not explain the observed patterns. Nevertheless, there is a paucity of this data in the northern hemisphere (9 studies) compared with the southern hemisphere (35 studies). Possible mechanisms contributing to unbalanced age and sex mortality, as well as its demographic effects, and implications for management and conservation, are discussed below.

2.4.1. Sex-specific bycatch

2.4.1.1. Possible mechanisms contributing to sex-specific bycatch

Although offspring sex-ratios in seabirds can vary with age, quality and timing of breeding (Velando, Graves & Ortega-ruano 2002; Weimerskirch *et al.* 2005; Blanchard *et al.* 2007), there is little evidence for any consistent sex-biases at hatching or recruitment at the population level (Weimerskirch *et al.* 2005;

Awkerman *et al.* 2007b; Donald 2007). Therefore, the patterns observed here indicate that sex-skewed bycatch is unlikely to be due to the underlying population sex-ratio. Hypotheses proposed to explain sex-related vulnerability to bycatch include sex-specific differences in at-sea distribution, and differential access to bait and discards related to sexual size-dimorphism and aggression (Ryan & Boix-hinzen 1999; Nel *et al.* 2002b; Bugoni *et al.* 2011; Barbraud *et al.* 2012).

It has been suggested that the competitive advantage of males foraging behind fishing vessels explains male-biased bycatch events (Ryan & Boix-hinzen 1999; Awkerman *et al.* 2006); however, there is little direct evidence to support this. Instead, in multi-species foraging aggregations, differences in body size between taxa are more important determinants of access to feeding opportunities than sex per se (Bugoni *et al.* 2011; Jiménez *et al.* 2012; Stauss *et al.* 2012; Bicknell *et al.* 2013). In contrast, sex-biased bycatch appears to be much better explained by sex-specific differences in distribution. For instance, in the southern hemisphere, our analysis showed a significantly higher frequency of male-biased bycatch in sub-Antarctic areas, but a trend towards the opposite pattern in subtropical waters; this is consistent with tracking and stable isotope results from a number of different sub-Antarctic seabird species during the breeding season, showing that females tend to forage farther from the colony and spend more time in subtropical waters compared with males (Nel *et al.* 2002a; Phillips *et al.* 2004, 2005, 2011; Hedd *et al.* 2014; Thiers *et al.* 2014; Weimerskirch *et al.* 2014; Jiménez *et al.* 2015a). In the northern hemisphere, where the bycatch data was more taxonomically heterogeneous and the sample size much smaller (15 species within 28 samples, 23%), overall patterns of sex-biased bycatch are less clear. Nevertheless, differential distribution at sea has also been identified as a

cause of male-biased mortality of common guillemot (*Uria aalge*) in coastal gillnets of Monterey Bay (California) (Nevins 2004), and for the male-skewed bycatch of both Laysan (*Phoebastria immutabilis*) and black-footed (*P. nigripes*) albatrosses off Alaska compared with the relatively balanced or female-biased sex-ratios of birds bycaught in Hawaiian waters (Beck, Nevins & Hester 2013). In the Baltic Sea, the sex-ratios of diving ducks bycaught in gillnets largely reflects the sex proportions observed in their wintering grounds (Stempniewicz 1994), supporting the hypothesis of differential distribution as the main driver of observed bycatch bias. Therefore, the overall predominance of males in seabird bycatch that we found in our study probably reflects the higher proportion of samples obtained in subpolar areas (68%), where the seabird mortality tend to be skewed toward males.

2.4.1.2. Demographic effects of sex-specific bycatch

The immediate effect of sex-biased bycatch could lead to skewed adult sex ratios and thus a reduction in effective population size (Mills & Ryan 2005; Weimerskirch *et al.* 2005; Donald 2007). For example, long-term demographic studies of wandering, black-browed (*Thalassarche melanophris*) and waved albatrosses (*Phoebastria irrorata*) all indicate sex-biases in survival that may be related to sex-specific bycatch (Weimerskirch & Jouventin 1987; Croxall *et al.* 1998; Arnold, Braut & Croxall 2006; Awkerman *et al.* 2006)(Arnold *et al.*, 2006; Awkerman *et al.*, 2006; Croxall *et al.*, 1998; Weimerskirch and Jouventin, 1987). Nonetheless, it is very difficult to measure directly the demographic impact of sex-skewed mortality in fisheries because: (1) until now, there was a lack of systematic sex-specific seabird bycatch data across global fisheries; (2) there is often uncertainty about the provenance of bycaught birds, making it difficult to

directly link events at sea with demographic monitoring on land; (3) there is a paucity of long-term demographic studies across multiple taxa and locations (Lewison *et al.* 2004, 2012; Anderson *et al.* 2011; Žydelis *et al.* 2013); and (4) there is uncertainty about other factors influencing sex differences in survival, such as relative predation risk, sex-specific costs of reproduction, variation in feeding strategies, or engagement in aggressive interactions (Weimerskirch *et al.* 2005; Donald 2007). Mills and Ryan (2005) modelled the impact of sex-biased bycatch in wandering albatross and showed that even moderate increase in female mortality (2-4% per year) reduces fecundity by 9–27% compared with unbiased mortality. This effect may explain the steep decline in the wandering albatross at South Georgia (Croxall & Prince 1990; Croxall *et al.* 1998; Poncet *et al.* 2006; Jiménez *et al.* 2015a). Population-level effects of sex-biased bycatch have been observed in situations where there is reliable information on both bycatch rates and demographic traits. For example, in the waved albatross, which breeds almost entirely on Española Island (Galápagos Islands), there is a skew in the adult population towards females as a result of the strongly male-biased mortality (82%) in artisanal fisheries off Peru and Ecuador (Awkerman *et al.* 2006, 2007b). In the wandering albatross at Possession Island (Crozet), the lower survival of females, attributed to higher mortality in pelagic longline fisheries, has also led to a male-biased population (Weimerskirch *et al.* 2005), and the same is expected at South Georgia where females have a greater overlap with tuna fisheries in subtropical waters and consequently are bycaught more frequently than males (Jiménez *et al.* 2015a). Distorted sex ratios can also result in indirect effects on population dynamics, including unexpectedly high rates of extra-pair paternity in female-biased populations (Huyvaert *et al.* 2000), or reduced breeding success due to aggressive nest intrusions by unpaired males resulting

in egg loss and infanticide in male-biased populations (Taylor, Leonard & Boness 2001; Awkerman *et al.* 2007a). These indirect effects, in tandem with the reduction of effective population size, can potentially increase the deleterious effects of bycatch on seabirds.

2.4.2. Age-specific bycatch

2.4.2.1. Possible mechanisms contributing to age-specific bycatch

Our review suggests that age-skewed seabird bycatch is common across global fisheries, with 68% of the bycatch samples skewed towards adults and 24% skewed towards immatures. The overall higher mortality of adults seems to agree with our initial prediction that dominant adults would outcompete immatures for foraging opportunities behind fishing vessels (Croxall & Prince 1990). However, we must be cautious interpreting this result because the higher mortality of adults may largely reflect the typical age structure of seabird populations, which tend to be characterized by more adults than immatures (Nur & Sydeman 1999). Detailed information on age-structure is lacking for most species and populations. Nevertheless, strong biases in both adult and immature bycatch suggest some extrinsic factors are in operation, and not that bycatch rates simply reflect the natural age ratios.

The degree to which different age classes interact with fisheries is not well understood (Lewison *et al.* 2012). However, some authors have proposed that juveniles may be more susceptible to bycatch because they favour scavenging over natural foods that may be more difficult to catch, or because of their naivety in avoiding fishing gear (Shealer 2002; Lewison *et al.* 2012; Fayet *et al.* 2015). Indeed, lack of experience while foraging around nets was considered to be the

main reason for immature-biased mortality of pursuit-diving seabirds (Österblom *et al.* 2002; Bregnballe & Frederiksen 2006). However, this is not a consistent pattern - in our study, 50% of the 12 samples of pursuit-diving seabirds of known age class drowned in nets were skewed towards adults, whereas 33% were skewed towards immatures. Naivety of young birds has also been suggested as the explanation for immature-skewed mortality in longlines, and potentially by trawls (Prince *et al.* 1994; Gales *et al.* 1998), but, again, this pattern was not supported by our data, which shows a large proportion of adults bycaught in these fisheries.

Based on the available data we suggest that a degree of spatial segregation at-sea by age is a better explanation for the observed age-specific susceptibility to bycatch, rather than differences in competitive capacity or experience in avoiding fishing gear. In the southern hemisphere, immature birds disperse further north and spend more time in subtropical waters, whereas adults (especially breeders) are more likely to stay in sub-Antarctic waters (Olmos 1997; Phillips *et al.* 2005; Weimerskirch, Åkesson & Pinaud 2006; Weimerskirch *et al.* 2014; Bugoni & Furness 2009; Catry *et al.* 2013). This pattern seems to be reflected in the significantly higher mortality of adults in subpolar areas in our analysis, which mainly resulted from the consistent adult-biased bycatch in diverse fisheries across sub-Antarctic waters (Bartle 1991; Gales *et al.* 1998; Gandini *et al.* 1999; Ryan & Boix-hinzen 1999; Nel *et al.* 2002b; Robertson & Bell 2002; Seco Pon, Gandini & Favero 2007; Thompson 2010a; b). On the other hand, in subtropical areas, where there are often more immatures (Phillips *et al.* 2005, 2006; Copello, Seco Pon & Favero 2013; Weimerskirch *et al.* 2014), our analyses indicated more samples biased to this younger age class (43%) in comparison to fisheries in sub-Antarctic waters (17%). Although the proportion of

immatures bycaught in subtropical areas is highest during summer (up to 100%), when most adults return to their breeding areas (Ryan, Keith & Kroese 2002; Petersen *et al.* 2010), immatures can also predominate in bycatch during winter (Murray *et al.* 1993; Neves & Olmos 1997; Gales *et al.* 1998; Roma 2009). The significantly higher bycatch of adults in trawl and demersal longline fisheries within the subpolar region is likely to reflect the same large-scale pattern, since those fisheries operate in shelf and slope waters closer to colonies (Bartle 1991; Gandini *et al.* 1999; Nel *et al.* 2002b; Robertson, Bell & Scofield 2003), whereas pelagic longliners operate in much more pelagic waters and at lower latitudes of the subpolar region (Gales *et al.* 1998; Thompson 2010a; Beck *et al.* 2013). This age-specific mortality associated with differential distribution at sea is not exclusive to albatrosses and petrels of the southern hemisphere. A range of other species in both hemispheres, including diving ducks, penguins, alcids, fulmars and gulls showed regional and seasonal patterns of age-specific bycatch likely to reflect differential overlap with fisheries; these seem to be linked to age-related differences in distribution as a consequence of breeding constraints, moult cycles, migration or age-specific foraging strategies (Stempniewicz 1994; Thompson *et al.* 1998; Gandini *et al.* 1999; Nevins 2004; Phillips *et al.* 2010; Cardoso *et al.* 2011). The significant effect of region on age ratios of seabirds bycaught on longlines but not in gillnets may be related to the characteristics of the affected seabird. It is unclear whether the taxa that are at greatest risk from gillnets (alcids, diving ducks) show large-scale age-segregation by latitude, or even if they do, they may not be killed in gillnets in some parts of their range.

2.4.2.2. *Demographic effects of age-specific bycatch*

Globally, mortality of adults in fisheries is thought to have deleterious effects not just on albatrosses and petrels, but also diving ducks, alcids and penguins (Darby & Dawson 2000; Smith & Morgan 2005; Thompson 2010b; Cardoso *et al.* 2011; Žydelis *et al.* 2013). In many cases, there is insufficient data on bycatch rates of different age classes to accurately estimate the impacts of, or predict the response to, potential management regimes (including changes in fishing effort distribution, or bycatch mitigation). These problems are exacerbated in the absence of robust data on demographic rates, particularly given the difficulties of disentangling effects of mortality in fisheries from other factors affecting breeding populations, such as environmental changes, depletion of prey stocks, introduced predators, habitat deterioration etc.

Although adult mortality has the most immediate and pronounced negative effect, chronic mortality of immatures can reduce recruitment below the minimum level needed to maintain population stability (Prince *et al.* 1994; Nur & Sydeman 1999; Sherley *et al.* 2015). Juvenile survival in seabirds is normally lower than adults (Nur & Sydeman 1999), but there is evidence that fisheries can reduce immature survival rates of some species even further. For example, negative trends in juvenile survival of black-browed albatross from South Georgia are correlated with the increase in pelagic longline fishing effort off South Africa (Croxall *et al.* 1998; Tuck, Polacheck & Bulman 2003; Arnold *et al.* 2006), which is the primary destination of young birds from that population (Phillips *et al.* 2005). Therefore, the higher susceptibility of juveniles to bycatch in pelagic longline fisheries, which are the most widespread and largest-scale of those operating in subtropical waters of the southern hemisphere (Tuck *et al.* 2003; Anderson *et al.* 2011), may be contributing to the low immature survival of black-browed and other albatross populations in the Southern Ocean (Prince *et al.* 1994; Croxall *et*

al. 1998; ACAP 2010c; d). Indeed, high mortality of immatures in fisheries resulting in depressed recruitment levels appears to have been a major contributor to the decline of both black-browed and grey-headed (*Thalassarche chrysostoma*) albatrosses at South Georgia (Prince *et al.* 1994).

2.4.3. Implications for management and conservation

Seabirds are the most threatened group of birds; nearly half of the 346 species are known or suspected to be in decline, with one third threatened with extinction, including 17 critically endangered, 35 endangered, 49 vulnerable and 37 near threatened (Croxall *et al.* 2012), and there has been a 70% decline in monitored populations between 1950 and 2010 (Paleczny *et al.* 2015). Bycatch was identified as one of the two greatest threats, and the most pervasive threat at sea (Croxall *et al.* 2012). Hence, given the frequency and magnitude of both sex- and age-biases in seabird bycatch, and the demographic implications, we strongly recommend much improved data collection on the age and sex of birds killed by fisheries in on-board observing programs at national and international levels. The latter requires concerted and coordinated action by Regional Fishery Management Organisations (RFMOs). In addition to increased on-board observer effort, it is necessary to implement standardized protocols for retrieving carcasses and collecting biological samples to provide high quality information on seabird bycatch; this includes accurate information on sex (Fridolfsson & Ellegren 1999; Bugoni & Furness 2009), age (Bugoni & Furness 2009; Thompson 2010b), and improved attempts to identify provenance (Abbot *et al.*, 2006; Gómez-Díaz & González-Solís, 2007; Abbot *et al.*, 2014). These approaches are especially urgent in the northern hemisphere – despite high levels of seabird bycatch here, the number of studies reporting age and sex-specific totals is much

lower than in the southern hemisphere. Moreover, tracking studies that map the distributions and hence overlap with specific vessels of birds of different age class and sex, throughout the year, will greatly improve ecological risk assessments (Jiménez et al., 2015a; Komorose and Lewison, 2015). Likewise, integrated population models testing the effects of fisheries on seabird demography, including analyses of Potential Biological Removal (PBR), must take sex- and age-specific differences in bycatch rates to avoid underestimation of the PBR and potentially instituting management actions that are insufficient (Dillingham and Fletcher, 2011; Lewison et al., 2012). Together, this information can then be used by regional (i.e. national action plans) and international conservation initiatives (including the Agreement on the Conservation of Albatrosses and Petrels, ACAP), as well as local fisheries management organizations and RFMOs to identify regions and fleets where more prescriptive mitigation measures should be applied, and where monitoring of compliance needs to be more intensive to prevent severe impacts of bycatch on seabird populations (Croxall et al., 2013; Phillips, 2013; Phillips et al., 2016). However, because (1) there is low reliability of bycatch data globally, (2) populations are at risk from different fisheries across large areas, and (3) provenance of bycaught birds is often unknown, incorporating information on sex- and age-biased bycatch in seabird management and conservation remains challenging, and the data must be examined on a case-by-case basis.

2.5. Conclusion

Sex and age biases in seabird bycatch are common features across global fisheries, mainly related to differential at-sea distributions. Overall, bycatch of

adults and males was higher in subpolar regions and closer to colonies, whereas immatures and females were caught more frequently in subtropical waters. We found no compelling evidence that differences in sex and age ratios are related to the competitive advantage of males and adults foraging at fishing vessels, or to naivety of young birds around fishing gear. There is clear evidence that differences in capture rates by sex and age have implications for populations that differ from those of unbiased mortality. Despite this, the need to ensure information is obtained on sex and age of bycaught birds has been largely neglected by on-board observer programs in national and international fisheries. Given the ubiquity and population-level consequences of such biases, we believe that global efforts to map bycatch and understand their impacts (e.g. Lewison et al., 2014) should include age and sex information wherever possible.

**CHAPTER 3. Sex-specific effects of fisheries and
climate on the demography of sexually dimorphic
seabirds**



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ABSTRACT

Many animal taxa exhibit sex-specific variation in ecological traits, such as foraging and distribution. These differences could result in sex-specific responses to change, but such demographic effects are poorly understood. Here we test for sex-specific differences in the demography of northern (NGP, *Macronectes halli*) and southern (SGP, *M. giganteus*) giant petrels - strongly sexually size-dimorphic birds that breed sympatrically at South Georgia, South Atlantic Ocean. Both species feed at sea or on carrion on land, but larger males (30% heavier) are more reliant on terrestrial foraging than the more pelagic females. Using multi-event mark-recapture models we examine the impacts of long-term changes in environmental conditions and commercial fishing on annual survival and use two-sex matrix population models to forecast future trends. As expected, survival of male NGP was positively affected by carrion availability. Female survival was positively affected by meridional winds, and negatively affected by sea ice concentration and pelagic longline effort. El Niño Southern Oscillation (ENSO) positively affected both sexes equally. SGP survival did not differ between sexes and was positively correlated with the Southern Annular Mode (SAM). Two-sex population projections indicate that future environmental conditions are likely to benefit giant petrels, however, any potential increase in pelagic longline fisheries could reduce female survival and population growth. Our study reveals that sex-specific ecological differences can lead to divergent responses to environmental drivers (i.e. climate and fisheries). Moreover, because such effects were not apparent when all individuals are considered together, ignoring such differences could underestimate the relative influence of change.

3.1. Introduction

Male and female animals often differ in aspects of their physiology, morphology, behaviour, reproductive roles and social interactions (Ruckstuhl & Neuhaus 2006; Breed & Moore 2016). These differences can cause sex-related variation in ecological and demographic traits, and ultimately sex-specific demographic responses to environmental change (Kraus, Eberle & Kappeler 2008; Oro *et al.* 2010; Jenouvrier *et al.* 2012; Vaughn, Turnross & Carrington 2014).

Understanding how species and populations respond to global climate change and anthropogenic effects is the major challenge in modern ecology. In the oceans, biodiversity and ecosystem functioning are threatened by changing temperatures, decreasing pH, fisheries harvesting, and habitat degradation (Halpern *et al.* 2008; Sydeman *et al.* 2015). These changes are particularly deleterious for large marine vertebrates, given their slow reproductive rates and high trophic status, but determining the impacts of change is challenging because of the complexity of direct and indirect effects and because they integrate processes over large spatio-temporal scales (Weimerskirch *et al.* 2003; Sydeman *et al.* 2015). For example, fisheries may have negative effects via bycatch (Nel *et al.* 2002b; Tuck *et al.* 2011) or positive effects via provision of food subsidies (Votier *et al.* 2004) and climate change may have positive effects by altering wind (Weimerskirch *et al.* 2012) or negative effects via reducing food availability (Reid & Croxall 2001; Sydeman *et al.* 2015). Such complex effects are also predicted to vary in their relative influence on males and females in species with sexual size dimorphism, or sex differences in foraging distributions, reproductive roles or

other aspects of behaviour (Martínez-Abraín *et al.* 2006; Oro *et al.* 2010; Lewis *et al.* 2015).

Parts of the Atlantic sector of the Southern Ocean are amongst the fastest-warming regions on Earth (Meredith & King 2005). Here oceanographic and atmospheric changes have produced a range of ecosystem-level disturbances, affecting a diversity of marine predators (Atkinson *et al.* 2004; Trathan *et al.* 2007). This region, and subtropical waters to the north, have also been exploited by large-scale commercial fisheries, causing unsustainable levels of bycatch and ecological change (Croxall & Nicol 2004; Tuck *et al.* 2011; Jiménez *et al.* 2014). Several studies have investigated the effects of climate change and fisheries on life history traits of land-based marine vertebrates in the Southern Ocean (Barbraud *et al.* 2012; Forcada & Hoffman 2014; Descamps *et al.* 2016); however, very few have examined sex-specific responses (Olsson & Van der Jeugd 2002; Jenouvrier *et al.* 2012; Pardo *et al.* 2013), even though sex-related differences in morphology and life-history are common among these taxa.

The northern giant petrel *Macronectes halli* (hereafter NGP) and southern giant petrel *M. giganteus* (hereafter SGP) offer an ideal model to investigate sex-specific responses to environmental changes in the fast changing Southern Ocean. These closely related congeners breed across the sub-Antarctic and are the most sexually size-dimorphic of all seabirds, with males up to 30% heavier and 15% larger than females (González-Solís 2004). They forage either at sea (from the ice edge to the sub-tropics) or on land where they are the dominant avian scavenger and predator of penguins and pinnipeds (Hunter 1983, 1984). The strong sexual size-dimorphism results in marked sexual segregation during incubation; males monopolise scavenging opportunities on land, forcing females

to forage at sea (González-Solís *et al.* 2000; González-Solís 2004). Later in the breeding season (when carrion availability has declined), and during winter, both sexes forage predominantly at sea (González-Solís *et al.* 2008). However, while this results in greater overlap between sexes during winter, a degree of sexual segregation is maintained with females overlapping more with demersal and trawl fisheries (González-Solís *et al.* 2000, 2008; Otley *et al.* 2007; Phillips *et al.* 2009).

Here, we used long-term capture-mark-recapture (CMR) data from both giant petrel species at Bird Island, South Georgia, to test for sex-specific effects of climate cycles, oceanographic conditions, and fisheries on demography. We used multi-event CMR models to estimate vital rates, and a two-sex demographic model to investigate the influence of sex-specific effects of environmental drivers on population growth rate. We expect high values of the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO) to have negative effects on giant petrel survival via reductions in krill availability (Trathan *et al.* 2007; Descamps *et al.* 2016). We also hypothesised that female survival in both species will be lower and more sensitive to variation in fishing effort and oceanographic conditions, and that male survival would be more sensitive to variation in carrion availability, especially in NGP, given their dominance as scavengers on land during the early breeding season (Hunter 1983; González-Solís *et al.* 2000).

3.2. Methods

3.2.1. Species, study site and data collection

We studied NGP and SGP on Bird Island (54° 00' S, 38° 03' W), South Georgia, which is the only site in the Atlantic Ocean where both species nest

sympatrically (Hunter 1984). Giant petrels lay a single egg without replacement, in early October for NGP, and mid-November for SGP. Incubation lasts 60 days and chicks fledge 110-120 days after hatching. Therefore, the breeding seasons of NGP and SGP encompass October-March and November-May, respectively.

In total, c.350 pairs of NGP and c. 150 pairs SGP in a well-demarcated study area were monitored annually during austral summers 2000/01 – 2014/15 (hereafter, 2001 refers to the breeding season in austral summer 2000/01 etc.). For details of the monitoring protocol, see Brown *et al.* (2015). Briefly, all breeding birds were fitted with an individually identifiable metal ring, and a coloured plastic ring engraved with a unique four-digit alpha-numeric code, and sexed from bill length (González-Solís *et al.* 2000). Active nests were checked every 4-5 days until both partners were identified, and visited weekly for the remainder of the breeding season until the outcome of the reproductive attempt was known.

3.2.2. The general model

In a multi-event modelling framework (Pradel 2005), events observed in the field provide information on the underlying biological (including non-observable) states of marked individuals. Multi-event models were built and fitted using E-SURGE v.1.9.0 (Choquet, Rouan & Pradel 2009), based on the observation of three possible events; “0” (not encountered), “1” (encountered as a successful breeder) or “2” (encountered as a failed breeder). Five states were defined: two observable states corresponding to successful (S) and failed breeders (F), and three unobservable states, corresponding to post-successful breeders (PS, non-breeding birds that were successful breeders in the previous season), post-failed breeders (PF, non-breeding birds that were failed breeders in the previous season), and dead (Figure 3.1, Table S3.1). This modelling

approach allows us to estimate annual adult survival for each species (probability of an adult surviving the breeding season and the following winter), based on 1,376 encounter histories of NGP (623 males and 753 females), and 668 of SGP (334 males and 354 females) (Table S3.2). As the study was conducted in a well demarcated area, and over the 15 years <1% of the total monitored population was observed breeding in adjacent areas (which are checked each year); emigration was not considered.

3.2.3. Model selection and goodness-of-fit

There is currently no test available to assess goodness-of-fit (GOF) for multi-event models. To check whether data met the basic assumptions underlying capture-mark-recapture models, a GOF test for the Cormack Jolly Seber model (CJS) was applied to a simplified (single state) version of the encounter histories, while also checking for sex-specific differences in resighting heterogeneity in U-CARE 2.2 (Pradel, Gimenez & Lebreton 2005; Choquet *et al.* 2009). Under the CJS assumptions, this comprised two tests and their sub-components: Test 2 (sub-components 2.CT + 2.CI) examines heterogeneity in recapture probabilities and trap-dependent effects; and Test 3 (sub-components 3.SR + 3.Sm) checks the heterogeneity in survival probabilities and transience effects. As our multi-event model design accounts for differences in breeding probabilities according to previous breeding states, it automatically corrects for trap-dependence effects, which are common in seabirds that often defer (skip) breeding. Thus GOF can be conducted excluding Test 2 (Barbraud & Weimerskirch 2012). Models were compared using QAICc and when two models had $\Delta QAICc < 2$ the most parsimonious was chosen (Lebreton, Burnham & Clobert 1992). We tried different structures of encounter probabilities, including time (year), sex and their

interactions, comparing them in order to obtain the best starting model. We then selected the best effect model for encounter probability, then breeding success and, subsequently, survival.

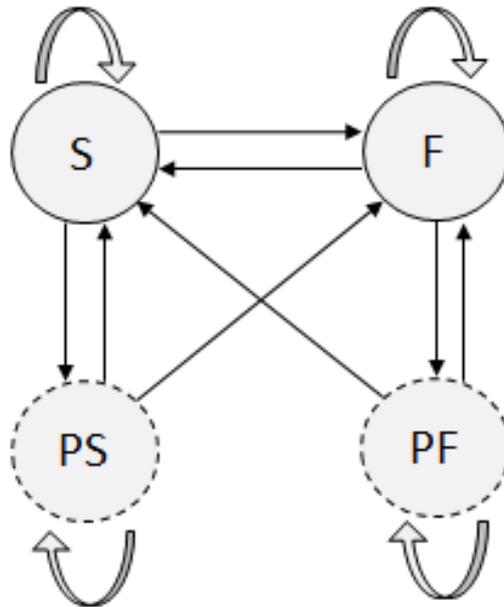


Figure 3.1. Life-cycle graph used to parameterise the multi-state model with five states: S = Successful breeder, F = Failed breeder, PS/F = Unobservable post successful/failed breeder. Arrows show the possible transitions among states. The state 'dead' is not presented in the figure as it can be reached from any other state.

3.2.4. Environmental covariates

3.2.4.1. Effect on demographic traits

We examined the effect of covariates suspected to influence adult survival based on previous knowledge of seabird and giant petrel ecology, for all birds and for each sex separately. Because giant petrels can be highly pelagic, but that also forage on land, we considered a large number of variables. These were (1) large-scale climatic indices, El Niño Southern Oscillation (ENSO) and Southern Annular Mode (SAM); (2) conditions in at-sea foraging areas, including sea

surface temperature (SST), Sea Ice Concentration (SIC), Net Primary Productivity (NPP), wind speed (zonal and meridional components), Antarctic krill *Euphasia superba* density, and fisheries; and (3) carrion availability on land, expressed as the number of fur seal pups born in a study beach at Bird Island (Figure 3.2). Relationships among covariates were examined by comparing their de-trended and standardized values using a Pearson's correlation matrix (Appendix S3.1). There was a strong negative correlation between SIC and SST ($r = -0.84, -0.75; p < 0.01$; Appendix S3.1); thus SST was dropped, and SIC retained as a candidate variable since we were more interested in the oceanographic drivers than SST *per se*.

Each variable was scaled to $\bar{x} = 0$ and $\sigma = 1$ (Schielzeth 2010) before constraining the models using a logit link function. Subsequently, we examined the magnitude of these effects using analysis of deviance (ANODEV), which compares the deviance of models where the demographic trait is time-dependent, constant, or constrained by one or more covariates (Grosbois *et al.* 2008). The derived R^2 metric expresses the percentage of temporal variation in a demographic trait that is explained by a covariate. For all explanatory variables we examined the influence on both long-term (basic models) and short-term variability (de-trended models). De-trended models reduce the risk of detecting spurious correlations when both the trait and covariate change in tandem over time (Grosbois *et al.* 2008). However, we also fitted the basic models (without de-trending), to reduce the risk of committing Type II errors. The influence of a covariate was considered statistically significant if the 95% confidence interval of the corresponding slope excluded zero, and if the p-value from ANODEV test ≤ 0.05 (Grosbois *et al.* 2008).

For the climatic indices and at-sea conditions in wintering areas, monthly values from April-September and June-October were averaged to provide a single annual mean value for NGP and SGP, respectively, with the offset in timing reflecting the difference in laying dates (Hunter 1984).

3.2.4.2. Large scale climatic indices

ENSO and SAM are large-scale climatic indices known to affect oceanography and marine productivity (Trathan *et al.* 2007; Meredith *et al.* 2008; Descamps *et al.* 2016). The ENSO generates warm sea surface temperature (SST) anomalies in the equatorial Pacific that are propagated to the Southern Ocean via atmospheric and oceanographic teleconnections (Meredith *et al.* 2008). We utilized the Bivariate EnSo Timeseries (BEST index) as a proxy of ENSO variability (Smith & Sardeshmukh 2000), with a 2 year lag to account for the average time that positive values of ENSO take to appear as SST anomalies in the Atlantic sector of the Southern Ocean (Meredith *et al.* 2008). Positive SST anomalies have been correlated with poor foraging conditions for a range of marine vertebrates (Trathan *et al.* 2007; Whitehouse *et al.* 2008), and thus are expected to negatively affect giant petrels. The SAM is a circumpolar atmospheric process that influences the Atlantic sector of the Southern Ocean almost immediately (~1 month), and is associated with warm SST anomalies, stronger circumpolar winds and changes in sea ice extent and concentration (Thompson & Wallace 2000; Trathan *et al.* 2007). Therefore, changes in SAM may influence giant petrel foraging efficiency, related to wind conditions or food availability at sea. Monthly values for BEST index were obtained from the Climate Diagnostics Centre of NOAA (<http://www.cdc.noaa.gov/people/cathy.smith/best/>, Figure 3.2a)

and monthly values of SAM were obtained from the Climate Prediction Centre of NOAA (<http://www.cpc.ncep.noaa.gov/>, Figure 3.2b).

3.2.4.3. Conditions in at-sea foraging areas

At-sea distributions during nonbreeding were mapped for each giant petrel species, based on 130 and 126 tracks of individual NGP and SGP, respectively, fitted with Global Location Sensors (GLS loggers; British Antarctic Survey, Cambridge, UK) in summer 1999/2000 (Figure S3.1). Subsequently, we extracted the data for the model covariates from all of the 5 x 5° cells within the 50% utilisation distributions (UDs) for oceanographic characteristics (SST, NPP and wind components), as this was considered to reflect the conditions experienced in core areas; and the 90% UD for trawl, demersal and pelagic longline fishing effort, which was considered to better reflect the potential encounters with fishing vessels (Pardo *et al.* 2017). Data on krill biomass and sea ice cover (SIC) were obtained from fixed sampling areas (see below).

- *Net primary productivity (NPP)*. Primary productivity at the base of the food web is an indicator of the ecosystem capacity to sustain animal biomass, and has been used as an index of predator food availability (Wakefield, Phillips & Matthiopoulos 2014). We used Net Primary Productivity (NPP), the quantity of carbon dioxide fixed by phytoplankton during photosynthesis, minus that released during respiration. Data were obtained from MODIS (<http://www.science.oregonstate.edu/ocean.productivity>) and Seawifs databases (<http://oceancolor.gsfc.nasa.gov/cms/data/seawifs>, Figure 3.2c).

- *Sea ice cover (SIC)*. Sea ice influences krill reproduction, growth and shelter, but also alters seabird foraging habitat by covering open water. Sea Ice Concentration (SIC) may influence giant petrels negatively, by reducing the size of foraging areas, or positively due to increased krill biomass. Remotely-sensed data on SIC were obtained from a polygon encompassing the Antarctic Peninsula and Scotia Sea (Figure 3.2d). Our initial analyses showed a strong negative correlation between SIC and SST ($r = -0.84, -0.75; p < 0.01$); thus SST was dropped, and SIC retained as a candidate variable since we were more interested in the oceanographic drivers than SST *per se*.
- *Krill biomass*. Antarctic krill *Euphasia superba* is a key component of Antarctic food webs, and across the Southern Ocean, the abundance of krill often shows a positive correlation with survival or breeding success of marine vertebrates (Croxall *et al.* 1992; Trathan *et al.* 2007; Descamps *et al.* 2016). Given the importance of krill in their diets (Hunter 1983, 1985), we expected a positive effect of krill availability on the survival of giant petrels. As a proxy of krill availability, we used krill density measured in annual acoustic surveys of the Western Core Box (WCB) area northwest of South Georgia previously the wintering period (Fielding *et al.* 2014, Figure 3.2e). Data was not available for the last two years of the study, thus, for modelling purpose, these missing values were replaced by the average of the last two years of data.
- *Wind speed*. Changes in wind regimes can directly influence foraging efficiency, and sex-specific differences in foraging performance in relation to wind are expected in size-dimorphic seabirds, driven primarily by differences in wind-loading (Phillips *et al.* 2004; Weimerskirch *et al.* 2012;

Lewis *et al.* 2015). As giant petrels have high wing loadings (149-163 Nm⁻²) (Warham 1977), we expect a positive influence of wind speed on their survival, particularly on the larger males. Wind data were obtained from QuickSCAT and ASCAT datasets (<http://cersat.ifremer.fr/data/products/catalogue>), expressed as average zonal (west-east) and meridional component (north-south) (Figure 3.2f, 3.2g).

- *Fisheries.* Giant petrels benefit from fisheries by scavenging on discards (Copello & Quintana 2009), but face the risk of incidental mortality by hooking on longlines when attempting to retrieve baits (Nel *et al.* 2002b; Sullivan *et al.* 2006; Yeh *et al.* 2013), or collision with trawl warp or monitoring cables (Sullivan *et al.* 2006). We predicted that females of both species will be more affected by fisheries, since they forage at lower latitudes than males, and are much more likely to forage on the Patagonian Shelf (González-Solís *et al.* 2000, 2008; Wakefield, Phillips & Matthiopoulos 2009) therefore overlap more with both demersal and pelagic longline fisheries, which often have high bird bycatch rates (Yeh *et al.* 2013; Jiménez *et al.* 2014, 2016; Tamini *et al.* 2015). We collated information on longline and trawl fisheries effort (number of hooks and hours trawled, respectively) in the southwest Atlantic, based on pelagic longline fisheries reported to ICCAT (International Commission for the Conservation of Atlantic Tuna), demersal longline fisheries reported to CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), and by the fleets of Argentina, Chile and Falklands, and trawl effort reported by the fleets of Argentina, Chile and the Falklands (Figure S3.2). Total annual effort for trawl (Figure 3.2h), demersal longline (Figure

3.2i) and pelagic longline (Figure 3.2j) fisheries were extracted from those operating within the 90% UD of the tracked giant petrels (see above). For modelling purpose, missing data for the last 2-4 were replaced by the average of the last two years of data. Giant petrels benefit from fisheries by scavenging on discards (Bugoni *et al.* 2010; Krüger *et al.* 2017a), but face the risk of incidental mortality by hooking on longlines when attempting to retrieve baits (Nel *et al.* 2002b; Yeh *et al.* 2013), or collision with trawl warp or monitoring cables (Sullivan *et al.* 2006). We predicted that females of both species will be more affected by fisheries, since they are more likely to forage on the Patagonian Shelf (González-Solís *et al.* 2000, 2008) and at lower latitudes than males, therefore overlap more with trawl, demersal and pelagic longline fisheries (Yeh *et al.* 2013; Jiménez *et al.* 2014, 2016; Tamini *et al.* 2015). We collated information on longline and trawl fisheries effort (number of hooks and hours trawled, respectively) in the southwest Atlantic, based on pelagic longline fisheries reported to ICCAT (International Commission for the Conservation of Atlantic Tuna), demersal longline fisheries reported to CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), and by the fleets of Argentina, Chile and Falklands, and trawl effort reported by the fleets of Argentina, Chile and the Falklands (Figure S3.2). Total annual effort for trawl (Figure 3.2h), demersal longline (Figure 3.2i) and pelagic longline (Figure 3.2j) fisheries were extracted from those operating within the 90% UD of the tracked giant petrels (see above). For modelling purpose, missing data for the last 2-4 were replaced by the average of the last two years of data.

3.2.4.4. Carrion availability

In contrast to most other marine vertebrates, giant petrels obtain a major portion of food on land during the breeding season, mainly scavenging but also depredating burrowing petrels, penguins and seal pups (Hunter 1983, 1985). The major sources of carrion at South Georgia are dead Antarctic fur seal *Arctocephalus gazella* males and pups. We predicted that survival of both giant petrel species will be affected by carrion availability; however, the effects are likely to be strongest for male NGP, which spend the most time on land feeding on fur seal carcasses (Gonzalez-Solís *et al.* 2000; González-Solís 2004). In years when more female fur seals give birth, more fur seal bulls spend time ashore competing for mating, and we therefore used the number of fur seal pups born in a study beach at Bird Island, monitored for the same period as our study, as proxies of carrion availability (Figure 3.2k).

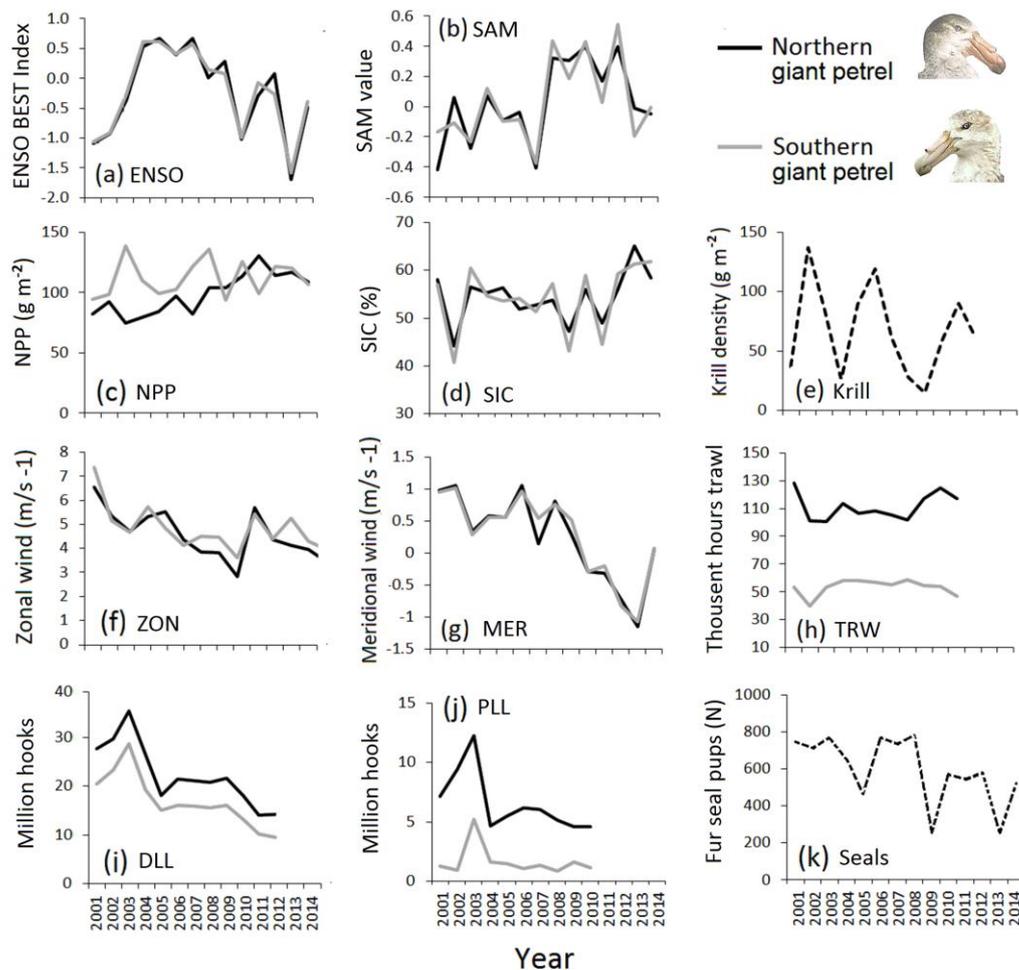


Figure 3.2. Annual variation in covariates (raw data) included as candidate predictors in models of survival of northern (black line) and southern (grey lines) giant petrels. Black dotted lines indicate covariates with common values for both species. (a) ENSO, El Niño Southern Oscillation, 2 year lag; (b) SAM, Southern Annular Mode, 1 month lag; (c) NPP, net primary productivity; (d) SIC, sea ice concentration, (e) krill density in the western core box, South Georgia (Fielding *et al.* 2014); (f) ZON, zonal and (g) MER, meridional wind speed; (h) TRW, trawl effort; (i) DLL, demersal and (j) PLL, pelagic longline effort; and (k) Seals, number of fur seal pups born in the study beach at Bird Island (British Antarctic Survey unpublished data). See Appendix S1 for details data sources.

3.2.5. Male-female survival differences

First, in order to explore annual differences, the survival of males (S_m) and females (S_f) was expressed as a proportional annual survival differential ΔS ($(S_m - S_f)/S_f * 100$; Jenouvrier *et al.* 2010). Secondly, in order to investigate

environmental drivers of survival of each sex, we constructed CMR models where variation in survival of only males or only females was constrained by covariates. A covariate effect was considered significant if the 95% confidence intervals of the corresponding slope did not include zero (Grosbois *et al.* 2008).

3.2.6. The two-sex matrix model

In order to explore the potential effects of sex differences in survival in response to environmental drivers on population growth rate, we developed two-sex population matrix models for both giant petrel species (Appendix S3.2, Caswell 2001), using the package “Pobpio” (Stubben, Milligan & Maintainer 2016) in R (R Development Core Team 2011). Potential future changes in survival as influenced by the covariates were explored by generating new survival estimates according to the magnitude and direction of the effects (slopes) for each sex, and following likely scenarios of environmental changes as supported by the literature (see Appendix S3.3). This involved calculating the expected change in survival (Ec) as $Ec = slope * (Smax - Smin)$ if the predicted trend for the covariate was positive and as $Ec = -slope * (Smax - Smin)$ if the predicted trend was negative, where $slope$ is the covariate effect, $Smax$ and $Smin$ are the maximum and minimum survival estimate for each sex from the $time*sex$ model. Subsequently, new survival values were calculated by adding the Ec to the average survival value for each sex. More details on the demographic modelling and supporting information justifying the assumptions on future trends of each influential covariate are presented in Appendix S3.3.

3.3. Results

3.3.1. Goodness of fit and model selection

The GOF based on Test 3, which is a sum of the χ^2 statistic and associated degrees of freedom (df) of tests 3.RS and 3.SM for each sex, indicate that the CJS model did not fit the data well for either NGP (males: $\chi^2 = 68.5$, $df = 27$, $P < 0.001$; females: $\chi^2 = 58.0$, $df = 28$, $P < 0.001$) or SGP (males: $\chi^2 = 72.0$, $df = 26$, $P < 0.001$; females: $\chi^2 = 56.2$, $df = 26$, $P < 0.001$) (Table S2). However, Test 3 leads to reasonable global variance inflation factors ($\hat{c} < 3$) for both NGP ($\hat{c} = 2.25$) and SGP ($\hat{c} = 2.46$), calculated for each specie as $\hat{c} = (\text{GOF}_{\text{males}} + \text{GOF}_{\text{females}}) / (\text{df}_{\text{males}} + \text{df}_{\text{females}})$. Therefore, for each species, we incorporated the global \hat{c} value into E-SURGE to perform model selection using the Akaike's Information Criterion corrected for overdispersion and small sample sizes (QAICc, Burnham & Anderson 2002).

Our initial model had survival varying by time, sex and previous state (S, F, PS, PF); however, in order to reduce the number of parameters, we compared breeders (pooled S/F) with non-breeders (PS/PF). Breeding probability was fixed as 1, because in our model all observed individuals are breeders (SB or FB), and therefore the encounter probability is a better proxy of breeding probability. Breeding success varies by time and previous state, however, and so to reduce the number of parameters we compared successful/post-successful individuals (S/PS) with failure/post-failure (F/PF), assuming the population consists of high and low quality individuals.

3.3.2. Encounter probability

The model with encounter probability varying by sex, age and state suggested a lack of fit, high parameter identifiability and high uncertainty around survival estimates. However, the model performed well after removal of the sex effect. Encounter probability varied over time but did not vary by state and thus time-dependent encounter probabilities were used in subsequent models for both species of giant petrel (Table 3.2, Figure S3.3).

3.3.3. Annual adult survival probability

Mean annual survival (\pm CI 95%) of NGP (0.91, 0.90 - 0.92), and SGP (0.92, 0.90-0.93) was similar. The linear model was the best-supported non-covariate model for both species, indicating significant decline in survival of NGP (linear vs time-dependent, Δ QAICc = 14.2; $R^2 = 0.71$, $P_{\text{ANODEV}} < 0.001$, slope \pm SE = -0.48 ± 0.05) and SGP (linear vs constant, Δ QAICc = 6.0, $R^2 = 0.42$, $P_{\text{ANODEV}} < 0.012$, slope = -0.42 ± 0.10 , Table 3.3, Figure 3.3).

Annual variation in survival at the population level in relation to covariates

There was a complex relationship between annual survival of NGP and the explanatory variables. There was a negative influence of zonal wind ($R^2 = 0.36$, $P_{\text{ANODEV}} = 0.03$, slope = -0.19 ± 0.09) and SIC ($R^2 = 0.33$, $P_{\text{ANODEV}} = 0.04$, slope = -0.16 ± 0.08), and a positive correlation with the meridional wind component ($R^2 = 0.38$, $P_{\text{ANODEV}} = 0.02$, slope = 0.22 ± 0.09) and ENSO ($R^2 = 0.32$, $P_{\text{ANODEV}} = 0.04$, slope = 0.18 ± 0.09). The model with additive effects of zonal winds and SIC accounted for the highest proportion of temporal variability in survival ($R^2 = 0.55$, $P_{\text{ANODEV}} = 0.02$; Table 3.3, Figure 3.3). Annual survival of SGP was positively correlated with SAM ($R^2 = 0.39$, $P_{\text{ANODEV}} = 0.02$, slope = 0.29

± 0.08 ; Table 3.3, Figure 3.3). The model with additive effects of SAM and zonal speed explained the highest proportion of temporal variability in survival ($R^2 = 0.66$, $P_{ANOVA} < 0.01$); however, zonal wind alone was not significant (Table 3.3, Figure 3.3).

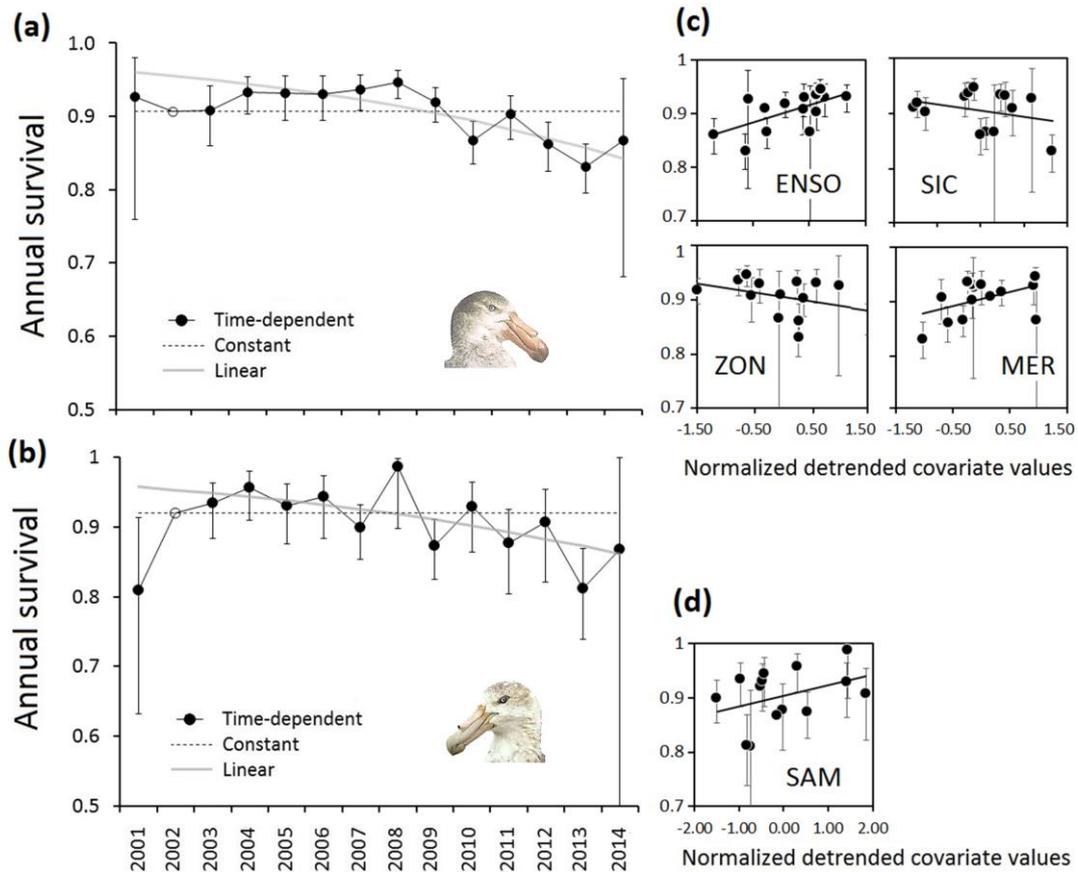


Figure 3.3. Variation in annual survival ($\pm 95\%$ CI) of northern (a) and southern (b) giant petrels, and correlation between annual survival and the significant covariates in survival models for each species (c, d). ENSO, El Niño Southern Oscillation; SAM, Southern Annular Mode; SIC, sea ice cover; zonal (ZON) and meridional (MER) wind components. Solid grey and dashed black lines indicate the linear trend and constant models, respectively. The trend line in “c” and “d” shows the slope of the linear correlation between the annual survival and the scaled values of de-trended covariates. Open circles in “a” and “b” indicate that survival could not be estimated so the average was plotted, and they were removed from the plots “c” and “d”.

Sex-specific survival and drivers

In both species, average survival was higher in male than females by $\Delta S = 2.2\%$; however, only for NGP was the sex-dependent model better supported than the model without a sex effect (sex vs constant, $\Delta QAI Cc = 2.4$; Table 3.2, Figure 3.4). Nevertheless, the magnitude of the difference between the sexes was similar in both species; survival (\pm CI 95%) of male and female NGP was 0.92 (0.90-0.93) and 0.90 (0.88-0.91) respectively, and of male and female SGP was 0.93 (0.90-0.94) and 0.91 (0.89-0.93), respectively. The observed range of variation in ΔS from 2001 to 2014 was [-3.9%, 12.2%] for NGP and [-6.7%, 16.5%] for SGP. Male and female survival in both species showed a significant negative linear trend over time, supported by the QAI Cc score and significant slopes (Table 3.3, Figure 3.4); therefore the interpretation of sex-specific responses was based on de-trended models only. For NGP, the negative and positive effect of SIC and meridional wind, respectively, were only expressed in female survival; the negative effect of zonal wind was only expressed in male survival; ENSO had a positive and similar effect on male and female survival; fur seal pup production had a positive effect on male survival, and; pelagic longline effort had a negative effect on female survival (Figure 3.5). For SGP, the effect of the environmental variables also varied by sex; SAM had a significant positive effect only on female survival (Figure 3.5).

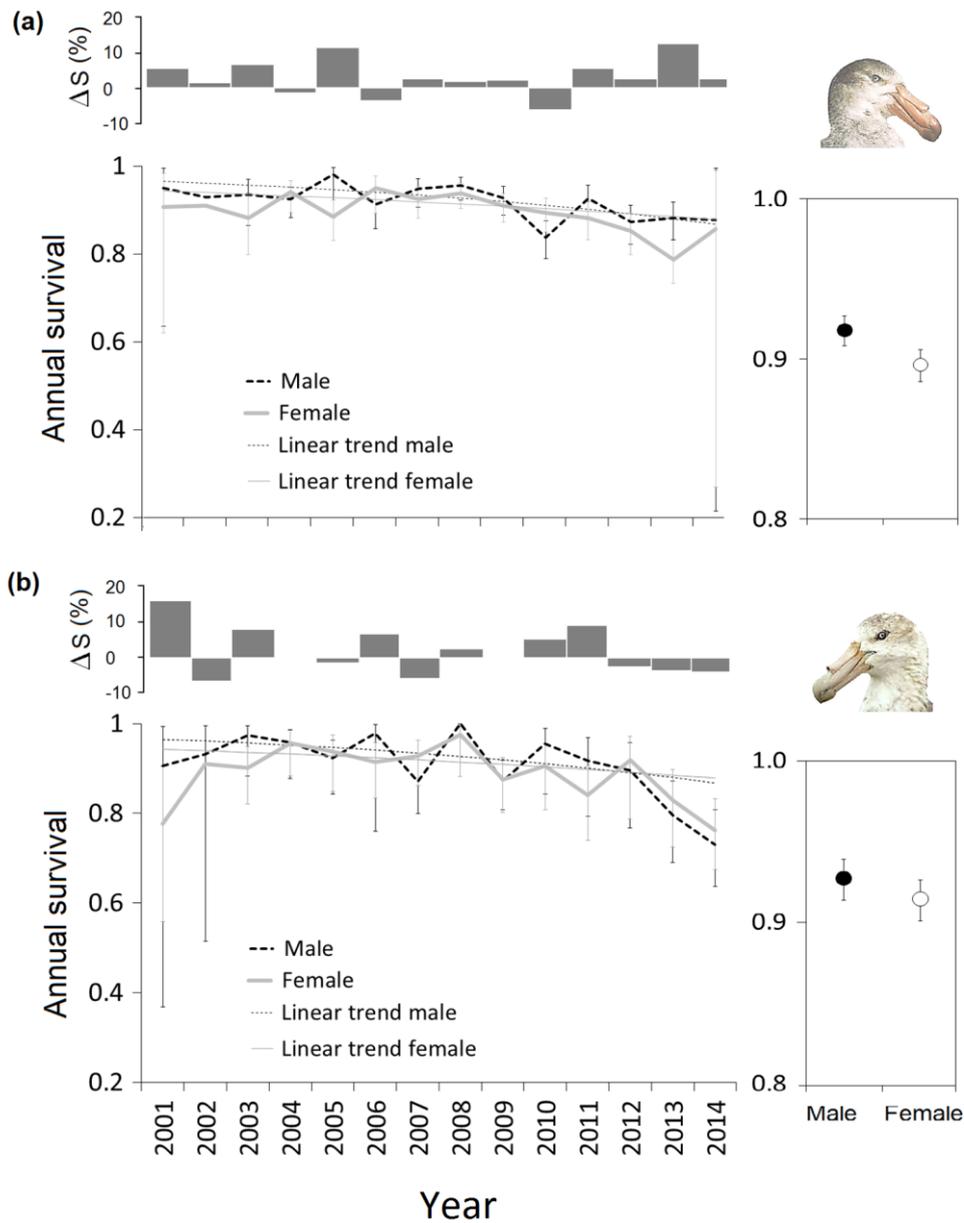


Figure 3.4. Sex-specific survival of (a) northern and (b) southern giant petrels. Left panels show the annual variation in survival of males and females, and the male-female survival differential (ΔS), which expresses the percentage difference in male survival relative to female. Right panels show the average sex-specific survival. Error bars are the $\pm 95\%$ confidence intervals.

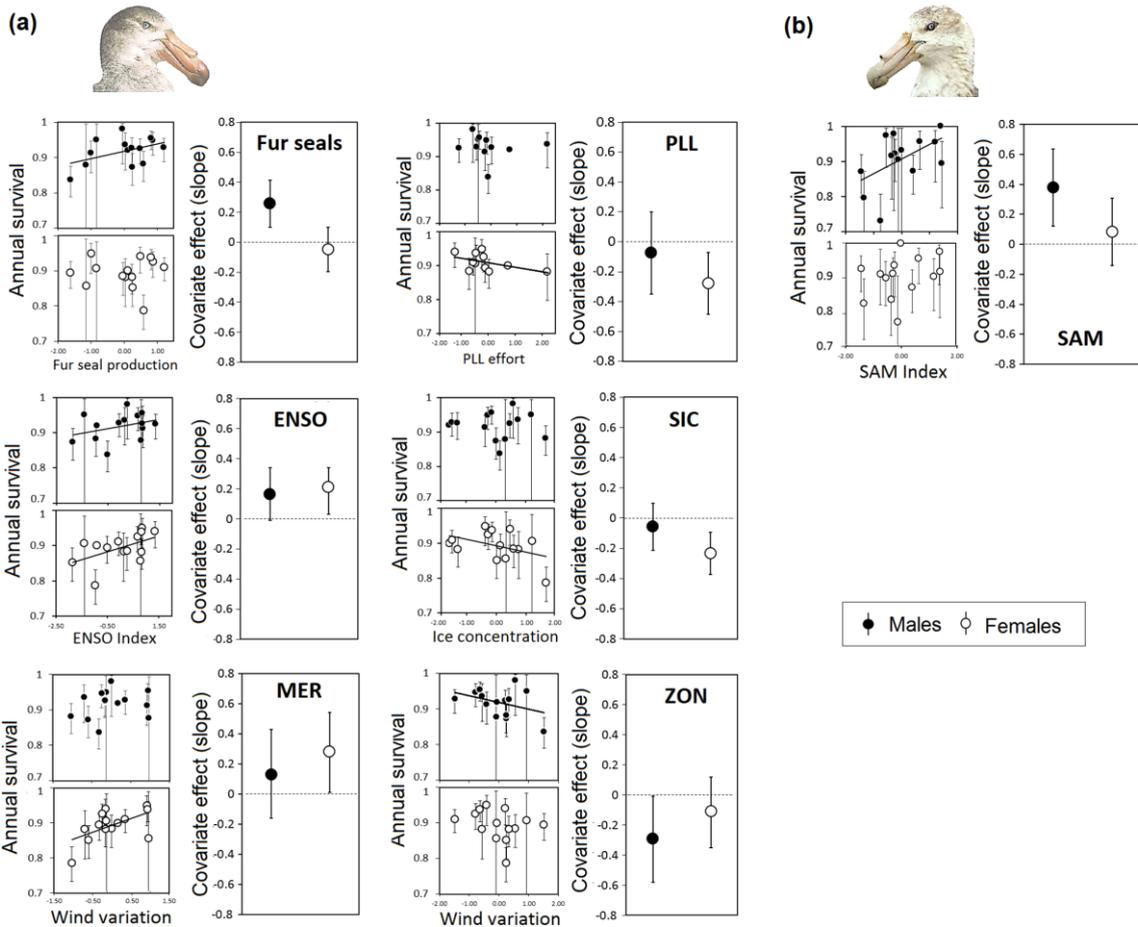


Figure 3.5. Relative effect of explanatory variables on male and female survival of (a) northern giant petrels, and (b) southern giant petrels. The scatterplots show annual survival of males and females (from the sex- and time-dependent model) as function of explanatory variables (de-trended and scaled values), and the vertical panels show the covariate effect (slope) on male and female survival. Fur seal productivity (Fur seals), El Niño Southern Oscillation (ENSO), Southern Annular Mode (SAM), sea ice concentration (SIC), zonal (ZON) and meridional (MER) wind speed (mph) and pelagic longline effort (PLL, millions of hooks).

3.3.4. Trends in environmental drivers and population growth

For NGP, the predicted increase in the frequency of ENSO is likely to have a positive impact on both male and female survival; however, the projected reductions in SIC and increases in meridional wind component may benefit

females, whereas the expected reduction in Antarctic fur seal pup production are likely to have negative effects on the survival of males (Table 3.4, Figure 3.5). Because of uncertainties in the future trend in pelagic longline effort within foraging areas, we tested scenarios of increasing or decreasing effort, which is expected to affect only the survival of female giant petrels. The deterministic population growth rate (λ ; lambda) based on the average values for male and female survival was 0.999. Taking into account the cumulative effects of predicted changes on the influential covariates; the estimated lambda is 1.014 if pelagic longline effort remains stable, and 1.003 and 1.012 for increased and decreased pelagic longline effort respectively. However, the model based on the average survival rates of males and females for the last five years of the study period, which were 4-5% lower than the average for all years, resulted in the lowest population growth rate ($\lambda = 0.971$) (Table 3.4, Figure 3.6).

For SGP, the population growth based on the average values of male and female survival was 0.998, and the only influential covariate was SAM, which is predicted to increase in the future, with a positive effect on male survival only, and increasing population growth ($\lambda = 1.034$). Conversely, the model based on the average survival rates of males and females for the last five years of the study, which were 3-4% lower than the average for all years, resulted in the lowest population growth rate ($\lambda = 0.974$) (Table 3.4, Figure 3.6).

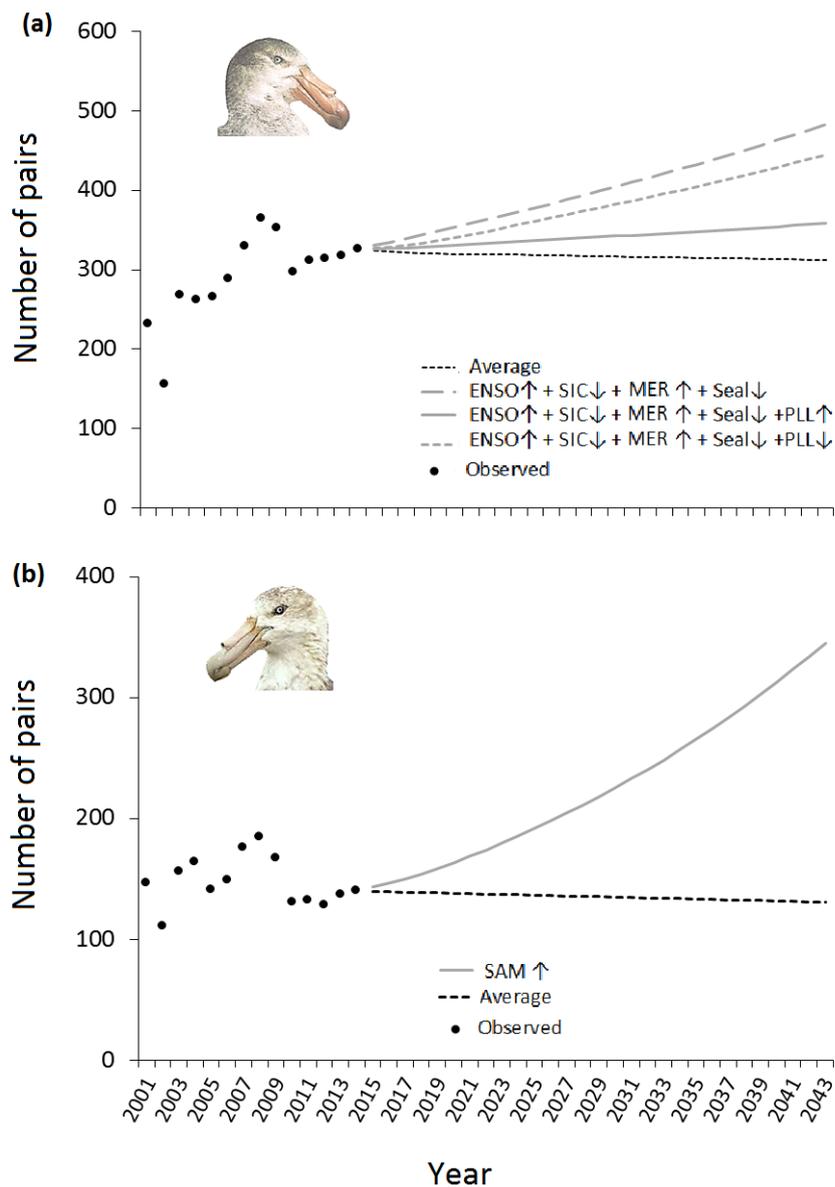


Figure 3.6. Average population trajectories of (a) northern giant petrels, and (b) southern giant petrels, based on the estimated vital rates and on predicted trends for the explanatory variables. In (a) “Combined PLL+” and “Combined PLL-” refers to the cumulative impact of all influential covariates and considering increases and decreases, respectively, in pelagic longline effort (PLL) within the foraging area (northern giant petrels only). Population projections as influenced by predicted trends in Southern Annular Mode (SAM), El Nino Southern Oscillation (ENSO), sea ice concentration (SIC), meridional wind speed (MER) and fur seal pup production (Seal) are also presented.

3.4. Discussion

This is one of the few studies to examine sex-specific effects of environmental variation and fishing effort on survival rates in a marine vertebrate (Olsson & Van der Jeugd 2002; Martínez-Abraín *et al.* 2006; Jenouvrier *et al.* 2012). We showed that the survival of giant petrels of one or both species was influenced by large-scale climatic indices, oceanographic characteristics, availability of fur seal carrion, and fisheries. We found interspecific differences, and, as expected, both species showed sex-specific responses to environmental variability. These interspecific differences may be related to allochrony, since NGP breed six weeks earlier, but may also be related to the large error founds for SGP survival estimates, making it difficult to detect significant effects. Possible ecological links underlying these relationships, and the causes and implications of differences between species and sexes are discussed below.

3.4.1. Climate oscillation and environment variability

Previous research has revealed either positive or negative effects of ENSO and SAM on pinnipeds and seabirds breeding in the Southern Ocean, and sometimes contrasting responses among sympatric species, or allopatric populations of the same species (Barbraud *et al.* 2012; Descamps *et al.* 2016). Overall, there was a significant positive influence of ENSO and meridional wind speed, as well as a negative influence of zonal wind speed and sea ice cover (SIC) on NGP survival, whereas there was a significant positive effect only of SAM on survival of SGP. Positive phases of ENSO and SAM are linked to warmer sea conditions (Trathan *et al.* 2007), although we did not detect this correlation in our covariate datasets (Appendix S3.1). Considering the positive and negative influence of ENSO and SIC, respectively, on NGP survival, and the strong

negative relationship between SIC and SST ($r = -0.75$, $p < 0.01$; Appendix S3.1); it seems that mortality of giant petrels is lower in relatively warm than cold years, in contrast to our initial prediction. This may be explained by two non-mutually exclusive mechanisms. First, warm conditions may increase the extent of ice-free waters and thus of giant petrel foraging areas, as with some other Antarctic seabirds (Descamps *et al.* 2016). Second, warm conditions reduce the survival of Antarctic fur seal pups and penguin fledglings (Beauplet *et al.* 2005; Trivelpiece *et al.* 2011; Horswill *et al.* 2014), and thus increase carrion availability.

Stronger winds directly increase flight speed and thus improve foraging performance of long distance surface seizers like giant petrels (Warham 1977; Weimerskirch *et al.* 2012), which likely explains the significant positive relationship between meridional winds and NOGP survival. However, the inverse relationship between zonal winds and NGP survival is contrary to our predictions and therefore may be because of some other indirect effects, like wind-driven changes in SIC beyond or fixed SIC sampling area (Holland & Kwok 2012).

Although Antarctic krill is a key component in the diet of both giant petrel species during breeding (Hunter 1983), we found no significant effect of krill density in the annual acoustic survey area to the northwest of the colony. This may be due to their ability to switch to a number of alternative prey, including squid, carrion or other seabirds (Hunter 1983; Phillips *et al.* 2011), or because we were unable to sample krill throughout the extensive foraging ranges of giant petrels during wintering (Figure S3.2, González-Solís *et al.* 2008).

3.4.2. Fisheries

Giant petrel mortality was formerly high in demersal longline fisheries around sub-Antarctic islands (Ashford *et al.* 1994; Nel *et al.* 2002b); however, this type of fishing is prohibited around South Georgia during the summer, and during the winter currently catches very few seabirds. As a result, local bycatch would not be an issue for giant petrels during our study period. Elsewhere, giant petrel bycatch has been recorded in trawl (Sullivan *et al.* 2006) and pelagic longline fisheries (Tuck *et al.* 2011). Despite this, we found no evidence for a significant negative relationship between those fisheries and the overall survival of both species, although there was a negative relationship between pelagic longline effort and female NGP survival. Female giant petrels are more likely to attend demersal longline vessels than males, at least during the breeding season (Otley *et al.* 2007), and during winter overlap more in areas with poorly managed pelagic longline fisheries than males (González-Solís *et al.* 2008; Phillips *et al.* 2009).

For scavenging species, like the giant petrels, availability of fishing discards (including offal) can be beneficial (Votier *et al.* 2004; Bugoni *et al.* 2010; Krüger *et al.* 2017a). However, based on our de-trended data, there was no evidence of this for giant petrels at Bird Island. Nonetheless, without de-trending, there was a significant positive influence of trawl effort on the survival of the SGP ($R^2 = 0.38$, $P_{ANODEV} = 0.02$; slope = 0.38 ± 0.11), and of demersal longline effort on the survival of both species (NGP: $R^2 = 0.39$, $P_{ANODEV} = 0.02$, slope = 0.52 ± 0.07 ; SGP: $R^2 = 0.32$, $P_{ANODEV} = 0.03$; slope = 0.36 ± 0.10), suggesting a positive effect in the long term (Table S3.3). Although giant petrels at South Georgia have limited access to discards during the early breeding season (Hunter 1983),

discards are probably more important later in breeding and during winter, when birds forage primarily at sea (Gonzalez-Solis et al. 2008).

3.4.3. Sex-specific responses to environmental variability

As predicted for these dimorphic species with divergent foraging ecology and distribution, there were sex-specific relationships between survival and our covariates. These effects were not apparent when analysis was conducted at the population-level, highlighting the importance of considering such within population variation. Although there was no overall significant influence of fur seal production on annual survival ($P_{\text{ANODEV}} > 0.05$), there was a significant positive influence on the survival of male NGP. This is consistent with their higher reliance on carrion during breeding; 94% of the birds foraging at fur seal carcasses during the breeding season were male NGP (Hunter 1983). Moreover, higher fur seal pup production at South Georgia may increase carrion availability during the following winter, providing scavenging opportunities on post-weaning pups depredated by leopard seals (Schwarz *et al.* 2013), benefiting male giant petrels that remain around South Georgia year round. Consistent with our other predictions about more pelagic females, the negative effect of SIC (potentially related to reducing at-sea foraging areas) and meridional winds was mainly for female NGP (Figure 3.5). This result is consistent with Weimerskirch *et al.* (2012) who found that shifts in meridional winds primarily affected female foraging performance of wandering albatross *Diomedea exulans*. The positive effect of ENSO on NGP survival affected males and females equally. This is probably because ENSO influences oceanographic conditions at a basin scale, thus affecting foraging areas of males and females through the year (Trathan *et al.* 2007; Barbraud *et al.* 2012).

3.4.4. Future prospects for giant petrels in a rapidly changing ecosystem

Despite the rapidity of change in the Atlantic sector of the Southern Ocean (Meredith & King 2005; Whitehouse *et al.* 2008) giant petrels are expected to cope better with future climate changes than obligate krill-dependent species (Reid & Croxall 2001; Atkinson *et al.* 2004; Trathan *et al.* 2007), because of their diverse foraging behaviours. Our two-sex population models predict that, under most scenarios, numbers of NGP and SGP will increase in future, while the population growth rate based on the average values of male and female survival tended to be relatively stable under the current environmental conditions (Figure 3.6).

Although warm conditions are likely to benefit giant petrels, in the long term these positive effects may not last, because persistent positive SST anomalies can lead to broader ecosystem disruptions in Antarctic food webs, and potentially the collapse of krill stocks (Atkinson *et al.* 2004; Meredith & King 2005). Negative effects of warming climate on krill populations will first become evident at the northern distributional limits, such as around South Georgia, and also at the Antarctic Peninsula, where temperatures have increased by 2.3 °C in the last 80 years (Meredith & King 2005; Whitehouse *et al.* 2008). Long term reductions in krill abundance may also lead to population declines of Antarctic fur seal and macaroni penguins *Eudyptes chrysolophus* (Forcada *et al.* 2005; Trathan *et al.* 2007; Forcada & Hoffman 2014; Horswill *et al.* 2014), possibly increasing carrion in the short-term, although if numbers decline they may ultimately have a negative impact (Hunter 1983). Additionally, as demonstrated by our models, increased

pelagic longline effort could have negative population-level effects, especially via increased bycatch of females (Gianuca, Phillips & Votier 2017).

3.5. Conclusion

Survival of giant petrels is influenced by large-scale climatic indices, oceanographic characteristics, the availability of seal carrion, and fisheries, but with contrasting effects for males and females. Modelled population trajectories of both species match the observed trends at Bird Island, and the future environmental changes are likely to benefit their population growth. However, a potential increase in pelagic longline fisheries could reduce female survival. The present study provides a better understanding of how sexual size dimorphism of a land-based marine predator can drive sex-specific responses to environmental fluctuations and anthropogenic factors, with implications for population trajectories. This reinforces the need for greater consideration of sex differences in ecological and demographic studies of dimorphic species, as well as in the management of anthropogenic impacts.

Table 3.1. Results of goodness of fit chi-square statistics (χ^2), and associated degrees of freedom (df) and *p-value*, for male and female northern and southern giant petrels.

	Male			Female		
	χ^2	df	p-value	χ^2	df	p-value
<i>Northern giant petrel</i>						
Test 3.SR	17.5	13	0.179	13.1	13	0.436
Test 3.SM	48.3	14	<0.001	44.9	15	<0.001
Sum Text 3	65.8	27	<0.001	58.0	28	<0.001
<i>Southern giant petrel</i>						
3.SR	21.1	13	0.07	20.4	12	0.06
3.Sm	50.9	13	<0.001	35.8	14	0.001
Sum Test 3	72.0	26	<0.001	56.2	26	<0.001

Table 3.2. Summary of model selection to estimate encounter probabilities of northern and southern giant petrels, K is the number of parameters in the model.

Model	K	Deviance	QAICc	Δ QAICc
<i>Northern giant petrel</i>				
time	94	18780.5	8537.5	0.0
time + state	96	18780.5	8541.6	4.1
time * state	107	18780.5	8564.2	26.8
state	84	18910.4	8574.7	37.2
constatnt	83	18942.6	8586.9	49.5
<i>Southern giant petrel</i>				
time	95	10628.9	4498.7	0.0
time + state	96	10628.9	4500.8	2.1
constant	83	10709.7	4506.1	7.4
state	84	10734.5	4518.2	19.6
time * state	107	10628.9	4524.1	25.5

Table 3.3. Model selection to estimate adult annual survival of northern and southern giant petrels and the effects of candidate explanatory covariates. Detrended covariate models are shown along with the time*sex-, time- and sex-depended, as well as the constant and linear the trend models. The slope \pm SE is shown only for the covariates that had a significant effect on survival (p ANODEV \leq 0.05).

Model*	K	Deviance	QAICc	Δ QAICc	R2 (%)	P ANODEV	Slope \pm SE
<i>Northern giant petrel</i>							
SIC+ZON	48	18780.3	8443.5	0.0	55	0.018	
SIC	47	18786.3	8444.1	0.6	33	0.040	-0.16 \pm 0.05
ZON	47	18786.5	8444.2	1.7	36	0.031	-0.19 \pm 0.09
MER	47	18784.8	8443.5	1.4	38	0.024	0.22 \pm 0.10
ENSO	47	18786.6	8444.3	0.8	32	0.045	0.18 \pm 0.06
SIC+WIN+ENSO	49	18779.2	8445.0	1.6	59	0.037	
TRW	47	18790.3	8445.9	2.4	18	0.149	0.14 \pm 0.07
PLL	47	18790.5	8446.0	2.5	17	0.158	-0.19 \pm 0.08
Linear	46	18795.1	8446.0	2.5	71	<0.001	-0.48 \pm 0.05
Seal	47	18791.2	8446.3	2.8	15	0.195	0.11 \pm 0.05
Krill density	47	18792.6	8446.9	3.4	9	0.310	
DLL	47	18793.0	8447.1	3.6	8	0.355	
SAM	47	18794.8	8447.9	4.4	1	0.749	
NPP	47	18795.1	8448.0	4.5	0	0.932	
Time	57	18768.4	8456.4	13.0			
Time x sex	71	18736.3	8470.7	27.2			
Sex	46	18850.9	8470.8	27.3			
Constant	45	18860.9	8473.2	29.7			
<i>Southern giant petrel</i>							
SAM + ZON	48	10621.8	4397.7	0.0	66	0.004	
SAM	47	10629.5	4398.8	1.1	39	0.023	0.28 \pm 0.40
SAM + ZON + ENSO	49	10621.7	4399.7	2.0	66	0.016	
ZON	47	10633.7	4400.5	2.8	24	0.091	
Linear	46	10640.4	4401.1	3.4	42	0.012	-0.42 \pm 0.10
ENSO	47	10636.6	4401.6	3.9	14	0.214	
DLL	47	10638.2	4402.3	4.6	8	0.348	
Krill	47	10638.4	4402.4	4.6	7	0.371	
MER	47	10638.4	4402.4	4.7	7	0.375	
SIC	47	10639.4	4402.8	5.1	4	0.522	
PLL	47	10639.6	4402.9	5.2	3	0.610	
NPP	47	10639.8	4402.9	5.2	2	0.581	
Seal	47	10640.4	4403.2	5.5	0	0.891	
TRW	47	10640.4	4403.2	5.5	0	0.982	
Constant	45	10661.0	4407.4	9.7			
sex	46	10658.9	4408.6	10.9			
Time	57	10612.3	4412.4	14.7			
Time x sex	71	10597.2	4435.4	37.7			

* Abbreviations: ENSO, El Nino Southern Oscillation; SAM, Southern Annular Mode, NPP, net primary productivity; SIC, sea ice concentration; ZON, zonal wind speed; MER, meridional wind component; Krill, krill density; Seal, Antarctic fur seal carrion availability; TRW, trawl effort; DLL, demersal longline effort; and PLL, pelagic longline effort.

Table 3.4. Survival values for male and female giant petrels, as influenced by predicted trends in the influential covariates (See Appendix S3.3). Future expected change (Ec) in survival as influenced by the covariates were calculated by multiplying the covariate slope by the range (max - min) of interannual variation in survival of each sex (NGP, M = 0.15, F = 0.20; SGP, M = 0.18, F = 0.19). New survival values were calculated by summing the Ec to the average value for each sex. Abbreviations: ENSO, El Nino Southern Oscillation; SAM, Southern Annular Mode, SIC, sea ice concentration, Seal, Antarctic fur seal carrion availability; PLL, pelagic longline effort.

Variable	Trend	Slope		Change in survival (Ec)		New survival values		Lambda
		M	F	M	F	M	F	
<i>Northern giant petrel</i>								
ENSO	+	0.24	0.22	0.03	0.04	0.95	0.94	1.025
SIC	-	ns	-0.23	0	0.05	0.92	0.95	1.019
MER	+	ns	0.28	0	0.06	0.92	0.99	0.987
Seal	-	0.24	ns	-0.04	0	0.89	0.9	0.993
PLL ↑	+	ns	-0.25	0	-0.05	0.92	0.85	0.993
PLL ↓	-	ns	-0.25	0	0.05	0.92	0.95	1.020
ENSO+MER+SIC+seal						0.90	0.94	1.011
ENSO+MER+SIC+seal+PLL↑						0.90	0.91	0.999
ENSO+MER+SIC+seal+PLL↓						0.90	0.95	1.016
Average survival						0.92	0.9	1.002
Average Last 5 years						0.88	0.85	0.975
<i>Southern giant petrel</i>								
SAM	+	0.38	ns	0.07	0	1	0.91	1.037
Average survival						0.93	0.91	0.997
Average last 5 years						0.89	0.88	0.973

**CHAPTER 4. Effects of environmental variation and fisheries on
the demography of two allochronic predators in the Southern
Ocean**



Submitted to *Oecologia*

ABSTRACT

Synchronizing timing of breeding with optimal environmental conditions is critical for successful reproduction, and has a major influence on population dynamics. Therefore, sympatric species that differ in breeding schedules (i.e. allochronic species) may respond differently to environmental change and anthropogenic impacts. We conducted a longitudinal study on two marine top predators, northern (NGP, *Macronectes halli*) and southern (SGP, *M. giganteus*) giant petrels that breed sympatrically on sub-Antarctic islands, but differ in timing of breeding by ~6 weeks to investigate how allochrony influenced responses to the same drivers. We used multi-event models to compare adult survival, breeding probability and breeding success at South Georgia. Subsequently, we tested for the effect of a suite of environmental variables, including fisheries, on breeding success. Finally, we examined the influence of reproductive rates on population growth. Mean adult survival of NGP and SGP were similar (91% and 92%, respectively), and breeding probability was higher in NGP (0.92) than SGP (0.83). Both species had higher breeding success in warmer years, and when Antarctic fur seal *Arctocephalus gazella* carrion availability was higher. As NGP breed earlier, they have greater access to this food resource, which peaks during their chick-rearing period when SGP are still incubating. This tends to increase chick survival and buffers the effects of wider environmental variability. Fisheries had little effect in either species. Matrix models predicted a slight increase in the NGP population ($\lambda = 1.017$) and a stable SGP population ($\lambda = 1.003$), matching observed trends for both species. Differential access to carrion availability during chick rearing due to allochrony contributes to the lower fecundity of SGP, and seems to drive the divergent population trajectories of the two species at South Georgia following the post-hunting recovery of the local fur seal population.

4.1. Introduction

Sympatric populations of closely related species that have similar ecological requirements often differ in the timing of their life-cycle events (e.g. migration or reproduction). Such phenological mismatch (allochryony) plays an important role in resource partitioning (Gonzalez-Solis *et al.* 2000; Navarro *et al.* 2013), genetic differentiation and ultimately speciation (Monteiro & Furness 1998; Friesen *et al.* 2007). Allochryony is also important in terms of responses to environmental variability and anthropogenic impacts; matches or mismatches with key environmental drivers can result in phenological changes with potential demographic consequences (Stenseth & Mysterud 2002; Miller-rushing *et al.* 2010). However, we still understand little about how changes in phenology will affect populations, and the underlying role of allochryony in driving divergent responses to environmental changes in sympatric species (Miller-rushing *et al.* 2010; Reed, Jenouvrier & Visser 2013b).

Synchronizing timing of breeding with optimal environmental conditions is critical for successful reproduction and hence has a major influence on population dynamics. This is especially important at high latitudes, where suitable biotic (e.g. food availability) and abiotic (e.g. climatic) conditions are highly time-constrained for many animals (Reed *et al.* 2013a; b; Youngflesh *et al.* 2017). Polar and sub-polar areas are also experiencing very rapid changes in climate (Moritz, Bitz & Steig 2002; Whitehouse *et al.* 2008; Hoegh-Guldberg & Bruno 2010), resulting in changes to phenology and widespread ecological disruption, especially in marine ecosystems (Atkinson *et al.* 2004; Sydeman *et al.* 2015; Poloczanska *et al.* 2016). The Southern Ocean and adjacent subtropical waters have also been exploited by large-scale commercial fisheries. Fisheries have had negative

impacts on many species via unsustainable bycatch (Croxall & Nicol 2004; Barbraud *et al.* 2012). The cumulative and interactive impacts of changing climate and fisheries have resulted in widespread ecological disruptions of marine ecosystems, with direct and indirect effects on population dynamics of land-based top predators (Trathan *et al.* 2007; Trivelpiece *et al.* 2011; Pardo *et al.* 2017). Phenological mismatch among sympatric land-based predators with similar foraging strategies and life-histories may influence the specific responses to environmental change and anthropogenic impacts; however, as far as we are aware, no study has sought to disentangle the effect of allochrony from other interspecific traits.

In this context, sibling species, the northern (NGP, *Macronectes halli*) and southern (SGP, *M. giganteus*) giant petrel offer an ideal opportunity for studying the role of allochrony in response to environmental change. They have wide marine distributions in the Southern Ocean and breed in sympatry on sub-Antarctic islands, sharing very similar life-history characteristics and ecology, but NGP breed around six weeks earlier than SGP (Marchant & Higgins 1990). This difference in timing of breeding is the key factor in maintaining reproductive isolation, although hybridization can still occur (Brown *et al.* 2015). Both species forage at-sea on Antarctic krill *Euphausia superba* and other marine prey (from the ice edge to the sub-tropics), and also extensively on land, mostly scavenging dead and moribund penguins and pinnipeds (Hunter 1984; Patterson *et al.* 2008). At South Georgia, the only site in the Atlantic where both species breed in sympatry (Hunter 1984), because NGP breed earlier, they are better able to exploit Antarctic fur seal (*Arctocephalus gazella*) carrion (pups and dead bulls), which peaks during early-mid chick-rearing of NGP (Figure 4.1). At this time, SGP are still incubating (Hunter 1984; Gonzalez-Solis *et al.* 2000). From the early

1960s to mid-1990s, the population of Antarctic fur seals increased at South Georgia, recovering after near extinction from intense hunting (Payne 1977; Forcada & Hoffman 2014). Over the same period the NGP population also increased, whereas the SGP population was stable or declining (Hunter 1985; González-Solís *et al.* 2000). NGP also have greater access than SGP during their respective chick-rearing periods to carrion in the form of macaroni penguin (*Eudyptes chrysolophus*) chicks (Williams & Croxall 1991), mostly consumed after crèche. However, late in the breeding season once carrion availability is much reduced, both NGP and SGP feed almost entirely on fish and krill, or scavenge behind fishing vessels (Otley *et al.* 2007; González-Solís *et al.* 2008). Hence, because of allochrony, both species face different conditions according to reproductive stage, and therefore environmental and fishing effort variability will potentially have differing consequences (Atkinson *et al.* 2004; Meredith & King 2005; Whitehouse *et al.* 2008).

Here we conducted a longitudinal study of giant petrel demography using capture-mark-recapture and matrix population models, to investigate the roles of terrestrial and marine environmental variability and fisheries in driving reproduction and population dynamics. This includes the first robust analysis of the influence of annual changes in carrion availability on land (Antarctic fur seal productivity). We expected the higher population growth rates for NGP at Bird Island (South Georgia) to be explained by higher breeding success, which covaries with carrion availability, whereas reproduction in SGP was expected to show a greater influence of variability in conditions at sea (Hunter 1984; Gonzalez-Solís *et al.* 2000). Fisheries within marine foraging areas were expected to enhance the breeding success of both species via food provisioning

in the form of discards (Nel *et al.* 2003; Votier *et al.* 2004; Copello & Quintana 2009).

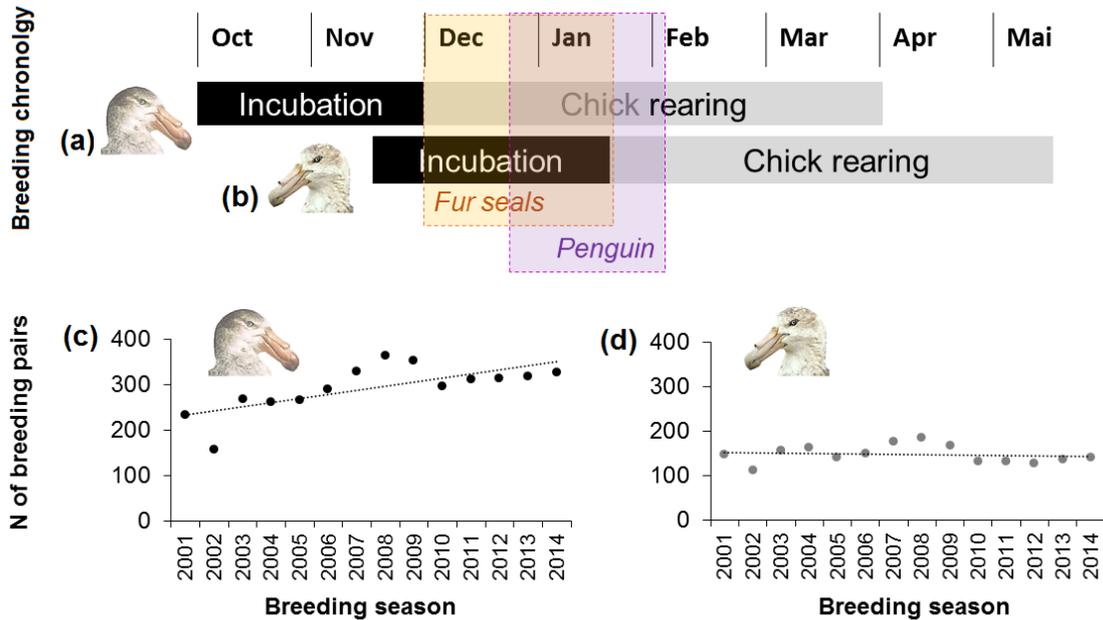


Figure 4.1. Simplified breeding chronology (upper panel), and number of breeding pairs in the study area at Bird Island, South Georgia in 2001-2014 (British Antarctic Survey, unpublished data) of (a, b) northern giant petrels and (c, d) southern giant petrels. Note the mismatch between the timing of chick-rearing of southern giant petrels and the peak availability of carrion from Antarctic fur seals and macaroni penguin chicks (shaded rectangles, Williams & Croxall 1991; Boyd 1993).

4.2. Methods

4.2.1. Species, study site and data collection

We studied NGP and SGP breeding at Bird Island (54° 00' S, 38° 03' W), South Georgia. Giant petrels lay a single egg without replacement in early October for NGP and mid-November for SGP. Overall, incubation lasts 60 days and chicks fledge 110-120 days after hatching. Therefore, the breeding seasons

of NGP and SGP encompass October-March and November-May respectively (Figure 4.1).

We monitored c. 350 pairs of NGP and c. 150 pairs of SGP in a well demarcated study area in austral summers 2000/01–2014/15 (hereafter, 2001 refers to the breeding season in austral summer 2000/01 etc.). For details of the monitoring protocol, see Brown *et al.* (2015). Briefly, all breeding birds were fitted with a British Trust for Ornithology metal ring and a coloured plastic ring engraved with a unique three-character alphanumeric code, and sexed from bill length. All nests were staked and mapped using handheld Global Positioning System (GPS) loggers. Active nests were checked every 4-5 days until both partners were identified, and visited weekly for the remainder of the breeding season until the outcome of the reproductive attempt was known.

4.2.2 The general CMR model

In order to investigate the effects of environmental variability on breeding success and to estimate other relevant life history traits for population dynamics, we modelled individual adult capture histories using multi-event models built and fitted in E-SURGE v.1.9.0 (Choquet *et al.* 2009). Based upon the observation of three possible events; “0” (not encountered), “1” (encountered as a successful breeder) or “2” (encountered as a failed breeder); we defined five states: two observable, corresponding to successful (SB) and failed breeders (FB), and three unobservable states (Figure 3.1, Table S3.1), corresponding to post-successful breeders (PS, non-breeding birds that were successful breeders in the previous season), post-failed breeders (PF, non-breeding birds that were failed breeders in the previous season), and dead (undifferentiated from permanently emigrated birds, but there is very high breeding site fidelity in this species). This modelling

approach allows the estimation of multiple life-history traits simultaneously: adult annual survival (probability of an adult bird surviving the breeding season and the following winter), breeding probability (probability of a bird laying an egg if alive), and breeding success (probability of fledging a chick if breeding). The estimation of demographic traits were based on 1,376 encounter histories (Table S3.2) of northern (623 males and 753 females) and 668 southern giant petrels (334 males and 354 females). As the study was conducted in well demarcated areas, and over 15 years, <1% of the colour-ringed population was observed breeding outside that area, emigration was not considered.

4.2.3. Model selection and goodness-of-fit

There is currently no test available to assess goodness-of-fit (GOF) for multi-event models. To check whether data met the basic assumptions underlying capture-mark-recapture models, a GOF test for the Cormack Jolly Seber model (CJS) was applied to a simplified (single state) version of the encounter histories, and potential sex-specific differences in resighting heterogeneity were checked in U-CARE 2.2 (Pradel *et al.* 2005; Choquet *et al.* 2009). Under the CJS assumptions, this comprised two tests and their sub-components: Test 2 (sub-components 2.CT + 2.CI) examines heterogeneity in recapture probabilities and trap-dependence; and Test 3 (sub-components 3.SR + 3.Sm) checks the heterogeneity in survival probabilities and transience effects. As our multi-event model design accounts for differences in breeding probabilities according to previous breeding states, it automatically corrects for trap-dependence, which is common in seabirds that often defer (skip) breeding (Pardo *et al.* 2017). Thus GOF can be conducted excluding Test 2 (Barbraud & Weimerskirch 2012).

Models were compared using QAICc (Δ QAICc) and when two models had Δ QAICc <2, the most parsimonious was chosen (Lebreton *et al.* 1992).

4.2.4. Environmental covariates

4.2.4.1. Effect of the covariates on demographic traits

We examined the effect of covariates suspected to influence breeding success. Because giant petrels can be highly pelagic, but that also forage on land, we considered a large number of variables related to: (1) large scale climatic indices, (2) conditions in marine foraging areas (including fisheries), and (3) onshore prey and carrion availability. Relationships among covariates were examined by comparing their de-trended values using Pearson's correlation coefficient (Table A3). Each variable was scaled to $\bar{x} = 0$ and $\sigma = 1$ (Schielzeth 2010) before inclusion as a covariate in models where variation in breeding success were constrained to be a function of one or more environmental drivers. Subsequently, we examined the magnitude of these effects using analysis of deviance (ANODEV; Grosbois *et al.* 2008). The derived R^2 metrics expresses the percentage of temporal variation in breeding success that is explained by a covariate. We examined the influence of all explanatory variables on both the long-term and short-term variability using basic and de-trended models, respectively. The advantages of using de-trended models are that it allows spurious correlations to be detected, which may arise if both the trait and the covariate show unrelated long-term trends (Grosbois *et al.* 2008). However, by also fitting the basic models, we reduced the risk of committing Type II errors. The influence of a covariate was considered to be statistically significant if the 95% confidence interval of the slope excluded zero, and if the p-value from ANODEV test was ≤ 0.05 (Grosbois *et al.* 2008). For each covariate, monthly

values were averaged throughout the breeding season of each species, in order to provide a single annual value.

4.2.4.2. Mapping at-sea foraging areas

In order to insure our covariates were spatially representative of both giant petrels, we mapped at-sea distributions during the breeding period for each species using tracking data collected at Bird Island, South Georgia (Figure 4.2). Tracking involved 20 g or 30 g satellite-tags (platform terminal transmitter or PTT-100; Microwave Telemetry) or, on males only, 68 g GPS loggers (BGDL-II; Shizuoka University, Japan) deployed during incubation (n = 7 NGP and 19 SGP), brood-guard (n = 18 NGP and 24 SGP) or post-guard chick-rearing (n = 15 NGP and 20 SGP) in austral summer 2005/06 (British Antarctic Survey, unpublished data). Trip start and end times were determined from PTT and GPS locations, and the patterns of saltwater immersion from concurrent deployment of leg-mounted loggers (British Antarctic Survey, Cambridge, UK). Separate utilisation distributions (UDs) were generated using kernel analysis for each breeding stage and species, and weighted according to the duration of each stage to produce a combined breeding-season UD. Data on oceanographic covariates (SST, NPP and wind components) used in the capture-mark-recapture models for breeding were extracted from all of the 5 x 5° cells within the 50% UD as this was considered to reflect the conditions experienced in core areas, whereas data on total trawl and demersal longline fishing effort were extracted from the 90% UD, which was considered to better reflect the potential encounters with fishing vessels (Pardo *et al.* 2017). Large climatic indices are expressed as global indices, and data on krill biomass and sea ice concentration

(SIC) were obtained from fixed sampling areas. Descriptions of the environmental covariates, assumptions and sources are presented below.

4.2.4.3. Large scale climatic indices

The El Niño Southern Oscillation (ENSO) generates warm sea surface temperature (SST) anomalies in the equatorial Pacific that are propagated to the Southern Ocean via atmospheric and oceanographic teleconnections (Murphy *et al.* 2007a; Meredith *et al.* 2008). We utilized the Bivariate EnSo Timeseries (BEST index) as a proxy of ENSO variability (Smith & Sardeshmukh 2000). We included a 2 year lag to account for the average time that positive values of ENSO take to generate SST anomalies in the Atlantic sector of the Southern Ocean (Meredith *et al.* 2008). Positive SST anomalies have been correlated with poor foraging conditions in a range of top predators, and thus are expected to negatively affect reproductive output of giant petrels. The Southern Annual Mode (SAM) is a circumpolar atmospheric process that influences the Atlantic sector of the Southern Ocean almost immediately (~1 month lag), and is associated with warm SST anomalies, stronger circumpolar winds and changes in sea ice extent and concentration (Thompson & Wallace 2000; Murphy *et al.* 2007a). Therefore, SAM may have a positive influence both on foraging efficiency and food availability at sea. Monthly values for BEST index were obtained from the Climate Diagnostics Centre of NOAA (<http://www.cdc.noaa.gov/people/cathy.smith/best/>) (Figure 4.3a) and monthly values of SAM were obtained from the Climate Prediction Centre of NOAA (<http://www.cpc.ncep.noaa.gov/>) (Figure 4.3b).

4.2.4.4. Conditions in at-sea foraging areas

There was a negative correlation between sea surface temperature (SST) and sea ice concentration (SIC) for both giant petrel species (NGP, $r = -0.81$;

SGP, $r = -0.72$; $p < 0.01$); and a positive correlation between SST and net primary productivity (NPP), significant for SGP ($r = 0.59$, $p = 0.03$) and marginally significant for NGP ($r = 0.48$, $p = 0.08$). Thus SST was dropped, and SIC and NPP retained as a candidate variable since we were more interested in the oceanographic drivers than SST per se.

- *Net primary productivity (NPP)* - Primary production can be used as an indicator of ecosystem capacity for sustaining animal biomass, and is assumed to be directly related to food availability (Wakefield *et al.* 2014). Thus we predicted a positive influence of NPP on breeding success of giant petrels. NPP is considered to reflect the quantity of carbon dioxide fixed by phytoplankton during photosynthesis minus the amount released during respiration. Data were obtained from MODIS (<http://www.science.oregonstate.edu/ocean.productivity>) and Seawifs databases (<http://oceancolor.gsfc.nasa.gov/cms/data/seawifs>) (Figure 4.3c).
- *Sea ice concentration (SIC)* - Sea ice influences krill reproduction, growth and shelter, and also alters seabird foraging habitat availability by covering open water. Sea Ice concentration (SIC) may influence giant petrel reproduction negatively, by reducing the extent of suitable foraging areas, or positively by increasing krill biomass (Hunter 1983). Remotely-sensed data on SIC were obtained from a polygon encompassing the Antarctic Peninsula and Scotia Sea (http://nsidc.org/data/seaice_index/archives.html) (Figure 4.3d).
- *Wind speed* - Changes in airflow can directly influence the foraging efficiency of seabirds with potential consequences for reproduction and, ultimately, demography (Weimerskirch *et al.* 2012). Giant petrels have

high wing loadings (154 Nm^{-2} , Spear & Ainley 1997) and we expect a positive influence of wind speed on breeding success. Data on wind speed (m/s), including the meridional (Figure 3e) and zonal components (Figure 4.3f) were obtained from QuickSCAT and ASCAT datasets (<http://cersat.ifremer.fr/data/products/catalogue>).

- *Krill density* – Antarctic krill is a key component of Antarctic food webs, and in the Southern Ocean is positively correlated with reproductive performance of several marine vertebrates (Croxall *et al.* 1992; Forcada *et al.* 2005; Murphy *et al.* 2007a). We expect a similarly positive relationship with giant petrel reproduction because krill is an important dietary component (Hunter 1983, 1985). Here we included krill density (g m^{-2}) measured in the Western Core Box (WCB) survey area northwest of South Georgia (Fielding *et al.* 2014) (Figure 4.3g).
- *Fisheries* – Breeding giant petrels may obtain benefits from fisheries in the form of discarded fish and offal (Copello & Quintana 2009; Krüger *et al.* 2017a). We obtained information on the spatial-temporal distribution of fishing effort of south Atlantic longline (number of hooks) and trawl (hours trawled) fisheries from the Commonwealth Scientific and Industrial Research Organisation (CSIRO, Hobart); which constitutes the most comprehensive multi-fisheries data set currently available. There was overlap between demersal longline and trawl fisheries from Argentina and the Falklands with the 90% UD of NGP (Figure S4.1), whereas no fishery overlapped with the 90% UD of SGP during breeding (Figure 4.2). Therefore summed effort for trawl (Figure 4.3h) and demersal longline (Figure 4.3i) fisheries within the 90% UD, which are known to produce high

amount of discards, were included in models for NGP only (Zeller *et al.* 2018).

4.2.4.5. Carrion availability

At our study site, the most abundant sources of terrestrial food are Antarctic fur seals and macaroni penguins, available dead, moribund or through predation. Therefore we used the number of fur seal pups produced on a long-term study beach (British Antarctic Survey, unpublished data; Figure 4.3j), and fledged macaroni penguin chicks in a monitored colony (Horswill *et al.* 2014; Figure 4.3k), as proxies of terrestrial food availability in Bird Island. Because the impact of giant petrels is mostly on fledglings when they first go to sea (Horswill *et al.* 2014), total chicks fledged (number of pairs x breeding success) provides a better proxy of penguin availability than breeding numbers. We predict that both giant petrel species will be affected by the variation in carrion availability, but that the effects were likely to be stronger for NGP, since the peak coincides with their early chick-rearing period.

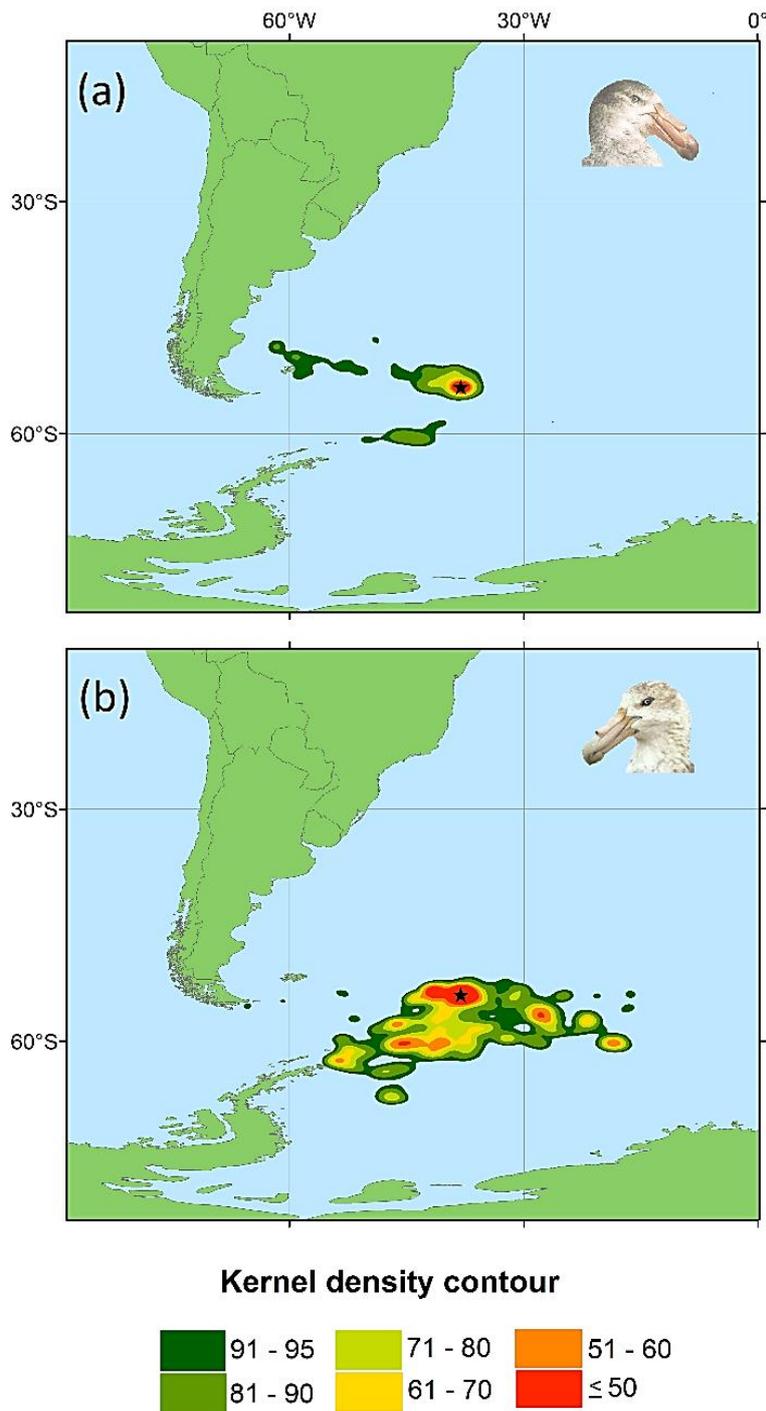


Figure 4.2. Utilization distributions (UDs; %) for (a) northern giant petrels ($n = 40$ adults) and (b) southern giant petrels ($n = 63$ adults) during the breeding period based on tracking data collected at Bird Island, South Georgia (black star). Data on oceanographic covariates used in the capture-mark-recapture models were extracted from all $5 \times 5^\circ$ cells that overlapped with the 50% UD.

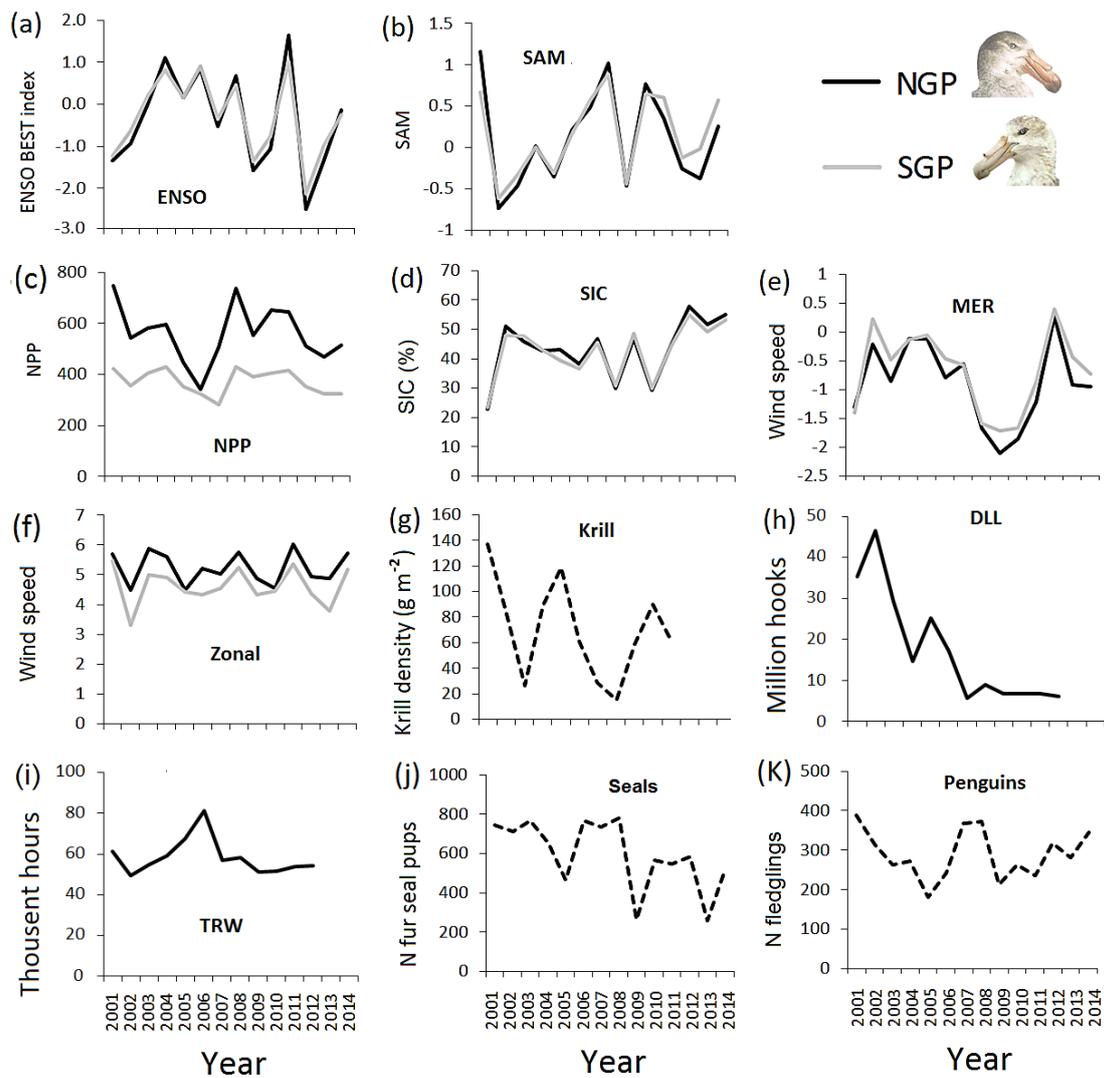


Figure 4.3. Annual variation in explanatory covariates during the breeding season. Data for northern giant petrel (NGP), southern giant petrel (SGP), or both species are represented by solid black, solid grey or dashed black lines, respectively. (a) El Niño Southern Oscillation - ENSO (BEST index) with 2 year lag; (b) Southern Annular Mode - SAM with 1 month lag; (c) net primary productivity - NPP and; (d) sea ice concentration - SIC; (e) meridional - MER and (f) zonal - ZON wind components; (g) krill density in the western core box, South Georgia (Fielding *et al.* 2014); (h) number of fur seal pups born in the long-term study beach (British Antarctic Survey, unpublished data); (i) number of fledged macaroni penguin chicks (Horswill *et al.* 2014); and (j) fishing effort of demersal longline - DLL and (k) trawl - TRW fisheries.

4.2.5. Population projections

To make predictions about changes in the population size of the two species we built a population projection matrix with six juvenile and one adult stage class, and assuming that all individuals recruit at 8 years old (Hunter 1984). For each species, we used mean values of the demographic parameters estimated in the CMR models, except for juvenile survival, which we obtained from Hunter (1984). Subsequently, based on number of breeding pairs observed in 2014 and assuming a stable stage distribution from our population model, we estimated the total population in 2015, including the number of juveniles and non-breeding adults. The matrix model was $N_{t+1} = \mathbf{A}N_t$, where N_t is a vector comprising the number of individuals in each age class at time t , and \mathbf{A} is the population projection matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & F \\ \phi_j & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_j & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_j & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_j & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_j & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_j & \phi_a \end{bmatrix}$$

Stages represented in \mathbf{A} refer to ϕ_j = juvenile survival, ϕ_a = adult survival and F = fecundity, defined as $F = P * R * \phi_a * f$, where P = breeding probability, R = breeding success and f = proportion of females in the population, assumed to be 0.5.

This demographic model allowed us to calculate the deterministic population growth rate (λ), and to estimate the sensitivity of λ to changes in survival and fecundity via elasticity analyses, which estimates the proportional change in the population growth rate for a proportional change in each vital rate. Subsequently, we investigated how changes in fecundity has influenced the

annual variation in the population growth rate over the study period, by calculating annual values of λ for considering the variation in breeding success while fixing survival as the average.

4.3. Results

4.3.1. Goodness of fit

The GOF based on Test 3 (Table 4.1), which is a sum of the χ^2 statistic and associated degrees of freedom (df) of tests 3.RS and 3.SM for each sex, indicated that the CJS model did not fit the data correctly for northern giant petrels (males: $\chi^2 = 68.5$, $df = 27$, $P < 0.001$; females: $\chi^2 = 58.0$, $df = 28$, $P < 0.001$) or southern giant petrels (males: $\chi^2 = 72.0$, $df = 26$, $P < 0.001$; females: $\chi^2 = 56.2$, $df = 26$, $P < 0.001$). However, Test 3 leads to reasonable global variance inflation factors ($\hat{c} < 3$) for the two species ($\hat{c} = 2.25$ and $\hat{c} = 2.46$, respectively; calculated as $\hat{c} = (\text{GOF}_{\text{males}} + \text{GOF}_{\text{females}}) / (\text{df}_{\text{males}} + \text{df}_{\text{females}})$). Therefore, we incorporated the global \hat{c} value into E-SURGE to perform model selection using the Akaike's Information Criterion corrected for overdispersion and small sample sizes (QAICc, Burnham & Anderson 2002).

4.3.2. Resighting probability

A set of candidate umbrella models differing in parameters for encounter probabilities were compared in order to obtain the best starting model in terms of parameter fit and identifiability. In the starting model, survival varied by time; breeding probability varied by state, and breeding success varied by time and state. According to the AICc scores, encounter probabilities of NGP and SGP varied over time and states (Table 4.2, Figure S3.3).

4.3.3. Adult annual survival and breeding probability

Average adult annual survival ($\pm 95\%$ CI) for NGP and SGP was 0.91 (0.90-0.92) and 0.92 (0.91-0.93), respectively, and average breeding probability ($\pm 95\%$ CI) for NGP and SGP was 0.92 (0.90-0.93) and 0.83 (0.80-0.87), respectively.

4.3.4. Breeding success

For both species, the time-dependent model without state dependency had stronger support than models that did include differences among states ($\Delta QAI Cc = 4.7$ and 28.5 for NGP and SGP respectively; Table 4.3, Table S4.2). Breeding success of NGP was higher and less variable than that of SGP (respective mean and range of 0.61, 0.37-0.92, and 0.48, 0.03-0.93). Annual breeding success of the two species was positively correlated ($R^2 = 0.34$, $P = 0.03$) and declined significantly during the study period, 2001-2014 (Table 4.3, Figure 4.4). Covariate effects are presented below, based on basic models, or on de-trended models when the covariate showed a clear trend over time (fur seal pup production – negative, and SIC - positive).

Northern giant petrel

NGP breeding success was positively correlated with the number of fur seal pups born each year (de-trended, $R^2 = 0.36$, $P_{ANO DEV} = 0.029$, slope = 0.30 ± 0.05) and the ENSO (basic, $R^2 = 0.27$, $P_{ANO DEV} = 0.058$, slope = 0.28 ± 0.04); together these explained 52 % of temporal variability in this trait ($P_{ANO DEV} = 0.003$; Table 4.3, Figure 4.4). Breeding success was not related to any of the other environmental variables.

Southern giant petrel

SGP breeding success was also positively correlated with the number of fur seal pups born each year (de-trended, $R^2 = 0.38$, $P_{\text{ANODEV}} = 0.024$, slope = 0.59 ± 0.08) and the ENSO (basic, $R^2 = 0.29$, $P_{\text{ANODEV}} = 0.046$, slope = 0.57 ± 0.07); together these explained 57 % of temporal variability in this trait ($P_{\text{ANODEV}} = 0.006$; Table 4.3, Figure 4.4). Breeding success was not significantly related to any other variable.

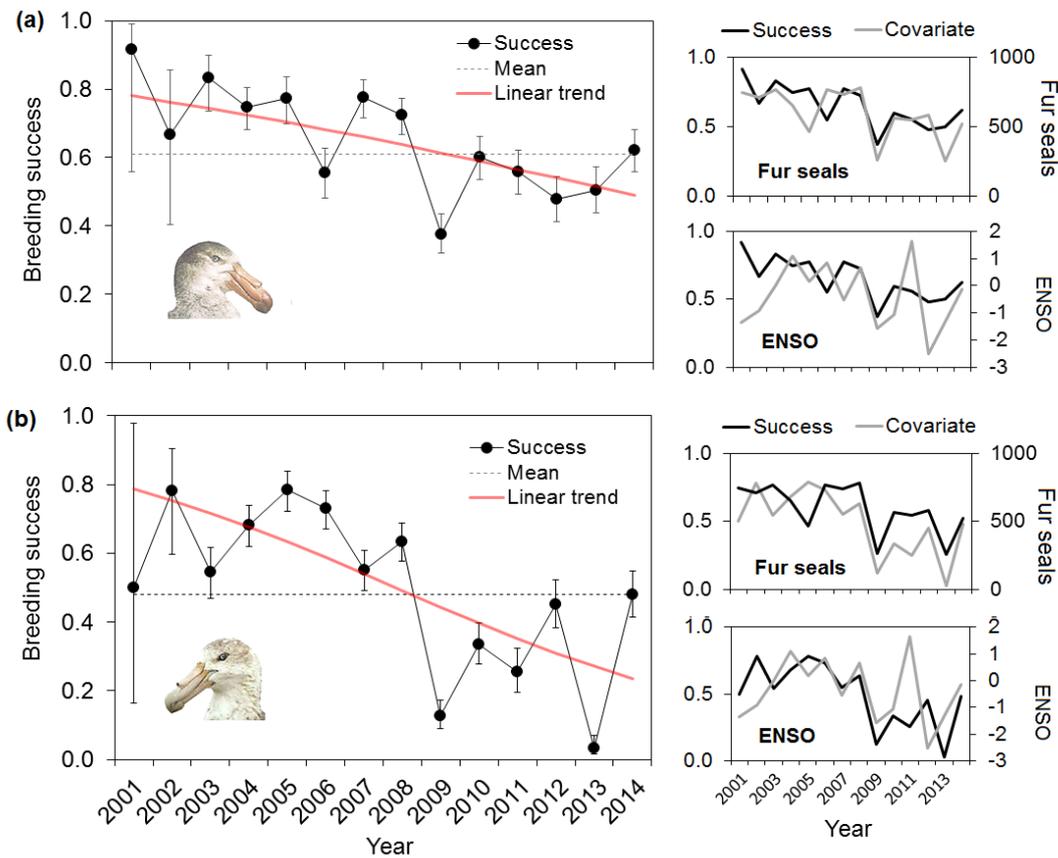


Figure 4.4. Annual variation in breeding success ($\pm 95\%$ CI) of (a) northern giant petrels, and (b) southern giant petrels at Bird Island (South Georgia), and relationship with the significant covariates (right panels); number of newly born Antarctic fur seal pups, 'Fur seals'; and El Niño Southern Oscillation, ENSO. Red and dashed black lines in the left panels refer to the linear trend and constant models, respectively.

4.3.5. Population growth rate

Northern giant petrel

The deterministic population growth rate (λ) for NGP based on the average survival and breeding success over the time series was 1.017, and the estimated total population in 2015 based on the stable stage distribution and the number of breeding pairs in 2014, was 1466 individuals, of which 48% were adults (Figure 4.5). The sensitivity and elasticity analyses showed that the growth rate is mainly sensitive to adult survival, which produced an 8.5 fold increase in lambda compared to juvenile survival and fecundity (Table 4.4). Population growth rate over the time series was predominantly positive or stable, varying from 0.989 to 1.046, with a tendency to stabilization from 2009 to 2014. There was a significant positive relationship ($R^2 = 0.480$, $P = 0.006$) between the population growth rate and the number of Antarctic fur seal pups born each year (Figure 4.5), but no significant relationships with the other environmental covariates.

Southern giant petrel

The deterministic population growth rate for SGP was 1.003, and the total estimated population in 2015 was 594 individuals, of which 55% were adults (Figure 5). The sensitivity and elasticity analyses showed that the growth rate is mainly sensitive to adult survival, which produced an 11-fold increase in lambda compared to juvenile survival or fecundity (Table 4.4). The population growth rate over our time series varied from 0.936 to 1.048, and showed a shift from predominantly positive values from 2001 to 2008 ($\lambda > 1$), to a negative phase from 2009 to 2014 (Figure 4.6). There was a significant positive relationship ($R^2 = 0.591$, $P = 0.001$) between population growth rate and the number fur seal pups (Figure 4.6). As with NGP, there were no significant

relationships between annual population growth rate of SGP and the other environmental covariates.

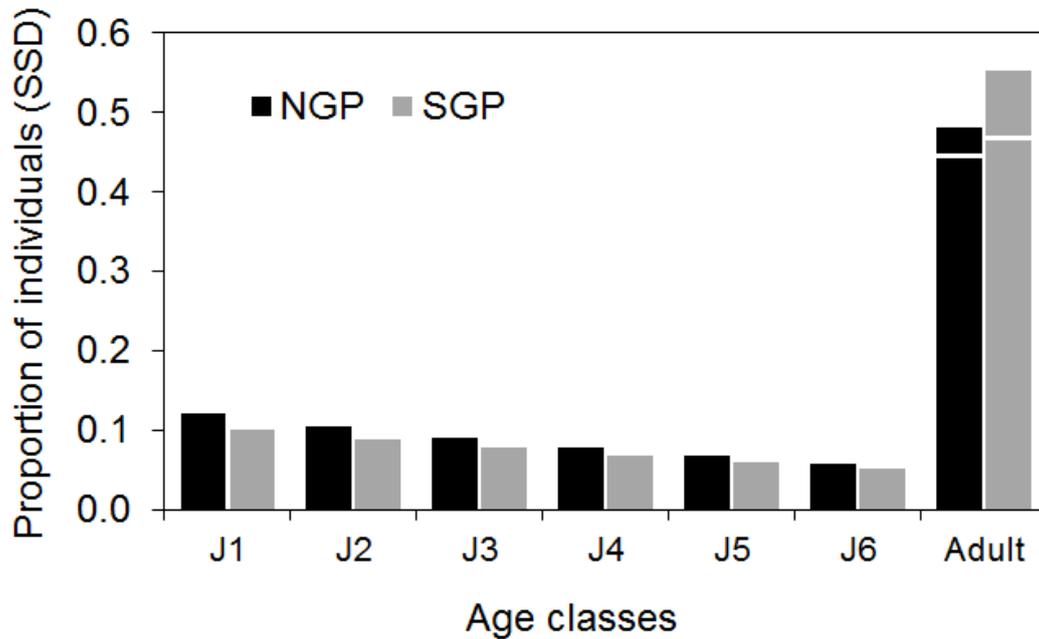


Figure 4.5. Proportion of individuals of the population in each age class, obtained from the stable stage distribution (SSD), for northern (NGP) and southern (SGP) giant petrels at Bird Island (South Georgia). J1-J6 refers to juvenile stages from one to 6 years old. The estimated population sizes in 2015 for northern and southern giant petrels were 1466 and 594 individuals, respectively. The top of the “Adult” columns, split by the white line, represent the mean proportion of non-breeding adults based on the estimated breeding probabilities for NGP (0.92) and SGP (0.83).

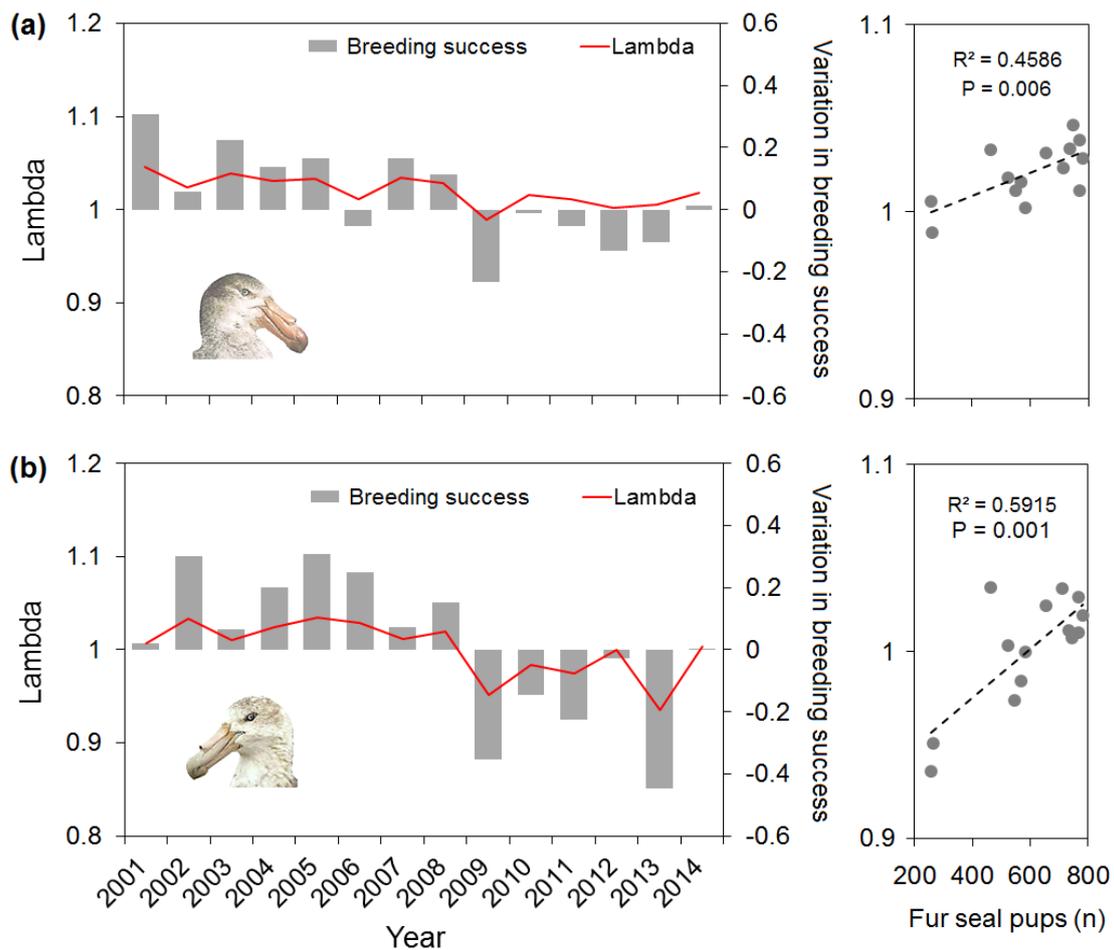


Figure 4.6. Annual variation in reproduction (breeding success, grey columns) relative to the mean, and in the deterministic population growth rate (red line). Variation in reproduction represents the proportional difference between the estimated value of the trait in a given year (from the time-dependent model) and the mean value over the study period (from the constant model), for both northern (a) and southern (b) giant petrels. The right-hand panels show the relationship between population growth rate and the number of Antarctic fur seal pups in the study beach, with the Pearson correlation statistic (R^2) and the corresponding P-value, and dashed lines shows the linear trend of the relationship.

4.4. Discussion

This is one of the few studies to examine the effects of environmental variability on sympatric, allochronic top predators. The correlation (*Pearson's r* = 0.59, $p = 0.03$) between annual variation in breeding success of NGP and SGP

suggests that similar drivers influence reproduction of both species. Possible ecological links underlying the relationships between reproduction and explanatory variables, including the role of allochrony in explaining the interspecific differences in responses to change are discussed below.

4.4.1. Prey and carrion availability on-shore

Annual fur seal pup production had a positive influence on breeding success of both species, but the effect was slightly weaker for NGP than SGP (slopes \pm SE of 0.30 ± 0.05 and 0.59 ± 0.05 , respectively). This is contrary to our initial predictions that NGP would be more strongly influenced by carrion availability based on their higher consumption of fur seals (Gonzalez-Solís *et al.* 2000). Hence, it appears that even though less carrion is consumed by SGP, its relative availability from year-to-year has a stronger influence on their breeding outcome. This situation would arise if in years of relatively low fur seal abundance, NGP can still feed their chicks with carrion but SGP have minimal access during a more critical period of their reproduction (late incubation to early chick-rearing), which has a greater impact on their breeding success. Not only are meals of fur seal carrion considerably more energy-dense ($\sim 10.7 \text{ kJ g}^{-1}$) than those of other prey types, such as krill ($\sim 4.4 \text{ kJ g}^{-1}$) or penguin ($\sim 7.6 \text{ kJ g}^{-1}$), but seal carrion is available closer to giant petrel nest sites and so require less foraging effort than feeding at sea (Hunter 1985; González-Solís *et al.* 2008). In some years, very little ($<1\%$ by mass) of the diet of SGP chicks is fur seal carrion (Hunter 1983), and under these conditions, they may be more likely to fail. That would explain the extremely poor breeding success of SGP in 2009 (0.14) and 2013 (0.03), which coincide with the poorest years for fur seal production (Figure 5).

Despite macaroni penguins representing a large proportion of the food of both giant petrel species during chick rearing (Hunter 1983, 1985), variations in the number of fledged penguins was not correlated with breeding success of NGP or SGP. This may be because of the superabundance of penguin carrion even in years with relatively low numbers - several million macaroni penguins breed on Bird and Willis islands (Croxall & Prince 2009), or possibly because most of the macaroni penguins that are consumed are adults killed or injured as they come ashore in heavy seas. The strong influence of fur seal carrion on giant petrels breeding success, despite the high availability of penguins, may also be related to a higher energetic cost of depredating fledglings and injured adult penguins near-shore (Horswill 2014), than that required to secure larger and more energy-dense meals of fur seal carrion (Hunter 1985).

4.4.2. Climatic oscillation and oceanographic conditions

Large scale climatic indices have either positive or negative effects on pinnipeds and seabirds breeding in the Southern Ocean. This creates contrasting responses among sympatric species or allopatric populations (Trathan *et al.* 2007; Barbraud *et al.* 2012; Descamps *et al.* 2016), but with more negative than positive relationships in the Atlantic sector of the Southern Ocean (Descamps *et al.* 2016). Climate-driven fluctuations in declines in krill availability have been linked to low breeding performance and population declines in a range of land-based predators (Reid & Croxall 2001; Bohec *et al.* 2008; Forcada & Hoffman 2014); however, we found no relationship between breeding success of giant petrels and krill density in the survey area to the northwest of the colony. This may be due to their ability to switch to a range of alternative prey, including fish, squid, other seabirds and carrion on land (Hunter 1983, 1985; Phillips *et al.* 2011),

or because we were unable to sample krill throughout the extensive foraging ranges of giant petrels during breeding (Figure 4.2; González-Solís *et al.* 2008).

The positive relationship between the breeding success of giant petrels and ENSO, of which the positive phases are linked to warmer sea temperatures (Murphy *et al.* 2007a), suggests that giant petrels breed better in warmer than colder years. This relationship may be explained by two non-mutually exclusive mechanisms. First, warm conditions may increase the extent of ice-free waters and thus of giant petrel foraging areas, as with some other Antarctic seabirds (Descamps *et al.* 2016). Second, warm conditions reduce body condition and survival of Antarctic fur seal pups and pre-fledging macaroni penguins (Beauplet *et al.* 2005; Trivelpiece *et al.* 2011; Horswill *et al.* 2016), and thus increase carrion availability. However, in the long term these positive effects may not last, because persistent warm anomalies can lead to broader ecosystem disruptions in Antarctic food webs, and potential collapse of krill stocks (Atkinson *et al.* 2004; Murphy *et al.* 2007a; Trathan *et al.* 2007). Long term reductions in krill abundance may also lead to population declines of Antarctic fur seal and macaroni penguins (Forcada *et al.* 2005; Trathan *et al.* 2007; Forcada & Hoffman 2014; Horswill *et al.* 2014), secondarily impacting giant petrels (Hunter 1983, 1985). This indirect effect may already be operating, as the decline of the Antarctic fur seal population from South Georgia, confirmed by our fur seal survey (Figure 3h), is associated with increasing frequency of climatic-driven reductions in krill availability (Forcada *et al.* 2005; Forcada & Hoffman 2014), with clear impacts on the breeding success of both giant petrels species (Figure 4.4).

Both giant petrel species show high foraging versatility (Hunter 1983, 1985; Gonzalez-Solís *et al.* 2000), and in the 1980s (when the NGP population

was much smaller) were estimated to consume roughly 690,000 penguins and 580,000 other seabirds at South Georgia each year (Hunter 1985). Hence, persistent reductions in availability of krill or fur seal pups can increase predation pressure of giant petrels on penguins and other seabird prey (Hunter 1985; Dilley *et al.* 2013; Horswill *et al.* 2014), similar to sites in the northern hemisphere where the consumption of smaller seabirds by predatory seabirds increased as food availability at sea decreased (Phillips, Thompson & Hamer 1999; Stenhouse & Montevecchi 1999; Votier *et al.* 2004).

4.4.3. Fisheries

Availability of fisheries discards (including offal) can have a positive effect on populations of scavenging seabirds (Thompson & Riddy 1995; Votier *et al.* 2004; Bugoni *et al.* 2010), including SGP from the Antarctic Peninsula (Krüger *et al.* 2017a). Although there was no evidence of this for giant petrels at Bird Island based on our detrended model, without detrending, there was a positive but marginally non-significant influence of demersal longline on the long-term breeding success of NGP ($R^2 = 0.25$, $P_{\text{ANODEV}} = 0.07$; slope = 0.56 ± 0.09). Although giant petrels at South Georgia have limited access to fisheries discards during early breeding (Hunter 1983, 1985), discards are presumably more important later in the season when they forage primarily at sea. This would explain why a general reduction in fishing effort (and hence discard availability) over time (Figure 4.3g) matches the negative trend in breeding success of NGP. The lack of overlap between SGPs tracked during breeding and fisheries at the Patagonian Shelf is supported by the sightings behind demersal longline vessels around the Falklands only of banded NGPs and not SGPs from our study population (Otley *et al.* 2007). Indeed, the tracked SGPs overlapped only with the

icefish and krill fisheries close to South Georgia, which provide negligible discards (Croxall & Nicol 2004).

4.4.4. Population growth rate

Adult survival was the most sensitive parameter influencing population growth rate in both giant petrel species, which was expected because their slow reproductive rates and high longevity, like other large marine vertebrates (Lewison *et al.* 2004). However, the demographic data and models for our study system indicate that survival of both species was very similar (NGP= 0.91, SGP= 0.92) and close to the average of 25 annual-breeding Procellariiforms (average= 0.91, min= 0.72, max= 0.97; Schreiber & Burger 2002). The annual variation in the population growth rate of both giant petrels was therefore mainly driven by differences in breeding success, which was strongly related to variations in fur seal carrion availability. The period of relatively stable NGP and declining SGP numbers from 2009 to 2014 coincided with the years with the lowest fur seal pup production – 23% lower than the average over our time series. Therefore, due to allochrony, the mismatch between SGP chick-rearing and the peak of carrion availability made them more vulnerable to annual variation in fur seal productivity than NGP, contributing to their lower and more variable breeding success and to the divergent population trajectories. Furthermore, the probability of skipping breeding was twice as high in SGP (0.17) than in NGP (0.08), also contributing to overall lower fecundity of SGP and their lower population growth rate.

4.5. Conclusions

The differences in population growth rate between NGP ($\lambda = 1.017$) and SGP ($\lambda = 1.003$) seemed to be strongly influenced by lower breeding success of SGP, as both species have similar, and high annual survival. These differences in fecundity were partly related to the privileged access of NGP to fur seal carrion due to allochrony, providing empirical evidence for the relationship between NGP population growth and the recovery of Antarctic fur seals at South Georgia suggested in previous studies. The combined effect of declines in krill availability and fur seal productivity may also have increased predation pressure of giant petrels on penguins and other seabird prey.

Table 4.1. Results of goodness of fit chi-square statistics (χ^2), and associated degrees of freedom (df) and *p-value*, for CMR models.

	Male			Female		
	χ^2	df	p-value	χ^2	df	p-value
Northern giant petrel						
Test 3.SR	17.5	13	0.179	13.1	13	0.436
Test 3.SM	48.3	14	<0.001	44.9	15	<0.001
Sum Test 3	65.8	27	<0.001	58.0	28	<0.001
Southern giant petrel						
Test 3.SR	21.1	13	0.07	20.4	12	0.06
Test 3.SM	50.9	13	<0.001	35.8	14	0.001
Sum Test 3	72.0	26	<0.001	56.2	26	<0.001

Table 4.2. Summary of model selection to estimate resighting probabilities of northern and southern giant petrels, K is the number of parameters in the model.

Model	k	Deviance	QAICc	Δ QAICc
Northern giant petrel				
Time	43	18894.9	8484.3	0.0
Time+state	45	18889.8	8486.1	1.8
Time*state	56	18861.4	8495.8	11.5
State	31	19160.7	8578.1	93.8
Constant	30	19180.0	8584.7	100.4
Southern giant petrel				
Time	43	10638.5	4411.7	0.0
State+time	45	10646.4	4419.0	7.3
State*time	56	10631.5	4435.6	23.9
Constant	30	10827.1	4461.8	50.1
State	31	11269.2	4643.6	231.9

Table 4.3. Model selection estimating breeding success of northern and southern giant petrels and the effects of candidate explanatory covariates. Survival and breeding probability were maintained constant in all models. Covariate models are shown along with time-dependent, constant and linear trend models. The slope \pm SE is shown only for the covariates that had a significant effect (ANODEV $p \leq 0.05$) on the temporal variation in breeding success (in bold). Abbreviations in model definition as follow. For previous state (inside parenthesis), “s” and “f” for successful and failed breeder, and “ps” and “pf” for post successful and post failed breeder, respectively. For covariates, ENSO, El Niño Southern Oscillation; SAM, Southern Annular Mode; PEN, number of macaroni penguin fledged; and seal, number of newly born Antarctic fur seal pups.

Model definition	K	Deviance	QAICc	Δ QAICc Overall	Δ QAICc Trait	P_{ANODEV}	R^2 (%)	Slope \pm SE
Northern giant petrel								
Time	30	18921.7	8469.9	0.0	0.0			
(s,ps f pf)*time	45	18864.2	8474.7	4.7	4.7			
(s ps, f pf)*time	46	18862.7	8476.1	6.1	6.1			
(s f, ps pf)*time	56	18861.4	8495.8	25.9	25.9			
Linear	18	19203.9	8571.1	101.2	101.2	0.034	32	-0.42 \pm 0.05
Constant (intercept)	17	19335.5	8627.7	157.7	157.7			
<u>Basic covariate models</u>								
Seal+ENSO	19	19118.6	8535.3	65.3	0.0	0.003	52	
Seal	18	19135.1	8540.6	70.7	5.3	0.005	49	0.39 \pm 0.04
ENSO	18	19225.0	8580.5	110.6	45.3	0.056	27	0.28 \pm 0.04
<u>De-trended covariate models</u>								
PEN+seal+ENSO+SAM	22	19035.8	8504.5	34.6	0.0	0.090	60	
PEN+seal+SAM	21	19059.3	8513.0	43.0	8.5	0.079	51	
PEN+seal	20	19065.4	8513.6	43.7	9.1	0.034	49	
PEN	19	19070.6	8513.9	44.0	9.4	0.008	48	0.39 \pm 0.05
Seal	19	19101.2	8527.5	57.6	23.0	0.029	36	0.30 \pm 0.05
SAM	19	19114.4	8533.4	63.5	28.9	0.045	32	0.30 \pm 0.05
Southern giant petrel								
Time	30	10692.6	4407.2	0.0	0.0			
(s f,ps pf)*time	56	10631.5	4435.6	28.5	28.5			
(s ps,f pf)*time	45	10738.4	4456.4	49.3	49.3			
(s, f ps pf)*time	45	10744.6	4459.0	51.8	51.8			
Linear	18	11081.4	4540.8	133.7	133.7	0.012	40	-0.80 \pm 0.08
Constant (intercept)	17	11338.1	4643.2	236.0	236.0			
<u>Basic covariate models</u>								
Seal+ENSO	19	10971.1	4498.0	90.9	25.5	0.006	57	
Seal	18	10991.2	4504.2	97.0	31.7	0.003	54	0.77 \pm 0.07
ENSO	18	11150.0	4568.7	161.6	96.2	0.046	29	0.57 \pm 0.07
<u>De-trended covariate models</u>								
Seal	19	10932.5	4482.3	75.2	0.0	0.024	38	0.59 \pm 0.08

**CHAPTER 5. Age-specific variation in demographic traits of
northern and southern giant petrels**



In preparation for submission to Oikos

ABSTRACT

Age and experience affect key life-history traits, influencing demographic and evolutionary processes in a variety of ways. However, few studies have investigated the effects of phenological mismatch on ageing patterns, and the interaction between age and experience shaping early adulthood performance. Here, we test for the effects of age and experience on the survival and reproduction of two allochronic, congeneric, long-lived seabirds presenting divergent population trajectories, the northern (NGP, *Macronectes halli*) and southern giant petrel (SGP, *M. giganteus*) at South Georgia, Antarctic. Breeding success of both giant petrel species improved markedly with age until around 20 years, driven by within-individual factors, but SGP showed lower breeding success and earlier reproductive senescence. Pre-fledging body mass showed a broadly quadratic relationship with parental age, suggesting that the age-specific pattern in breeding success was partially related to variation in foraging performance. In early adulthood, inexperienced individuals (first-time breeders) had lower breeding success and subsequent survival. Furthermore, we showed that pre-fledging body mass increased rapidly with parental age among first-time breeders in both species, but breeding success did not, disentangling the effects of foraging performance and breeding experience *per se* on early adulthood breeding success. Our results suggest that, due to allochrony, NGP rear their chicks under higher availability of seasonally limited, high-calorific, land-based food (pinniped and penguin carrion), which may delay its reproductive senescence by increasing chick survival and, potentially, by improving adulthood performance due to better neonatal nutrition. These findings provide empirical evidence shedding new light on how phenological mismatch can influence reproductive senescence.

5.1. Introduction

Age influences many life-history traits, affecting demographic and evolutionary processes in a variety of ways; hence, the study of age-effects on demography is a major field in population ecology (Caswell 2001; Ricklefs 2010a). Age-related variation in fitness traits (survival and reproduction), are well documented in birds and mammals, with performance increasing in early adulthood followed by a plateau and subsequent decline in later life (Caswell 2001; Froy *et al.* 2017; Lemaitre & Gaillard 2017). This pattern is usually related to within-individual change, for instance the advantages of increased experience through early adulthood, the higher foraging and reproductive ability of middle-age individuals, and physiological senescence in later life (Ricklefs 2010b; Desprez *et al.* 2014; Froy *et al.* 2017).

The evolutionary mechanism of senescence, or aging, which is the decline of physiological functions with age is poorly understood (Dev 2015), and it is unlikely to be adaptive since it impairs reproductive performance (Kirkwood 1977). The mutation-accumulation theory (Medawar 1952) suggests that the strength of natural selection decreases with age, such that more deleterious mutations would accumulate. This hypothesis is aligned with the antagonistic-pleiotropy theory (Williams 1957), which involves positive selection for genes conferring short-term effects on survival or reproduction in early adulthood, despite negative effects on health and fitness later in life. Alternatively, the disposable soma theory suggests that longevity is determined through “longevity assurance mechanisms”, which provide optimal trade-off between reproduction and somatic maintenance for an organism’s ecological context (Kirkwood & Holliday 1979). Despite the fact that there is little consensus on which of these

three, non-mutually exclusive theories is more is more important, empirical support for disposable soma theory and antagonistic pleiotropy as evolutionary mechanisms of senescence is much stronger than for mutation accumulation (Nussey *et al.* 2013).

In terms of reproduction, performance could also improve with age because of among-individual differences, such as the selective disappearance through mortality of low quality individuals that bred poorly, or selective appearance in the population of individuals that invested less in reproduction and so survived longer (Aubry *et al.* 2009; Zhang *et al.* 2015). Furthermore, environmental conditions may influence aging rates by affecting the cost of reproduction (Proffitt *et al.* 2007; Lemaître *et al.* 2013; Lemaître & Gaillard 2017) and neonatal nutrition, which is known to affect adulthood performance (Blount *et al.* 2003; Van De Pol *et al.* 2006; Nussey *et al.* 2007). In early adulthood, age-effects on breeding success can vary in more complex ways. For instance, among first-time breeders, performance may increase with age, as older individuals are more experienced in terms of foraging (Martin 1995; Lemaître & Gaillard 2017), or decrease, indicating that the birds that recruit late are low-quality phenotypes (Aubry *et al.* 2009; Nussey *et al.* 2013; Fay *et al.* 2016). Although survival and reproduction are strongly influenced by extrinsic factors, like weather and food availability (Forcada *et al.* 2005; Milligan, Holt & Lloyd 2009; Frederiksen *et al.* 2014), and synchronising life-cycle events with ideal conditions is critical for optimal performance (Miller-rushing *et al.* 2010; Reed *et al.* 2013b; Youngflesh *et al.* 2017), we have a poor understanding of how phenological mismatch can affect age-related variation in vital rates. This is particularly important in the face of rapid changes in climate that has caused shifts in

phenology of a range of taxa (Parmesan 2006; Visser 2008), with potentially major demography implications (Miller-rushing *et al.* 2010).

Recent evidence suggest that environmental conditions (e.g. food availability) can influence aging patterns, with faster senescence under lower environment quality (van de Pol & Verhulst 2006; Lemaître *et al.* 2013; Oro *et al.* 2014). However, how changes in phenology can affect aging patterns via mismatch with optimal environmental conditions is poorly understood. Thus, comparisons among sympatric species that exploit similar ecological niches, but differ in their phenology (i.e., allochronic species), may provide useful insights into the role of phenological mismatch and environmental conditions in reproductive senescence. In this context, the northern (NGP, *Macronectes halli*) and southern giant petrel (SGP, *M. giganteus*) are a valuable species-pair for studying the role of phenological mismatch on ageing patterns. They have wide marine distributions in the Southern Ocean and breed in sympatry on sub-Antarctic islands, but NGP breed around six weeks earlier than SGP (Marchant & Higgins 1990). They forage on Antarctic krill *Euphausia superba* and other marine prey (from the ice edge to the sub-tropics), and also extensively on land, mostly scavenging dead and moribund penguins and pinnipeds (Hunter 1984; Patterson *et al.* 2008). At South Georgia, the only site in the Atlantic where both species breed in sympatry (Hunter 1984), because NGP breed earlier, they are better able to exploit Antarctic fur seal (*Arctocephalus gazella*) carrion (pups and dead bulls), which peaks during early to mid chick-rearing of NGP, when SGP are still incubating (Hunter 1984; Gonzalez-Solís *et al.* 2000). However, late in the breeding season once carrion availability is much reduced, both species feed almost entirely at sea, although SGP still perform longer foraging trips (González-Solís, Croxall & Afanasyev 2008). Hence, because of allochrony, both species

face different environmental conditions according to reproductive stage, which can result in interspecific differences in reproductive costs (Hunter 1984; González-Solís *et al.* 2008). This is likely to affect patterns of reproductive ageing, with potential demographic implications (Van De Pol *et al.* 2006; Miller-rushing *et al.* 2010; Lemaitre & Gaillard 2017). Indeed, the number of NGP increased over the same period as the population of Antarctic fur seals recovered at South Georgia (Payne 1977; Boyd 1993; Forcada & Hoffman 2014), whereas the SGP population was stable or declining (Hunter 1985; González-Solís *et al.* 2000).

Here, we conducted a longitudinal study to examine reproductive ageing patterns in these two allochronic, sibling species, which show divergent population trajectories, and also compared survival and age-specific variation in reproductive traits between inexperienced and experienced breeders in early adulthood. We predict, as observed in most long-lived vertebrates, that performance of both species will improve during early adult life, but will then decrease, associated with senescence. Further, we predict that NGP will exhibit reproductive senescence later in life, assuming that their higher access to carrion during chick rearing may attenuate the constraints of environmental variability on their late-life reproductive success. In early adulthood, survival and reproductive performance of inexperienced breeders is predicted to be lower than that of experienced breeders, because they have more limited foraging and breeding skills, and potentially incur a higher cost of reproduction (i.e. reduced subsequent survivorship). Given the interactive effects of age and experience in early adulthood, breeding performance may increase with age, suggesting within-individual improvement, or decrease with age, revealing the effects of individual heterogeneity (later recruitment of lower quality individuals).

5.2. Methods

5.2.1. Species, study site and data collection

We studied NGPs and SGPs on Bird Island (54° 00' S, 38° 03' W), South Georgia. Giant petrels lay a single egg without replacement in early October (NGP), or mid-November (SGP). Incubation lasts 60 days and chicks fledge 110-120 days after hatching. Therefore, the breeding seasons of NGP and SGP encompass October-March and November-May, respectively.

In total, c.350 pairs of NGP and c. 150 pairs of SGPs in a well-demarcated study area were monitored annually during austral summers 2000/01 – 2015/16 (hereafter, 2001 refers to the breeding season in austral summer 2000/01 etc.). For details of the monitoring protocol, see Brown *et al.* (2015). Briefly, all breeding birds were fitted with an individually identifiable metal ring, and a coloured plastic ring engraved with a unique four-digit alpha-numeric code, and sexed from bill length (González-Solís *et al.* 2000). All nests were staked and mapped using handheld Global Positioning System (GPS) loggers. Active nests were checked every 4-5 days until both partners were identified, and visited weekly for the remainder of the breeding season until the outcome of the reproductive attempt was known. Chicks of NGP and SGP were ringed, weighed and bill length measured shortly before fledging (on 2-5 March and 10-13 April, respectively). Bill length measurements from chicks with fully grown bills (> 80 days, Hunter 1984) were used for sexing; birds were considered to be males if bill length was >92 cm for NGP (González-Solís & Gonzalez-solis 2004) and >90 cm for SGP (González-Solís & Croxall 2006). From the breeding season of 2006 onwards, active nests were checked daily during incubation in order to obtain accurate laying dates. Many of the birds in the long-term study area were of known age,

having been ringed as chicks in the early 1980s by Hunter (1984), and subsequently.

5.2.2. Age-related variation in reproductive traits

We investigated the effect of age on the following breeding traits: breeding success (probability of fledging from a laid egg, binary trait: 0= failed or 1= successful); laying date (first egg dates from 2006 onwards were 17 and 29 September for NGP and SGP, respectively), and pre-fledging body mass (g) of chicks with 80-108 days old for both species (average \pm sd, NGP: 93.8 ± 4.8 , SGP: 91.5 ± 3.9).

Age-effects on breeding success at the population level were modelled using data from 854 breeding attempts by 186 (86 male, 96 female, 4 undetermined) known-age NGP, and 487 breeding attempts by 136 (70 male, 62 female, 4 undetermined) known-age SGP. Effects on laying date and pre-fledging body mass were modelled in separate analyses, since laying dates were not recorded before 2006, and body mass was unavailable for some chicks. To account for sexual size-dimorphism and chicks weighted with different ages, a term for chick sex and another for age were included in models of pre-fledging mass.

Subsequently, we compared age-specific variation in these reproductive traits between inexperienced (birds breeding for the first time) and experienced breeders (birds that had bred at least once) during early adulthood (7-12 years old). The interaction between age and breeding experience in early adulthood was modelled using a reduced dataset including only breeding seasons from 2006 onwards. Because nest monitoring became comprehensive in the study

area from 2003, any bird recorded as a first breeder in 2006 that had actually bred before must have skipped the previous three seasons, which would be uncommon for a near-annual breeder. In addition, we excluded individuals not recorded breeding until 12+ years (Figure S5.1). Thus, by removing the first years of data, as well as the very old individuals recorded as first-time breeders, we reduced the risk of misclassifying experienced birds as inexperienced individuals.

5.2.2.1. Statistical analysis

The relationships between age and reproductive traits were modelled using Generalized Linear Mixed Models (GLMMs). Where the number of samples per age class was <10, age classes were collapsed to avoid lack of statistical power and biased results. Breeding success was modelled as a binary trait using a binomial error distribution and logit link function. A Gaussian error distribution was used to model laying date and pre-fledging mass (Zuur *et al.* 2009). All models included individual as a random effect to account for the non-independence of observations, and year as a fixed effect, to account for annual variation in environmental conditions. Models with fixed effects were compared against the null model (intercept and random effects only) using Akaike Information Criterion (AIC), where the best model is taken to be that with the lowest AIC value. AIC differences of < 2 are not considered to be meaningfully different (Zuur *et al.* 2009). All analyses were performed using the lme4 (Bates *et al.* 2014) package in R (version 2.14.0).

5.2.3. Comparative survival between inexperienced and experienced breeders in early adulthood

5.2.3.1. The general model

In order to investigate differences in the survival and breeding probabilities of inexperienced and experienced birds, we built and fitted multi-event Capture-Mark-Recapture models using E-SURGE v.1.9.0 (Choquet *et al.* 2009). In a multi-event modelling framework (Pradel 2005), events observed in the field provide information on the underlying biological (including non-observable) states of marked individuals. Our model was based on the observation of six possible events; “0” (not encountered), “1” (marked as chick), “2” (breeding by first the time - successful), “3” (breeding by the first time - failed), “4” (breeding by the second or subsequent times – successful) and “5” (breeding by the second or subsequent times – failed). From these observations we built the model shown in Figure 5.1. Seven states were defined: five observable states corresponding to chick (C), inexperienced successful (IS) and inexperienced failed breeders (IF), experienced successful (ES) and experienced failed breeders (EF); one unobservable state, corresponding to post-breeder (PB); and death (Figure 5.1). This modelling approach allows the simultaneous estimation of resighting, survival and breeding probabilities, as well as of breeding success in early adulthood (7-12 years old), accounting for differences between inexperienced and experienced breeders. Breeding success estimates were compared with the results from the GLMMs. This CMR analysis was based on encounter histories of 2,368 and 877 NGP and SGP, respectively, marked as chicks from the 2000 to 2015 breeding seasons (Table S5.1). Given the high longevity and late age at recruitment of giant petrels, and the relatively short duration of the long-term monitoring study, age-specific survival or juvenile survival could be estimated. As the study was conducted in a well demarcated area, and over the 16 year study period <1% of the total monitored population was observed breeding in adjacent areas (which are checked each year); emigration was not considered.

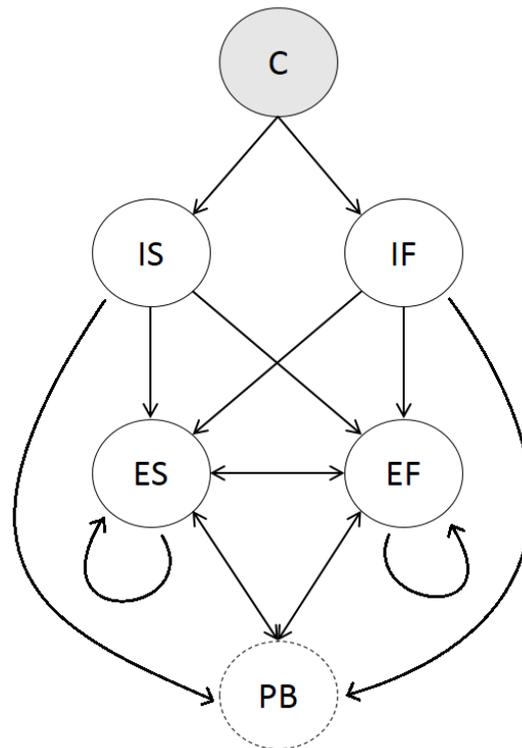


Figure 5.1. Life-cycle used to parameterise the multi-event model with seven states: C = Chick, IS = Inexperienced successful breeder, IF = Experienced failed breeder, ES = Experienced successful breeder, EF = Experienced failed breeder and PB = Unobservable post-breeder state. Arrows show the possible transitions among states. The state `dead` is not presented in the figure as it can be reached from any other state.

5.2.3.2. Model selection and goodness-of-fit

There is currently no test available to assess goodness-of-fit (GOF) for multi-event models. To check whether data met the basic assumptions underlying CMR models, a GOF test for the Cormack-Jolly-Seber model (CJS) was applied to a simplified (single state) version of the encounter histories after suppressing the first encounter (birds marked as chicks), while also checking the effect of

experience (experienced vs inexperienced) on resighting heterogeneity in U-CARE 2.2 (Pradel *et al.* 2005; Choquet *et al.* 2009). Under the CJS assumptions, this comprised two tests and their sub-components: Test 2 (sub-components 2.CT + 2.CI) examines heterogeneity in recapture probabilities and trap-dependence effects; and Test 3 (sub-components 3.SR + 3.Sm) checks the heterogeneity in survival probabilities and transience effects. As our multi-event model design accounts for differences in breeding probabilities according to previous breeding states, it automatically corrects for trap-dependence, which are common in seabirds that often defer (skip) breeding (Pardo *et al.* 2017). Thus GOF can be conducted excluding Test 2 (Barbraud & Weimerskirch 2012).

Models were compared using QAICc (Δ QAICc) and when two models had Δ QAICc <2 the most parsimonious was chosen (Lebreton *et al.* 1992). We tried different structures of dependence for resighting probabilities, including time, breeding performance in the previous season, and experience; and compared them to obtain the best initial model. We then selected the best effect model for encounter probability, then breeding success and, subsequently, survival. In our initial model, survival varied with experience and breeding success in the previous season, with experience-dependence in breeding probabilities and experience- and time-dependence in breeding success. We then compared models emphasising experience (IS/IF vs ES/EF) or success in the previous season (IS/ES vs IF/IS), always differentiating the “chick” state (first encounter).

5.3. Results

5.3.1. Age-related variation in breeding traits

Mean breeding success of NGP (0.58, 0.56-0.61) was significantly higher than that of SGP (0.39, 0.3-0.43; $Z= 6.82$, $P < 0.01$). Breeding success of both species improved through early life to around 20 years, followed by a plateau in NGP, and a decline in SGP; SGP also showed higher variation around this pattern (Figure 5.2). These observed trends were supported by the model selection, where the relationship between breeding success and age was better explained by a polynomial ($\Delta AIC: 3.5$) function in NGP, with a plateau after the peak, and a quadratic function ($\Delta AIC: 2.2$) in SGP, with a marked decline after the peak (Table S5.2).

Mean pre-fledging mass varied significantly with sex but not between species. After accounting for sexual size dimorphism and chick age, there was a significant non-linear relationship between age and pre-fledging body mass in NGP ($\Delta AIC: 14.0$), characterized by improvement through early life to around 20 years old, followed by a gradual decline. Significant patterns of age-related variation in pre-fledging mass were not detected in SGP (Table S2. Figure 5.2).

Laying date of NGP varied slightly but significantly as a non-linear (polynomial) function of age ($\Delta AIC: 4.2$); laying dates became later with age during early adult life (from 7 to 20 years old), after which they reached a plateau. There was a significant linear relationship between age and laying dates of SGP ($\Delta AIC: 17.7$), which was not improved by quadratic or polynomial terms, with laying dates slightly delayed as age increased (Figure 5.2). In both giant petrel

species, the highest variation in laying dates was observed among birds ≤ 15 years old.

5.3.2. Interactive effects of age and experience on breeding traits in early adulthood

In early adulthood in NGP (7-12 years old), experience explained variation in breeding success better than age alone ($\Delta AIC = 4.5$); however, the interactive effect of age and experience received similar support (Table S5.2). The breeding success of inexperienced breeders varied little with age and was significantly lower (mean, 95% CI = 0.26, 0.18-0.35; $Z = 2.65$, $P < 0.01$) than that of experienced birds of the same age (0.43, 0.35-0.51), except that experienced birds of 9 years old had relatively low breeding success (Figure 5.2). For SGPs, the models with age or experience terms better explained the variation in breeding success and received similar support (Table S5.2). The breeding success of inexperienced birds decreased from 7 to 9 years old and then improved, and was significantly lower (0.20, 0.12-0.28; $Z = 1.77$, $P = 0.04$) than that of experienced breeders of the same age (0.30, 0.21-0.39), apart from 10 year old birds (Figure 5.2).

The significantly lower breeding success of new recruits compared to experienced breeders is aligned with the results from the CMR analysis. The models with additive effects of time and experience were well-supported for both giant petrel species ($\Delta QAICc$ NGP = 7.1, SGP = 18.3), with lower breeding success in first breeders (Table S5.3, Figure 5.3, Figure S5.2).

For NGPs, the models with age or the interaction between age and experience better explained the variation in pre-fledging body mass, and received

similar support. Variation in pre-fledging mass of SGP was better explained by experience, age or their interaction (Table S5.2). Pre-fledging mass improved rapidly with parental age in first-time breeders of both giant petrel species, and slower in experienced NGPs, whereas no age-effect was detected in experienced SGPs (Figure 5.2).

According to the model selection, laying dates of NGP were better explained by experience, or additive effects of experience and age; however, there was no clear trend. For SGP, the null model (intercept only) was the best supported, indicating no significant age- or experience-related variation in laying dates (Figure 5.2, Table S5.2).

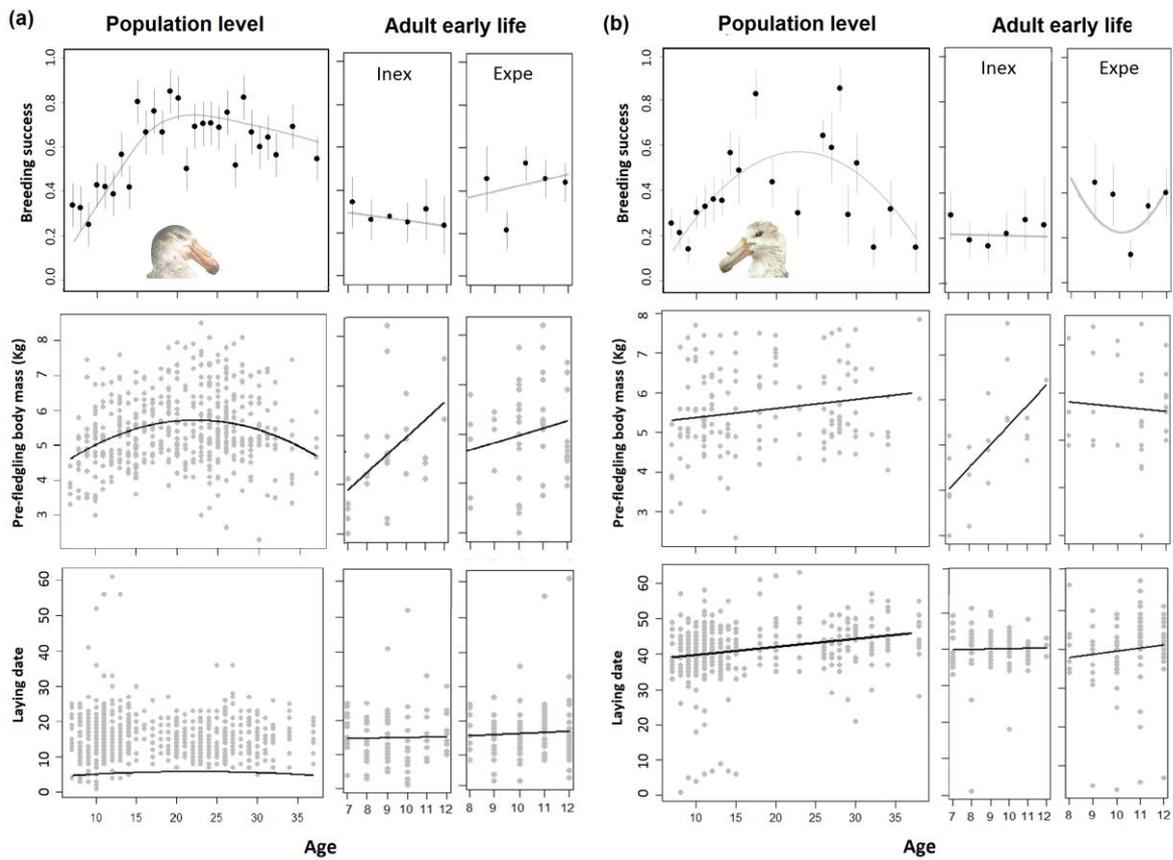


Figure 5.2. Age-specific variation in breeding success (top), pre-fledging mass of chicks, (middle) and laying date (bottom) at the population level, and between inexperienced and experienced breeders in early adulthood in northern and southern giant petrels. The dark solid circles show the average breeding success by age, and the associated standard error. The lines represents the predicted values for each trait from the linear, quadratic or polynomial model, according to the best supported model for each trait.

5.3.3. Experience-related variation in early adult survival

Goodness of fit and model selection - The GOF based on Test 3 (Table 5.1), which is a sum of the χ^2 statistic and associated degrees of freedom (df) of tests 3.RS and 3.SM, indicated that the CJS model fitted the data well for both NGP (males: $\chi^2 = 12.8$, df = 10, $P \geq 0.17$) and SGP (males: $\chi^2 = 10.5$, df = 13, $P \geq 0.22$).

Encounter probability - The model with encounter probability varying by experience and time was the best supported model for both NGP ($\Delta\text{QAICc} = 16.6$) and SGP ($\Delta\text{QAICc} = 18.3$); thus, experience- and time-dependent encounter probabilities were used in subsequent models for both species (Table 5.2). Annual encounter probability varied between 0.70 - 0.94 in the NGP and 0.37 - 0.73 in the SGP (Figure S5.2).

Survival - The experience-dependent survival model was the best supported for NGP ($\Delta\text{QAICc} = 11.6$); specifically, first-time birds had lower survival (mean \pm SE = 0.87 ± 0.05) than experienced breeders (0.93 ± 0.03) (Figure 5.3, Table 5.2). However, because of the small sample size, survival of SGP in relation to age and experience could not be reliably estimated by our model (Figure 5.3).

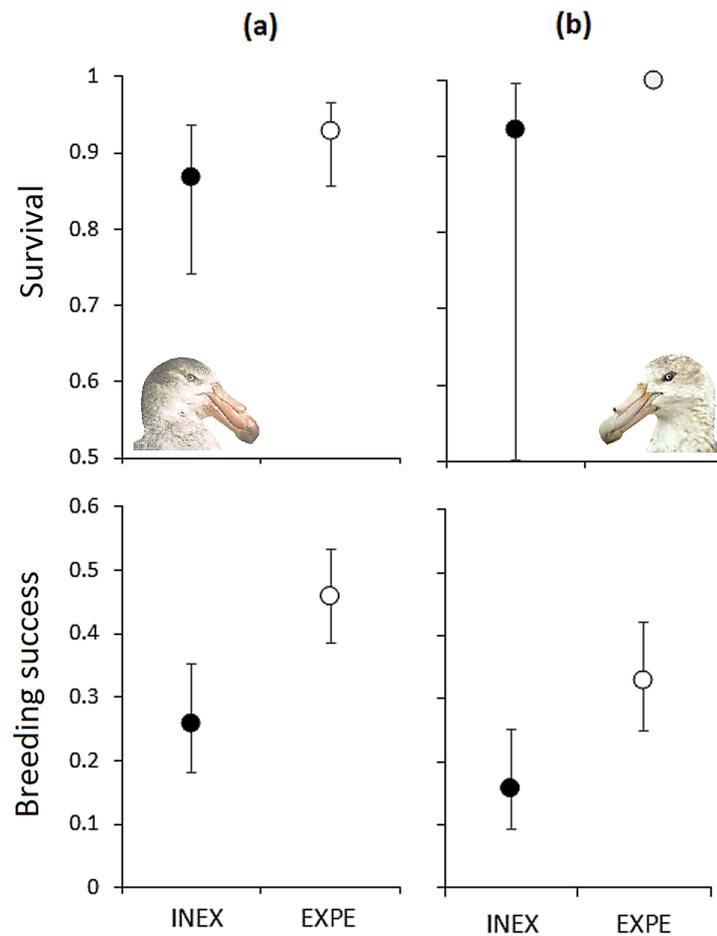


Figure 5.3. Mean survival (top) and breeding success (bottom) of inexperienced (INEX) and experienced (EXPE) northern giant petrels (a) and southern giant petrels (b) during early adulthood, as estimated by the CMR analysis. Error bars indicate 95% Confidence Intervals. Survival could not be reliably estimated for southern giant petrel.

5.4. Discussion

Our study found evidence of marked age-related variation in reproductive traits of giant petrels, with divergent pattern of reproductive senescence between these two sympatric and allochronic long-lived vertebrates. Furthermore, by decomposing changes in reproductive output in early adult life according to breeding experience, we provided empirical evidence for the role of experience

in determining successful breeding, and for the higher cost of reproduction on subsequent survival of new recruits in relation to experienced breeders.

5.4.1. Age-related variation in reproductive traits

Consistent with our predictions, breeding success of both giant petrel species improved markedly in early adult life, and reproductive senescence started earlier in the SGP (Figure 5.2). The improvement in breeding success with age in both species, as observed in other animals, is likely driven by within-individual enhancements in foraging and breeding experience in early adulthood (Martin 1995; Nussey *et al.* 2013; Froy *et al.* 2017). Because of the taxonomic proximity, and virtually identical ecology and life history of these two sibling species, the divergent pattern in reproductive aging is likely related to environmental constraints rather than to interspecific differences in intrinsic somatic ageing. Food availability is one of the most important drivers of breeding success of animals (Stempniewicz 1994; Milligan *et al.* 2009). Not surprisingly, in the krill-centred food web of the Southern Ocean, climate-driven fluctuations in prey availability are correlated with variation in the breeding performance of a range of land-based marine predators (Croxall *et al.* 1992; Forcada *et al.* 2005; Murphy *et al.* 2007a; Trathan *et al.* 2007). Both species of giant petrel feed extensively at sea and on the same prey, including krill, and are therefore largely subject to the same fluctuations in the quality of the marine environment (González-Solís *et al.* 2008). However, because of allochrony, only NGP have reliable access to fur seal carrion during chick rearing (Hunter 1983). The higher availability of this seasonally limited, high calorific (10.5 kJ g^{-1} , Hunter 1985) land-based resource near nesting sites may attenuate the effects of reproductive senescence on NGP by increasing chick survival (This thesis, Chapter 4), as well

as reducing the cost of foraging at sea (González-Solís *et al.* 2008), which is high in giant petrels compared to other procellariiformes (Warham 1977; Obst & Nagy 1992). This would explain the delayed reproductive ageing of NGP compared to SGP, which do not have reliable access to this land-based resource, since reproductive senescence is known to be influenced by reduced foraging performance of old individuals (Catry *et al.* 2006; Proffitt *et al.* 2007; MacNulty *et al.* 2009; Zimmer *et al.* 2011). This explanation is consistent with recent longitudinal studies comparing reproductive aging in mammals and birds between wild and semi-captivity, or high and low quality environments, suggesting that increased resource availability can mitigate the effects of reproductive senescence (Parga & Lessnau 2005; Douhard *et al.* 2014; Oro *et al.* 2014; Ichino *et al.* 2015; Lemaitre & Gaillard 2017). Additionally, accordingly to the 'silver spoon' hypothesis, the reliable access of NGP to fur seal carrion during chick rearing is likely to attenuate its reproductive senescence due to positive effects of high-quality neonatal nutrition on somatic functions that influence adulthood performance (Birkhead, Fletcher & Pellatt 1999; Blount *et al.* 2003; van de Pol & Verhulst 2006; Douhard *et al.* 2014; Lemaitre & Gaillard 2017). The mechanistic explanation for the influence of early life nutrition on adulthood ageing rates is poorly understood. Theories and empirical evidence suggest that low-quality neonatal nutrition affects organ formation (Birkhead *et al.* 1999), immune function or antioxidant activity (Blount *et al.* 2003; Ricklefs 2010b), however there is a lot of debate on what is more important, as well as a broad agreement that longitudinal studies in wild populations are needed (Van De Pol *et al.* 2006; Ricklefs 2010b; Lemaitre & Gaillard 2017).

The high breeding success of both species from 7 to around 20 years, followed by a decline with age only in SGP, potentially driven by phenological

mismatch to optimal environmental conditions, suggests that the pattern of age-specific variation in breeding success of giant petrels is strongly influenced by within-individual improvement through early life and senescence, rather than selective disappearance (earlier mortality) of individuals that invested more in reproduction (Martin 1995; Nussey *et al.* 2013; Zhang *et al.* 2015). By decomposing breeding success according to age, we revealed that the average lower breeding success of SGP (0.39) vs NGP (0.58) at population level is partially driven by the low performance of senescent SGP individuals, providing empirical evidence of how patterns of reproductive senescence can influence population growth rate.

Pre-fledgling mass of NGP chicks also increased with parental age, plateaued, and gradually declined, suggesting that the pattern of age-specific breeding success was partially driven by age-related variation in foraging performance (Oro *et al.* 2014; Lemaitre & Gaillard 2017). Despite the earlier reproductive senescence of SGP, pre-fledgling mass gradually increased with parental age through early life; however, our small sample for SGP reduced our ability to detect age-related variation in this trait. Overall, there was no consistent pattern of age-related variation in laying dates; however, the highest discrepancies in laying dates were observed among individuals <15 years old, suggesting higher within-species phenological mismatch in early adulthood.

5.4.2. Interactive effects of age and experience on breeding traits in early adult life

According to our predictions, breeding success of both species was lower in inexperienced than experienced breeders of the same age (7-12 years); thus, experience-related differences had a stronger influence than age on breeding

success in the years after recruitment (Figure 5.3). Among inexperienced breeders, pre-fledging body mass increased steeply with recruitment age of the parent, suggesting rapid improvement in foraging ability in early adult life; however, this pattern was not reflected in breeding success, which varied little with age in inexperienced breeders. This may reflect the lack of breeding experience *per se* (e.g. mate synchrony, incubating, brooding and central place foraging; Martin 1995; Cam & Monnat 2000) limiting the breeding success of first-time breeders, independent of age-related variation in foraging abilities. These findings represent a valuable empirical contribution to disentangling the confounding effects of breeding experience *per se* and age-related improvement in foraging performance shaping age-specific breeding success in early adulthood.

5.4.3. Cost of reproduction on the survival of inexperienced and experienced breeders

Early life stages are critical periods when available resources must be partitioned between investment in growth, body maintenance and reproduction, (Tavecchia *et al.* 2001; Desprez *et al.* 2014; Fay *et al.* 2016). Reproduction is energetically expensive (Barbraud & Weimerskirch 2005; Speakman 2008), therefore, the first breeding event usually involves a particularly high cost that can be expressed through decreased survival, which is aggravated under conditions of high environmental variability (Barbraud & Weimerskirch 2005; Desprez *et al.* 2014). This would then explain the lower breeding success and subsequent survival of NGP inexperienced (first-time) breeders compared to birds with same age individuals that bred at least once before. Due to the lower sample size for

SGP and the related lack of statistical power, we were not able to compare survival between inexperienced and experienced breeders for this species.

5.5. Conclusions

Breeding success of both giant petrel species improved markedly with age until around 20 years, driven by within-individual factors, but SGP showed earlier reproductive senescence. In giant petrels, despite the fact that pre-fledging mass increased steeply with age, the lack of breeding experience *per se* limited the breeding success of first-time breeders, disentangling the role of experience and age-related variation in breeding performance in early adulthood. Our results suggest that, due to allochryony, the better access of NGP to seasonally limited resources during chick-rearing may mitigate the effects of age-related senescence on their breeding success by increasing chick survival as well as enhancing adulthood performance due to better neonatal nutrition in relation to SGP. These findings represent empirical evidence on how phenological mismatch can influence demographic process and the role of environmental shaping patterns of reproductive senescence.

Table 5.1. Results of goodness of fit chi-square statistics (χ^2), and associated degrees of freedom (df) and *p-value* for northern and southern giant petrels.

	χ^2	df	p-value
<i>Northern giant petrel</i>			
Test 3.SR	9.1	6	0.167
Test 3.SM	3.7	4	0.452
Sum Test 3	12.8	10	-
<i>Southern giant petrel</i>			
Test 3.SR	2.3	7	0.939
Test 3.SM	8.2	6	0.224
Sum Test 3	10.5	13	

Table 5.2. Model selection to estimate probabilities of resighting, survival and breeding success, testing the effect of previous breeding outcome (successful or failed) and experience (inexperienced vs experienced breeders).

(a) Northern giant petrel					
Model definition	k	Deviance	QAICc	Δ AICc - trait	Δ AICc - overall
<i>Encounter</i>					
state(IS/IF, ES/EF)+time	39	1811.5	1890.7	0.0	1.6
state(IS, IF, ES, EF)+time	47	1811.5	1907.3	16.6	18.2
state(IS/ES, IF/EF)+time	45	1825.6	1917.2	26.5	28.2
time	37	3457.3	3532.4	1641.7	1643.3
state(IS/IF, ES/EF)	23	5317.2	5363.6	3472.9	3474.5
state(IS/IF, ES/EF)*time	41	5281.5	5364.8	3474.1	3475.8
state(IS/ES, IF/EF)*time	41	5292.1	5375.5	3484.8	3486.4
state(IS, IF/ES/EF)*time	41	5295.6	5378.9	3488.2	3489.9
<i>Breeding success</i>					
state(IS/IF, ES/EF)+time	32	1824.3	1889.1	0.0	0.0
time	31	1833.4	1896.1	7.1	7.1
constant	23	1857.2	1903.7	14.6	14.6
state(IS/IF, IF/EF)	24	1847.0	1895.4	6.3	6.3
state(IS/IF, IF/EF)*time					
<i>Survival</i>					
state(C, IS/IF, ES/EF)	32	1824.3	1889.1	0.0	0.0
state(C, IS/ES, IF/EF)	38	1823.5	1900.7	11.6	11.6
state(C/IS/IF, ES/EF)	37	1853.6	1928.7	39.6	39.6
state(C, IS, IF/ES/EF)	38	1853.6	1930.8	41.7	41.7
(b) Southern giant petrel					
Model definition	k	Deviance	QAICc	Δ QAICc - trait	Δ QAICc - overall
<i>Encounter</i>					
state(IS/IF, ES/EF)+time	39	1398.4	1479.4	0.0	14.5
state(IS, IF, ES, EF)+time	46	1401.5	1497.7	18.3	32.8
state(IS/ES, IF/EF)+time	44	1414.2	1506.1	26.6	41.2
time	37	2305.5	2382.2	902.8	917.3
state(IS/IF, ES/EF)	23	3605.3	3652.3	2172.9	2187.4
state(IS/IF, ES/EF)*time	43	3579.8	3669.5	2190.1	2204.6
state(IS/ES, IF/EF)*time	43	3596.9	3686.6	2207.2	2221.7
state(IS, IF/ES/EF)*time	43	3613.7	3703.4	2224.0	2238.5
<i>Breeding success</i>					
state(IS/IF, ES/EF)+time	32	1401.1	1467.2	0.0	2.3
time	31	1406.2	1470.2	3.0	5.2

constant	23	1442.9	1490.0	22.8	25.1
state(IS/IF, IF/EF)	24	1491.7	1540.9	73.7	75.9
state(IS/IF, IF/EF)*time	43	3596.9	3686.6	2219.4	2221.7
<u>Survival</u>					
state(C, IS IF/ES/EF)	37	1388.2	1464.9	0.0	0.0
state(C, IS/IF, ES/EF)	32	1401.1	1467.2	2.3	2.3
state(C, IS/ES, IF/EF)	37	1395.0	1471.7	6.8	6.8
constant	30	4550.2	4614.1	3149.2	3149.2

CHAPTER 6. General discussion



6.1. Overview

In this thesis I have combined an analytically robust literature review to quantify the extent of age and sex-specific variation in seabird bycatch by fisheries and performed a comprehensive longitudinal study involving capture-mark-recapture analysis (CMR) and matrix population models (PPMs), to address effects of fisheries, environmental variability and climate oscillation on population dynamics of northern and southern giant petrels. Together, this study has provided not only a better understanding of the global impact of fisheries on seabird populations, but also provides valuable empirical evidence for variation in demographic traits by sex, age and phenology, and how responses to change may vary according to subcomponents of the populations. In a broader context, this thesis has implications for management and conservation, as well as providing insight into life-history tactics and for better understating the impacts of environmental change on marine vertebrates.

6.2. Implications for management and conservation

Seabirds are the most threatened group of birds, with one third threatened with extinction (Croxall *et al.* 2012), and a 70% decline in monitored populations between 1950 and 2010 (Paleczny *et al.* 2015). Fisheries bycatch is a major threat, and understanding sex- and age-bias in bycatch has been identified as important for assessing population-level impacts (Lewison *et al.* 2012; Phillips *et al.* 2016). In **Chapter 2** I demonstrate that seabird bycatch tends to be biased by sex and age, mainly related to differential at-sea distributions. There is clear evidence that differences in capture rates by sex and age have implications for

populations that differ from those of unbiased mortality, therefore we strongly recommend improved data collection on the age and sex of birds killed by fisheries in observing programs at national and international levels, involving concerted and coordinated action by Regional Fishery Management Organisations (RFMOs) and international conservation initiatives (including the Agreement on the Conservation of Albatrosses and Petrels, ACAP). This information, combined with tracking technologies and demographic studies, are important to identify regions and fleets where bycatch is more likely to result in population-level impacts, and to improve targeting of bycatch mitigation and monitoring of compliance. These results were presented by Dr. Richard Phillips at the 8th Meeting of the ACAP Seabird Bycatch Working Group (SBWG8), 4 - 6 September 2017, in Wellington, New Zealand.

Giant petrels have been recorded as bycatch in pelagic and demersal logline, and in trawl fisheries, but the potential population level impact of this mortality was unknown. In **Chapter 3**, I combined longitudinal data, information on at-sea distribution and fishery effort, to quantify the potential impact of fisheries on the survival of giant petrels, which is a research priority for these two ACAP listed species (ACAP 2010a; b; Lewison *et al.* 2012). However, although giant petrel populations from South Georgia are not thought to be particularly threatened by bycatch, I detected a negative effect of pelagic longline effort on female NGP survival, which is consistent with the pattern of sex-biased bycatch described in Chapter 2. Increasing pelagic longline effort within the foraging areas of giant petrels, without the implementation of effective bycatch mitigation measures (Melvin, Guy & Read 2014; ACAP 2016), could result in negative population effects by increasing female mortality, and reducing the effective population size (Awkerman *et al.* 2007b; Jiménez *et al.* 2016).

6.3. Population ecology and responses to environmental change

In **Chapter 3** and **Chapter 4** I show that annual survival and breeding success of NGP and SGP was influenced mainly by climatic oscillation and oceanographic conditions, as observed in other marine vertebrates (Grosbois *et al.* 2008; Forcada & Hoffman 2014; Descamps *et al.* 2016). Large scale climatic indices have either positive or negative effects on pinnipeds and seabirds breeding in the Southern Ocean, with contrasting responses among sympatric species or allopatric populations (Trathan *et al.* 2007; Barbraud *et al.* 2012; Descamps *et al.* 2016), but more negative than positive relationships in the Atlantic sector of the Southern Ocean (Descamps *et al.* 2016), contrasting with the positive effects of warming conditions that I detected on the survival and reproduction of giant petrels. Several studies have investigated the effects of climate change and fisheries on life history traits of land-based marine vertebrates in the Southern Ocean (Forcada *et al.* 2005, 2008, Barbraud *et al.* 2011, 2012; Descamps *et al.* 2016); however, this study became one of the few providing empirical evidence that survival responses to change can vary by sex (Olsson & Van der Jeugd 2002). As expected, survival of male NGP was positively affected by carrion availability, whereas the more pelagic females were positively affected by conditions at sea, with positive effects of meridional winds, and negative effects of sea ice concentration and pelagic longline effort. Despite fisheries were not influential in the short term variability (de-trended models), results from basic models suggest that discards from demersal longline and trawl fisheries in wintering area may influence positively the survival of giant petrels.

Overall, the breeding success of both giant petrels was positively influenced by Antarctic fur seal carrion and climatic oscillation, but because SGP breed later, they have less access to this food resource during chick-rearing, so tended to have lower fledging success. The matrix models predicted a long-term increase for NGP ($\lambda = 1.017$) and stability for SGP ($\lambda = 1.003$), matching the observed trends for both species. As survival rates of NGP and SGP were similar (1% higher for SGP), and comparable with other long-lived seabirds, differences in fecundity due to breeding phenology relative to carrion availability therefore seem to be driving the divergent population trajectories of the two species at South Georgia, following the recovering of fur seal populations from intense hunting. According with the findings in **Chapter 5**, this better access of NGP to seasonally limited resources during chick-rearing not only contributes for a higher breeding success, but also seems to mitigate the effects of somatic senescence on their breeding success due to positive pervasive effects of high-quality neonatal nutrition, explaining the earlier reproductive senescence of SGP. These findings sheds a new light on how phenological mismatch can influence demographic process and on the role of environmental conditions on reproductive senescence, which among the poorest understood processes in population ecology (Miller-rushing *et al.* 2010; Lemaitre & Gaillard 2017).

6.4. Concluding remarks

This research demonstrates how sex- and age-specific differences in ecology, or phenological mismatch, can lead to divergent responses to environmental drivers with implication for population dynamics, Moreover, because such effects were not apparent when all individuals are considered together, ignoring them could underestimate the relative influence of change,

which can be detrimental in terms of conservation. Giant petrels inhabit one of the fastest climate-warming regions on Earth. The positive effects of warm conditions on the demographic rates of giant petrels, in the opposite directions as observed for a range of marine vertebrates in the same ecosystem, show that it is necessary studies across multiple taxa to comprehend the ambiguity of population responses to climate change. However, despite warmer conditions benefit giant petrels in short term, in the long term this effects may not last, as persistent warm sea temperatures could lead to collapse of the krill centred food web. Finally, these findings in this thesis sheds a new light on how phenological mismatch can influence demographic process and on the role of environmental conditions on reproductive senescence, which are among the poorest understood processes in population ecology (Miller-rushing et al. 2010; Lemaitre & Gaillard 2017).

APPENDICES

Table S2.1. List of the species included in this study.

Family	Common name	Specie	IUCN*
Albatrosses (Diomedidae)	Wandering albatross	<i>Diomedea exulans</i>	VU
	Antipodean albatross	<i>Diomedea antipodensis</i>	VU
	Northern royal albatross	<i>Diomedea sanfordi</i>	EN
	Southern royal albatross	<i>Diomedea epomophora</i>	VU
	Black-browed albatross	<i>Thalassarche melanophris</i>	NT
	Campbell albatross	<i>Thalassarche impavida</i>	VU
	White-capped albatross	<i>Thalassarche steadi</i>	NT
	Shy albatross	<i>Thalassarche cauta</i>	NT
	Salvin's albatross	<i>Thalassarche salvini</i>	VU
	Grey-headed albatross	<i>Thalassarche chrysostoma</i>	EN
	Buller's albatross	<i>Thalassarche bulleri</i>	NT
	Atlantic yellow-nosed albatross	<i>Thalassarche chlororhynchos</i>	EN
	Indian yellow-nosed albatross	<i>Thalassarche carteri</i>	EN
	Laysan albatross	<i>Phoebastria immutabilis</i>	NT
	Black-footed albatross	<i>Phoebastria nigripes</i>	NT
	Waved albatross	<i>Phoebastria irrorata</i>	CR
Petrels (Procellariidae)	Southern giant petrel	<i>Macronectes giganteus</i>	LC
	Northern giant petrel	<i>Macronectes halli</i>	LC
	Northern fulmar	<i>Fulmarus glacialis</i>	LC
	Flesh-footed shearwater	<i>Puffinus carneipes</i>	LC
	White-chinned petrel	<i>Procellaria aequinoctialis</i>	VU
	Short-tailed shearwater	<i>Puffinus tenuirostris</i>	LC
	Sooty shearwater	<i>Puffinus griseus</i>	NT
	Grey petrel	<i>Procellaria cinerea</i>	LC
Sea ducks (Merginae)	Grey-faced petrel	<i>Pterodroma gouldi</i>	LC
	Tufted duck	<i>Aythya fuligula</i>	LC
	Greater scaup	<i>Aythya marila</i>	LC
	Long-tailed duck	<i>Clangula hyemalis</i>	VU
	Velvet scoter	<i>Melanitta fusca</i>	EN
	Common scoter	<i>Melanitta nigra</i>	LC
Penguins (Spheniscidae)	Common eider	<i>Somateria mollissima</i>	LC
	Yellow-eyed penguin	<i>Megadyptes antipodes</i>	EN
	Magellanic penguin	<i>Spheniscus magellanicus</i>	NT
Auks (Alcidae)	Humboldt penguin	<i>Spheniscus humboldti</i>	VU
	Common guillemot	<i>Uria aalge</i>	LC
Gulls (Laridae)	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	LC
	Glaucous-winged gull	<i>Larus glaucescens</i>	LC
Cormorants (Phalacrocoracidae)	Glaucous gull	<i>Larus hyperboreus</i>	LC
	Great cormorant	<i>Phalacrocorax carbo</i>	LC
Grebes (Podicipodidae)	Spotted shag	<i>Phalacrocorax punctatus</i>	LC
	Great crested grebe	<i>Podiceps cristatus</i>	LC

* IUCN Status: LC, Least concern; NT, Near threat; VU, Vulnerable; EN, Endangered; CR, Critically endangered.

Appendix S3.1. Analyses of correlation (Pearson’s correlation test) among de-trended candidate covariates on the survival of northern (a) and southern (b) giant petrels. Within the foraging areas of both species, sea surface temperature (SST) was positively correlated with net primary productivity (NPP) and negatively correlated sea ice concentration (SIC). Therefore, in order to reduce the number of covariates to minimising the risk of spurious correlation (Grosbois *et al.* 2008; Frederiksen *et al.* 2014), we dropped SST kept SIC and NPP; since we are more interested in the oceanographic features associated with it SST than in the temperature *per se*. Pelagic effort was positively and negatively correlated with demersal logline effort and trawl effort. Southern Annular Mode (SAM) was positively correlated with NPP. Grey rows and columns indicate the covariates and corresponding correlations removed from our data set.

(a) Northern giant petrel												
	SAM	ENSO	DLL	PLL	TRW	NPP	SST	SIC	Krill	ZON	MER	Seals
SAM		0.78	0.70	0.39	0.46	0.00	0.33	0.09	0.67	0.81	0.60	0.75
ENSO	0.08		0.26	0.16	0.99	0.92	0.27	0.26	0.58	0.09	0.21	0.24
DLL	-0.11	-0.32		0.01	0.11	0.91	0.10	0.72	0.81	0.18	0.64	0.81
PLL	-0.25	-0.40	0.70		0.02	0.75	0.46	0.85	0.08	0.63	0.31	0.68
TRW	-0.22	0.00	-0.45	-0.61		0.20	0.86	0.72	0.23	0.20	0.64	0.57
NPP	0.71	-0.03	0.03	0.09	-0.37		0.04	0.03	0.56	0.77	0.79	0.33
SST	0.28	0.32	-0.46	-0.22	0.05	0.55		0.00	0.30	0.56	0.92	0.23
SIC	-0.47	-0.32	0.11	0.05	0.11	-0.59	-0.75		0.43	0.13	0.14	0.39
Krill	-0.13	-0.16	-0.07	0.49	-0.35	0.17	0.30	-0.23		0.69	0.94	0.26
ZON	0.07	-0.47	-0.38	-0.14	0.37	-0.09	-0.17	0.43	0.12		0.22	0.01
MER	0.15	0.36	-0.14	-0.29	-0.14	-0.08	0.03	-0.41	0.02	-0.35		0.51
Seals	0.09	0.34	0.07	-0.12	-0.17	0.28	0.34	-0.25	-0.33	-0.65	-0.19	

(b) Southern giant petrel survival												
	SAM	ENSO	DLL	PLL	TRW	NPP	SST	SIC	Krill	ZON	MER	Seals
SAM		0.76	0.57	0.74	0.38	0.08	0.77	0.96	0.20	0.09	0.47	0.86
ENSO	0.09		0.20	0.69	0.13	0.98	0.21	0.51	0.62	0.58	0.11	0.27
DLL	-0.17	-0.37		0.05	0.07	0.81	0.28	0.60	0.69	0.15	0.59	0.74
PLL	-0.10	0.12	0.52		0.08	0.60	0.53	0.25	0.65	0.04	0.59	0.77
TRW	-0.26	0.42	-0.51	-0.48		0.29	0.46	0.20	0.96	0.70	0.28	0.55
NPP	0.48	0.01	-0.07	0.15	-0.31		0.02	0.13	0.73	0.19	0.04	0.42
SST	0.08	0.36	-0.31	-0.18	0.22	0.61		0.00	0.30	0.92	0.28	0.36
SIC	0.02	-0.19	0.15	0.33	-0.37	-0.42	-0.84		0.49	0.74	0.31	0.14
Krill	-0.36	-0.14	0.12	-0.14	-0.02	0.10	0.30	-0.20		0.95	0.76	0.26
ZON	0.46	-0.16	-0.41	-0.54	-0.11	0.37	0.03	0.10	-0.02		0.06	0.63
MER	-0.21	0.44	-0.16	0.16	0.31	-0.55	-0.31	0.29	-0.09	-0.52		0.65
Seals	-0.05	0.32	-0.10	0.09	0.18	0.24	0.26	-0.41	-0.33	-0.14	0.13	

Appendix S3.2. Two-sex demographic model

In order to investigate the effect of sex-specific variations in survival in response to environmental drivers on population growth rate, we built and analysed a two-sex population matrix models (Caswell 2001, Figure S3.2a) combining functions of the packages “Pobpio” (Stubben *et al.* 2016) and “Popdemo” (Stott, Hodgson & Townley 2016) in R (R Development Core Team 2011).

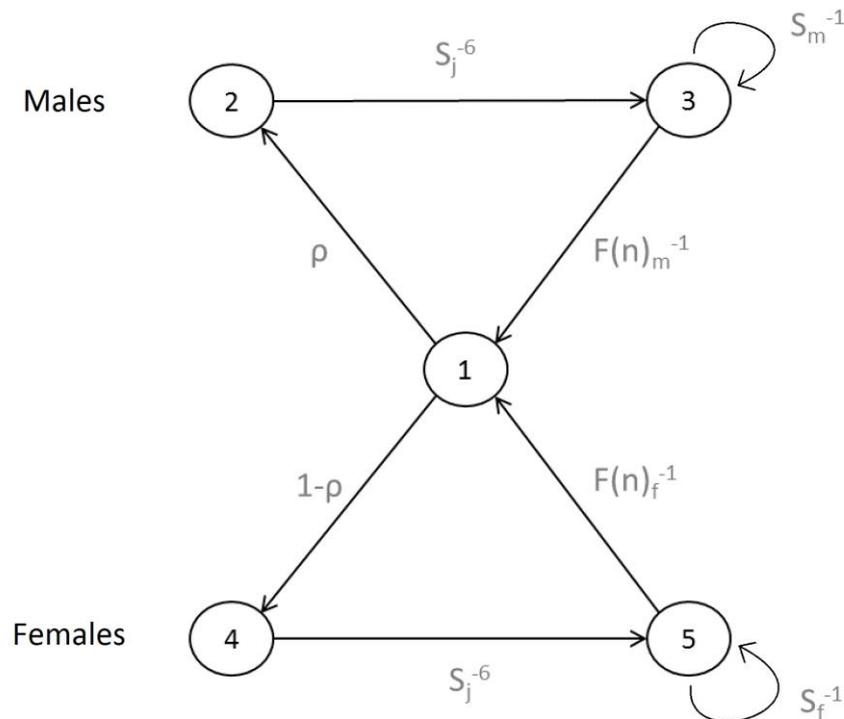


Figure S3.2a. Life-cycle for the two-sex population model. S_j , juvenile survival; S_m : male survival; S_f , female survival; $F(n)_m$, male fertility function; $F(n)_f$, female fertility function; ρ , proportion of males at birth.

We first build a deterministic two-matrix model with six juvenile and one adult stage class, assuming a post-breeding census and that all individuals mature at 7 years old. We used mean values of the demographic parameters for each sex as estimated by our CMR models (**Table S3.2a**), except for juvenile survival, which was obtained from the literature (Hunter 1984), and the number of breeding pairs observed in 2014. We then estimated the deterministic growth rate and the stable age distribution, which allowed us to calculate the population size for each species, including juveniles and non-breeding adults. The matrix

model was $N_{t+1} = \mathbf{A}N_t$, where N_t is a vector comprising the number of individuals in each age class at time t , and \mathbf{A} is the population projection matrix:

$$\mathbf{A} = \begin{bmatrix}
 0 & 0 & 0 & 0 & 0 & 0 & 0 & F(n)m & 0 & 0 & 0 & 0 & 0 & 0 & 0 & F(n)f \\
 \rho & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 1-\rho & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_m & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_j & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_f
 \end{bmatrix}$$

Stages representation in \mathbf{A} refer to S_f = juvenile survival, S_m = male survival, S_f = female survival, ρ = proportion of males at birth and $F(n)m/F(n)f$ = male and female per capita fertility function, which is derived from the harmonic birth function $B(n)$, calculated as $B(n) = 2kN_mN_f/N_m+N_f$, where k = clutch size (1 in our species), N_m = number of males and N_f = number of females. Then, the fertility functions are calculated as $F(n)m$ or $F(n)f = B(n)/N_m+N_f$.

Table S3.2a. Survival and fertility parameters for the northern and southern giant petrels.

Parameter	Northern giant petrel	Southern giant petrel
Adult male survival	0.92	0.93
Adult female survival	0.90	0.91
Juvenile survival	0.88	0.88
Breeding probability	0.83	0.83
Chicks per breeding pair	0.61	0.48
Proportion of male at birth	0.50	0.50

Appendix S3.3. Predicted trends in environmental factors

Bellow we justified the assumptions we have made about the more likely future trends for each influential covariate, and how that may influence male and female survival.

El Nino Southern Oscillation (ENSO) is a southern hemisphere-scale climate process that influences the interannual variability in sea surface temperatures and winter sea ice distribution and dynamics. Positive SST anomalies in the equatorial pacific (ENSO region) are correlated with warming waters in the South Georgia area with 2-2.5 years lag. The southwest Atlantic sector of the Southern Ocean is one of the fastest warming regions on earth, with positive SST anomalies increasing in intensity and frequency during the past half century, associated with increasing the frequency and intensity of ENSO events (Atkinson *et al.* 2004; Meredith & King 2005). This positive trend in ENSO and its positive SST anomalies around South Georgia region is predicted to carry on, thus we assumed a positive trend in the future. For instance, the predicted positive trend in ENSO events are expected to influence positively northern giant petrel of both sexes equally.

Sea ice concentration (SIC) predictions are highly variable around Antarctic, due to complex oceanographic and atmospheric interactions. Within our study area, which is one of the fastest warming regions on earth, SIC was negatively correlated with SST ($r = -0.75$ and -0.84 , $p < 0.01$). Therefore, reductions in SIC are projected to continue in the future, associated with warming SST, nevertheless SIC is also influenced by atmospheric and oceanographic circulation patterns. We expect that reduction in SIC will affect female northern giant petrel strongly, while affecting the survival of males slightly.

A shift to positive values of the **Southern Annular Mode (SAM)** has been observed during the past decades and it is projected continue, therefore we assumed a positive trend in SAM values in the future. The continuation of the current positive trend is likely to affect positively the survival of male southern giant petrel.

Average **wind speed** as well as its zonal component are predicted to increase at the high latitudes while meridional winds are likely to decrease, following the observed trend in recent decades and influenced by a future shift of SAM to positive values (Weimerskirch *et al.* 2012).

Fur seal pup production in South Georgia is likely to decline due to increasing intensity and frequency of positive SST anomalies linked to ENSO events. The link between fur seal pup production and positive SST are the changes in abundance, size and distribution of krill, as a consequence of changes in sea ice and circulation dynamics (Forcada *et al.* 2005, 2008; Meredith & King 2005; Murphy *et al.* 2007a; b). The anomalies at South Georgia were likely associated with the development of physical– biological processes that altered the local environment and food supply of Antarctic fur seal females over time scales longer than their breeding cycle (Forcada *et al.* 2005, 2008). Reductions in fur seal productivity are likely to affect negatively the survival of male northern giant petrels.

Pelagic longline effort (PLL) is likely to shift poleward under the future climatic scenarios, as is the northern range of distributions of both giant petrel species from our study populations (Krüger *et al.* 2017b). Therefore we do not expect changes in the overlap or risk of bycatch of giant petrels under predicted climate scenarios. However, since fisheries are also influenced by other factors, including government policy and industry pressure, and can also adapt and shift target species, we tested scenarios with increasing or decreasing PLL longline effort, which are expected to have negative or positive effects, respectively on female northern giant petrel survival.

Table S3.1. Detailed E-Surge matrices. The 5 states are S=Successful Breeder, F=Failed Breeder, PS=Sabbatical Post-Successful Breeder, PF=Sabbatical Post-Failed Breeder and D=Dead; and additional states for breeding probabilities include Sb=Breeding Post-Successful Breeder, Fb=Breeding Post-Failed Breeder, PSb=Breeding after Sabbatical Post-Successful Breeder, PFb=Breeding after Sabbatical Post-Failed Breeder. There are 3 transition probabilities that allow the estimation of survival (s), breeding (b) and success (k) probabilities with potential intermediate states. Events in the recapture probabilities matrix are 0=Not Seen, 1=Seen Successful Breeder, 2=Seen Failed Breeder.

INITIAL STATE

Probability to start in each state

S	F	PS	PF
i	*	-	-

TRANSITIONS

Survival probability

	S	F	PS	PF	D
S	s	-	-	-	*
F	-	s	-	-	*
PS	-	-	s	-	*
PF	-	-	-	s	*
D	-	-	-	-	*

Breeding probability

	Sb	PS	Fb	PF	PSb	PFb	D
S	b	*	-	-	-	-	-
F	-	-	b	*	-	-	-
PS	-	*	-	-	b	-	-
PF	-	-	-	*	-	b	-
D	-	-	-	-	-	-	*

Breeding success

	S	F	PS	PF	D
Sb	k	*	-	-	-
PS	-	-	*	-	-
Fb	k	*	-	-	-
PF	-	-	-	*	-
PSb	k	*	-	-	-
PFb	k	*	-	-	-
D	-	-	-	-	*

EVENT

Encounter probability

	0	1	2
S	*	p	-
F	*	-	p
PS	*	-	-
PF	*	-	-
D	*	-	-

Table S3.2. Summary of sex-specific capture histories (reduced m-array) northern (a, top) and southern (b, bottom) giant petrels from Bird Island, South Georgia. i denotes the occasion, R_i is the number of individuals released at the occasion i , m_{ij} is the number released at occasion i that were next encountered at occasion j , r_i is the total number reencountered among the R_i originally released at occasion i , and m_j is the total number of individuals encountered at occasion j .

(a) Northern giant petrel																
Males																
i	R_i	2	3	4	5	6	7	8	9	10	11	12	13	14	15	r_i
1	17	13	1	1	1	0	0	0	0	0	0	0	0	0	0	16
2	30		17	12	0	0	0	0	0	0	0	0	0	0	0	29
3	104			80	10	2	0	1	1	0	0	1	0	1	0	96
4	260				211	17	5	5	0	0	0	0	0	0	0	238
5	247					146	60	25	2	0	0	0	0	0	0	233
6	185						132	32	1	1	0	0	0	0	0	166
7	218							184	19	0	0	0	0	2	0	205
8	314								280	16	0	2	0	0	0	298
9	339									286	17	2	2	0	1	308
10	329										231	35	4	0	1	271
11	264											197	33	8	0	238
12	263												185	35	3	223
13	254													198	22	220
14	282														243	243
m_j		13	18	93	222	165	197	247	303	303	248	237	224	244	270	
Females																
i	R_i	2	3	4	5	6	7	8	9	10	11	12	13	14	15	r_i
1	18	11	0	4	0	0	0	0	1	0	0	0	0	0	0	16
2	26		15	7	1	0	0	0	1	0	0	0	0	0	0	24
3	100			76	7	1	1	1	0	0	0	1	0	0	0	87
4	259				200	18	12	4	3	0	1	0	0	0	0	238
5	249					143	53	12	3	1	1	0	0	0	0	213
6	185						139	26	3	3	0	0	0	1	0	172
7	244							200	19	1	2	0	0	0	2	224
8	320								280	13	0	2	2	0	0	297
9	361									291	15	10	4	2	1	323
10	342										258	28	5	4	1	296
11	298											228	20	2	3	253
12	310												224	26	3	253
13	292													208	18	226
14	306														257	257
m_i		11	15	87	208	162	205	243	310	309	277	269	255	243	285	
(b) Southern giant petrel																
Males																
i	R_i	2	3	4	5	6	7	8	9	10	11	12	13	14	15	r_i
1	18	2	11	2	0	0	0	0	0	0	0	0	0	0	0	15
2	13		4	8	0	0	0	0	0	0	0	0	0	0	0	12
3	100			67	26	1	1	0	0	0	0	1	0	0	0	96
4	131				89	23	7	1	0	1	0	0	0	0	0	121
5	145					70	47	10	1	0	1	0	1	0	0	130
6	105						49	45	4	0	0	0	0	0	0	98
7	116							75	22	0	2	0	0	0	0	99
8	148								113	25	5	0	0	0	0	143

9	151									93	21	9	5	0	0	128
10	131										71	31	7	5	4	118
11	102											50	24	9	1	84
12	104												53	28	3	84
13	108													57	19	76
14	109														74	74

<i>m_j</i>	2	15	77	115	94	104	131	140	119	100	91	90	99	101		
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Females																	
<i>i</i>	<i>R_i</i>	<i>m_{ij}</i>														<i>r_i</i>	
1	27	0	12	8	0	0	0	0	0	0	0	0	0	0	0	0	20
2	11		5	6	0	0	0	0	0	0	0	0	0	0	0	0	11
3	101			78	7	2	2	0	0	0	0	0	0	0	0	0	89
4	171				114	30	10	2	3	0	0	0	0	0	0	0	159
5	156					71	50	17	0	0	0	0	0	0	0	0	138
6	121						75	29	3	0	0	0	0	0	0	0	107
7	142							106	23	2	0	0	0	0	0	0	131
8	169								126	25	6	1	1	0	0	0	159
9	178									115	23	6	2	2	1	0	149
10	150										101	17	4	4	0	0	126
11	132												65	35	4	2	106
12	102													67	16	3	86
13	129														81	20	101
14	124															89	89

<i>m_i</i>	0	17	92	121	103	137	154	155	142	130	89	109	107	115		
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Table S3.3. Description of all models and model selection per parameter (encounter probability, breeding success and survival), including the model order (model), number of estimable parameters (k), deviance, QAICc, Δ QAICc among models estimating the same parameter (Δ QAICc Par.), and overall Δ QAICc among all the models (Δ QAICc Par.). For the covariate models, the R^2 , the P_{ANODEV} , and the significant covariate effects (slopes) with respective lower and upper 95% confidence intervals (CI-, CI+) are presented. Covariate effects which $P_{ANODEV} > 0.05$ are highlighted in bold. Abbreviations for covariates as follow. ENSO, El Nino Southern Oscillation; SAM, Southern Annular Mode; SST, sea surface temperature; NPP, Net Primary Productivity; SIC, sea ice concentration; 'krill', krill density; ZON, zonal wind intensity; MER, meridional wind intensity; DLL, demersal longline effort; PLL, pelagic longline effort; TRW, trawl effort; 'seal', number of newly born Antarctic fur seal pups in the previous season.

(a) Northern giant petrel									
Model-Parameters	K	Deviance	QAICc	Δ QAICc Par.	R^2	P_{ANODEV}	Slope	CI-	CI+
Encounter									
Time-dependent	94	18780.5	8537.5	0.0					
Time + state	96	18780.5	8541.6	4.1					
Time*state	107	18780.5	8564.2	26.8					
State-dependent	84	18910.4	8574.7	37.2					
Constant	83	18942.6	8586.9	49.5					
Breeding success									
Time-dependent	69	18780.5	8486.3	0.0					
State (S/F, PS/PF)*time	94	18780.5	8537.5	51.2					
State (S/PS, F/PF)*time	96	18736.3	8521.9	35.7					
Constant	56	19210.9	8651.1	164.8					
Survival									
Linear trend	46	18795.1	8446.0	0.0	71	<0.001	-0.48	-0.59	-0.38
Time-dependent	57	18768.4	8456.4	0.0					
State(S, F/PS/PF)*time*sex	99	18587.4	8461.9	5.5					
State(S/PS, F/PF)*time*sex	99	18594.7	8465.2	8.7					
Time*sex	71	18736.3	8470.7	14.3					
Sex-dependent	46	18850.9	8470.8	14.4					
Constant	45	18860.9	8473.2	16.8					
<u>Basic covariate models</u>									
MER	46	18777.4	8438.1	0.0	90	<0.001	0.41	0.28	0.53
ENSO	46	18801.0	8448.6	10.5	55	0.002	0.38	0.29	0.46
DLL	46	18821.6	8457.8	19.6	42	0.012	0.42	0.21	0.64
SIC	46	18833.1	8462.9	24.8	30	0.043	-0.35	-0.45	-0.27
TRW	46	18838.1	8465.1	27.0	25	0.071	-0.31	-0.51	-0.10
SAM	46	18845.5	8468.4	30.3	17	0.148	-0.21	-0.37	-0.05
NPP	46	18854.6	8472.4	34.3	7	0.368	ns		
PLL	46	18857.6	8473.8	35.6	4	0.517	ns		
ZON	46	18859.5	8474.6	36.5	1	0.680	ns		
Krill	46	18859.9	8474.8	36.7	1	0.726	ns		
<u>Detrended covariate models</u>									
MER_d	47	18784.8	8443.5	1.4	38	0.024	0.22	0.02	0.41
ZON_d	47	18785.5	8443.8	1.7	36	0.031	-0.19	-0.38	-0.01
SIC_d	47	18786.3	8444.1	2.0	33	0.040	-0.16	-0.26	-0.05
ENSO_d	47	18786.6	8444.3	2.2	32	0.045	0.18	0.06	0.30
PLL_d	47	18790.5	8446.0	3.9	18	0.151	-0.19	-0.36	-0.03
Seal-1_d	47	18791.2	8446.3	4.2	17	0.164	0.11	0.00	0.21
Krill_d	47	18792.6	8446.9	4.8	15	0.208	ns		

TRW_d	47	18793.6	8447.4	5.3	6	0.440	ns			
DLL_d	47	18794.1	8447.6	5.5	4	0.526	ns			
SAM_d	47	18794.8	8447.9	5.8	4	0.506	ns			
<i>Sex-specific models</i>										
SIC_d_F	48	18813.0	8458.0	0.0	20	0.149	-0.23	-0.38	-0.09	
MER_d_F	48	18814.6	8458.7	0.7	17	0.185	0.28	0.01	0.54	
ZON_d_F	48	18822.0	8462.0	4.0	3	0.560	ns			
Seal_d_F	48	18816.9	8459.7	1.7	13	0.254	ns			
PLL_d_F	48	18818.2	8460.3	2.3	10	0.308	-0.28	-0.48	-0.07	
ENSO_d_F	48	18818.7	8460.6	2.5	9	0.332	0.18	0.03	0.34	
Linear_F	47	18824.0	8460.9	2.8	40	0.047	-0.27	-0.48	-0.05	
Seal_d_M	48	18826.1	8463.9	5.8	15	0.213	0.26	0.10	0.41	
ZON_d_M	48	18826.8	8464.	6.1	14	0.229	-0.29	-0.58	-0.01	
Linear_M	47	18836.4	8466.4	8.3	26	0.158	-0.48	-0.63	-0.32	
ENSO_d_M	48	18833.2	8467.0	9.0	5	0.503	0.16	-0.01	0.34	
MER_d_M	48	18834.6	8467.6	9.6	3	0.611	ns			
SIC_d_M	48	18835.8	8468.2	10.1	1	0.782	ns			
PLL_d_M	48	18836.1	8468.3	10.3	0	0.848	ns			
(b) Southern giant petrel										
Model-parameters	K	Deviance	QAICc	Δ QAICc	Par.	R ²	P _{ANODEV}	Slope	CI-	CI+
Encounter										
Time	95	10628.9	4498.7	0.0						
Time+state	96	10628.9	4500.8	2.1						
Constant	83	10709.7	4506.1	7.4						
State	84	10734.5	4518.2	19.6						
Time*state	107	10628.9	4524.1	25.5						
Breeding success										
Time	69	10628.8	4444.0	0.0						
State(S/PS,F/PF)*time	96	10597.2	4487.9	43.9						
State(S,PS/F/PF)*time	95	10628.8	4498.6	54.6						
Constant	56	11274.3	4678.0	234.4						
Survival										
Linear	46	10640.4	4401.1	0.0	42	0.012	-0.42	-0.59	-0.24	
Constant	45	10661.0	4407.4	6.3						
sex	46	10658.9	4408.6	7.5						
Time	57	10612.3	4412.4	11.3						
Time*sex	71	10597.2	4435.4	34.3						
State(S,PS/F/PS)*time*sex	99	10546.4	4467.8	66.7						
State(S/PS,F/PF)*time*sex	99	10573.4	4478.7	77.6						
<i>Basic covariate models</i>										
MER	46	10637.4	4399.9	0.0	48	0.006	0.30	0.18	0.42	
ENSO	46	10639.9	4400.9	1.0	43	0.011	0.35	0.21	0.49	
NPP	46	10643.3	4402.3	2.4	36	0.023	-0.31	-0.47	-0.16	
DLL	46	10645.3	4403.1	3.2	32	0.034	0.36	0.16	0.56	
PLL	46	10649.9	4405.0	5.1	23	0.084	0.32	0.08	0.56	
Seal	46	10653.9	4406.6	6.7	14	0.180	0.21	0.04	0.39	
SIC	46	10655.1	4407.1	7.2	12	0.223	0.26	0.02	0.50	
Krill	46	10659.1	4408.7	8.8	4	0.792	ns			
TRW	46	10659.1	4408.7	8.8	4	0.795	ns			
SAM	46	10660.9	4409.4	9.5	0	1.000	ns			
<i>Detrended covariate models</i>										
SAM+ZON_d	48	10621.8	4397.7	0.0	66	0.004				
SAM_d	47	10629.5	4398.8	1.1	39	0.023	0.29	0.12	0.45	
SAM+ZON+ENSO_d	49	10621.7	4399.7	2.0	66	0.016				
ZON_d	47	10633.7	4400.5	2.8	24	0.091	-0.23	-0.41	-0.05	
Linear	46	10640.4	4401.1	3.4	42	0.012	-0.42	-0.59	-0.24	
ENSO_d	47	10636.6	4401.6	3.9	14	0.214	0.20	0.01	0.39	
DLL_d	47	10638.2	4402.3	4.6	8	0.348	ns			
Krill_d	47	10638.4	4402.4	4.6	7	0.371	ns			
MER_d	47	10638.4	4402.4	4.7	7	0.375	ns			
SIC_d	47	10639.4	4402.8	5.1	4	0.526	ns			
PLL_d	47	10639.6	4402.9	5.2	3	0.581	ns			
NPP_d	47	10639.8	4402.9	5.2	2	0.620	ns			
Seal_d	47	10640.4	4403.2	5.5	0	0.891	ns			
TRW_d	47	10640.4	4403.2	5.5	0	0.982	ns			
<i>Sex-specific models</i>										
Male_SAM_d	48	10637.9	4404.2	0.0	25	0.097	-0.20	-0.41	0.01	
Male_Linear	47	10646.4	4405.6	1.4	30	0.043	-0.46	-0.71	-0.21	
Male_ZON_d	48	10644.8	4407.0	2.8	5	0.490	ns			

Male_ENSO_d	48	10646.3	4407.6	3.4	0	0.870	ns		
Linear_F	47	10653.0	4408.3	4.1	16	0.154	-0.27	-0.48	-0.05
Female_ZON_d	48	10648.9	4408.7	4.5	10	0.310	ns		
Female_ENSO_d	48	10649.0	4408.7	4.5	10	0.317	ns		
Female_SAM_d	48	10652.6	4410.2	6.0	1	0.732	ns		

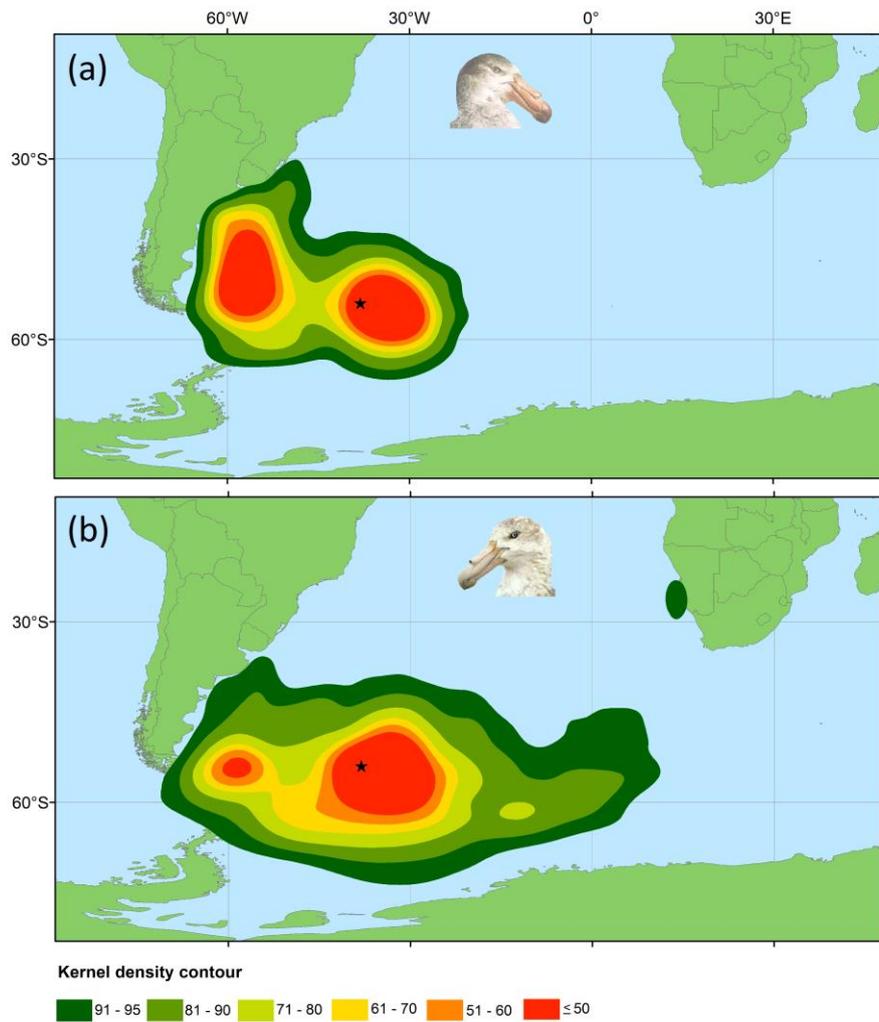


Figure S3.1. Utilization distributions (UDs; %) for northern (a) and southern (b) giant petrels during the nonbreeding (wintering) periods based on tracking data collected at Bird Island, South Georgia (black star). Data on oceanographic covariates used in the capture-mark-recapture models for breeding and nonbreeding periods were extracted from the 50% UD, and on fishery covariates from all 5 x 5° cells that overlapped with the 90% UD.

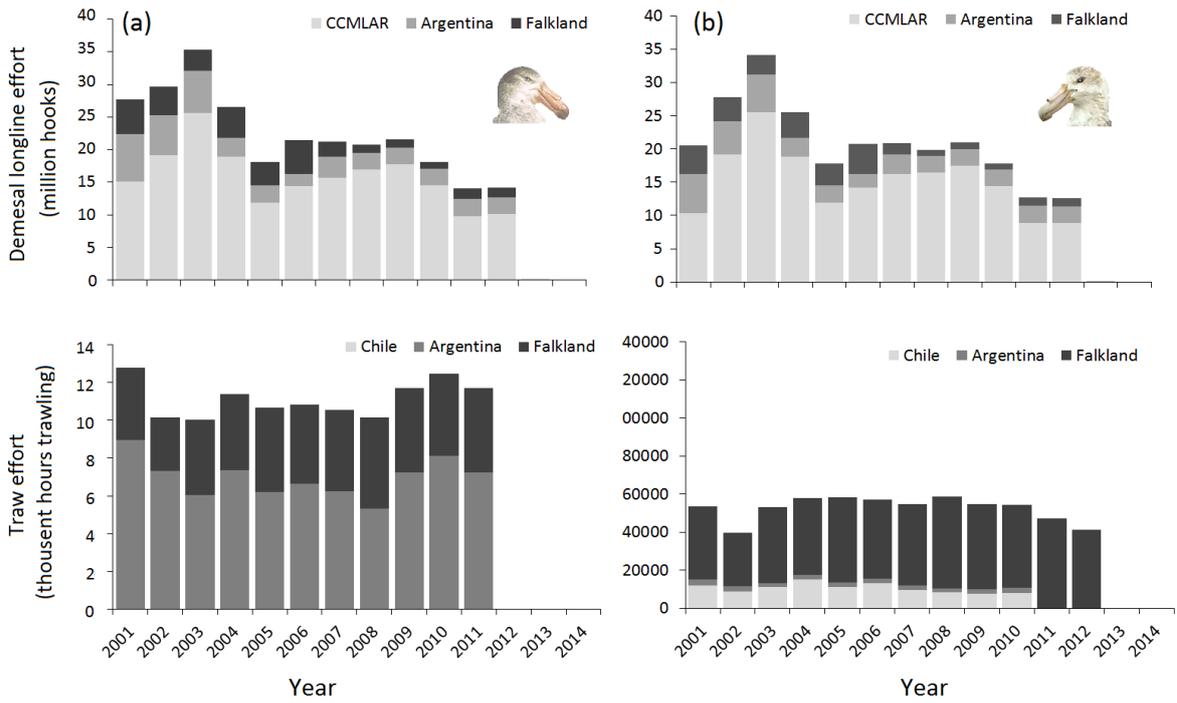


Figure S3.2. Contribution of each country fleet to the total effort of demersal logline (top) and trawl (bottom) within the wintering foraging areas of northern (a) and southern (b) giant petrels.

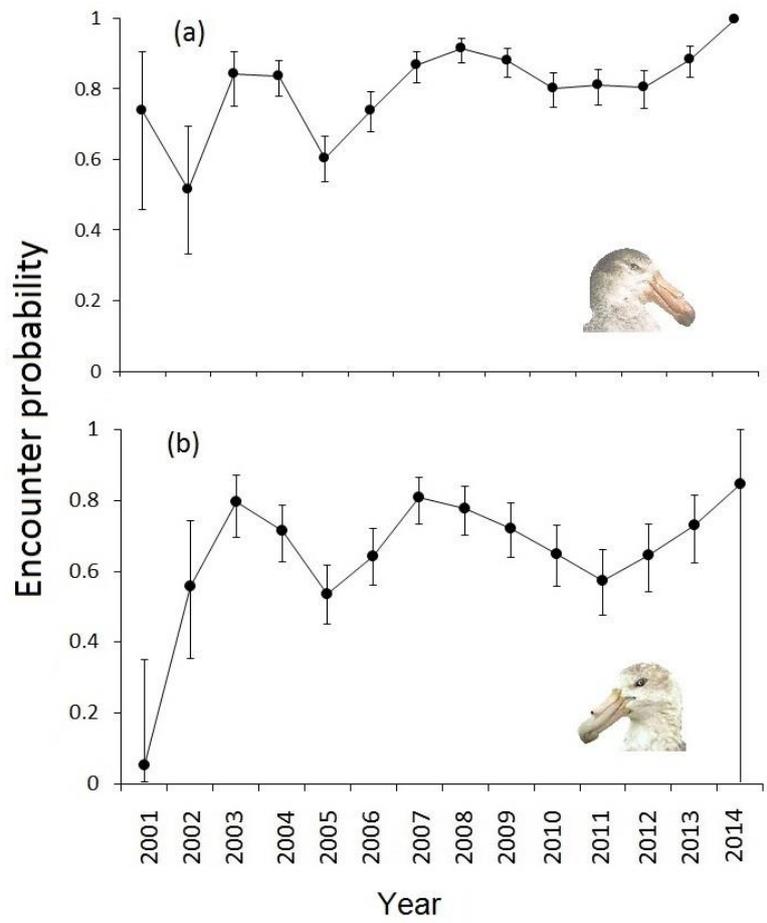


Figure S3.3. Temporal variation (\pm 95% CI) in encounter probabilities of northern (a) and southern (b) giant petrels.

Table S4.1. Pearson’s correlation matrix showing relationships among the scaled and de-trended covariate values included in the demographic models for northern (a) and southern (b) giant petrels. For Abbreviations as follow: ENSO, El Nino Southern Oscillation; SAM, Southern Annular Mode; SST, sea surface temperature; NPP, Net Primary Productivity; SIC, sea ice concentration; ‘krill’, krill density; ZON, zonal wind intensity; MER, meridional wind intensity; DLL, demersal longline effort; TRW, trawl effort; ‘seal’, number of newly born Antarctic fur seal pups; ‘PEN’, number of macaroni penguin fledged.

(a) Northern giant petrel												
	ENSO	SAM	SST	NPP	SIC	Krill	ZON	MER	DLL	TRW	Seal	PEN
ENSO		0.47	0.29	1.00	0.55	0.30	0.04	0.86	0.32	0.18	0.28	0.41
SAM	0.21		0.02	0.02	0.00	0.91	0.14	0.09	0.15	0.51	0.05	0.04
SST	0.30	0.60		0.08	0.00	0.94	0.52	0.03	0.05	0.70	0.57	0.75
NPP	0.00	0.61	0.48		0.03	0.97	0.11	0.05	0.65	0.04	0.52	0.11
SIC	-0.17	-0.85	-0.81	-0.57		0.66	0.52	0.01	0.20	0.44	0.49	0.58
Krill	-0.30	0.03	0.02	-0.01	-0.13		0.26	0.56	0.21	0.79	0.12	0.59
ZON	0.55	0.41	0.19	0.44	-0.19	-0.32		0.52	0.45	0.87	0.10	0.28
MER	-0.05	-0.46	-0.57	-0.53	0.69	0.17	-0.19		0.43	0.61	0.69	0.98
DLL	-0.29	-0.41	-0.53	-0.13	0.36	0.36	-0.22	0.23		0.41	0.59	0.93
TRW	0.38	0.19	0.11	-0.55	-0.23	0.08	0.05	0.15	-0.24		0.51	0.44
Seal	0.31	0.53	0.17	0.19	-0.20	-0.44	0.45	0.12	-0.16	0.19		0.03
PEN	-0.24	0.55	-0.10	0.44	-0.16	-0.16	0.31	-0.01	0.03	-0.23	0.58	

(b) Southern giant petrel										
	ENSO	SAM	SST	NPP	SIC	Krill	ZON	MER	Seal	PEN
ENSO		0.44	0.29	0.51	0.48	0.35	0.23	0.98	0.28	0.38
SAM	0.22		0.06	0.60	0.05	0.67	0.01	0.05	0.03	0.05
SST	0.30	0.52		0.03	0.00	0.76	0.13	0.02	0.61	0.59
NPP	0.19	0.15	0.59		0.08	0.66	0.06	0.08	0.95	0.82
SIC	-0.20	-0.54	-0.72	-0.48		0.29	0.18	0.02	0.55	0.56
Krill	-0.27	-0.13	0.09	0.13	-0.31		0.84	0.73	0.13	0.63
ZON	0.34	0.67	0.42	0.51	-0.38	-0.06		0.10	0.17	0.35
MER	-0.01	-0.53	-0.61	-0.48	0.63	0.10	-0.45		0.90	0.69
Seal	0.31	0.58	0.15	-0.02	-0.17	-0.42	0.39	0.04		0.03
PEN	-0.25	0.54	-0.16	-0.07	-0.17	-0.14	0.27	-0.12	0.58	

Table S4.2. Model selection estimating encounter probability and breeding success of northern and southern giant petrels and the effects (Slope) of candidate explanatory covariates on success. Survival and breeding probability were maintained constant in all models. Abbreviations in model definition as follow. For previous state (inside parenthesis), “s” and “f” for successful and failed breeder, and “ps” and “pf” for sabbatical post-successful and post-failed breeder, respectively. For covariates ENSO, El Niño Southern Oscillation; SAM, Southern Annular Mode; NPP, Net Primary Productivity; SIC, sea ice concentration; ‘krill’, krill density; ZON, zonal wind intensity; MER, meridional wind intensity; DLL, demersal longline effort; TRW, trawl effort; ‘seal’, number of newly born Antarctic fur seal pups; ‘PEN’, number of macaroni penguin fledged.

Model definition	K	Deviance	QAICc	QAICc Trait	QAICc Overall	P _{ANODEV}	R2	Slope	CI-	CI+
(a) Northern giant petrel										
<u>Encounter probability</u>										
Time	43	18894.9	8484.3	0.0	14.4					
Time+state	45	18889.8	8486.1	1.8	16.2					
Time*state	56	18861.4	8495.8	11.5	25.9					
State	31	19160.7	8578.1	93.8	108.2					
Constant (intercept)	30	19180.0	8584.7	100.4	114.8					
<u>Breeding success</u>										
Time	30	18921.7	8469.9	0.0	0.0					
(s,f ps pf)*time	45	18864.2	8474.7	4.7	4.7					
(s ps,f pf)*time	46	18862.7	8476.1	6.1	6.1					
(s f, ps pf)*time	56	18861.4	8495.8	25.9	25.9					
Linear	18	19203.9	8571.1	101.2	101.2	0.036	32	-0.42	-0.53	-0.31
Constant (intercept)	17	19335.5	8627.7	157.7	157.7					
Basic covariate models										
Seal+ENSO	19	19118.6	8535.3	0.0	65.3	0.003	52			
Seal+ENSO+SAM	20	19118.0	8537.0	1.7	67.1	0.003	53			
Seal	18	19135.1	8540.6	5.3	70.7	0.006	48	0.39	0.30	0.47
ENSO	18	19225.0	8580.5	45.3	110.6	0.056	27	0.28	0.20	0.36
DLL	18	19234.7	8584.8	49.6	114.9	0.070	25	0.56	0.39	0.73
SAM	18	19251.3	8592.2	57.0	122.3	0.105	20	0.30	0.20	0.40
PEN	18	19268.5	8599.9	64.6	129.9	0.154	16	0.24	0.15	0.33
SIC	18	19281.8	8605.8	70.5	135.9	0.206	13	-0.23	-0.32	-0.13
MER	18	19293.6	8611.0	75.8	141.1	0.267	10	0.17	0.09	0.25
ZON	18	19302.2	8614.8	79.6	144.9	0.325	8	0.17	0.08	0.26
TRW	18	19314.9	8620.5	85.2	150.6	0.439	5	0.14	0.05	0.23
NPP	18	19315.2	8620.6	85.4	150.7	0.427	5	0.13	0.05	0.22
krill	18	19326.1	8625.5	90.2	155.5	0.576	2	-0.10	-0.20	0.00
De-trended models										
PEN+seal+ENSO+SAM_d	22	19035.8	8504.5	0.0	34.6	0.090	60			
PEN+seal+SAM_d	21	19059.3	8513.0	8.5	43.0	0.079	51			

PEN+seal_d	20	19065.4	8513.6	9.1	43.7	0.034	49				
PEN_d	19	19070.6	8513.9	9.4	44.0	0.009	47	0.34	0.25	0.44	
Seal_d	19	19101.2	8527.5	23.0	57.6	0.029	36	0.30	0.21	0.39	
SAM_d	19	19114.4	8533.4	28.9	63.5	0.045	32	0.30	0.20	0.40	
ENSO_d	19	19153.1	8550.6	46.1	80.7	0.149	18	0.19	0.10	0.27	
ZON_d	19	19156.5	8552.1	47.6	82.2	0.164	17	0.19	0.10	0.28	
MER_d	19	19171.3	8558.7	54.2	88.8	0.256	12	0.13	0.05	0.21	
NPP_d	19	19175.7	8560.6	56.1	90.7	0.293	10	0.13	0.04	0.22	
krill_d	19	19189.4	8566.7	62.2	96.8	0.457	5	-0.08	-0.19	0.02	
DLL_d	19	19191.2	8567.5	63.0	97.6	0.481	5	0.09	-0.04	0.22	
SIC_d	19	19191.2	8567.5	63.0	97.6	0.488	4	-0.07	-0.17	0.03	
TRW_d	19	19194.4	8569.0	64.5	99.1	0.544	3	-0.03	-0.13	0.07	
(b) Southern giant petrel	K	Deviance	QAICc	QAICc Trait	QAICc Overall	P _{ANODEV}	R2	Slope	CI-	CI+	
<u>Encounter probability</u>											
Time	43	4410.6	4411.7	0.0	0.0						
State+time	45	4417.8	4419.0	7.3	7.3						
State*time	56	4433.7	4435.6	23.9	23.9						
Constant	30	4461.3	4461.8	50.1	50.1						
State	31	4643.0	4643.6	231.9	231.9						
<u>Breeding success</u>											
Time	30	4406.6	4407.2	0.0	0.0						
(s f,ps pf)*time	56	4433.7	4435.6	28.5	28.5						
(s ps,f pf)*time	45	4455.2	4456.4	49.3	49.3						
(s, f ps pf)*time	45	4457.7	4459.0	51.8	51.8						
Linear	18	4540.6	4540.8	133.7	133.7	0.012	40	-0.80	-0.96	-0.64	
Constant	17	4643.0	4643.2	236.0	236.0						
Basic covariate models											
Seal+ENSO+MER	20	4472.3	4472.5	65.4	0.0	0.003	67				
Seal+ENSO	19	4497.8	4498.0	90.9	25.5	0.006	57				
Seal	18	4504.0	4504.2	97.0	31.7	0.003	54	0.77	0.63	0.91	
ENSO	18	4568.5	4568.7	161.6	96.2	0.046	29	0.57	0.43	0.70	
MER	18	4611.2	4611.4	204.3	138.9	0.208	13	0.37	0.25	0.50	
SIC	18	4615.6	4615.8	208.6	143.3	0.242	11	-0.39	-0.53	-0.25	
ZON	18	4624.9	4625.1	218.0	152.6	0.339	8	0.39	0.23	0.55	
PEN	18	4639.4	4639.6	232.5	167.1	0.619	2	0.15	0.03	0.27	
SAM	18	4641.7	4641.9	234.8	169.4	0.703	1	0.12	-0.01	0.25	
Krill	18	4644.9	4645.1	238.0	172.6	0.952	0	0.02	-0.12	0.16	
NPP	18	4644.9	4645.1	238.0	172.6	0.961	0	-0.01	-0.13	0.10	
De-trended models											
Seal_d	19	4482.1	4482.3	75.2	0.0	0.024	38	0.59	0.43	0.74	
Seal+PEN_d	20	4482.8	4483.1	75.9	0.8	0.084	39				
Seal+PEN+SAM_d	21	4483.1	4483.4	76.2	1.0	0.182	40				
SAM_d	19	4515.2	4515.5	108.3	33.1	0.157	17	0.38	0.23	0.52	
PEN_d	19	4518.8	4519.1	111.9	36.8	0.190	15	0.33	0.19	0.46	
ZON_d	19	4524.5	4524.7	117.5	42.4	0.257	12	0.37	0.20	0.54	
ENSO_d	19	4524.8	4525.0	117.9	42.7	0.262	11	0.32	0.17	0.47	
MER_d	19	4526.1	4526.3	119.1	44.0	0.281	10	0.27	0.14	0.40	

NPP_d	19	4536.8	4537.0	129.8	54.7	0.528	4	-0.15	-0.27	-0.03
SIC_d	19	4537.5	4537.7	130.6	55.4	0.555	3	-0.18	-0.33	-0.02
Krill_d	19	4541.7	4541.9	134.7	59.6	0.799	1	0.07	-0.07	0.21

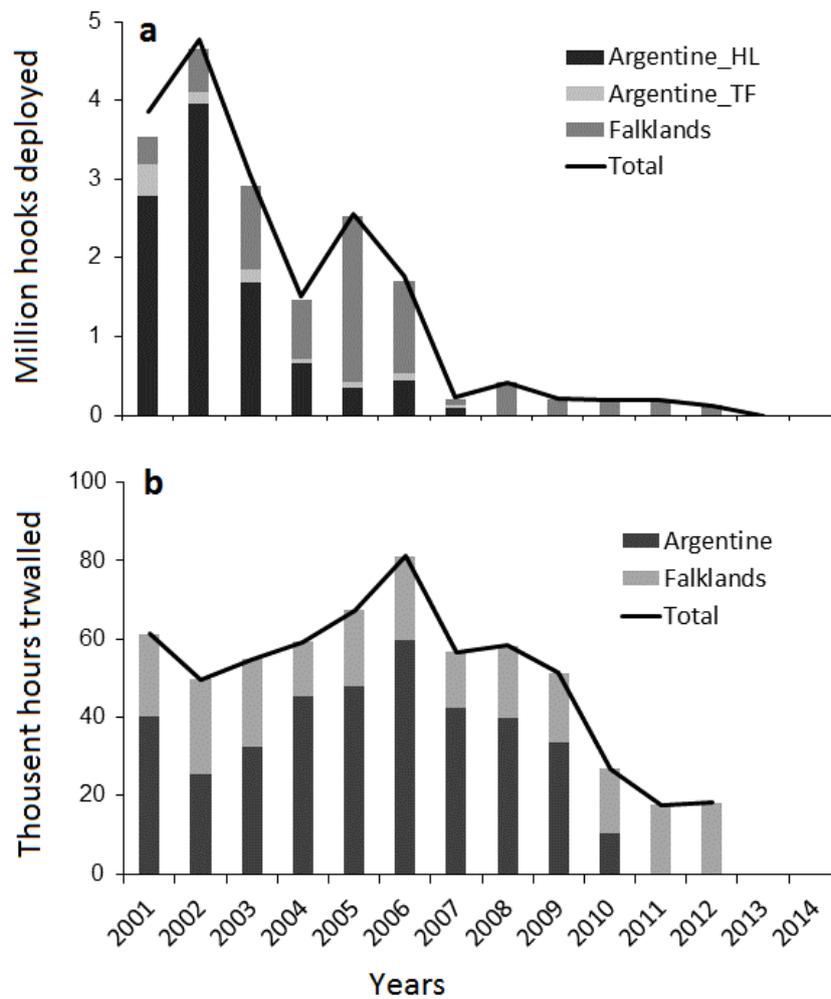


Figure S4.1. Contribution of each fleet to the total effort of demersal longline (a) and trawl (a) super fleets within the breeding foraging areas of northern giant petrels. Argentine demersal longline effort is split in hake (HL, *Merluccius* spp) and toothfish (TF, *Dissostichus* spp).

Table S5.1. Summary of capture histories (reduced m-array) of northern giant petrels (a, top) and southern giant petrels (b, bottom) at Bird Island, South Georgia. i denotes the occasion, R_i is the number of individuals released at the occasion i , m_{ij} is the number released at occasion i that were next encountered at occasion j , r_i is the total number reencountered among the R_i originally released at occasion i , and m_j is the total number of individuals encountered at occasion j .

<i>(a) Northern giant petrel</i>																	
i	R_i	M_{ij}															r_i
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	29	0	0	0	0	0	0	3	1	4	1	3	0	0	0	0	12
2	52		0	0	0	0	0	0	1	3	4	8	2	3	1	1	23
3	67			0	0	0	0	0	0	1	0	1	0	1	1	0	4
4	216				0	0	0	0	0	0	0	3	5	3	2	2	15
5	182					0	0	0	0	0	0	2	3	2	2	2	11
6	145						1	0	0	0	0	0	2	4	8	4	19
7	128							1	0	0	0	0	0	3	1	5	10
8	242								4	0	0	0	0	0	3	4	11
9	252									5	0	0	0	0	0	0	5
10	135										12	1	0	0	0	0	13
11	186											11	4	1	0	0	16
12	180												17	8	1	1	27
13	166													21	5	1	27
14	187														41	0	41
15	254															45	45
m_i		0	0	0	0	0	1	4	6	13	17	29	33	46	65	65	
<i>(b) Southern giant petrel</i>																	
i	R_i	M_{ij}															r_i
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	24	0	0	0	0	0	0	7	5	2	0	2	0	0	0	0	16
2	14		0	0	0	0	0	0	2	2	1	4	4	1	0	0	14
3	54			0	0	0	0	0	0	2	1	1	0	1	2	0	7
4	75				0	0	0	0	0	0	0	3	2	7	3	1	16
5	96					0	0	0	0	0	0	2	1	4	2	1	10
6	81						0	0	0	0	0	0	0	2	3	2	7
7	97							0	0	0	0	0	0	0	1	9	10
8	94								5	0	1	1	0	0	0	1	8
9	116									5	3	1	0	0	1	1	11
10	29										4	2	0	1	1	0	8
11	56											3	1	4	1	0	9
12	49												9	4	5	0	18
13	73													10	3	2	15
14	40														18	7	25
15	103															21	21
m_i		0	0	0	0	0	0	7	12	11	10	19	17	34	40	45	

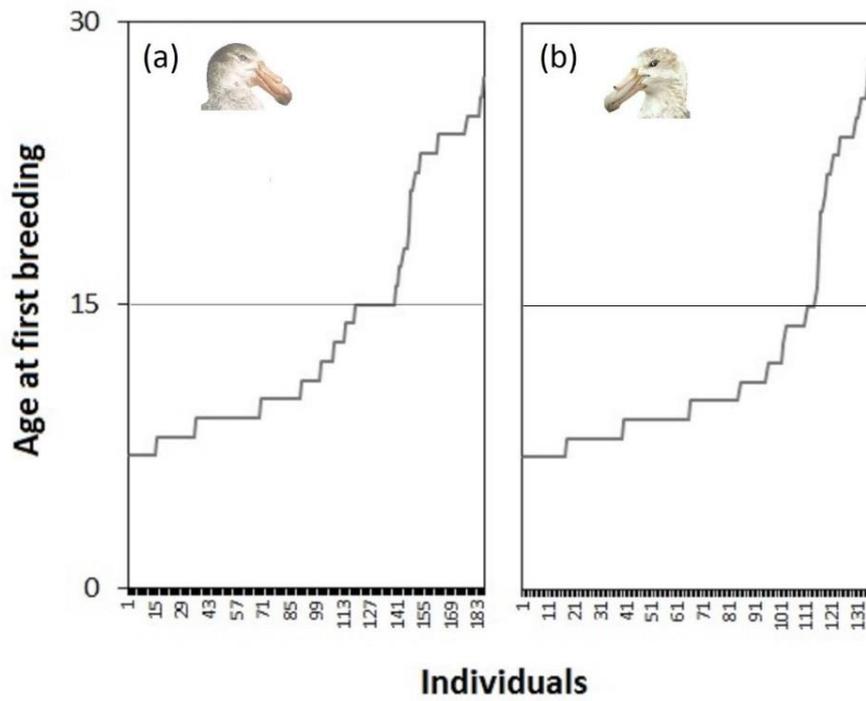


Figure S5.1. Age of northern giant petrels (a) and southern giant petrels (b) at first recorded reproduction (recruitment). The horizontal line indicates the cut-off point used for recruitment age. Birds older than this threshold were likely to have been missed when breeding for the first time.

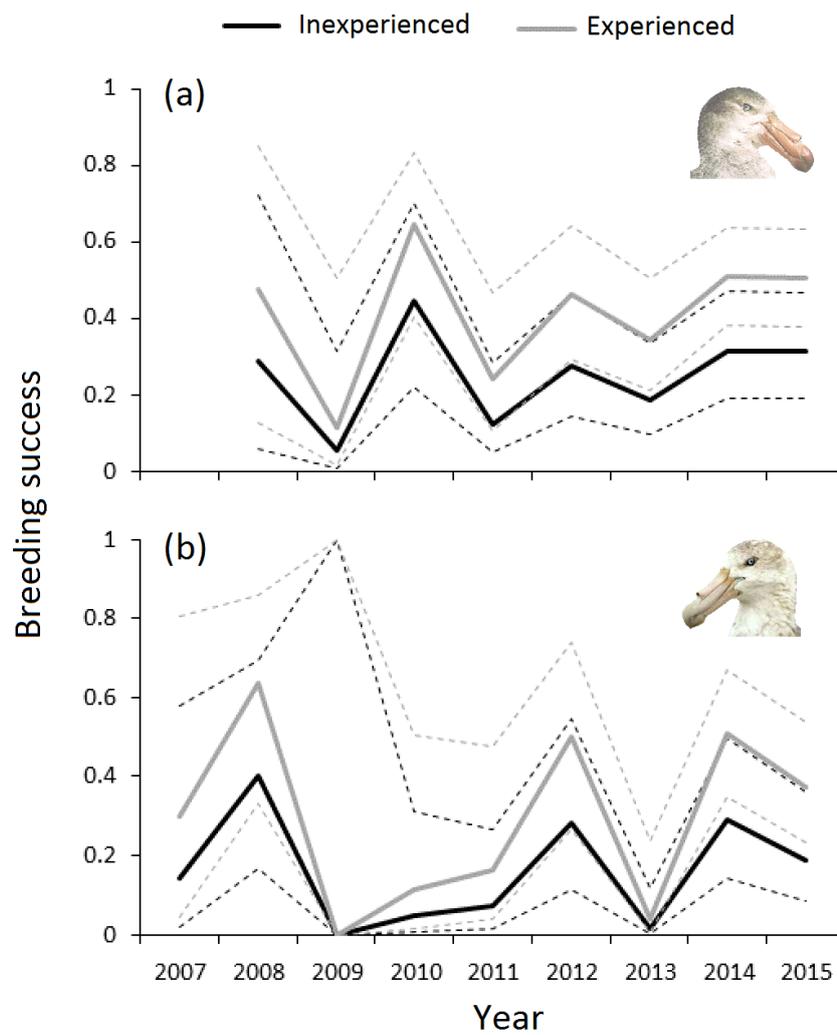


Figure S5.2. Annual variation in breeding success of northern giant petrels (a) and southern giant petrel (b) according to breeding experience. The dashed lines indicate \pm 95% confidence intervals.

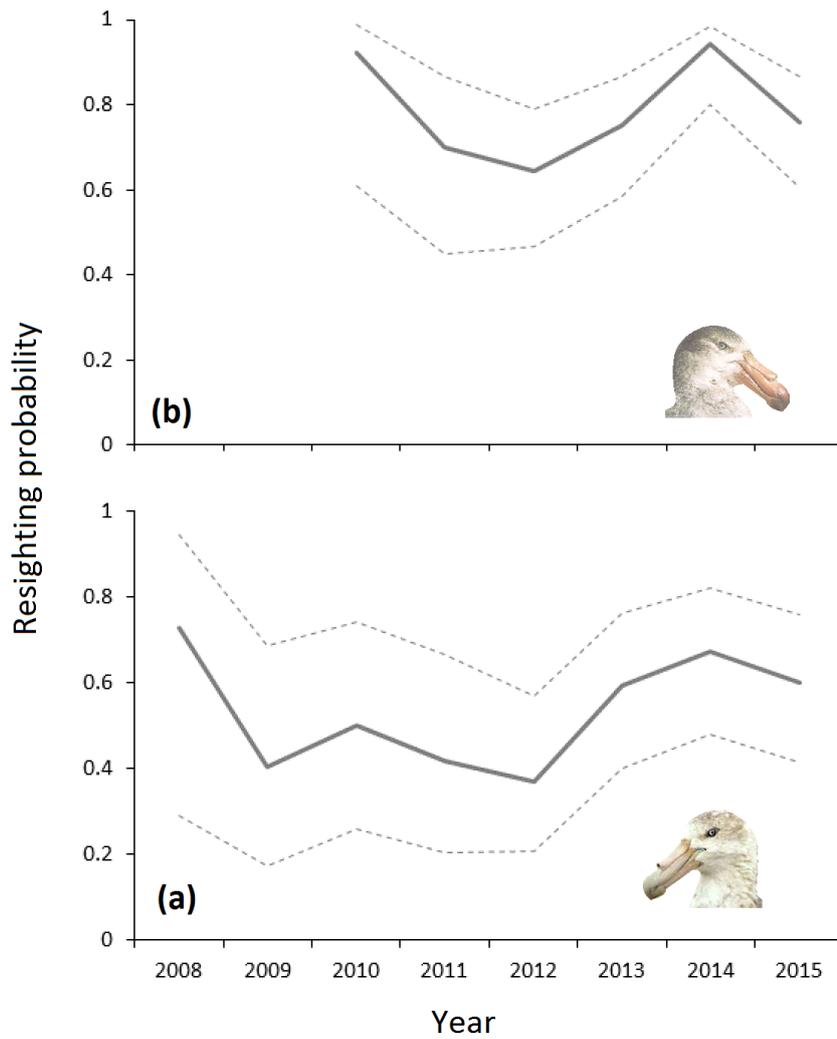


Figure S2. Annual variation in resighting probability of northern giant petrels (a) and southern giant petrels (b) that were experienced breeders. The dashed lines indicates $\pm 95\%$ confidence intervals.

Table S5.2. Model selection examining breeding success, chick pre-fledging mass and laying dates as function of parental age and experience, at the population level and in early adulthood.

(a) Northern giant petrel					
Model	d.f.	Deviance	AIC	AIC	Residual d.f.
Population level					
<i>Breeding success</i>					
Polynomial	6	1068	1055.5	0	884
Quadratic	5	1069	1059	3.5	885
Linear	4	1076	1068.1	12.6	886
Year	3	1093	1086.7	31.2	887
Intercept	2	1157	1152.7	97.2	888
<i>Pre-fledgling mass</i>					
Polynomial	7	961.1	977.1	1.1	369
Quadratic	6	962	976	0	370
Linear	5	978	990	14	371
Year	4	980.3	990.3	14.3	372
intercept	3	1444	1450.1	474.1	495
<i>Laying date</i>					
Polynomial	6	4308	4320.1	0	709
Quadratic	5	4314	4324.3	4.2	710
Linear	4	4320	4327.8	7.7	711
Intercep	3	4324	4329.6	9.5	712
Early adult life					
<i>Breeding success</i>					
exp*age_Q	7	414.2	328.2	4.8	195
exp+age_Q	6	314.9	326.9	3.5	196
exp*age_L	6	314.2	326.2	2.8	196
exp*age_L	5	315.1	325.1	1.7	197
age_L	4	319.9	327.9	4.5	198
exp	4	314.4	323.4	0	198
intercep	3	322.5	328.5	5.1	199
<i>Pre-fledgling mass</i>					
exp*age_Q	9	208.3	226.3	3.3	83
exp+age_Q	8	208.6	224.6	1.6	84
exp*age_L	8	209.4	225.4	2.4	84
exp*age_L	7	210.9	224.9	1.9	85
age_L	6	211	223	0	86
exp	6	219.1	231.1	8.1	86
chick_sex	5	221	231	8	87
<i>Laying date</i>					

exp*age_Q	8	1607	1623	2.2	240
exp+age_Q	7	1607	1621.3	0.5	241
exp*age_L	7	1610	1623.5	2.7	241
exp*age_L	6	1610	1621.9	1.1	242
age_L	5	1612	1621.7	0.9	243
exp	5	1611	1620.8	0	243
intercep	4	1616	1624	3.2	244
(b) Southern giant petrel					
Model	d.f.	Deviance	AIC	AIC	Residual d.f.
Population level					
<i>Breeding success</i>					
Quadratic	5	607.08	617.08	0	482
Polynomial	6	607.27	619.27	2.19	481
Linear	4	624.98	632.98	15.9	483
Year	3	628.24	634.24	17.16	484
intercept	2	649.6	653.6	36.52	485
<i>Pre-fledgling mass</i>					
Constant	3	567.9	573.9	151.9	186
Linear	5	410.4	422.4	0.4	146
Year	4	412	422	0	147
Polynomial	7	408.5	424.5	2.5	144
Quadratic	6	409.9	423.9	1.9	145
<i>Laying date</i>					
Linear	4	2588.9	2596.9	0	403
Constant	3	2608.6	2614.6	17.7	404
Polynomial	6	2587.6	2599.6	2.7	401
Quadratic	5	2588.3	2598.3	1.4	402
Early adult life					
<i>Breeding success</i>					
exp*age_Q	7	210.3	224.3	4.5	195
exp+age_Q	6	210.3	222.3	2.5	196
exp*age_L	6	211.1	223.1	3.3	196
exp*age_L	5	211.1	221.1	1.3	197
age_L	4	211.8	219.8	0	198
exp	4	213.6	221.6	1.8	198
intercep	3	217	223	3.2	199
<i>Pre-fledgling mass</i>					
exp*age_Q	9	130.3	148.3	3.8	45
exp+age_Q	8	130.5	146.5	2	46
exp*age_L	8	130.4	146.4	1.9	46
exp*age_L	7	130.9	144.9	0.4	47
age_L	6	132.5	144.5	0	48
exp	6	132.6	144.6	0.1	48
chick_sex	5	136.9	146.9	2.4	49
<i>Laying date</i>					

exp*age_Q	8	1299.9	1315.9	5.4	193
exp+age_Q	7	1299.9	1313.9	3.4	194
exp*age_L	7	1300.1	1314.1	3.6	194
exp+age_L	6	1300.5	1312.5	2	195
age_L	5	1301.7	1311.7	1.2	196
exp	5	1300.6	1310.5	0	196
intercept	4	1302	1310.5	0	197

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