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Sex-specific effects of fisheries and climate on the demography of sexually dimorphic seabirds

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Abstract

1. 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.

2. 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 adult survival and use two-sex matrix population models to forecast future trends.

3. As expected, survival of male NGP was positively affected by carrion availability, but negatively affected by zonal winds. Female survival was positively affected by meridional winds and El Niño–Southern Oscillation (ENSO), and negatively affected by sea ice concentration and pelagic longline effort. Survival of SGPs did not differ between sexes; however, survival of males only was positively correlated with the Southern Annular Mode (SAM).

4. 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.

5. 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 may not be apparent when all individuals are considered together, ignoring sex differences could underestimate the relative influence of a changing environment on demography.

KEYWORDS
giant petrels, *Macronectes giganteus*, *Macronectes halli*, sex-specific effects, sexual size dimorphism, South Georgia, Southern Ocean, survival

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1 | INTRODUCTION

Male and female animals often differ in aspects of their physiology, morphology, behaviour, reproductive roles and social interactions (Breed & Moore, 2015; Ruckstuhl, 2006). These differences can cause sex-related variation in ecological and demographic traits, and ultimately sex-specific demographic responses to environmental change (Jenouvrier et al., 2012; Kraus, Eberle, & Kappeler, 2008; Oro, Torres, Rodríguez, & Drummond, 2010; Vaughn, Turnross, & Carrington, 2014).

Understanding how species and populations respond to global climate change and anthropogenic effects is a major challenge in modern ecology. In the oceans, biodiversity and ecosystem functioning are threatened by changing temperatures, decreasing pH, expanding fisheries and habitat degradation (Halpern et al., 2008; Sydeman, Poloczanska, Reed, & Thompson, 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 (Sydeman et al., 2015; Weimerskirch, Inchausti, Guinet, & Barbraud, 2003). For example, fisheries may have negative effects via bycatch (Nel, Ryan, & Watkins, 2002; 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, Louzao, Grissac, & Delord, 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 (Lewis, Phillips, Burthe, Wanless, & Daunt, 2015; Martínez-Abraín et al., 2006; Oro et al., 2010).

Parts of the Atlantic sector of the Southern Ocean are among the fastest warming regions on Earth (Meredith & King, 2005). There, oceanographic and atmospheric changes have produced a range of ecosystem-level disturbances, affecting a diversity of marine predators (Atkinson, Siegel, Pakhomov, & Rothery, 2004; Trathan, Forcada, & Murphy, 2007). This region, and subtropical waters to the north, has also been exploited by large-scale commercial fisheries, causing unsustainable levels of bycatch and ecological change (Croxall & Nicol, 2004; Jiménez, Phillips, Brazeiro, Defeo, & Domingo, 2014; Tuck et al., 2011). 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; Descamps et al., 2016; Forcada & Hoffman, 2014); however, very few have examined sex-specific responses (Jenouvrier et al., 2012; Olsson & Van der Jeugd, 2002; Pardo, Barbraud, Authier, & Weimerskirch, 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 ideal models

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 & Gonzalez-solis, 2004). They forage either at sea (from the ice edge to the subtropics) 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 monopolize scavenging opportunities on land, forcing females to forage at sea (González-Solís, Croxall, & Wood, 2000; Granroth-Wilding & Phillips, 2018). Later in the breeding season (when carrion availability has declined), and during winter, both sexes forage predominantly at sea (González-Solís, Croxall, & Afanasyev, 2008), including around fishing vessels (Jiménez, Domingo, Abreu, & Brazeiro, 2011; Otley et al., 2007; Weimerskirch, Capdeville, & Duhamel, 2000). Although this results in greater overlap between sexes during winter, a degree of sexual segregation is maintained with females overlapping more than males with demersal longline, trawl (González-Solís et al., 2008, 2000; Otley et al., 2007; Phillips, Bearhop, McGill, & Dawson, 2009) and, potentially, pelagic longline fisheries (Phillips et al., 2009; Thiers et al., 2014).

Here, we used long-term capture–mark–recapture (CMR) data from breeding adults of 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 expected high values of the Southern Annular Mode (SAM) and El Niño–Southern Oscillation (ENSO) to have negative effects on adult giant petrel survival via reductions in krill availability (Descamps et al., 2016; Trathan et al., 2007). We also predicted that survival of the more pelagic females in both species would be lower and more sensitive to variation in fishing effort and oceanographic conditions than that of males, which instead would be more sensitive to variation in carrion availability, especially in NGP, given their dominance as scavengers on land during the early breeding season (González-Solís et al., 2000; Hunter, 1983).

2 | MATERIALS AND METHODS

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 of 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, Techow, Wood, and Phillips (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.

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 S1). Based on 1,376 encounter histories of NGP (623 males and 753 females) and 688 of SGP (314 males and 374 females), we estimated key demographic rates for each species, calculated as probabilities of transition from one state to the next. The estimated demographic rates were (a) adult overwinter survival (probability of an adult surviving from one breeding season to the next), (b) encounter probability (probability of a surviving adult being encountered in the next season), (c) breeding probability (probability of an adult encountered alive laying an egg) and (iv) breeding success (probability of a breeding bird fledging a chick), which for population modelling purposes was assumed as the number of chicks per breeding pair. The GEPAT matrix underlying our model, provided in Appendix S1, shows that non-breeding individuals are unobservable, so their encounter probability = 0. The study was conducted in a well-demarcated area, and over the 15 years, breeding site fidelity was high with <1% of the monitored population observed breeding in adjacent areas (checked each year). Therefore, emigration was not considered.

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 (Choquet et al., 2009; Pradel, Gimenez, & Lebreton, 2005). Under the CJS assumptions, this comprised two tests and their subcomponents: Test 2 (subcomponents 2.CT + 2.CI) examines heterogeneity in recapture probabilities and

trap-dependent effects; and Test 3 (subcomponents 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-dependent effects, which are common in seabirds that often defer (skip) breeding. Thus, GOF can be conducted excluding Test 2 (Pardo et al., 2017). Test 3 was associated with reasonable global variance inflation factors; therefore, for each species, we incorporated the ĉ value into E-SURGE to perform model selection using the second-order Akaike's information criterion (QAICc) corrected for overdispersion and small sample sizes (Burnham & Anderson, 2002). When two models had ΔQAICc < 2, the most parsimonious was chosen (Lebreton, Burnham, & Clobert, 1992). We selected the best structure for encounter probabilities, comparing models with time (year), sex and their interaction. We then selected the best structure for breeding probability, then breeding success and, subsequently, survival, while keeping the selected structure from the previous step.

2.4 | Sex differences in survival

First, to explore annual differences, the survival of males (Sm) and females (Sf) was expressed as a proportional annual survival differential ΔS (($Sm-Sf$)/Sf*100; Jenouvrier, Caswell, Barbraud, & Weimerskirch, 2010). Second, to investigate environmental drivers of adult survival of each sex, we constructed CMR models in which variation in survival of only males or only females was constrained by potentially influential covariates selected based upon previous knowledge of seabird and giant petrel ecology (Appendix S2). Including age in the models and accounting for covariate effects on juvenile survival would be valuable. However, intensive monitoring started in the early 2000s and insufficient birds at the study site had been ringed previously as chicks to enable us to build age-specific models or calculate juvenile survival.

2.5 | Environmental covariates

2.5.1 | Effect on survival

Because giant petrels can be highly pelagic, but can also forage on land, we considered a large number of variables (Appendix S2). These were (a) large-scale climatic indices: El Niño–Southern Oscillation (ENSO) and Southern Annular Mode (SAM); (b) conditions in at-sea foraging areas, including sea surface temperature (SST), sea ice concentration (SIC), net primary productivity (NPP), wind speed (zonal – ZON and meridional – MER components), Antarctic krill *Euphausia superba* density and fisheries; and (c) carrion availability on land, expressed as the number of fur seal pups born in a study beach at Bird Island (Figure 1). For both giant petrel species, SST was negatively correlated with SIC (NGP, $r = -0.75$, $p < 0.01$; SGP, $r = -0.84$, $p < 0.01$) and positively correlated with NPP (NGP, $r = 0.55$, $p = 0.04$; SGP, $r = 0.51$, $p = 0.02$), so we dropped SST and retained SIC and NPP as candidate variables, since we were more interested in the
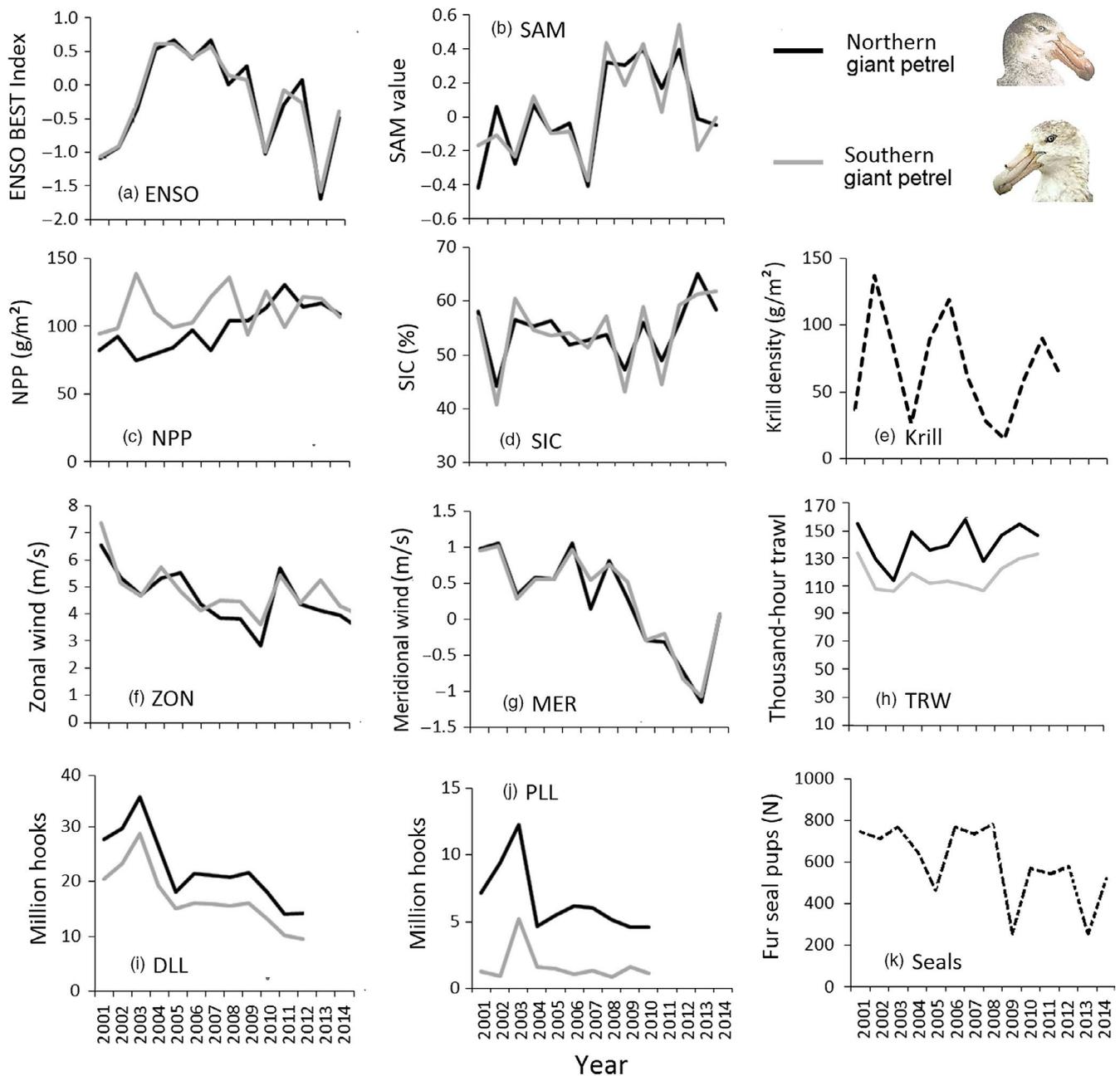
FIGURE 1   Annual variation in covariates (raw data) included as candidate predictors in models of survival of northern (black line) and southern (grey lines) giant petrels. Black dotted lines indicate covariates with common values for both species. (a) ENSO, El Nino–Southern Oscillation, 2-year lag; (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 S2 for details on data sources

oceanographic drivers associated with SST than temperature per se (Table S2.1).

Each variable was standardized to $\bar{x} = 0$ and $\sigma = 1$ (Schielzeth, 2010) before constraining the models using a logit link function. Subsequently, we ran models including covariate effects and examined the magnitude of these effects on adult males or females surviving using analysis of deviance (ANODEV), which we calculated as the fraction of temporal variation explained by each covariate (Grosbois et al., 2008). Because we detected significant linear trends in the

survival of both giant petrel species, as well as in some covariates, to decrease the risk of detecting spurious correlations when both the trait and covariate change in tandem over time, we examined the influence of environmental drivers on adult survival using detrended models (Grosbois et al., 2008). The influence of a covariate was considered statistically significant if the 95% confidence interval of the corresponding slope excluded zero (Grosbois et al., 2008).

For the climatic indices and at-sea conditions in wintering areas, monthly values from April–September and June–October were

TABLE 1 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	ΔQAICc
Northern giant petrel				
Time	94	18,780.5	8,537.5	0.0
Time + state	96	18,780.5	8,541.6	4.1
Time * state	107	18,780.5	8,564.2	26.8
State	84	18,910.4	8,574.7	37.2
Constant	83	18,942.6	8,586.9	49.5
Southern giant petrel				
Time	95	10,628.9	4,498.7	0.0
Time + state	96	10,628.9	4,500.8	2.1
Constant	83	10,709.7	4,506.1	7.4
State	84	10,734.5	4,518.2	19.6
Time * state	107	10,628.9	4,524.1	25.5

averaged to provide a single winter mean value for NGP and SGP, respectively, with the offset in timing reflecting the difference in laying dates (Hunter, 1984).

2.5.2 | Spatial extent of environmental covariates

At-sea distributions of non-breeding birds were mapped for each giant petrel species, based on 130 and 126 tracks of different individuals of NGP and SGP, respectively, fitted with Global Location Sensors (GLS loggers; British Antarctic Survey, Cambridge, UK) in summer 1999/2000 (Figure S2.1; based on data in González-Solís et al., 2008). Subsequently, we extracted the data for the model covariates from all of the 5 × 5° cells within the 50% utilization 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% UDs 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 Appendix S2).

2.6 | The two-sex matrix model

To explore the potential effects of sex differences in survival in response to environmental drivers on population growth rate, we developed a series of stochastic, two-sex population matrix model for each giant petrel species (Appendix S3, Caswell, 2001) 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. This involved calculating the expected change in survival (Ec) as Ec = slope*(logit(S_{max}) – logit(S_{min})), where slope is the mean (±SE) covariate effect, and S_{max} and S_{min} are the maximum and minimum survival

estimate for each sex from the time*sex model. Subsequently, new survival values were calculated by adding or subtracting the *Ec* to the mean (± *SE*) survival value for each sex (depending on the expected direction of the effect). More details on the demographic modelling and supporting information justifying the assumptions on future trends of each influential covariate are presented in Appendix S3 and S4.

3 | RESULTS

3.1 | Goodness-of-fit and model selection

The GOF based on Test 3 indicated that the CJS model did not fit the data well for either NGP (males: χ^2 = 68.5, df = 27, p < 0.001; females: χ^2 = 58.0, df = 28, p < 0.001) or SGP (males: χ^2 = 72.0, df = 26, p < 0.001; females: χ^2 = 56.2, df = 26, p < 0.001) (Table S1). However, Test 3 was associated with reasonable global variance inflation factors ($\hat{c}$ < 3) for both NGP ($\hat{c}$ = 2.25) and SGP ($\hat{c}$ = 2.46), calculated for each species as $\hat{c} = \left(\chi^2_{males} + \chi^2_{females} \right) / (df_{males} + df_{females})$. Therefore, for each species, we incorporated the global $\hat{c}$ value into E-SURGE to perform model selection (Burnham & Anderson, 2002).

Our initial model had survival varying over time, by sex and previous state, which compared breeders (successful and failed pooled) with non-breeders (post-successful and post-failed pooled). Breeding probability was kept constant (intercept only), because in our model all observed individuals are breeders (successful or failed breeder), and therefore, the breeding probability is confounded with encounter probability. Breeding success varied over time and by previous state. Table S2 shows the model selection for the complete set of models run for each species.

3.2 | Encounter probability

The model with encounter probability varying by sex, year and state suggested a lack of fit, low 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 1, Figure S2).

3.3 | Annual adult survival probability

Mean annual survival (± 95% CI) of NGP (0.91, 0.90–0.92) and SGP (0.92, 0.90–0.93) was similar. The linear trend model was the best-supported non-covariate model for both species, indicating a significant decline in survival of both NGP (slope ± SE = −0.48 ± 0.05) and SGP (slope = −0.42 ± 0.10, Table 2).

In both species, mean survival was higher in males than females and the magnitude of the difference between the sexes was similar (NGP, ΔS = 2.22%; SGP, ΔS = 2.20%); however, only

TABLE 2 Model selection to estimate adult annual survival of northern and southern giant petrels and the effects of significant explanatory covariates that had a significant effect on the temporal variation in annual survival

	K	Deviance	QAICc	ΔQAICc	% R^2	P_{ANODEV}	Slope	CI−	CI+
(a) Northern giant petrel									
Model—Parameters									
Linear trend	46	18,795.1	8,446.0	0.0	71	<0.001	−0.48	−0.59	−0.38
Time	57	18,768.4	8,456.4	10.5					
Time*sex	71	18,736.3	8,470.7	14.3					
Sex	46	18,850.9	8,470.8	14.4					
Constant	45	18,860.9	8,473.2	16.8					
Sex-specific covariate models									
Female_PLL	48	18,818.2	8,457.8	0.6	10	0.308	−0.28	−0.48	−0.07
Female_SIC	48	18,813.0	8,458.0	0.8	20	0.149	−0.23	−0.38	−0.09
Female_MER	48	18,814.6	8,458.7	1.5	17	0.185	0.28	0.01	0.54
Female_ENSO	48	18,818.7	8,460.6	3.4	9	0.332	0.21	0.03	0.34
Female_Linear	47	18,824.0	8,460.9	3.7	40	0.047	−0.27	−0.48	−0.05
Male_Seal	48	18,826.1	8,463.9	6.7	15	0.213	0.26	0.1	0.41
Male_ZON	48	18,827.9	8,464.1	7.0	14	0.229	−0.29	−0.58	−0.01
Male_Linear	47	18,836.4	8,466.4	9.2	26	0.158	−0.48	−0.63	−0.32
(b) Southern giant petrel									
Model—parameters									
Linear trend	46	10,640.4	4,401.1	0.0	42	0.012	−0.42	−0.59	−0.24
Constant	45	10,661.0	4,407.4	6.3					
Sex	46	10,658.9	4,408.6	7.5					
Time	57	10,612.3	4,412.4	11.3					
Time*sex	71	10,597.2	4,435.4	34.3					
Sex-specific covariate models									
Male_SAM	48	10,637.9	4,404.2	0.0	25	0.097	0.38	0.12	0.63
Male_Linear	47	10,646.4	4,405.6	1.4	30	0.043	−0.46	−0.71	−0.21
Female_Linear	47	10,653.1	4,408.3	4.1	16	0.154	−0.27	−0.48	−0.05

Note: Detrended covariate models are shown along with the time-dependent (Time), the sex-specific (Sex), the sex- and time-dependent (Time*sex), the constant and the linear trend models.

for NGP was the sex-dependent model better supported than the model without a sex effect (sex vs. constant, ΔQAICc = 2.4; Table 2, Figure 2). Mean survival (±95% CI) of male and female NGP was 0.92 (0.90–0.93) and 0.90 (0.88–0.91), respectively, and survival 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 (Table 2, Figure 2); therefore, the interpretation of sex-specific responses was based on detrended models only. For NGP, there was a negative effect of SIC and a positive effect of meridional wind and ENSO, but this was only apparent in female survival. There was a negative effect of zonal wind on male 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). For SGP, the effect of the environmental variables

also varied by sex; SAM had a significant positive effect, but only on male survival (Figure 3), whereas none of the tested covariates had statistically significant effects on female survival.

3.4 | Trends in environmental drivers and population growth

For NGP, the stochastic population growth rate (λ; lambda) based on the mean male and female survival across the time series (2001–2014) was 1.003 (95% confidence intervals: 0.997–1.008). Taking into account the cumulative effects of predicted changes on the influential covariates, λ was 1.017 (1.002–1.029) if pelagic longline effort remains stable, and 1.005 (0.979–1.024) and 1.025 (1.013–1.034) for increased and decreased pelagic longline effort, respectively (Table 3, Figure 4).

For SGP, the population growth based on the mean values of male and female survival was 0.999 (0.992–1.006), and the only
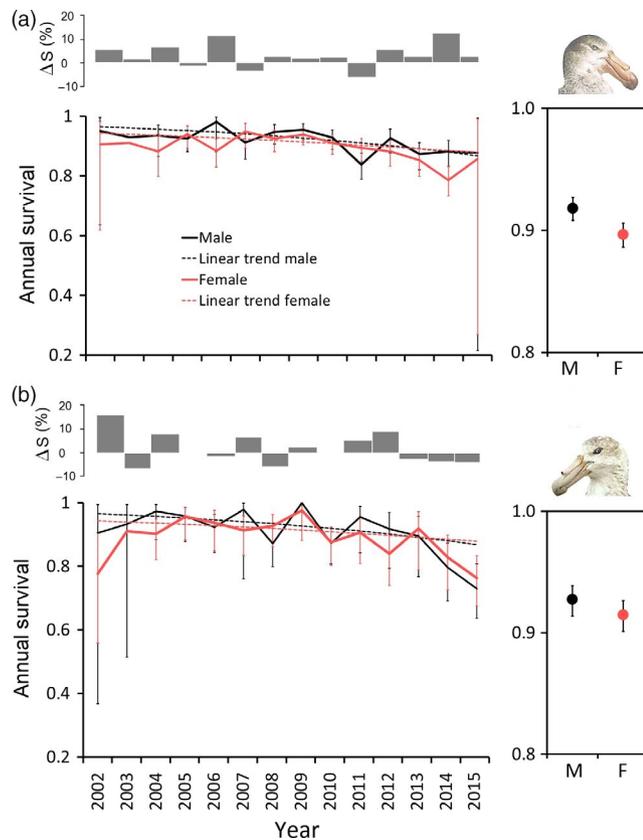
FIGURE 2 Sex-specific survival of (a) northern and (b) southern giant petrels. Left panels show the annual variation in survival of males and females, and the male–female survival differential (ΔS), which expresses the percentage difference in male survival relative to female. Right panels show the mean sex-specific survival. Error bars are the ±95% confidence intervals

influential covariate was SAM, which is predicted to increase in the future, with a positive effect on male survival only, increasing λ to 1.021 (0.996–1.035) (Table 3, Figure 4).

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 (Jenouvrier et al., 2012; Martínez-Abraín et al., 2006; Olsson & Van der Jeugd, 2002). Although the canalization theory (Fay, Weimerskirch, Delord, & Barbraud, 2015; Gaillard & Yoccoz, 2003) predicts a stronger buffering against environmental variability in adult survival (Jenouvrier, Barbraud, Cazelles, & Weimerskirch, 2005; Pardo et al., 2017), which is the most sensitive vital rate to the population growth rate of large seabirds, 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, highlighting the importance of considering such within-population variation. The interspecific differences may be related to allochrony, since

NGP breed six weeks earlier, but may also be related to the smaller sample size for SGP, making it difficult to detect significant covariate effects when they are not very strong. Possible ecological links underlying these relationships, and the causes and implications of differences between species and sexes are discussed below.

4.1 | Fur seal carrion

The significant positive influence of fur seal productivity on the survival of male NGPs is consistent with their higher reliance on carrion during breeding; 94% of the birds foraging on fur seal carcasses during the breeding season were male NGPs (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 *Hydrurga leptonyx* (Schwarz, Goebel, Costa, & Kilpatrick, 2013), benefiting male NGPs that remain around South Georgia year-round.

4.2 | 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). 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 S2). The positive effect of ENSO on survival of NGP females and the trend in this direction for males is likely because ENSO influences oceanographic conditions at a basin scale, thus affecting foraging areas of males and females throughout the year (Barbraud et al., 2012; Trathan et al., 2007). The negative effect of SIC on female NGP only is consistent with our predictions about more pelagic females. 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 S2), 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 increase 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, Barbraud, Chambellant, & Guinet, 2005; Horswill et al., 2014; Trivelpiece et al., 2011) and thus increase carrion availability. The positive effect of SAM on survival of male SGPs suggests that survival of this species is also higher in relatively warmer years.

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 (Fielding et al., 2014). This may be due to their ability to switch to a number of alternative prey, including squid, carrion or other seabirds (Hunter, 1983; Phillips, McGill, Dawson, & Bearhop, 2011), and fishing discards (Bugoni,
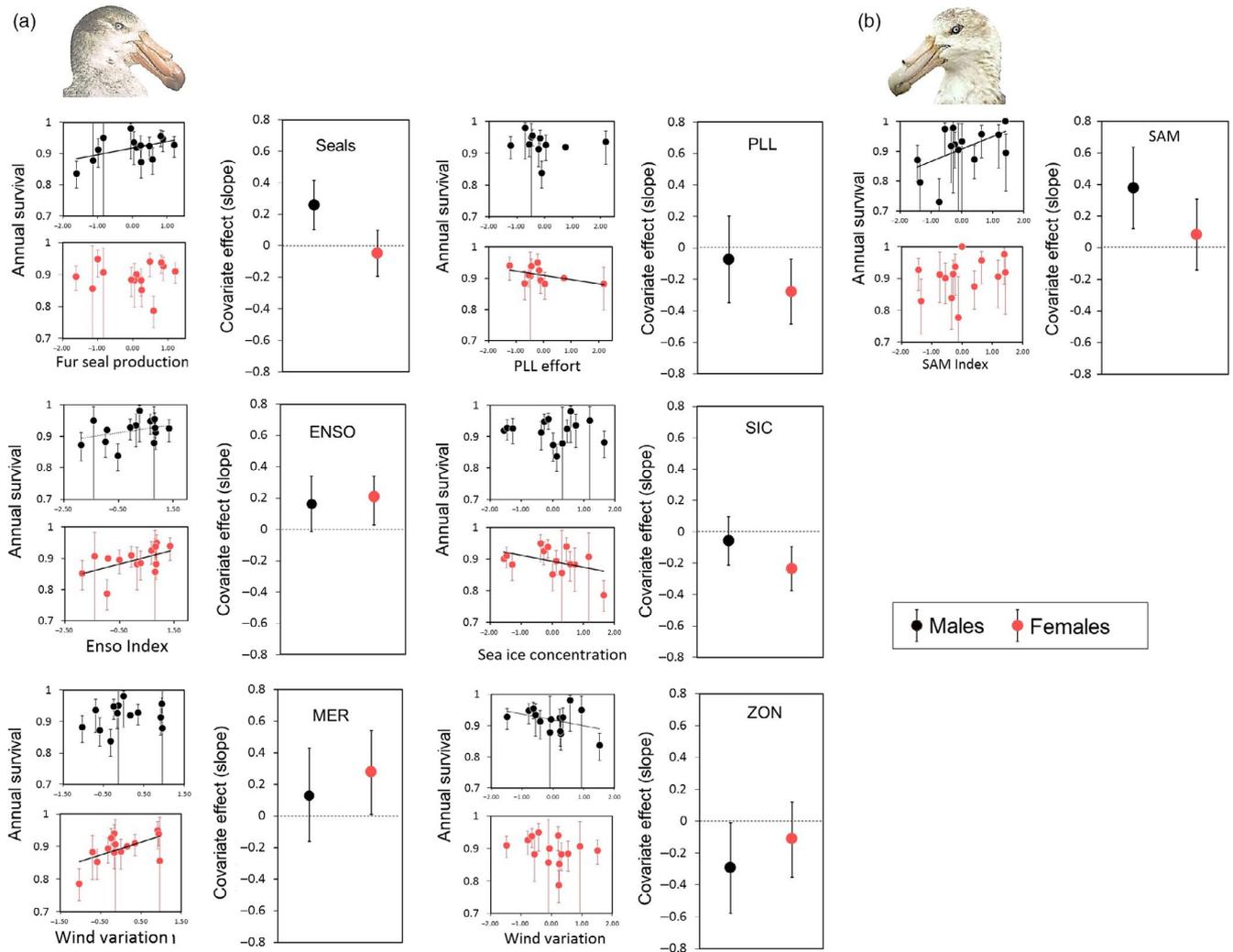
FIGURE 3 Relative effect of explanatory variables on male and female survival of (a) northern giant petrels and (b) southern giant petrels. The scatter plots show annual survival of males and females (from the sex- and time-dependent model) as function of explanatory variables (detrended and scaled values), and the vertical panels show the covariate effect (slope) on male and female survival. Fur seal productivity (Fur seals), El Nino–Southern Oscillation (ENSO), Southern Annular Mode (SAM), sea ice concentration (SIC), zonal (ZON) and meridional (MER) wind speed (ms^{-1}), and pelagic longline effort (PLL, millions of hooks). Error bars represent ±95% confidence intervals

Mcgill, & Furness, 2010; Copello, Quintana, & Pérez, 2008) or because we were unable to sample krill throughout the extensive foraging ranges of giant petrels during the winter (Appendix S2, González-Solís et al., 2008).

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 positive effect of meridional winds on female NGP survival. This sex-specific response supports our predictions about more pelagic females and is consistent with Weimerskirch et al. (2012) who found that shifts in meridional winds primarily affected foraging performance of female wandering albatross *Diomedea exulans*. However, the inverse relationship between zonal winds and male NGP survival is contrary to our predictions and may therefore indicate other indirect effects, such as wind-driven changes in oceanographic conditions (Holland & Kwok, 2012; Lee et al., 2017).

4.3 | Fisheries

Giant petrel mortality was formerly high in demersal longline fisheries around sub-Antarctic islands, impacting mainly females (Ashford, Croxall, Rubilar, & Moreno, 1994; Nel et al., 2002); however, this type of fishing is now prohibited around South Georgia during the summer, and during the winter seabird bycatch is negligible due to the mandatory adoption of mitigation measures. Accordingly, we found no effect of demersal longline effort on survival in our study populations. Elsewhere, giant petrel bycatch has been recorded in trawl (Sullivan, Reid, & Bugoni, 2006) and pelagic longline fisheries (Tuck et al., 2011), but with relatively low vulnerability to bycatch compared with albatrosses (Jiménez, Domingo, Abreu, & Brazeiro, 2012; Sullivan et al., 2006; Weimerskirch et al., 2000). Aligned with this, there was no significant effect of trawl fishing effort on the survival of either giant petrel species, although there was a negative relationship between pelagic longline effort and female NGP survival. Female giant petrels are more

TABLE 3 Survival values for male and female giant petrels, as influenced by predicted trends in the influential covariates (See Appendix S3)

Influential variable	Future trend	Mean slope		Ec		New survival		Mean OSR	λ (95% CI)
		Male	Female	Male	Female	Male	Female		
Northern giant petrel									
ENSO	+	ns	0.179	0.00	0.023	0.92	0.923	0.97	1.012 (1.004–1.020)
SIC	−	ns	−0.230	0.00	0.029	0.92	0.929	0.91	1.013 (1.006–1.021)
MER	+	ns	0.281	0.00	0.033	0.92	0.933	0.86	1.014 (1.002–1.026)
SEAL	−	0.260	ns	−0.056	0.00	0.864	0.90	0.72	0.985 (0.975–0.996)
PLL ↑	+	ns	−0.281	0.00	−0.050	0.92	0.85	1.97	0.990 (0.982–0.997)
PLL ↓	−	ns	−0.280	0.00	0.033	0.92	0.933	0.86	1.014 (1.004–1.024)
ENSO, MER, SIC, SEAL				−0.056	0.064	0.864	0.964	0.35	1.017 (1.002–1.029)
ENSO, MER, SIC, SEAL, PLL ↑				−0.056	0.043	0.864	0.943	0.45	1.005 (0.979–1.024)
ENSO, MER, SIC, SEAL, PLL ↓				−0.056	0.076	0.864	0.976	0.31	1.025 (1.013–1.034)
Mean survival						0.92	0.90	1.24	1.003 (0.997–1.008)
Southern giant petrel									
SAM	+	0.379	ns	0.046	0.00	0.976	0.91	2.45	1.021 (0.996–1.035)
Mean survival						0.93	0.91	1.29	0.999 (0.992–1.006)

Note: Expected change (Ec) in survival as influenced by the covariates was calculated by multiplying the covariate slope (± *SE*) by the range (logit(max)−logit(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 adding or subtracting the Ec to the mean survival value for each sex (in logit space, see Appendix S3). OSR is the mean operational sex ratio (OSR = N_m/N_f), and λ is the mean stochastic population growth rate ± 95% quantiles (or bootstrapped confidence intervals, CI).
Abbreviations: ENSO, El Nino–Southern Oscillation; SAM, Southern Annular Mode; SIC, sea ice concentration; MER, meridional wind; SEAL, Antarctic fur seal carrion availability; PLL, pelagic longline effort.

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 (Bugoni et al., 2010; Krüger, Paiva, Petry, & Ramos, 2017; Votier et al., 2004), particularly during winter for our study populations, when birds forage primarily at sea (González-Solís et al., 2008). However, based on our detrended models, there was no evidence of any positive effects of fishing discards on the survival of adult giant petrels from Bird Island.

## 4.4 | Future prospects for giant petrels in a rapidly changing ecosystem

Despite the rapid changes 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 (Atkinson et al., 2004; Reid & Croxall, 2001; 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 the future, whereas the growth rate based on the mean values of male and female survival suggested that population sizes would remain relatively stable under the current environmental conditions (Figure 4).

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 & Hoffman, 2014; Forcada, Trathan, Reid, & Murphy, 2005; Horswill et al., 2014; Trathan et al., 2007), 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 by-catch of females (Gianuca, Phillips, & Votier, 2017).

5 | CONCLUSIONS

Survival of giant petrels is influenced by large-scale climatic indices, oceanographic characteristics, the availability of seal carrion and

FIGURE 4 Mean (lines) ± 95% bootstrapped confidence intervals (polygons) population trajectories of (a to c) northern giant petrels and (d) southern giant petrels, based on the estimated vital rates and on predicted trends for the explanatory variables. Population projections are influenced by predicted trends in Southern Annular Mode (SAM), El Nino–Southern Oscillation (ENSO), sea ice concentration (SIC), meridional wind speed (MER), fur seal pup production (SEAL) and pelagic longline effort within the foraging area (PLL); '↑'and '↓'refer to the expected direction of change of each covariate in future, representing increases and decreases, respectively, and "♀"and "♂" indicate that females and males, respectively, are affected in each case
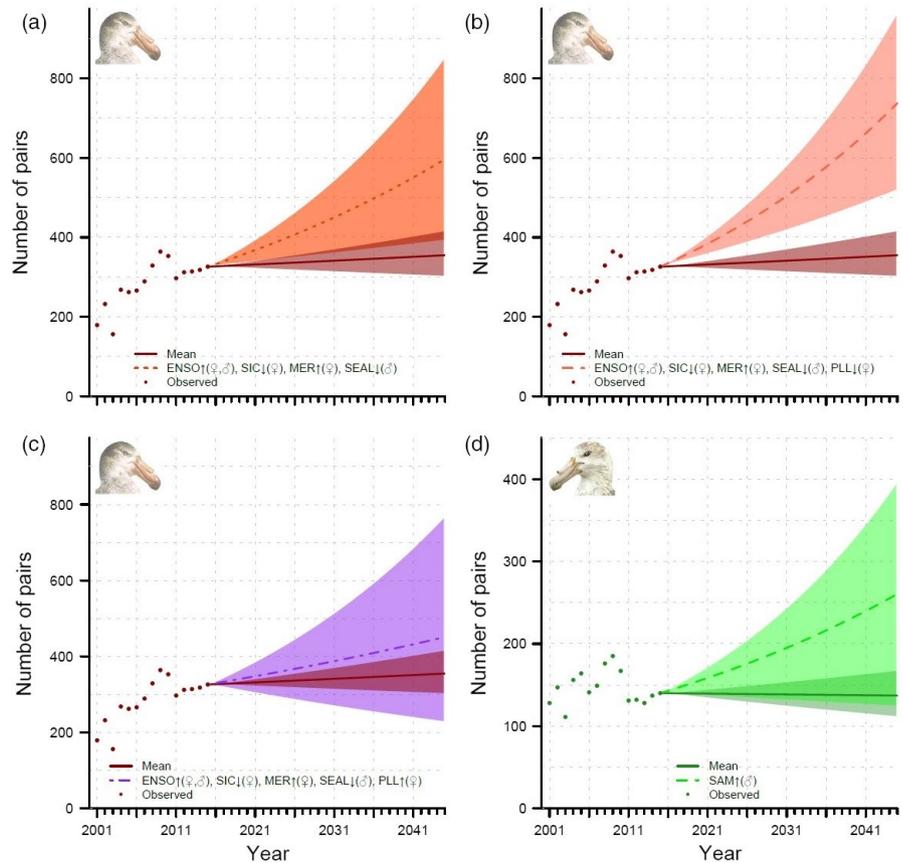
fisheries, but with contrasting effects for males and females. Modelled population trajectories of both species match the observed trends at Bird Island, and the future environmental changes are likely to benefit their population growth. However, a potential increase in pelagic longline fisheries could reduce female survival. The present study provides a better understanding of how sexual size dimorphism of a land-based marine predator can influence 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.

AUTHORS' CONTRIBUTIONS

D.G., S.C.V. and R.A.P. conceived and designed the study; R.A.P. oversees the long-term giant petrel study; A.G.W. manages the long-term demographic data; G.N.T. manages the global multi-fisheries dataset; J.F. oversees the long-term Antarctic fur seal study; L.I. extracted the remotely sensed covariates from the wintering areas; R.B.S. and D.G. conducted the stochastic population projection modelling; D.G. conducted all other the analyses, with inputs from D.P., R.C., R.P., S.C.V. and S.T., and drafted the manuscript; and all authors contributed substantially to revisions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Individual encounter histories for both species of giant petrels are available here: Dryad entry: https://doi.org/10.5061/dryad.37qt6nm (Gianuca et al., 2019). Data on climate indexes were obtained from the Climate Diagnostics Centre of NOAA (http://www.cdc.noaa.gov/people/cathy.smith/best/) and the Climate Prediction Centre of NOAA (http://www.cpc.ncep.noaa.gov/). Atmospheric and oceanographic data were obtained from MODIS (http://www.science.oregonstate.edu/ocean.productivity), SeaWiFS (https://oceancolor.gsfc.nasa.gov/data/seawifs/) and QuickSCAT/ASCAT (http://cersat.ifremer.fr/data/products/catalogue) databases. Krill data are available in Fielding et al., (2014). Publicly available fishery effort data were downloaded directly from ICCAT (https://www.iccat.int/en/t2ce.asp) or are provided in Tuck et al. (2015a): Dryad entry: https://doi.org/10.5061/dryad.7f63m (Tuck et al., 2015b). Data from several fisheries agencies are commercially sensitive and have not been archived, but

can be requested through the agency data managers: CCAMLR (www.ccamlr.org/), Falkland Islands (www.fis.com/falklandfish). The giant petrel tracking data can be downloaded from the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/contributor.php?contributor_xml:id=361; dataset ids: 497, 498, 499, 500, 1,385, 1,392, 1,393).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.