

Climate variability and breeding parameters of a transhemispheric migratory seabird over seven decades

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ABSTRACT: Climate variability affects physical oceanographic systems and environmental conditions at multiple spatial and temporal scales. These changes can influence biological and ecological processes, from primary productivity to higher trophic levels. Short-tailed shearwaters *Ardenna tenuirostris* are transhemispheric migratory procellariiform seabirds that forage on secondary consumers such as fish (myctophids) and zooplankton (euphausiids). In this study, we investigated the breeding parameters of the short-tailed shearwater from a colony of 100 to 200 breeding pairs at Fisher Island, Tasmania, Australia, for the period 1950 to 2012, with the aim to quantify the relationship between breeding parameters with large-scale climate indices in the Northern (i.e. Northern Pacific Index and Pacific Decadal Oscillation) and Southern Hemispheres (i.e. El Niño–Southern Oscillation and Southern Annular Mode). Through the use of generalised linear models, we found that breeding participation among short-tailed shearwaters was affected by climate variability with a 12-mo temporal lag. Furthermore, breeding success decreased in years of increased rainfall at the colony. These findings demonstrate that both large-scale climate indices and local environmental conditions could explain some of the variability among breeding parameters of the short-tailed shearwater.

KEY WORDS: Short-tailed shearwater · *Ardenna tenuirostris* · Trophic levels · Lag · Longitudinal study

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1. INTRODUCTION

Seabirds are higher trophic level species that are susceptible to climate variability on both local and regional scales (Napp & Hunt 2001, Jenouvrier 2013, Zador et al. 2013, Cushing et al. 2018). Oceanographic properties are influenced by large-scale physical forcing that alters atmospheric conditions, sea level pressure and ocean temperature, which in turn affect bottom-up processes, such as changes in primary and secondary productivity (Zador et al. 2013, Cushing et al. 2018). Variations in oceanographic

and climatic conditions can influence seabird nesting habitat, foraging grounds and resource availability, which could change their distribution, abundance, reproductive output and population growth (Frederiksen et al. 2004, Humphries & Möller 2017).

Climate variability in the Northern and Southern Hemispheres can be measured by large-scale climate indices. Shifts in these indices result in changes to prevailing weather, environmental conditions and oceanographic systems, which may affect biological and ecological processes (Stenseth & Mysterud 2002, Sprong et al. 2018). In the Northern Hemisphere, the

Pacific Decadal Oscillation (PDO) and the North Pacific Index (NPI) are the dominant climate drivers, and are known to influence seabird demography, abundance and distribution (Baduini et al. 2001, Hunt et al. 2002, Bond et al. 2011). The PDO operates on a quasi-decadal scale lasting 15 to 30 yr (Humphries & Möller 2017), and the NPI measures the strength of the Aleutian Low, an indicator of climate forcing in the Bering Sea (Trenberth & Hurrell 1994). In the Southern Hemisphere, the primary climate drivers are the El Niño–Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) (Grose et al. 2010), which have both been linked to the breeding performance of seabirds (Duffy 1990, Clucas 2011, Humphries & Möller 2017, Pardo et al. 2017). ENSO is a dominant climate index that fluctuates between 3 phases—neutral, warm (i.e. El Niño) and cool (i.e. La Niña)—and affects global climate, sea surface temperature (SST) and rainfall, while the SAM is the primary driver for climate variability in the Southern Hemisphere (Lovenduski & Gruber 2005, Stammerjohn et al. 2008, Sprogis et al. 2018) and is characterised by the movement of the westerly wind belt that circles Antarctica.

These 4 climate indices affect marine ecosystems on temporal scales from months to years (Trathan et al. 2007, Sallée et al. 2008). Low trophic order species can be rapidly affected by environmental changes; however, the effect on a predator population can take place months or even years later, as the changes in primary productivity propagate through the food web (Humphries & Möller 2017, Cox et al. 2018). Numerous studies have shown that the foraging success of seabirds affects their breeding performance, both directly during the breeding season (Pinaud & Weimerskirch 2002, Jenouvrier et al. 2018) and indirectly through carry-over effects during the non-breeding season (Shoji et al. 2015, Jenouvrier et al. 2018).

Procellariiformes (albatross, petrels and shearwaters) are seabirds with low production potential (e.g. low reproductive rates, single-egg clutch and delayed recruitment into the breeding population) (Warham 1990, Weimerskirch et al. 2001, Meathrel & Carey 2007). They are a trans-equatorial migratory seabird and spend the majority of their lives at sea, travelling great distances utilising a variety of habitats during the breeding and non-breeding periods. Consequently, they are exposed to a variety of weather, environmental conditions and oceanographic systems in both the Northern and Southern Hemispheres (Weimerskirch & Cherel 1998, Einoder et al. 2013, Yamamoto et al. 2015, Nishizawa et al. 2017).

One of the longest ecological studies (from 1947 to the present) of a procellariiform is that of the short-tailed shearwater *Ardenna tenuirostris* (formerly *Puffinus tenuirostris*) at Fisher Island, Tasmania, Australia. This population of birds has been monitored annually since 1947 through an extensive capture–mark–recapture (CMR) program (Serventy & Curry 1984, Wooller et al. 1990) that we used to investigate the breeding parameters of the short-tailed shearwater from Fisher Island and their relationship with large-scale climate indices from both the Northern and Southern Hemispheres. More specifically, we aim to: (i) investigate the annual trends in the breeding parameters of the short-tailed shearwater at Fisher Island; (ii) determine which climate indices have the most influence on breeding parameters; and (iii) identify any local environmental conditions that may also affect breeding success.

2. MATERIALS AND METHODS

2.1. Study species

The short-tailed shearwater is a medium-sized (500 to 800 g) burrow-nesting procellariiform (Skira 1990, Berlincourt & Arnould 2015), with pronounced pan-oceanic migration. Each September to October, birds return from their non-breeding grounds in the Northern Hemisphere to southeastern Australia to breed (Skira 1991). During the breeding season, shearwaters alternate short (local) and long foraging trips (Southern Ocean, across oceanic regions from longitude 80° E to 160° E) (Woehler et al. 2003, Raymond et al. 2010). The breeding season of the short-tailed shearwater begins in November, where one egg per successful breeding pair is laid. Laying is highly synchronised, with 95% of the eggs laid between 24 and 28 November. A breeding pair will not replace the single egg if it fails (Skira 1990). Hatching occurs from mid-to-late January (Carey 2010) and chicks fledge in mid-April to early May (Serventy 1967, Wooller et al. 1990). After the breeding season, adults and fledglings return to the North Pacific during the austral winter (Shaffer et al. 2006, Raymond et al. 2010, Vertigan et al. 2012).

2.2. Field site

The study colony is located on Fisher Island (40° 10' S, 148° 10' E), a 0.9 ha island in the Furneaux Island Group, Tasmania, Australia. All burrows on

the island have been marked with a number. Each year of the study, all new individuals captured in burrows during searches, including chicks, were banded with a uniquely numbered stainless-steel band, and the band and burrow numbers were recorded. If the bird was already banded, the band and burrow numbers were recorded. The methods used in the program to identify individuals and reproductive performance have been constant since 1947, and are further outlined in previous studies (Serventy 1967, Serventy & Curry 1984).

2.3. Shearwater breeding parameters

2.3.1. Breeding birds and chick numbers

From late November to mid-December each season, all burrows on the island were checked at least twice every 10 d to locate and identify both members of each breeding pair. Non-breeding (prospecting) birds generally only make short nocturnal visits to the island during the incubation and chick-rearing periods (Bradley et al. 1999), and tend to explore unoccupied burrows without taking up residency. While non-breeding birds constitute the majority of birds found on the surface within the colony (Serventy 1967), searching burrows minimises the likelihood of detecting a non-breeding bird. All burrows were checked again in late March to early April the following year and the presence or absence of chicks was recorded, with all new chicks banded. This study data set is continuous since 1947, with the exception of 2013 and 2014, when no breeding adults were recorded, and 1992, when the presence or absence of chicks was not recorded. In the first 3 yr of the study, there was a rapid increase in the number of breeding pairs, which could be attributed to initial difficulties in the establishment of the banding program. Consequently, we chose to remove the first 3 yr of data, from 1947 to 1949. We also chose to remove all data after 2012 due to the data gaps for breeding adults, to maintain consistency. Therefore, the time series used in this study is from 1950 to 2012.

2.3.2. Breeding success

Breeding success was calculated as the number of chicks in March divided by the number of burrows occupied by birds in December of the previous year. The number of eggs was not used to determine

breeding or hatching success, as the detection of eggs in burrows on Fisher Island was relatively low due to a lack of experience among observers, and the lengths and intricacies of the burrows themselves (Serventy & Curry 1984).

2.4. Breeding periods

To quantify the influence of climate on the breeding parameters of the short-tailed shearwater, 3 breeding periods were chosen in this study: (i) the pre-breeding/migration period (May to October), when the birds are building their body lipid reserves in the North Pacific Ocean in preparation for their return migration to southeastern Australia and subsequent breeding attempt (Yamamoto et al. 2015, Nishizawa et al. 2017); (ii) the early-breeding period (September to November), used to examine environmental variabilities that could affect adult condition and reproduction; and (iii) the chick-rearing period (December to March), where parental conditions/investment could be affected by environmental variabilities, which in turn could impact chick body condition and survival (Fay et al. 2015).

2.5. Temporal lags

Additionally, 3 temporal lags were chosen for each breeding period and incorporated into the analysis (Table 1). Temporal lag 1 (3 to 4 mo) was chosen to account for variation in spatial-temporal scales of oceanographic conditions, which may impact local resources (see Cox et al. 2018) and the direct effects of local environmental conditions such as poor weather conditions (Genovart et al. 2013, Fagundes et al. 2016) (Table 1). Temporal lags 2 (6 to 7 mo) and 3 (12 mo) were chosen as climate fluctuations, irradiation and wind stress can influence primary productivity (Sharples et al. 2006, Cox et al. 2018) and the propagation of lower trophic consumers, such as fish (myctophids) and zooplankton (euphausiids), which are a large component of the diet of short-tailed shearwaters (Nishizawa et al. 2017) (Table 1).

2.5. Environmental data

We used the PDO and NPI as indicators of Northern Hemisphere climatic conditions, and ENSO and SAM as indicators of Southern Hemisphere climatic conditions during the breeding periods. Monthly

Table 1. Breeding periods and temporal lags used in the generalised linear models to determine the influence of climate on breeding parameters of the short-tailed shearwater

Breeding period	Temporal lag 1 ⁽⁰⁾	Temporal lag 2 ^(-0.5)	Temporal lag 3 ⁽⁻¹⁾
Pre-breeding/migration (PB) May to October	May to August ^a (PB ⁰)	February to August ^a , the same year as the pre-breeding season (PB ^{-0.5})	November to October (PB ⁻¹)
Early breeding (EB) September to November	September to November (EB ⁰)	June to November the same year as the pre-breeding season (EB ^{-0.5})	December to November (EB ⁻¹)
Chick rearing (CR) December to March	December to March (CR ⁰)	September to March, the same year as the pre-breeding season (CR ^{-0.5})	April to March (CR ⁻¹)
^a Most short-tailed shearwaters migrate around September to October, so we did not include these months in this time period			

PDO values for the period 1949 to 2012 were obtained from the National Oceanic and Atmospheric Administration (NOAA) at: www.ncdc.noaa.gov/teleconnections/pdo/. The PDO index is calculated from the principal component of monthly SST anomalies in the North Pacific poleward of 20°N (Mantua & Hare 2002). The PDO values consist of persistent positive or negative temperature anomalies, classified as warm (positive value) or cool (negative value), which have been shown to impact marine ecosystems through changes in the species composition, distribution and abundance (Mantua & Hare 2002, Becker et al. 2007).

Monthly NPI means for the period 1949 to 2012 were obtained from NOAA at: https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Data/np.long.data (Hurrell 2017). The NPI is the mean sea-level pressure over the North Pacific Ocean 30° N to 65° N and 160° E to 140° W (Trenberth & Hurrell 1994). NPI measures the strength of the Aleutian Low in the atmosphere and is an indicator of climate forcing in the Bering Sea (Trenberth & Hurrell 1994, Zador et al. 2013). NPI has been linked to changes in physical ocean properties, such as sea-ice retreat (Zador et al. 2013), which can influence bottom-up processes, such as phytoplankton blooms.

Monthly Southern Oscillation Index (SOI) values for 1949 to 2012 were obtained from the Australian Bureau of Meteorology (BOM) at: www.bom.gov.au/climate/current/soi2.shtml. The SOI measures the difference in surface air pressure between Tahiti and Darwin (Trenberth 1997). It is also a key atmospheric index for ENSO and determines the strength of El Niño and La Niña events. El Niño events are sustained values of the index (lower than -8) and are associated with a warming of the central and eastern

tropical Pacific Ocean, whereas La Niña events are sustained values of the index (higher than +8) and are associated with oceanic cooling within these same areas (Trenberth 1997).

The SAM is the dominant mode of atmospheric variability at mid and high latitudes in the Southern Hemisphere. Monthly SAM data for 1957 to 2012 were extracted from the Natural Environment Research Council British Antarctic Survey at: www.nerc-bas.ac.uk/icd/gjma/sam.html (Marshall 2003). The SAM consists of both positive and negative states. During a positive SAM state, a strong westerly wind belt contracts toward Antarctica, causing high-pressure atmospheric systems over southern Australia that can result in either stable or dry conditions. Negative SAM values reflect the expansion of the strong westerly winds towards the equator, with low atmospheric pressure systems over southern Australia that can increase storm and rain events. These westerly winds are responsible for driving the circulation within the Southern Ocean (Lovenduski & Gruber 2005). Changes in wind patterns can affect the stirring of the water column, which can alter the depth in the mixed layer, impacting nutrient availability in the upper ocean, with follow-on consequences for biological production (Lovenduski & Gruber 2005).

Finally, we included monthly rainfall during the chick-rearing period (December to March), as localised rain events have been shown to influence the breeding parameters of burrowing seabirds (Serventy & Curry 1984, Bester et al. 2007). Monthly rainfall for the chick-rearing period between 1949 to 2012 was obtained from the Lady Barron station (<1 km from Fisher Island) from the Australian BOM at: www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_

nccObsCode=136&p_display_type=dailyDataFile&p_startYear=&p_c=&p_stn_num=099002.

2.6. Statistical analysis

Prior to model selection, a non-parametric measure of rank correlation (Spearman's ρ) was used to investigate correlation among the variables. Breeding success and the annual number of chicks were highly correlated; therefore, the annual number of chicks was removed from the analysis (Table S1 in the Supplement at www.int-res.com/articles/suppl/m642p191_supp.pdf). Correlations were found between several of the climate indices at each temporal lag (Tables S2 & S3 in the Supplement). For model parsimony, temporal lag 2 was excluded from the analysis based on rank correlation, as the relationship for each climate index (e.g. SAM) was strong (>0.75 correlation) between temporal lag 1 and/or 3 (Table S2). Removing temporal lag 2 also limits the number of model parameters, as constructing all possible models for each climate variable and temporal lag would create an unmanageable number of models. Additionally, PDO for the duration of pre-breeding/migration with temporal lag 1 (PDO PB⁰) and PDO with temporal lag 3 (PDO PB⁻¹) were highly correlated, thus only PDO PB⁻¹ was used in the analysis (Table S2). Additionally, SOI during the early-breeding period with temporal lag 1 (SOI EB⁰) and SOI with temporal lag 3 (SOI EB⁻¹) during the early-breeding period were correlated; therefore, SOI EB⁻¹ was used in the analysis. PDO PB⁻¹ and SOI EB⁻¹ were chosen as productivity lags can occur throughout the trophic levels, and over a 12-mo period the distribution and abundance of fish and krill may be affected (Jenouvrier 2013, Zador et al. 2013, Saba et al. 2014).

Generalised linear models were fitted to the data using the glm package in R version 3.5.0 (R Development Core Team 2019). The assumption of normality of residuals was checked using standard graphical methods (Zuur et al. 2010). Two models were subsequently used to investigate the relationship between breeding parameters and large-scale climate indices.

2.6.1. Model 1 — number of breeding shearwaters

The first model related the number of breeding birds arriving at Fisher Island to the suite of environmental covariates. Climatic variables based on the appropriate breeding period included in the full

model were: (i) NPI during the pre-breeding/migration period with temporal lag 1 (NPI PB⁰); (ii) NPI during the pre-breeding/migration period with temporal lag 3 (NPI PB⁻¹); (iii) PDO PB⁻¹; (iv) SOI EB⁻¹; (v) SAM during the early-breeding period with temporal lag 1 (SAM EB⁰); and (vi) SAM during the early-breeding period with temporal lag 3 (SAM EB⁻¹).

SAM EB⁰ was not significant and was removed from the analysis to limit the number of parameters within the model.

2.6.2. Model 2 — breeding success of shearwaters

The second model related breeding success to a number of climate variables in the Southern Hemisphere. Climatic and environmental variables based on the chick-rearing period included in the full model were: (i) SAM during the chick-rearing period with temporal lag 1 (SAM CR⁰); (ii) SAM during the chick-rearing period with temporal lag 3 (SAM CR⁻¹); (iii) rainfall during the chick-rearing period with temporal lag 1 (Rainfall CR⁰); (iv) SOI during the chick-rearing period with temporal lag 1 (SOI CR⁰); and (v) SOI during the chick-rearing period with temporal lag 3 (SOI CR⁻¹).

Model selection was conducted through the comparison of Akaike's information criterion (AIC), Akaike weights (w_i) and AIC differences (Δ_i). w_i were calculated to provide a measure of strength for each model (Anderson & Burnham 2004). Models with an AIC $\Delta_i < 2$ were considered to have equivalent support. To assess the most important covariate, in these cases, we used model averaging to provide a final model (Anderson & Burnham 2004). Model averaging was calculated as a sum of the w_i over the number of models where the covariate appears (Anderson & Burnham 2004).

3. RESULTS

There was considerable variability over the time period in both reproductive parameters (Fig. 1). There were 98 ± 29 breeding pairs per year when averaged across the entire time period. However, from the start of the survey period in 1950, there was a gradual decline in the number of breeding pairs, reaching 58 pairs in 1971 and 1973 (Fig. 1A). From the mid-1980s, the number of breeding pairs increased until 2007, when 160 breeding pairs were recorded (Fig. 1A). From 2007 to 2012, there was slight variation in the annual number of breeding

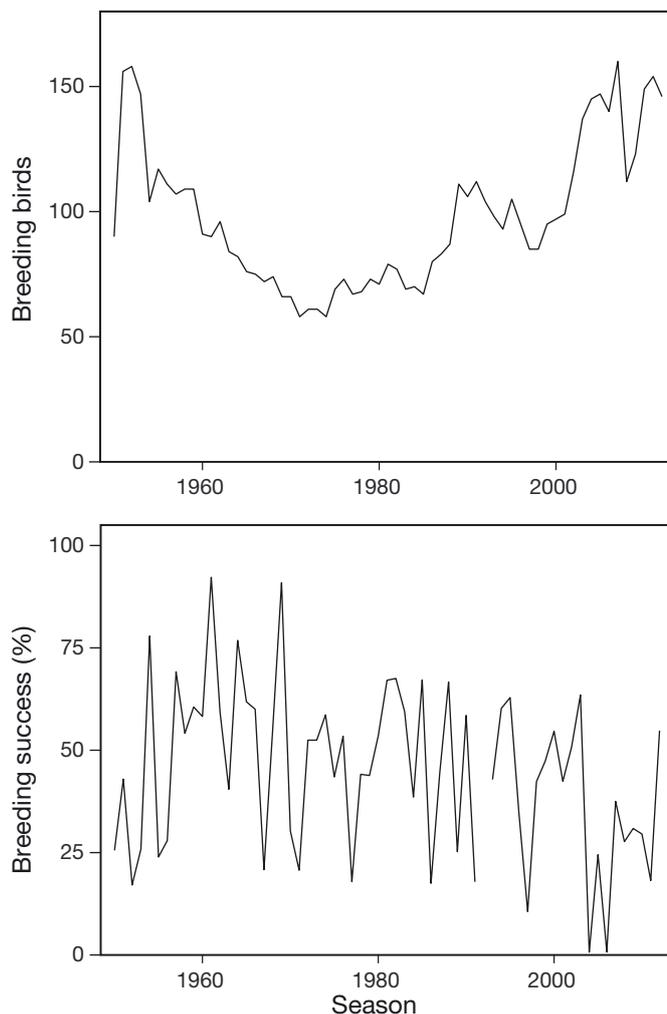


Fig. 1. Time series (1950 to 2012) of short-tailed shearwaters breeding at Fisher Island. (A) Annual number of breeding participants arriving to Fisher Island. (B) Annual variation of breeding success at Fisher Island

pairs. Breeding success fluctuated annually, with an average of $45 \pm 20\%$ across the entire time period. The lowest breeding success was recorded in 2004 and 2006 (less than 1%; Fig. 1B). The most successful breeding season was in 1961, when there was a 92% success rate (Fig. 1B).

3.1. Climatic variability and the number of breeding shearwaters

There were 6 models with an $AIC \Delta_i < 2$, containing all covariates (Table 2, Table S4 in the Supplement). After model averaging, SAM EB^{-1} explained the most variation (Table 3), with the number of birds arriving to the breeding colony increasing in years of positive SAM (Fig. 2). Furthermore, there was a negative relationship between the number of birds arriving at Fisher Island and NPI PB^0 and PDO PB^{-1} (Fig. 2). Lastly, the contribution of NPI PB^{-1} and SOI EB^{-1} to explain any variability within the model was marginal (Table 3).

3.2. Effects of climate variability and environmental conditions on shearwater breeding success

The full model, which contained all variables considered to be important, presented 4 models with an $AIC \Delta_i < 2$, with all covariates included in these models (Table 4, Table S5 in the Supplement). After model averaging, the covariate that

Table 2. Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag 1⁽⁰⁾ and temporal lag 3⁽⁻¹⁾ climate indices North Pacific Index (NPI), Southern Oscillation Index (SOI), Southern Annular Mode (SAM) and Pacific Decadal Oscillation (PDO) on the number of birds arriving to breed at Fisher Island. Models selected for model averaging with $AIC \Delta_i < 2$ are in bold. Only the top 10 models are displayed

Model no.	Intercept	NPI PB^0	NPI PB^{-1}	SAM EB^{-1}	SOI EB^{-1}	PDO PB^{-1}	df	logLik	AICc	Δ_i	Weight
5	94.632	NA	NA	10.952	NA	NA	3	-257.671	521.813	0.000	0.116
6	6899.754	-6.697	NA	12.412	NA	NA	4	-256.793	522.386	0.574	0.087
21	92.841	NA	NA	10.261	NA	-6.028	4	-256.816	522.432	0.618	0.085
22	7338.209	-7.131	NA	11.769	NA	-6.427	5	-255.790	522.805	0.992	0.071
23	7196.822	NA	-7.018	9.367	NA	-11.986	5	-255.824	522.872	1.059	0.068
19	8317.722	NA	-8.126	NA	NA	-13.752	4	-257.446	523.693	1.879	0.045
1	94.091	NA	NA	NA	NA	NA	2	-259.780	523.791	1.978	0.043
17	92.066	NA	NA	NA	NA	-6.946	3	-258.713	523.897	2.083	0.041
24	12254.749	-6.066	-5.927	10.789	NA	-11.399	6	-255.083	523.916	2.103	0.041
13	94.667	NA	NA	10.865	0.090	NA	4	-257.657	524.113	2.300	0.037

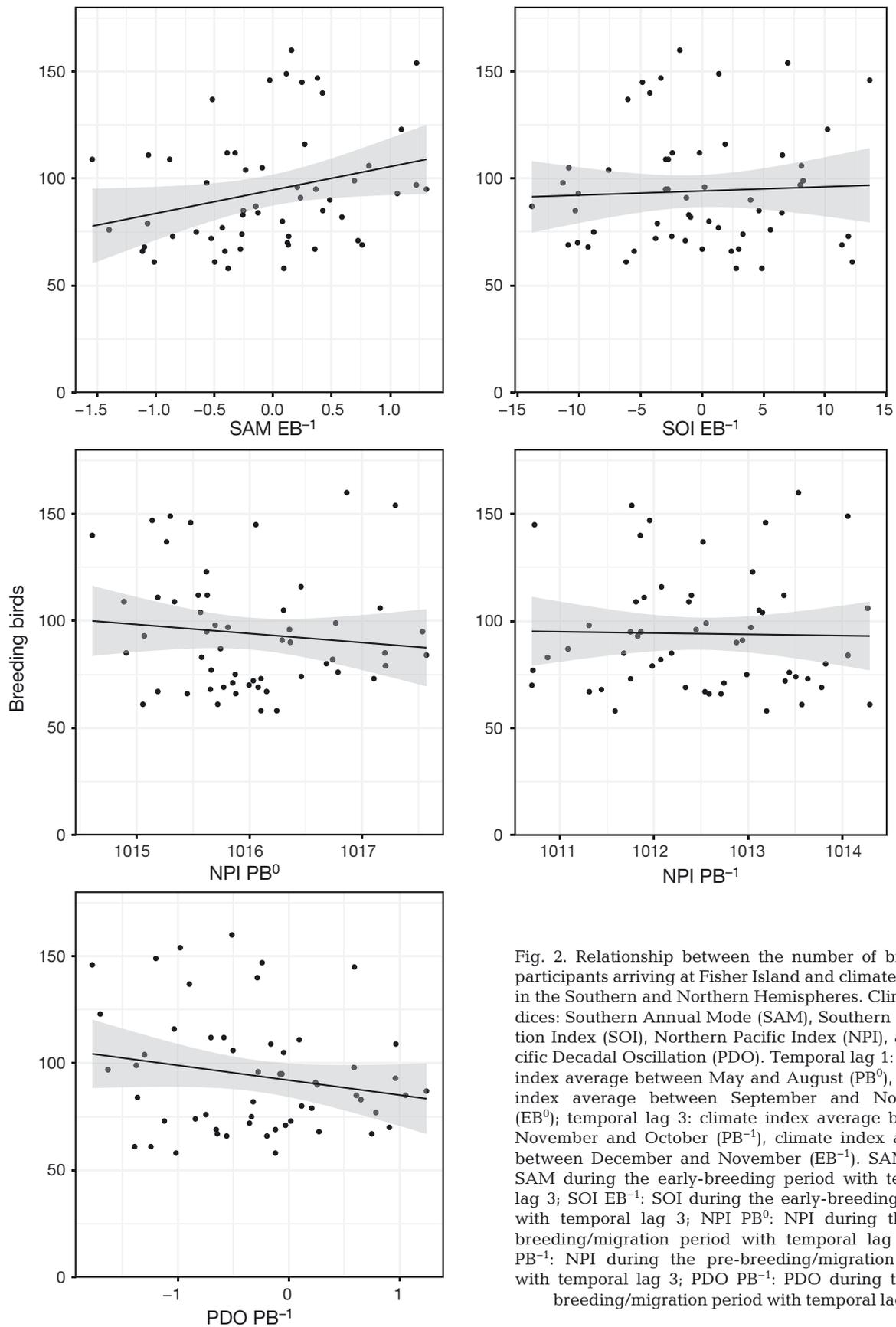


Fig. 2. Relationship between the number of breeding participants arriving at Fisher Island and climate indices in the Southern and Northern Hemispheres. Climate indices: Southern Annual Mode (SAM), Southern Oscillation Index (SOI), Northern Pacific Index (NPI), and Pacific Decadal Oscillation (PDO). Temporal lag 1: climate index average between May and August (PB^0), climate index average between September and November (EB^0); temporal lag 3: climate index average between November and October (PB^{-1}), climate index average between December and November (EB^{-1}). SAM EB^{-1} : SAM during the early-breeding period with temporal lag 3; SOI EB^{-1} : SOI during the early-breeding period with temporal lag 3; NPI PB^0 : NPI during the pre-breeding/migration period with temporal lag 1; NPI PB^{-1} : NPI during the pre-breeding/migration period with temporal lag 3; PDO PB^{-1} : PDO during the pre-breeding/migration period with temporal lag 3

Table 3. Models with an AIC $\Delta_i < 2$ and relative importance values of each climate index for temporal lag 1⁽⁰⁾ and temporal lag 3⁽⁻¹⁾ on the number of breeding birds arriving to breed at Fisher Island

	SAM EB ⁻¹	PDO PB ⁻¹	NPI PB ⁰	NPI PB ⁻¹	SOI EB ⁻¹
Importance	0.83	0.52	0.31	0.22	0.00
No. containing models	5	4	2	2	0

explained the greatest amount of variability of breeding success was localised rainfall, with years of higher rainfall associated with reductions in breeding success (Table 5, Fig. 3). SOI CR⁻¹ conditions demonstrated a positive relationship with breeding success. In contrast, as SOI CR⁰ values increased, this led to a decrease in breeding success (Fig. 3). The contribution of SAM CR⁻¹ and SAM CR⁰ was negligible (Table 5).

4. DISCUSSION

This 63-yr study has demonstrated that breeding performance of the short-tailed shearwater was influenced by climate indices, local weather and environmental conditions. The annual number of breeding birds arriving at Fisher Island was influenced by climate indices in both the Northern and Southern Hemispheres, while breeding success at Fisher Island was affected by local weather conditions (i.e. rainfall). Moreover, the breeding parameters within this study were affected by climate indices with a 12-mo temporal lag more so than climate indices lagged over the associated breeding period.

Table 5. Models with an AIC $\Delta_i < 2$ and relative importance values of each climate index and rainfall for temporal lag 1⁽⁰⁾ and temporal lag 3⁽⁻¹⁾ on breeding success at Fisher Island

	Rainfall CR ⁰	SOI CR ⁰	SOI CR ⁻¹
Importance	1.00	0.55	0.38
No. containing models	4	2	2

4.1. Lags in productivity transfer to breeding parameters of shearwaters

Lags in productivity transfer may occur throughout the food web, and have been associated with changes in breeding success, distribution, abundance and demographic parameters of several seabird species (Jenouvrier 2013), which is consistent with our findings in this study. Climatic variability influences environmental conditions, which can alter primary productivity and influence aspects of secondary production, such as the recruitment of fish and krill (Zador et al. 2013, Saba et al. 2014), which are both prey for short-tailed shearwaters. For example, in Antarctica, a 1-yr lag was found between primary production and the recruitment of Antarctic krill *E. superba* (Saba et al. 2014), which can influence food availability to higher trophic species. Due to the delay in energy transfer through the food chain (Sandvik et al. 2007, Sandvik & Einar Erikstad 2008), these effects are not observed immediately (Zador et al. 2013, Cox et al. 2018). Similarly, in the North Atlantic, breeding success of 13 species of seabirds was influenced by lagged variables of the North Atlantic Oscillation (NAO) and SST (Sandvik et al. 2007, Sandvik & Einar Erikstad 2008). During nega-

Table 4. AIC ranked model selection results to explain the effects of temporal lag 1⁽⁰⁾ and temporal lag 3⁽⁻¹⁾ for climate indices SOI and SAM, and rainfall on breeding success at Fisher Island. Models selected for model averaging with AIC $\Delta_i < 2$ are in bold. Only the top 10 models are displayed

Model no.	Intercept	Rainfall CR ⁰	SAM CR ⁰	SAM CR ⁻¹	SOI CR ⁰	SOI CR ⁻¹	df	logLik	AICc	Δ_i	Weight
10	0.619	-0.003	NA	NA	-0.005	NA	4	13.171	-17.491	0.000	0.163
2	0.632	-0.004	NA	NA	NA	NA	3	11.590	-16.682	0.810	0.109
18	0.639	-0.004	NA	NA	NA	0.005	4	12.544	-16.237	1.255	0.087
26	0.626	-0.003	NA	NA	-0.004	0.003	5	13.685	-16.066	1.426	0.080
4	0.634	-0.004	-0.022	NA	NA	NA	4	12.077	-15.303	2.188	0.055
9	0.454	NA	NA	NA	-0.006	NA	3	10.848	-15.197	2.296	0.052
12	0.621	-0.003	-0.008	NA	-0.005	NA	5	13.235	-15.164	2.327	0.051
14	0.621	-0.003	NA	-0.005	-0.005	NA	5	13.181	-15.058	2.434	0.048
6	0.638	-0.004	NA	-0.019	NA	NA	4	11.728	-14.605	2.887	0.038
20	0.640	-0.004	-0.017	NA	NA	0.004	5	12.849	-14.394	3.098	0.035

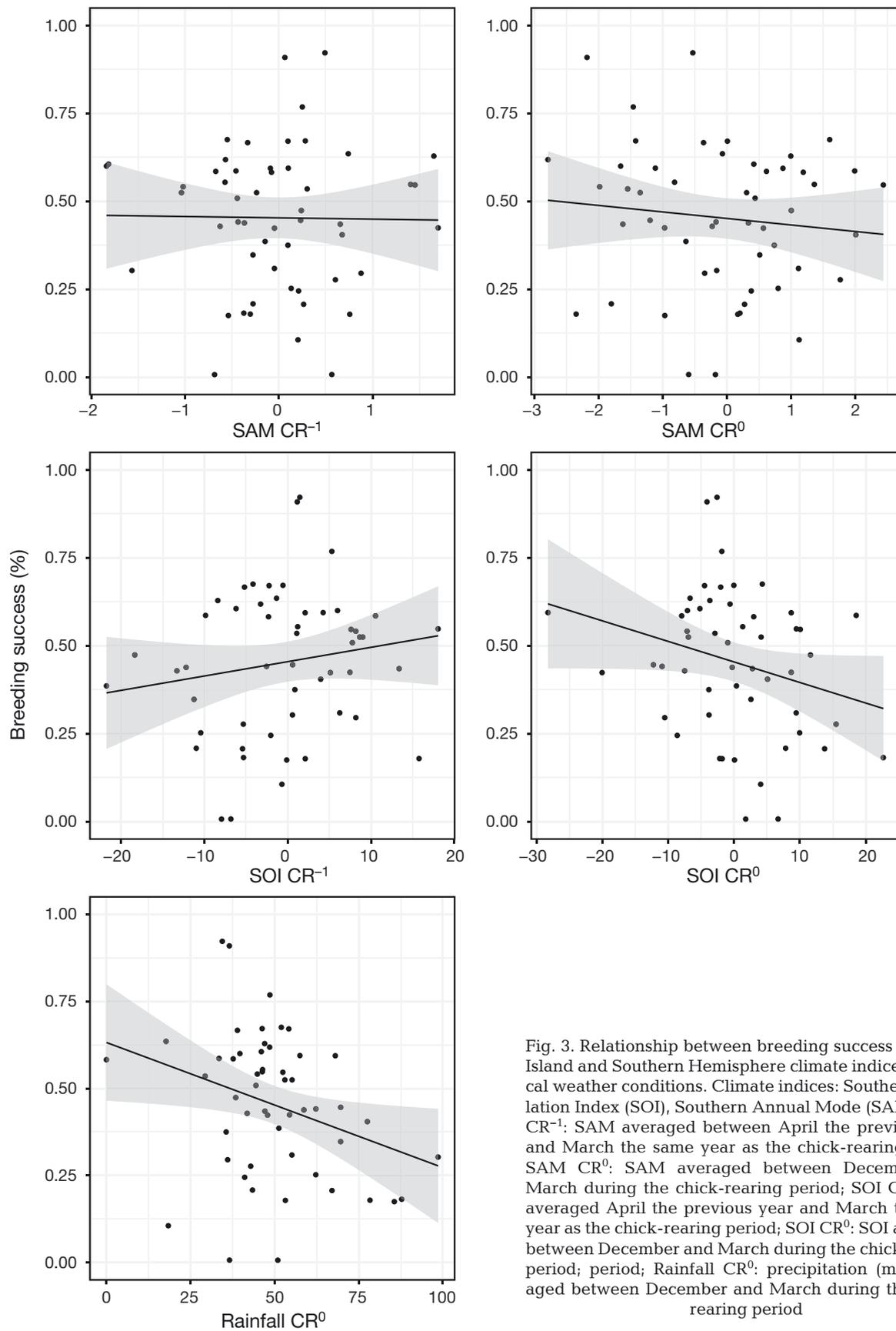


Fig. 3. Relationship between breeding success at Fisher Island and Southern Hemisphere climate indices and local weather conditions. Climate indices: Southern Oscillation Index (SOI), Southern Annual Mode (SAM). SAM CR⁻¹: SAM averaged between April the previous year and March the same year as the chick-rearing period; SAM CR⁰: SAM averaged between December and March during the chick-rearing period; SOI CR⁻¹: SOI averaged April the previous year and March the same year as the chick-rearing period; SOI CR⁰: SOI averaged between December and March during the chick-rearing period; Rainfall CR⁰: precipitation (mm) averaged between December and March during the chick-rearing period

tive NAO, values with a 1-yr lag and low SST with a 2-yr lag resulted in higher breeding success (Sandvik et al. 2007, Sandvik & Einar Erikstad 2008). Similarly, lower reproductivity in diving seabirds (e.g. murres and cormorants) have been demonstrated 1 to 2 yr after warmer SST in the Bering Sea (Zador et al. 2013).

4.2. Climatic variability and its influence on the number of breeding shearwaters

The low production potential of shearwaters requires long-term data to be able to assess their population dynamics and elucidate the effects of environmental perturbations on their abundance (Bradley et al. 1991). Environmental conditions can influence resource availability in both the non-breeding and breeding foraging grounds, which will in turn affect breeding participation of short-tailed shearwaters at Fisher Island, as body condition is an important determinant in the decision of whether to breed (Weimerskirch et al. 2001). The main reason for birds to skip a breeding event is a shortage in resource availability, which prevents them from acquiring sufficient food reserves to invest in reproduction (Chastel et al. 1995, Coulson 2008). Furthermore, resource acquisition and foraging behaviour during the non-breeding periods may have carry-over effects into the breeding season, as diminished body reserves can impact their ability to breed (Lovvorn et al. 2003, Bester et al. 2007).

4.2.1. Influence of Northern Hemisphere climate indices on the number of breeding shearwaters

Foraging grounds during the non-breeding period are important areas for birds to accumulate body lipid reserves before migration (Lovvorn et al. 2003, Bester et al. 2007). Over the last 50 yr, the climate in the Northern Hemisphere has experienced an increase in the intensity of the winter NAO, which has affected survival of the adult northern fulmar *Fulmarus glacialis* due to changes in resource availability (Grosbois & Thompson 2005). It is likely that similar effects have been felt among adult short-tailed shearwaters at Fisher Island, as demonstrated by fluctuations in the number of breeding participants. For example, the number of birds breeding at Fisher Island decreased 1 yr after warm phases of the PDO (positive index) and slightly increased with lower NPI values (i.e. stronger Aleutian Low) during the

pre-breeding period. The NPI is an indicator of the strength of the Aleutian Low, and the PDO has been shown to influence SST (Bond et al. 2011, Springer et al. 2018). Both climate patterns influence primary production and prey availability in the North Pacific through changes in ocean properties and sea ice dynamics. For example, a stronger Aleutian Low is linked to larger phytoplankton spring blooms in the Bering Sea (Iida & Saitoh 2007, Bond et al. 2011). Prior to migrating southwards, short-tailed shearwaters foraging in the Northern Pacific Ocean move further north, around the Bering and Chukchi Seas, as the distribution of krill shifts (Baduini et al. 2001, Yamamoto et al. 2015, Nishizawa et al. 2017). Consequently, any changes in bottom-up processes that influence krill abundance and availability will impact short-tailed shearwater populations prior to their migration south.

Furthermore, warm phases of the PDO (positive index) influence oceanographic properties and environmental conditions, which in turn affect the availability of zooplankton biomass in the surface waters (Jin et al. 2009, Bond et al. 2011). For example, high SST in the Bering Sea in 1997 redistributed the vertical distribution of euphausiids (i.e. krill) to deeper waters (Baduini et al. 2001). In the northern Gulf of Alaska during warm phases of the PDO, there was a decrease in the availability of euphausiids and capelin *Mallotus villosus*, which led to starvation of murres *Uria* spp. and decreased reproductive output of kittiwakes *Rissa* spp. (Hatch 2013). However, during cool phases of the PDO (negative index), the opposite occurred: resources increased, having a positive impact on both species (Hatch 2013). Therefore, it is highly likely that during a cool phase of the PDO, resource availability would increase, which would improve foraging success among short-tailed shearwaters prior to their migration south. Concurrently, this may have facilitated the accumulation of body lipid reserves and contributed to an increase in the number of breeding participants at Fisher Island.

4.2.2. Influence of Southern Hemisphere climate indices on the number of breeding shearwaters

In the Southern Hemisphere, the Southern Ocean is a key foraging area for short-tailed shearwaters during the pre-breeding and breeding periods, and is highly influenced by SAM. The number of breeding participants at Fisher Island increased under positive SAM conditions. When SAM is positive, winds inten-

sify, which causes stronger mixing of the water column and a deeper mixed layer. This, combined with increased upwelling, may influence nutrient availability within surface waters (Lefebvre et al. 2004). This may increase productivity, which would have flow-on effects throughout the food web. For example, early recruitment into a population of wandering albatross *Diomedea exulans* has been linked to positive SAM, thought to be due to increases of resource availability (Fay et al. 2017). Therefore, during a positive SAM event, ocean productivity may increase, having a positive influence on short-tailed shearwater abundance the following year.

SAM can affect the strength of the Antarctic Circumpolar Current (ACC) and the seasonal extent of sea ice around the Antarctic Continent, both of which have been shown to influence the productivity of the Southern Ocean (Constable et al. 2003, Lefebvre et al. 2004). Over the past 20 yr, SAM has been increasing, leading to changes in wind direction and intensity, with cooling waters shifting out from Antarctica and influencing the extent of sea ice (Stammerjohn et al. 2008). Changes in the timing of sea-ice formation and retreat, along with temperature, determine the intensity and location of phytoplankton spring blooms, affecting the availability and abundance of primary and secondary consumers (Nishizawa et al. 2017). These changes during positive SAM may be influencing productivity in the Southern Ocean (Lefebvre et al. 2004), leading to greater prey availability for seabirds such as short-tailed shearwaters in the following year (Nishizawa et al. 2017), resulting in higher breeding participation at Fisher Island.

Prior to breeding, short-tailed shearwaters undertake a foraging trip to the Southern Ocean (i.e. honeymoon period) to rebuild their body condition, which deteriorates during the long migration from the Northern Hemisphere (Lill & Baldwin 1983, Weimerskirch & Cherel 1998, Vertigan et al. 2012). Additional long foraging trips to the Southern Ocean are also undertaken by short-tailed shearwaters throughout the incubation period (Weimerskirch & Cherel 1998, Einoder et al. 2013, Berlincourt & Arnould 2015). These long foraging trips (1000 to 4000 km) are designed to replenish adult body condition, which deteriorates during the incubation period (Weimerskirch & Cherel 1998, Einoder et al. 2013). Short-tailed shearwaters forage across different oceanic regions within the Southern Ocean, including south of the Polar Front (PF), the Sub-Antarctic Front (SAF) and Antarctic waters (Woehler et al. 2003, Raymond et al. 2010, Berlincourt & Arnould

2015), feeding predominantly on myctophids (fish) and euphausiids (*E. vallentini*) (Weimerskirch & Cherel 1998, Connan et al. 2010, Einoder et al. 2013). When resources are low, breeding procellariiform species may skip breeding if it poses a risk to their own survival (Chastel et al. 1995, Weimerskirch et al. 2001). Therefore, breeding decisions of the short-tailed shearwater are likely to also be influenced by resource availability and foraging success within the Southern Ocean.

4.3. Influence of environmental conditions on the breeding success of shearwaters

Localised rainfall and ENSO were found to influence the breeding success of short-tailed shearwaters at Fisher Island, with rainfall having the greatest influence. Burrowing procellariiforms are adversely affected by heavy rainfall due to burrow flooding, which causes chick mortality and egg failure (Serventy & Curry 1984, Warham 1996, Bester et al. 2007, Fagundes et al. 2016). For example, young providence petrel *Pterodroma solandri* chicks were more vulnerable to rainfall conditions than older chicks (Bester et al. 2007), probably because their down is not water-repellent, resulting in them becoming waterlogged and unable to maintain core body temperature (Warham 1996). During this study, the mortality rate between eggs and chicks were not recorded; therefore, we were unable to determine at which stage of development rainfall had the greatest impact.

ENSO is a significant contributor to Australia's climate, altering environmental conditions that influence seabird ecology (Grose et al. 2010, Chambers et al. 2011). Nonetheless, the effects of ENSO in southeastern Australia on seabird populations are not well established (Chambers et al. 2011, Lit-zow et al. 2016). In our study, breeding success was influenced by ENSO; however, the nature of the relationship varied depending on the temporal lag. Breeding success decreased with negative values of SOI lagged over a 12-mo period, while breeding success increased with negative values of SOI lagged over 3 mo, during the chick-rearing period. This may suggest the environmental conditions 1 yr prior to short-tailed shearwater breeding affects prey availability. Therefore, in the case of negative SOI values, this may lead to lower resource availability. On the west coast of Australia, studies have highlighted the adverse effects of El Niño (i.e. sustained values of SOI lower than -8). For example,

warm surface waters caused by El Niño events can block nutrient upwelling, influencing primary production, which in turn affects the distribution and abundance of zooplankton, fish and higher trophic predators (Jenouvrier 2013). These El Niño events have been linked to delays in breeding and reduced breeding success for the wedge-tailed shearwater *Ardenna pacifica*.

However, there are a few possibilities to explain the contrasting results during the chick-rearing period for SOI. Local environmental conditions, such as wind, humidity and temperature, are influenced by ENSO, which may have impacted burrow conditions of the short-tailed shearwater during chick rearing. For example, local environmental conditions have been shown to influence the microclimate of the burrows of the Macaronesian shearwater *Puffinus lherminieri baroli*, which can impact chicks and influence breeding success (Fagundes et al. 2016). Therefore, the local environmental conditions during negative SOI values may have been advantageous for chick development, leading to an increase in breeding success. Secondly, short-tailed shearwaters are able to mitigate unfavourable environmental conditions due to their flexible foraging strategies. They frequent more distant foraging areas when resources are low (Berlincourt & Arnould 2015), providing a buffer during adverse conditions. Finally, only individuals of high fitness may be choosing to return to Fisher Island to breed more frequently (Bradley et al. 2000), therefore enabling them to successfully breed during negative SOI values. These possibilities require further exploration to unravel the relationship between ENSO and breeding success and to understand the ecological processes at play.

There are several other, non-resource, factors that may have contributed to some of the variability in breeding success at Fisher Island. For example, predation on short-tailed shearwater eggs occurred at Fisher Island during the 1980s from native water rats *Hydromys chrysogaster* (Bradley et al. 2000). While these effects have not been quantified, on Big Dog Island, within the Furneaux Island Group, approximately 8% of the short-tailed shearwater eggs laid were lost to 2 species of predators: water rats and the blotched blue-tongue lizard *Tiliqua nigrolutea* (Carey 2010). Furthermore, breeding success in short-tailed shearwaters is also influenced by the experience and quality of the pair-bonds, which, if lacking, may result in the abandonment of eggs and breeding failure (Wooller et al. 1990, Bradley et al. 1999, Meathrel & Carey 2007). This effect was not accounted for in the present study.

4.4. Final considerations

Long-lived seabirds integrate the variabilities in their marine environments in various manifestations—from foraging trip durations to demographic parameters. In many cases, these signals are direct: prey species' abundances during ENSO events in the Galapagos result in catastrophic breeding failures (Schreiber & Schreiber 1989, Boersma 1998), while long-term changes in SST altering the distributions and abundances of prey species over decades result in population decreases of 90% of rockhopper penguins at Subantarctic Campbell Island (Moors 1986).

Temporal and/or spatial correlates and lags between the environmental drivers and biological responses range from days to decades (Stommel 1963, Haurly et al. 1978) and disentangling short-term from long-term responses using seabirds such as short-tailed shearwaters requires long-term time series, as most species of long-lived seabirds do not recruit into breeding populations until they are several years old. Short-tailed shearwaters commence breeding by a mean age of 7 yr (Wooller et al. 1990, Bradley et al. 1991), providing an extended temporal window for environmental drivers to influence demographic parameters, often through resource availability (Ainley et al. 1995, Bost et al. 2015, Fay et al. 2015, 2017). This may also be the situation for the Fisher Island short-tailed shearwater breeding population, and further investigation is required to unravel further long-term population responses to environmental pressures.

Another key aspect of the bird's life history that will be affected by environmental factors is age-specific survival. For example, an early-life demographic study of the wandering albatross showed that juvenile females had a higher survival rate compared to that of males; however, in adult wandering albatross this was reversed, thus environmental and trophic conditions may impact survival differently depending on age (Fay et al. 2015, 2017). There are mark-recapture data available for each year of this long-term data set, and an analysis of these data will be the focus of future studies. However, because the breeding population on Fisher Island is quite small—20–80 chicks produced per year—this results in a data set in which annual resight data are relatively sparse. Also, the fact that recapture/resight effort varied considerably among years further complicates the issue, making interannual survival comparisons difficult (Desprez et al. 2013). Finally, imperfect detections further limit our ability to conduct a survival analyses, especially across the entire 70-yr time

series. Devising techniques that can tease relationships out of the considerable uncertainty which is a product of these small samples is beyond the scope of the present study.

The findings of this study highlight the importance of long-term monitoring to assess large-scale climate indices and local environmental conditions affecting seabirds' breeding parameters. Ecological lags are also an important factor to consider when identifying climate-induced effects, as any impacts to bottom-up processes (i.e. nutrient upwellings in the ocean) need time to filter through to the higher trophic levels. Given that ecosystem processes are complex and often difficult to quantify, other intrinsic and extrinsic factors not considered in the study may also contribute to the variability of breeding parameters of the short-tailed shearwater (e.g. breeding experience, inadequate pair bond and predation). To further understand impacts at the population level, demographic studies are needed to investigate the long-term impact on the short-tailed shearwater population in southeastern Australia.

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