



Where have all the petrels gone? Forty years (1978–2020) of Wilson’s Storm Petrel (*Oceanites oceanicus*) population dynamics at King George Island (Isla 25 de Mayo, Antarctica) in a changing climate

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Received: 27 July 2022 / Revised: 27 April 2023 / Accepted: 11 May 2023
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Abstract

Numerous seabird species are experiencing population declines, and this trend is expected to continue or even accelerate in the future. To understand the effects of environmental change on seabird populations, long-term studies are vital, but rare. Here, we present over four decades (1978–2020) of population dynamic and reproductive performance data of Wilson’s Storm Petrels (*Oceanites oceanicus*) from King George Island (Isla 25 de Mayo), Antarctica. We determined temporal trends in population size, breeding output, and chick growth rates, and related interannual variation in these variables to various environmental variables. Our study revealed a decline of 90% in population size of Wilson’s Storm Petrels in two colonies, and considerable changes in breeding output and chick growth rates. Temporal changes in breeding demographics were linked to interannual environmental variation, either causing changes in food availability (particularly Antarctic krill, *Euphausia superba*) or in nest burrow accessibility due to snow blocking the entrance. With the expected rise in air and sea surface temperatures, the predicted increases in precipitation over the Antarctic Peninsula will likely lead to increased snowstorm prevalence. Additionally, the rising temperatures will likely reduce food availability due to reduced sea ice cover in the wintering grounds of Antarctic krill, or by changing phyto- and zooplankton community compositions. The ongoing environmental changes may thus lead to a further population decline, or at the very least will not allow the population to recover. Monitoring the population dynamics of Antarctic seabirds is vital to increase our understanding of climate change-induced changes in polar food webs.

Keywords Antarctic seabird · Long-term data · Climate change · Breeding success · *Procellariiformes*

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Introduction

Seabirds form an integral part of marine ecosystems (Signa et al. 2021), not only connecting nutrient (e.g., Duda et al. 2020) and contaminant (Blais et al. 2005; Signa et al. 2013) flow between marine and terrestrial systems, but also linking marine habitats on a global scale (Pacyna et al. 2019; Signa et al. 2021; Wild et al. 2022). Their fundamental place in the food web means that seabirds are exceptionally susceptible to changes in marine environments, and that, in turn, makes them vulnerable to ongoing climate and anthropogenic changes. Indeed, many seabird species are under threat globally, with nearly half of the species experiencing population declines (Croxall et al. 2012; Dias et al. 2019). These population declines are likely caused by multiple factors including climate change and direct anthropogenic threats (Dias et al. 2019).

The effects of variation in environmental conditions on avian reproductive performance and demography are complex and may differ between species, area, phase in the annual cycle, and age groups (Bestley et al. 2020). Local weather conditions such as air temperature (Quillfeldt 2001; Jenouvrier et al. 2005; Ritz et al. 2005; Hahn et al. 2007), precipitation (Quillfeldt 2001; Hahn et al. 2007; Youngflesh et al. 2021), or wind conditions (Quillfeldt 2001; Ritz et al. 2005; Nevoux and Barbraud 2006; Hahn et al. 2007) can have contrasting and variable effects on various breeding parameters (Michielsen et al. 2019). Similarly, local and regional oceanographic conditions, such as sea ice extent (Ballerini et al. 2009; Hinke et al. 2014), or sea surface temperature (Barbraud et al. 2000; Jenouvrier et al. 2003; Hahn et al. 2007), and variation in large-scale environmental indices such as the Southern Annular Mode (SAM; or Antarctic Oscillation, AAO) can have diverse effects on both juvenile and adult survival (Nevoux and Barbraud 2006; Descamps et al. 2016; Abadi et al. 2017) or breeding success (Jenouvrier et al. 2005; Descamps et al. 2016; Sauser et al. 2018) with various time lags (Descamps et al. 2016; Pacoureaux et al. 2019).

Climate and oceanographic variation are undeniably interlinked, with large-scale indices affecting oceanographic variables on regional and local scales (Barbraud et al. 2012; Lee et al. 2019). While changes in local climate conditions may have direct effects on species' behaviour (Tarroux et al. 2016; Dehnhard et al. 2021) and breeding success (Quillfeldt 2001; Büßer et al. 2004; Michielsen et al. 2019), the effects may also be indirect through their effect on food availability (Quillfeldt 2001; Büßer et al. 2004; Lescroël et al. 2014; Jenouvrier et al. 2015). Birds breeding in adverse weather conditions may mitigate the negative effects on their offspring through adopting various strategies, such as chicks gaining large

fat reserves (Gębczyński and Jadwiszczak 2000) or going into facultative hypothermia (Gębczyński 1995; Kuepper et al. 2018). However, prolonged food deprivation will nevertheless lead to starvation (Büßer et al. 2004; Kuepper et al. 2018), negatively affecting chick growth and survival. In addition, food stress may exacerbate oceanographic effects under harsh weather circumstances (Ritz et al. 2005; Krüger et al. 2021).

Pelagic seabirds breeding in the Southern Hemisphere are more threatened compared to seabirds from other parts of the world, with over half of the species in decline (Croxall et al. 2012; Chambers et al. 2014). These declines are mostly linked to fisheries (e.g., overfishing and bycatch) and climate change (Dias et al. 2019). In addition to population declines, southern hemisphere seabird species show changes in phenology in response to climate change, with most Procellariidae populations and migratory species breeding in the Antarctic showing shifts towards later phenological events (Barbraud and Weimerskirch 2006; Chambers et al. 2014). This may lead to mismatches with prey phenology, eventually affecting reproductive performance and demography (Sauser et al. 2021).

The effects of environmental changes on breeding population size in seabirds are often delayed due to their longevity and late recruitment age (Gaston and Descamps 2011; Miles et al. 2015). Low breeding success due to unfavourable environmental conditions (Quillfeldt 2001; Jenouvrier et al. 2005, 2015; Nevoux and Barbraud 2006; Bestley et al. 2020) may only have a significant effect on population size years later due to lowered recruitment rates (Anchundia et al. 2014; Miles et al. 2015; Pacoureaux et al. 2019). This effect may be enhanced by low survival of juveniles in unfavourable environmental conditions reducing recruitment further (Forcada et al. 2008; Hinke et al. 2014).

Long-term studies are vital in understanding how inter-annual variation in environmental conditions affects population demographics in long-lived seabirds. Such studies are generally scarce, and especially so for species nesting in hard-to-reach remote areas in cracks and crevices such as the smallest member of the Procellariidae breeding in Antarctica: the Wilson's Storm Petrel, *Oceanites oceanicus*, (hereafter WSP) (Chambers et al. 2014). Except for a long-term study (1959–2004) on Antarctic seabird phenology, for which WSP annual arrival dates were scored (Barbraud and Weimerskirch 2006), the longest study of variation in breeding output spanned a decade (Büßer et al. 2008). WSPs play a crucial role in the Antarctic food web both as predator and prey (Büßer et al. 2008; Bestley et al. 2020) due to their high abundance (est. population size 8–200 million; Warham 1990; BirdLife International 2021). Therefore, changes in their breeding output and population dynamics may have substantial effects on the Antarctic marine ecosystem.

In this study, we summarised opportunistically assembled (mainly for purposes of various short-term studies) data on WSP population demographics and breeding performance collected at irregular intervals between 1978 and 2020 on King George Island (or Islas 25 de Mayo, hereafter KGI), South Shetland Islands, maritime Antarctic, with a total of 27 years with available data. WSP is the smallest endotherm breeding in the Antarctic region with a circumpolar breeding distribution (Olivier and Wotherspoon 2006), with colonies along the Antarctic coast, on islands in the Southern, Indian and Atlantic Ocean as far north as the Falkland Islands (Islas Malvinas) (Carboneras et al. 2017). WSP forages primarily on Antarctic krill (*Euphausia superba*), but also supplements its diet with other crustaceans, and small fish (Ridoux 1994; Quillfeldt 2002). Considering the sensitivity of Antarctic krill to climate change (Atkinson et al. 2004, 2019; Reiss et al. 2017), WSP may be especially vulnerable to changes in environmental conditions once they lead to changes in food abundance (Quillfeldt 2001), for example, through affecting chick provisioning rates (Büßer et al. 2004). Additionally, snowstorms are known to block the entrances of WSP burrows (Wasilewski 1986; Büßer et al. 2004), preventing adults from entering and laying eggs (Quillfeldt 2001) or provisioning chicks possibly leading to starvation (Gębczyński and Jadwiszczak 2000; Quillfeldt 2001; Kuepper et al. 2018), or hypothermia (Gębczyński 2003; Kuepper et al. 2018). Indeed, based on an estimated foraging range of ca. 500 km (Croxall and Prince 1980), the breeding season foraging habitat of WSP from KGI is found to the north and west of the Antarctic Peninsula, and therefore lies in one of the areas undergoing the most rapid warming worldwide (e.g., Ducklow et al. 2007). The temperature rise in this area has been about three times higher than the global mean (2 °C over the year; 6 °C in winter), leading to a reduction in winter sea ice extent by 10% per decade, and a shorter seasonal duration of sea ice cover (Clarke et al. 2007).

Locally, weather conditions may affect access to nest burrows on land and food availability at sea. The waters around KGI do not have a standing stock of Antarctic krill, but the predator species rely on krill swarms supplied by ocean currents from the Bellingshausen Sea (Sahrhage 1988; Quillfeldt 2001). Krill abundance is heavily reliant on sea ice cover (SIC) during the preceding winter (Loeb et al. 1997), thus, variation in SIC in the Bellingshausen Sea may affect food availability for WSP. The prevalence of westerly winds affects the distribution of krill stocks, and a decline in westerly winds is thus associated with lower food availability (Quillfeldt 2001; Büßer et al. 2008). Variation in SAM is associated with a change in wind conditions (Lee et al. 2019), and may therefore

affect food availability for krill-eating predators as well as precipitation events (Marshall et al. 2017).

Combining environmental data measured by remote sensing techniques and modern statistical techniques allows researchers to relate variability in long-term data collected decades before, to changes in environmental conditions on large temporal and spatial scales. Given the observed decline of various pelagic seabird species (Croxall et al. 2012; Dias et al. 2019), WSP is likely to follow the same trend despite the current classification as Least Concern and stable (Bird-Life International 2021). Indeed, surveys in 1984 and 2016 in Adélie Land, Antarctica showed a 40% decline in breeding pairs (Barbraud et al. 2017). The declining trend in WSP is further suggested by the apparent lower occupancy rate of nests and thus number of chicks in recent years compared to earlier studies in the same locations on KGI (Jabłoński 1986; Wasilewski 1986; Kostelecka-Myrcha and Myrcha 1989; Gębczyński and Jadwiszczak 2000; Aulsems et al. 2020). Similar to other seabirds (Dias et al. 2019), the possible causes for a population decline are likely manifold, mainly weather, climate and food availability related (Quillfeldt 2001, 2002; Büßer et al. 2004).

Here, we explored the link between environmental conditions and breeding population demographics of WSP. Given the reported decreasing trend in the population sizes of various krill-eating Antarctic predators (Croxall et al. 2012; Dias et al. 2019; Krüger et al. 2021), we expected to find lowered breeding output of WSP in more recent years compared to earlier years, and to find evidence for declining population sizes over time. Considering the phenological shifts of WSPs breeding on the coast of Adélie Land (Barbraud and Weimerskirch 2006), we expected that WSP reproductive phenology on KGI has also shifted to later in the year. Due to the elusive nature of the species, due to their pelagic lifestyle, nocturnal activity in the breeding colony, and tendency to breed in hard-to-reach cracks and crevices, measuring population size or age directly is nearly impossible. In addition to the opportunistic nature of our data, we thus used various measurements to describe population dynamics, and a suite of environmental variables. Therefore, the results presented in this study should be interpreted as trends which need to be confirmed with independent data.

Materials and methods

Study species and area

We studied WSP colonies on KGI (Fig. 1), in the vicinity of the Argentinian Base Carlini (62°14'S, 58°40'W; CA, formerly called Base Jubany) and the Henryk Arc-towski Polish Antarctic Station (62°09'S, 58°27'W; HA). WSP adults arrive at the colonies on KGI from September

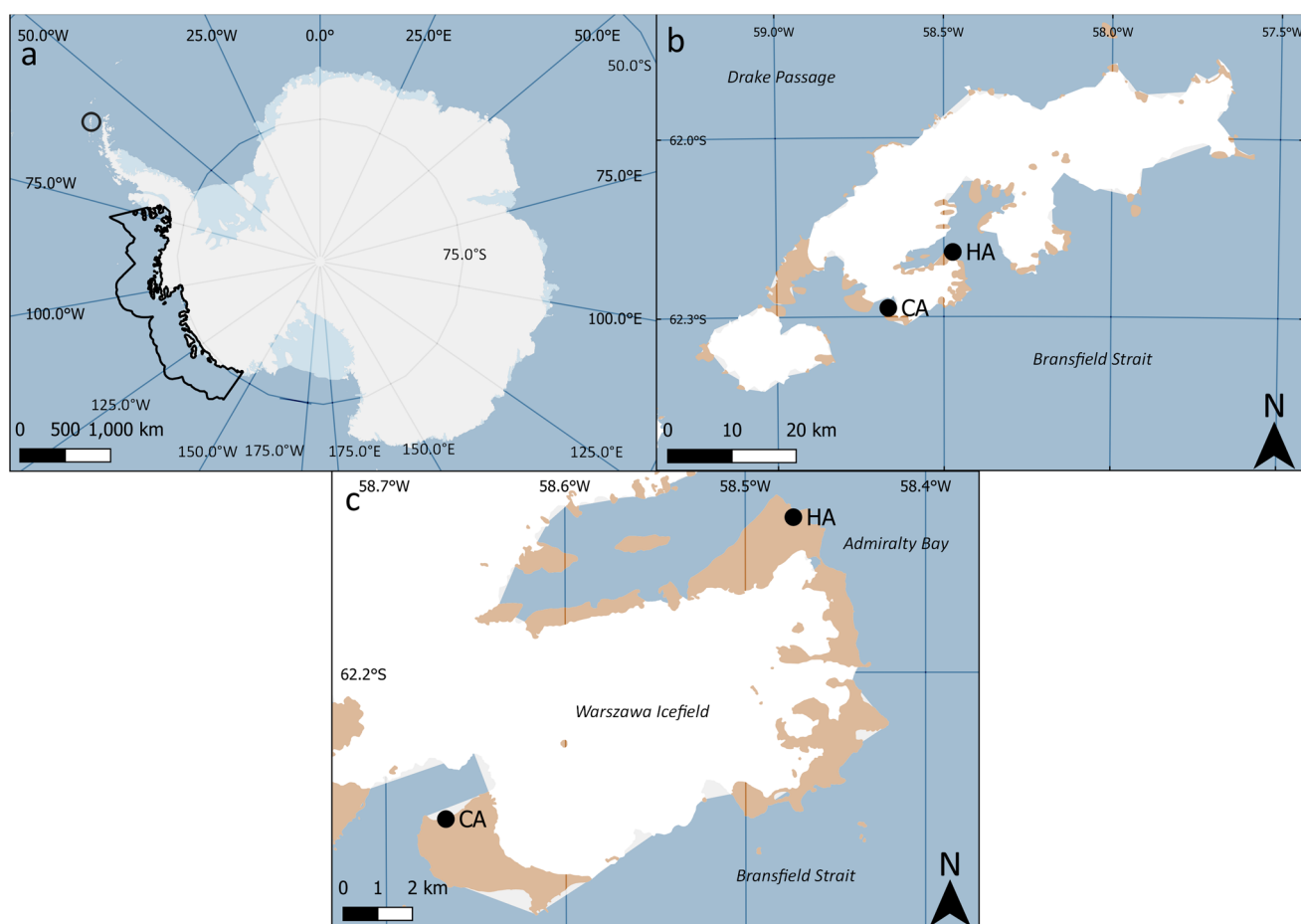


Fig. 1 Study area. The study area is located to the west of the Antarctic Peninsula (**a**) on King George Island (Isla 25 de Mayo), South Shetlands (**b**). The Wilson's Storm Petrel (*Oceanites oceanicus*) colonies at either side of the Warszawa Icefield were studied at the Argentinian Base Carlini and the Henryk Arctowski Polish Antarctic Station (**c**). The black circle in **a** shows King George Island (Isla 25 de

Mayo). The black outline in **a** shows the Bellingshausen Sea, from Spalding et al. 2007. The black dots in **b** and **c** show the locations of the research stations (CA = Argentinian Base Carlini; HA = Henryk Arctowski Polish Antarctic Station). The black arrows in **b** and **c** point North. Map source: Quantarctica (Matsuoka et al. 2018)

(Sierakowski 1991) to October (Wasilewski 1986), with eggs being laid from December to February (Wasilewski 1986). WSPs lay a single egg per season (Carboneras et al. 2017) which is incubated for 38–59 days. Partners are socially and genetically monogamous (i.e., there is no extra-pair paternity) and share parental duties during the breeding season (Wasilewski 1986; Quillfeldt 2001; Quillfeldt et al. 2001). The egg may be left unattended for several days, increasing the total length of incubation period (Beck and Brown 1972). The chick fledges at an age of 54–69 days (Beck and Brown 1972). Although there are no data on the age at first breeding for WSP, similar sized Storm Petrels generally start breeding between 2 and 4 years of age (Morse and Buchheister 1977; Bried and Bolton 2005; Okill and Bolton 2005; Sanz-Aguilar et al. 2009). Like all Procellariiformes, WSP is a long-lived species, with an estimated mean adult life expectancy of 10.4 years (Beck and Brown 1972) and a

maximum lifespan of approximately 30 years based on local ring recoveries.

Data collection

We studied WSP on KGI since 1978 at HA (Jabłoński 1986) and at CA since 1995 (Quillfeldt 2001). In total, we collected WSP breeding demographic data in seven breeding seasons at HA and 19 breeding seasons at CA (Table 1). At CA, we caught adults at night throughout the breeding season using a mist net at the same location in the Tres Hermanos colony in each study year. The population size in 1995–96 was estimated at 1400–2300 breeding pairs (Hahn et al. 1998). As a proxy of local population size, we calculated the number of birds caught per hour at CA between 1 and 3 h after sunset, to correct for the length of the catching events. Since we captured the birds at various times during the breeding season,

Table 1 Study years of Wilson's storm-petrel population demographic data collected on King George Island, South Shetland, maritime Antarctica

Colony	CA		HA	
	<i>n</i>	Year	<i>n</i>	Year
Adults caught per hour	15	1996; 1999; 2001; 2003–2007; 2013–2017; 2020	0	–
Foot spot ratio	14	1999–2001; 2003–2007; 2013–2017; 2020	0	–
Number of nests	19	1996; 1999–2009; 2013–2017; 2020	7	1979–1981; 1984; 1995; 2017–2018
Number of eggs	19	1996; 1999–2009; 2013–2017; 2020	4	1979; 1981; 1995; 2018
Laying success	19	1996; 1999–2009; 2013–2017; 2020	4	1979; 1981; 1995; 2018
Number of chicks	19	1996; 1999–2009; 2013–2017; 2020	7	1980–1981; 1984; 1990; 1995; 2017–2018
Hatching success	19	1996; 1999–2009; 2013–2017; 2020	6	1980–1981; 1984; 1995; 2017–2018
Hatching date	16	1996; 1998–2003; 2005–2009; 2015–2017; 2020	5	1980–1981; 1995; 2017–2018
Number of fledged chicks	16	1996; 1998–2007; 2013–2016; 2020	2	2017–2018
Fledging success	16	1996; 1998–2007; 2013–2016; 2020	2	2017–2018
Food loads	12	1996; 1998–2002; 2005–2007; 2015–2017	0	–
Tarsus growth rate	11	1996; 1998–2002; 2005; 2015–2017; 2020	4	1991; 1995; 2017–2018
Wing growth rate	11	1996; 1998–2002; 2005; 2015–2017; 2020	4	1991; 1995; 2017–2018
Body mass growth rate	11	1996; 1998–2002; 2005; 2015–2017; 2020	5	1979; 1991; 1995; 2017–2018
Maximum body mass	10	1998–2002; 2005; 2015–2017; 2020	5	1979; 1991; 1995; 2017–2018

Data was collected during several expeditions to the Argentinian Base Carlini (CA) and the Henryk Arctowski Polish Antarctic Station (HA). *n* = the number of years with data collected on the listed variables; Year = study years denoted as the year in January of the breeding season (e.g., the breeding season of 1996 spans September 1995 through May 1996)

we used the mean number of birds caught during the peak hours. The number of birds caught in mist nets did not differ significantly over the season (Online Resource 1). Since mist net captures often include non-breeding birds, we estimated the likelihood of an individual to be a breeder or pre-breeder by scoring whether foot web spots were absent (0; young bird; pre-breeder) or present (1; older bird; breeder) following Quillfeldt et al. 2000. The foot spot ratio of all adults caught in a year thus ranges from 0 (only young birds, or pre-breeders) to 1 (only older birds, or breeders).

We assembled all known data describing reproductive performance at both breeding sites, either from published materials (Jabłoński 1986; Wasilewski 1986) or our own studies, including unpublished data. We determined the number of potential nests as burrows from which we at least heard an adult WSP calling, or in which we found an egg or chick. We marked nests either permanently, or within a breeding season with markers being removed at the end of the study period. At CA we stored nest locations on an *x*–*y* grid with a local reference point in earlier years (1996–2001). We stored nest locations in a handheld GPS device (Garmin) in the years after 2001 at CA, and in 2017–2018 at HA. The teams that carried out data collection varied between years and colonies. However, we assumed search effort was similar between years or to have slightly increased in later years. We could not determine reproductive output at the individual or pair level due to the elusive behaviour of the species, because nest burrows are not

occupied every year, and research teams often arrived after egg laying and hatching had started. We used variation in hatching date between years to assess phenological changes, as laying date or fledging date could often not be recorded within the period research teams were present at the study sites. Therefore, as a measurement of colony-wide production, we calculated laying success and hatching success by dividing the number of eggs (including chicks found after hatching) and chicks, respectively, by the maximum number of active nests found in an area in previous years. However, care should be taken when interpreting these variables, as especially laying success may thus be underestimated if unhatched eggs were not found. We determined fledging success as the number of fledglings divided by the number of chicks in a given year, and considered it as NA in years with complete hatching failure.

Storm Petrel chick growth follows a sigmoid curve, with a period of exponential growth followed by a period of linear growth, ultimately reaching an asymptote (Quillfeldt and Peter 2000; Ausems et al. 2020). When a chick's hatching date was unknown, we estimated it based on the size of the chick's tarsus, provided it had not yet reached the asymptote (Quillfeldt and Peter 2000; Ausems et al. 2020). We measured chick body mass to the nearest 0.1 g with an electronic or spring scale, tarsus length to the nearest 0.1 mm with a calliper and wing length to the nearest 1 mm with a ruler. We calculated chick growth rates for individual chicks (Ausems et al. 2020) whenever possible, or for the entire year when

no individual data were available and we had to estimate it from published data. We assumed chicks had passed the linear body mass growth period after 20 days (Ausems et al. 2020), the age at which they generally reach their maximum body mass before losing weight to be able to fledge (Pollet et al. 2021). We log-transformed chick body mass using the natural logarithm before calculating the body mass growth rate. For chicks older than 20 days, we took the maximum recorded body mass and averaged that for all chicks per year, as an estimate of chick body condition. We calculated chick feeding rates (i.e., food load per day in g) for chicks at CA where we measured body mass daily, based on daily mass differences and the estimated metabolic loss during the day (Gladbach et al. 2009; Kuepper et al. 2018).

We defined the different breeding periods based on the median predicted hatching date per year. The non-breeding (NB) period starts at the end of the chick-rearing period of the previous year until 140 days before the median hatching date, the pre-breeding (PB) period runs from 140 to 50 days before the median hatching date, the incubation (IN) period from 50 days before until the median hatching date, and the

chick-rearing (CR) period from the median hatching date until 40 days after (Wasilewski 1986; Sierakowski 1991; Carboneras et al. 2017). NB covers the period when WSPs are absent from the colonies, but may be important for Antarctic krill development. PB covers the period when WSPs arrive at the colonies, and start courtship and egg production (Wasilewski 1986; Sierakowski 1991; Carboneras et al. 2017). For each breeding stage, we selected relevant environmental conditions which are summarised in Table 2.

Environmental conditions

To understand the effects of interannual variation in environmental conditions on breeding output, we selected environmental variables on local and regional scales with known effects. As local weather variables, we considered interannual variation in wind conditions (i.e., wind direction and wind speed), precipitation, sea surface temperature (SST), and 2 m air temperature. As regional variables, we included the hemisphere-wide SAM, which is a measure of the strength of the westerly winds, and SIC west of

Table 2 Response and explanatory variables used for the bootstrapped regression analyses per breeding stage of Wilson's storm-petrels breeding on King George Island, South Shetland, Maritime Antarctic

	Breeding stage			
	Non-breeding	Pre-breeding	Incubation	Chick-rearing
Response variables				
Adults caught (h^{-1})	✓	✓		
Foot spot ratio	✓	✓		
Laying success	✓	✓		
Hatching success	✓	✓	✓	
Hatching date	✓	✓	✓	
Tarsus growth	✓	✓	✓	✓
Wing growth	✓	✓	✓	✓
Body mass growth	✓	✓	✓	✓
Mean maximum body mass	✓	✓	✓	✓
Fledging success	✓	✓	✓	✓
Explanatory variables				
Sea ice cover (lag 0–5 years)	✓	✓		
Southern annular mode	✓	✓	✓	✓
Total precipitation		✓	✓	✓
Air temperature		✓	✓	✓
Wind speed		✓	✓	✓
Westerly winds		✓	✓	✓
Sea surface temperature		✓	✓	✓
Snowstorm days		✓	✓	✓

The tick marks (✓) indicate which breeding stage was relevant for each variable, while empty cells indicate that a breeding stage was not relevant. For the response variables, a tick mark indicates that environmental conditions in that breeding stage were used for bootstrapped regression analysis, while environmental conditions in breeding stages without tickmarks were excluded (e.g., environmental conditions during the chick-rearing period cannot have affected laying success). For the explanatory variables, tick marks indicate for which period data was extracted, while empty cells indicate for which period data was excluded from the analyses (e.g., air temperature at the breeding grounds during the non-breeding period is unlikely to have affected the breeding success in the following breeding seasons as the birds are absent)

the base of the Antarctic Peninsula, in the Bellingshausen Sea marine ecoregion (Fig. 1a; Spalding et al. 2007).

We extracted monthly average wind speed data ($\text{m}\cdot\text{s}^{-1}$) from the READER (REference Antarctic Data for Environmental Research) data base (British Antarctic Survey 2013) for CA (listed under its former name Jubany station). We downloaded wind direction in U (west–east axis) and V (north–south axis) components ($\text{m}\cdot\text{s}^{-1}$) using the Movebank database (<https://www.movebank.org>) from the ERA-interim (ECMWF Re-Analysis; European Centre for Medium-range Weather Forecast (ECMWF), 2011) datasets with a spatial resolution of 79 km grids. From the ERA5 datasets (fifth generation ERA), which have a spatial resolution of 31 km grids, we extracted daily precipitation totals in mm water equivalent and daily mean surface air temperature (K) for the breeding season (January–March) for CA for 1979–2020 (Muñoz Sabater 2019, 2021). We marked a possible snow blocking event, or snowstorm prevalence, when the total precipitation was > 10 mm in a 3-day rolling average, followed by a period ≥ 3 days with mean air temperatures below freezing. We chose these parameters based on field observations in the 2014/2015–2017/2018 breeding seasons.

We downloaded 0.25-degree Daily Optimum Interpolation SST data from NOAA (National Oceanic and Atmospheric Administration) (Huang et al. 2020) for the area between latitude 54–63°S and longitude 60–65°W using the *rerddap* package in R (Chamberlain 2021; R Core Team 2022) from the start of the data collection in 1982. SAM data were downloaded from <http://www.nerc-bas.ac.uk/icd/gjma/sam.html> (accessed 26-04-2021; Marshall 2003) for 1978–2020. We calculated monthly SIC for the Bellingshausen Sea marine ecoregion (Spalding et al. 2007) from remote sensing (Scanning Multichannel Microwave Radiometer, Special Sensor Microwave Imager, Special Sensor Microwave Imager/Sounder) sea ice concentration data (Fetterer et al. 2008). The spatial resolution of the sea ice concentration data is 25×25 km, with a temporal resolution of one day. Sea ice concentration values between 1% and 15% are statistically irrelevant because data values less than 15% from passive microwave instruments are too uncertain to use, and were thus ignored (i.e., set to NA) (Fetterer et al. 2008).

As westerly winds are connected with krill availability (Quillfeldt 2001), we calculated the proportion of days with westerly winds for each relevant time period. We considered days with wind speeds $> 5 \text{ m}\cdot\text{s}^{-1}$ for analyses. We calculated the sum of the precipitation for each breeding stage, and the sum of days with potential snow blocking events. For the other environmental variables, we calculated the anomaly from the monthly mean using all available data between 1978 and 2020. We then calculated the mean anomaly value for each breeding stage.

The mean length of Antarctic krill found in chick food has been reported to be 42.8 mm (Wasilewski 1986), which corresponds to krill of about four years old (Ikeda 1985). Additionally, Antarctic krill shows a multi-year abundance cycle (Hewitt 2003; Steinberg et al. 2015) and its abundance is closely related to sea ice cover (Hewitt 2003; Atkinson et al. 2008). Therefore, we analysed not only the correlation between breeding output and SIC of the preceding winter, but also of the SIC of the winters with time lags up to five years prior.

Statistical analyses

We performed all statistical analyses in R 4.0.5. (R Core Team 2022). Laying success, hatching success, the number of adults caught per hour, foot spot ratio, mean maximum body mass, and fledging success have single values associated with each year and colony, while hatching date, chick growth rates, and food load had multiple values per year coming from different nests.

We assessed demographic variation over time and in relation to changing environmental conditions using linear models (*lm*; package *stats*), and visually assessed model fit using QQ plots. We included year and the environmental conditions during the breeding stages relevant to the breeding variable (Table 2). Additionally, since the micro-climate of the nest burrow may affect chick growth (Michielsen et al. 2019) and 1/3 of the nests was measured at least twice (176 out of 535 nests), in analyses including hatching date or chick growth we used linear mixed-effects models (LMM) with the nest identity as a random effect (*lmer*; package *lme4*; Bates et al. 2015).

We assembled 27 years of data spanning over four decades, with the number of years in which each breeding variable was monitored ranging between 13 (chick growth parameters) and 24 (hatching success; Table 1). Although the considered data set is unique in terms of the temporal scale of data collection, the overall sample size (i.e., the number of study years) was rather moderate, thus resulting in models with wide confidence intervals. Therefore, we examined the significance of the estimates using a bootstrapping ($N = 1000$) procedure (Manly 2007). Additionally, we limited the number of explanatory variables in the models to one to prevent overfitting (Harrell 2015). We determined the results to be significant if the 95% confidence interval of the regression coefficients did not include zero. Since we expected temporal autocorrelation in the data (e.g., the number of adults caught in year $t + 1$ is likely affected by the number of adults caught in year t), we included year as an explanatory variable. Due to the large number of years without data collection, we could not include temporal autocorrelation structures in the models, which may complicate the interpretation of the results. The pairwise approach to

defining the linear models resulted in 333 bootstrapped pairwise linear models (Table 2), for which we did not use any p -value correction methods (Rothman 1990; Saville 1990; Althouse 2016). However, we accounted for the possibility of making Type I errors by interpreting the results on a larger scale than the individual comparisons (e.g., by their potential effects on food availability or nest burrow access).

To account for potential multicollinearity between environmental variables, we used the Pearson's correlation coefficient (*rcorr*; package *Hmisc*; Harrell Jr, 2021) to determine correlations between the environmental variables.

Results

Temporal trends in populations dynamics and breeding performance

The bootstrapped linear regression estimates for laying success (adjusted $R^2 = 0.41$; Fig. 2a) and hatching success (adjusted $R^2 = 0.29$; Fig. 2b) indicated significant decreases over time (Fig. 3a, b). Hatching date did not significantly increase or decrease over time (adjusted $R^2 = -0.01$; Fig. 2c; Fig. 3c). The number of adults caught per the season decreased significantly (adjusted $R^2 = 0.74$; Fig. 2d; Fig. 3d), but foot spot ratio did not change over the studied period (adjusted $R^2 = -0.07$; Fig. 2e; Fig. 3e). The mean number of adults caught per hour, during peak hours (1–3 h after sunset) was 123.0 in 1996–1999, compared to 12.2 in 2001–2020 (see also Online Resource 1 for total catch number per night), a 90.1% decline.

Chick growth rates showed diverging effects with tarsus growth rate significantly increasing over time (adjusted $R^2 = 0.16$; Fig. 2f; Fig. 3f), but with wing growth rate (adjusted $R^2 = 0.24$; Fig. 2g, Fig. 3g) and log body mass growth rate decreasing over time (adjusted $R^2 = 0.02$; Fig. 2h, Fig. 3h). Mean maximum chick body mass did not change significantly over time (adjusted $R^2 = 0.10$; Fig. 2i; Fig. 3i), and food loads did not change significantly over time either (adjusted $R^2 = 0.05$; Fig. 2j; Fig. 3j). Fledging success significantly increased (adjusted $R^2 = 0.12$; Fig. 2h; Fig. 3h).

Effects of environmental conditions on breeding parameters

Laying success was significantly, positively correlated with PB SIC in the preceding year and two years prior, and significantly, negatively correlated with pre-breeding precipitation (Fig. 2a). The adjusted R^2 for laying success ranged between -0.08 (SIC with a 3-year lag) and 0.37 (SIC in the preceding winter; Online Resource 2). Hatching success was also significantly, positively correlated with PB SIC in

the preceding year, as well as with the PB SST anomaly, the incubation air temperature anomaly, and negatively with precipitation during incubation (Fig. 2b). The adjusted R^2 for hatching date ranged between -0.07 (pre-breeding air temperature) and 0.27 (incubation air temperature; Online Resource 2). The mentioned environmental parameters were not correlated with each other for either laying success, or hatching success (p -value ≥ 0.05 ; Online Resource 3).

Hatching date was significantly correlated with non-breeding SIC with 0- up to 5-year lags, and with pre-breeding SIC with 2-, 3- and 5-year lags (Fig. 2c). It was positively correlated with non-breeding SIC in the preceding year, two years prior and three years prior, and with pre-breeding SIC two years prior and five years prior. Hatching date was negatively correlated with non-breeding SIC one year prior, four years prior and five years prior, and with pre-breeding SIC three years prior. SIC in the non-breeding period was significantly, positively correlated with SIC during the pre-breeding period (p -value < 0.05 ; Online Resource 3).

Hatching date was additionally significantly correlated with non-breeding SAM anomaly Fig. 2c). It was also significantly correlated with pre-breeding precipitation, SST anomaly and air temperature anomaly (Fig. 2c). Lastly, hatching date was significantly correlated with incubation precipitation, SAM anomaly, SST anomaly, air temperature anomaly, wind speed anomaly and westerly winds (Fig. 2c). The environmental predictors significantly correlated with hatching date showed various levels of correlation with each other (Online Resource 3). The adjusted R^2 for hatching date ranged between -0.08 (pre-breeding SIC with a 5-year lag) and 0.37 (incubation SST; Online Resource 2).

The log-transformed number of adults caught per hour, during peak hours (1–3 h after sunset) was significantly, positively correlated with pre-breeding SIC up to two years prior (Fig. 2d). Foot spot ratio was significantly, negatively correlated with non-breeding SIC four years prior, and with pre-breeding precipitation (Fig. 2e). The adjusted R^2 for the log-transformed number of adults caught per hour ranged between -0.11 (pre-breeding SAM) and 0.58 (pre-breeding SIC with a 2-year lag; Online Resource 2). None of the significant environmental predictors correlating the number of adults or foot spot ratio was significantly correlated with each other (Online Resource 3).

Food load was significantly, positively correlated with non-breeding SIC with lags between one and five years, and with pre-breeding SIC with 1-, 3- and 4-year lags, but negatively with pre-breeding SIC with a 5-year lag (Fig. 2j). Food load was significantly, negatively correlated with wind speed anomaly in the pre-breeding and incubation period, but positively with chick-rearing wind speed anomaly (Fig. 2j). Food load increased with air temperature anomaly during incubation, and incubation

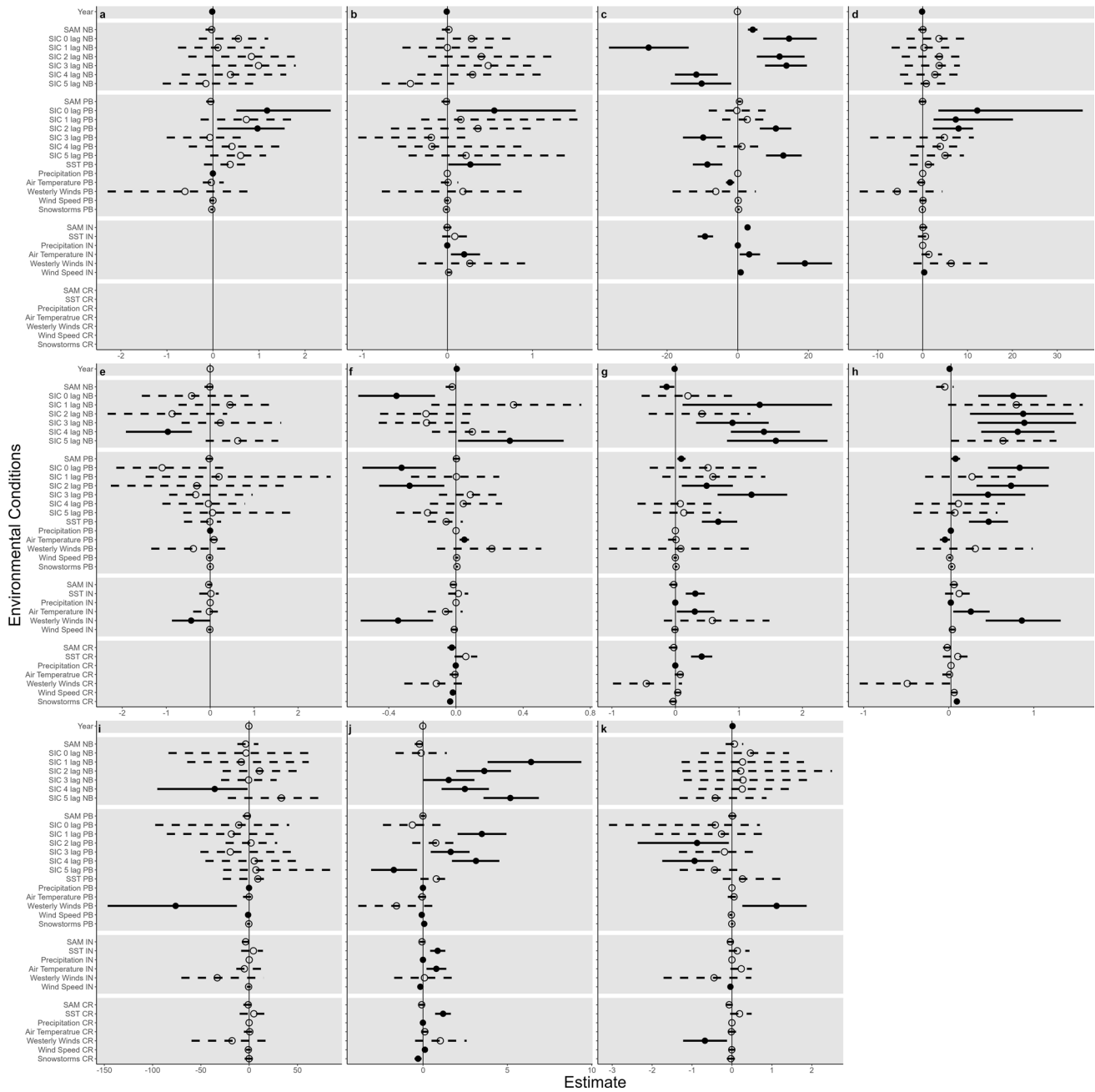


Fig. 2 Pairwise bootstrapped breeding and environmental LM/LMM estimates. The points show the mean bootstrapped estimates, the horizontal lines show the 95% CI, and the vertical solid line shows 0. We assumed significance if the 95% CI did not overlap with zero. Significant effects are shown with solid points and 95% CI lines, non-significant effects are with open points and dashed 95% CI lines. **a** laying success; **b** hatching success; **c** hatching date; **d** log adults

caught $\cdot h^{-1}$; **e** foot spot ratio; **f** chick tarsus growth ($mm\cdot d^{-1}$); **g** chick wing growth $mm\cdot d^{-1}$; **h** log chick body mass growth ($g\cdot d^{-1}$); **i** mean maximum chick body mass (g); **j** food loads (g); **k** fledging success. SAM=Southern Annular Mode, SIC=Sea Ice Cover in the Belling-shausen Sea (Fig. 1a) with 0–5 year lags, SST=Sea surface temperature, NB Non-breeding period, PB Pre-breeding period, IN Incubation period, CR Chick-rearing period. For sample sizes, see Table 1

and chick-rearing SST anomalies (Fig. 2j). Food load was significantly, negatively correlated with precipitation in the pre-breeding, incubation, and chick-rearing stage (Fig. 2j). Conversely, food load was significantly, positively correlated with pre-breeding snowstorm prevalence,

but negatively with chick-rearing snowstorm prevalence (Fig. 2j). The adjusted R^2 of food load ranged between 0.04 (pre-breeding SIC with a 1-year lag) and 0.09 (incubation SAM; Online Resource 2). The environmental predictors

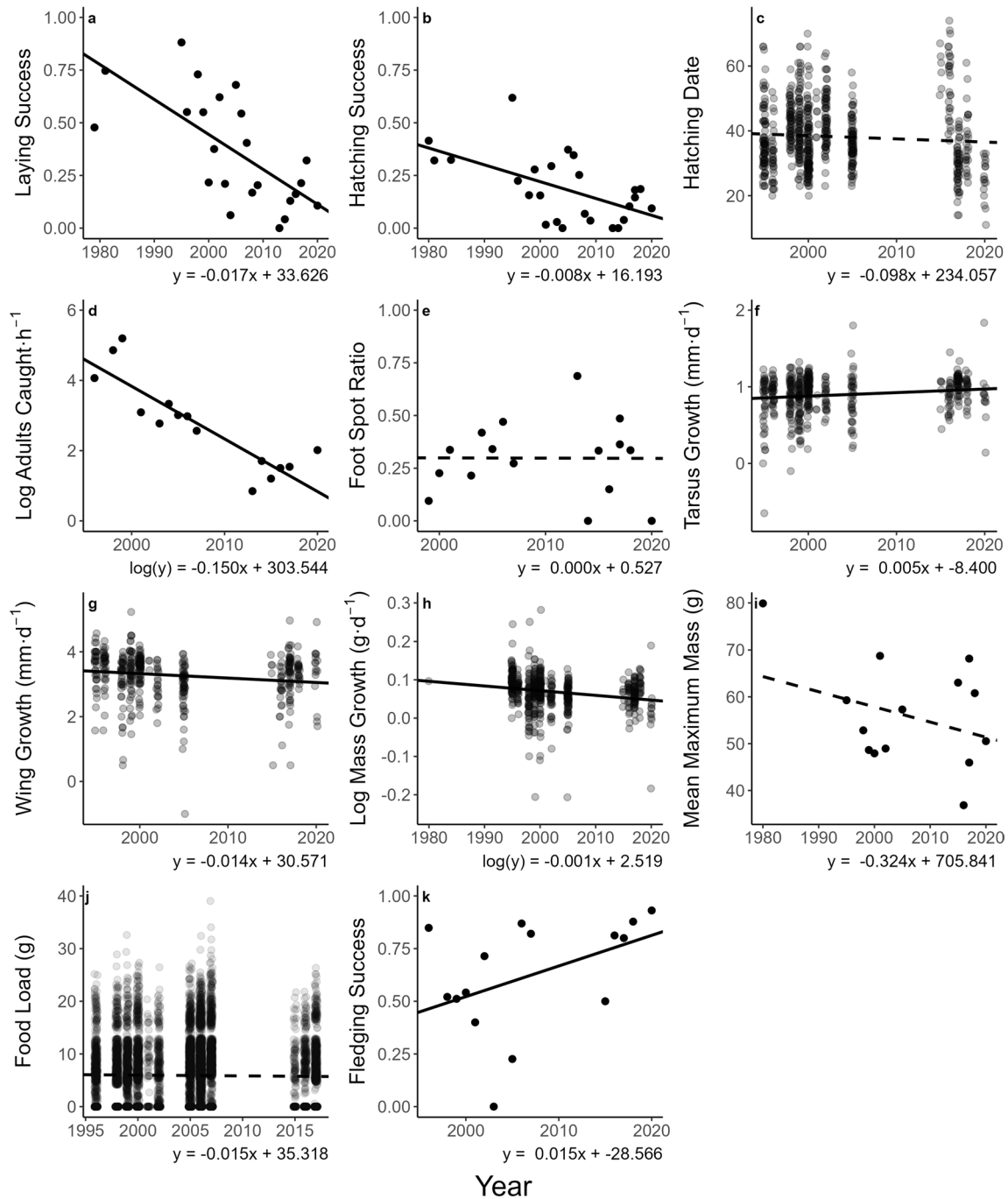


Fig. 3 Wilson's Storm-Petrel breeding variables regression over time. Significant relationships (Fig. 2) are shown with solid regression lines defined by the bootstrapped coefficients and intercepts, while non-significant correlations are shown with dashed lines. For each breeding variable the linear regression model is expressed below the panel. **a** laying success; **b** hatching success; **c** hatching date; **d** log

adults caught $\cdot h^{-1}$; **e** foot spot ratio; **f** chick tarsus growth ($mm \cdot d^{-1}$); **g** chick wing growth ($mm \cdot d^{-1}$); **h** log chick body mass growth ($g \cdot d^{-1}$); **i** mean maximum chick body mass (g); **j** food loads (g); **k** fledging success. Note that the single points in 1979 in panels h and i are based on measurements from multiple nests (Wasilewski 1986)

significantly correlated with hatching date showed various levels of correlation with each other (Online Resource 3).

Fledging success was significantly, negatively correlated with pre-breeding SIC with 2- and 4-year lags (Fig. 2k). It

was positively correlated with pre-breeding westerly winds but negatively with chick-rearing westerly winds (Fig. 2k). Lastly, fledging success was negatively correlated with wind speed anomaly during incubation (Fig. 2k). The adjusted

R^2 of fledging success ranged from -0.09 (chick-rearing wind speed) to 0.26 (pre-breeding SIC with a 4-year lag; Online Resource 2). None of the significant environmental predictors correlating with the number of adults or foot spot ratio was significantly correlated with each other (Online Resource 3).

Effects of environmental conditions on chick growth

Chick tarsus growth rate was significantly, positively correlated with SIC in the preceding year during the non-breeding and pre-breeding periods, and negatively with pre-breeding SIC 2 years prior (Fig. 2f). Tarsus growth rate was positively correlated with the pre-breeding air temperature anomaly, but negatively correlated with westerly winds during the incubation period (Fig. 2f). It was additionally negatively correlated with precipitation, wind speed anomaly, and snowstorm days during the chick-rearing period (Fig. 2f). The adjusted R^2 of chick tarsus growth rate ranged between 0.10 (pre-breeding SIC with a 4-year lag) and 0.27 (incubation westerly winds; Online Resource 2).

Chick wing length growth rate was significantly, positively correlated with non-breeding SIC with 1-, 3-, 4- and 5-year lags, non-breeding SAM anomaly (Fig. 2g). It was also significantly, positively correlated with pre-breeding SIC with 2- and 3-year lags, SAM, and SST anomalies (Fig. 2g). Wing length growth rate was additionally significantly, negatively correlated with incubation precipitation, and positively with incubation SST and air temperature anomalies (Fig. 2g). Lastly, wing length growth rate was significantly, negatively correlated with chick-rearing precipitation, and positively with chick-rearing SST anomaly (Fig. 2g). The adjusted R^2 for wing length growth rate ranged between 0.17 (chick-rearing air temperature) and 0.33 (pre-breeding SIC with a 5-year lag; Online Resource 2).

Log-transformed chick body mass growth rate was significantly, positively correlated with non-breeding SIC in the preceding year and up to 4 years prior (Fig. 2h). Pre-breeding SIC in the preceding year, and with 2- and 3-year lags were also significantly, positively correlated with log-transformed body mass growth rate, as were pre-breeding SAM and SST anomalies (Fig. 2h). Pre-breeding precipitation and air temperature anomaly had significant, negative effects on log-transformed chick body mass growth rate, as had incubation precipitation while incubation air temperature had a positive effect (Fig. 2h). Westerly wind prevalence during the incubation period had a positive effect on log-transformed chick body mass growth rate but westerly wind prevalence during the chick-rearing period had a negative effect (Fig. 2h). Wind speed anomaly and snowstorm prevalence during the chick-rearing period had significant, positive effects on log-transformed chick body mass growth rate (Fig. 2h). The adjusted R^2 for log-transformed chick body

mass growth rate ranged between 0 (non-breeding SIC with a 5-year lag, pre-breeding air temperature and wind speed, and incubation air temperature and SST) and 0.11 (pre-breeding SIC in the preceeding winter; Online Resource 2).

The significant environmental predictors affecting chick growth rates showed an extensive correlation with each other (p -values < 0.05; Online Resource 3). In addition to the significant, positive correlations between non-breeding SIC and pre-breeding SIC with various lags, the significant environmental predictors were intercorrelated at various levels (p -values < 0.05; Online Resource 3).

The annual mean maximum chick body mass was significantly, negatively correlated with non-breeding SIC four years prior, and with pre-breeding precipitation, wind speed anomaly, and westerly wind prevalence (Fig. 2i). The adjusted R^2 for mean maximum chick body mass ranged between -0.10 (pre-breeding SIC with a 5-year lag) and 0.36 (pre-breeding precipitation; Online Resource 2). Total precipitation and wind conditions during the pre-breeding period were significantly correlated with each other (p -values < 0.05), but not with pre-breeding SIC with a 4-year lag (p -value > 0.05; Online Resource 3).

Discussion

The WSP colonies on KGI showed significant changes in population demographics over the last four decades. At CA, the number of adults caught during peak hours (i.e., 1–3 h after sunset) decreased by 90.1%. While mist net captures often include non-breeders and may thus not directly reflect changes in the breeding population size (Quillfeldt et al. 2000; Sanz-Aguilar et al. 2010), this decline corresponds to a decrease in nests found around HA of up to 88.9% when comparing historical numbers (Jabłoński 1986) with the 2016/2017 and 2017/2018 breeding seasons (614 vs. 68 nests in the same area). At the Tres Hermanos colony near CA, a similar decline of 87.5% occurred in the numbers of nests found (1998: 224 nests vs. 2020: 28 nests found). Moreover, foot spot ratio did not change over the studied period, suggesting that the proportion of non-breeders did not change.

Jabłoński (1986) described several large colonies of WSP around HA in the breeding season of 1978/1979 which were abandoned or had shrunk in the breeding seasons of 2016/2017 and 2017/2018. Decreases in seabirds on KGI have been reported for multiple seabird species (Petty et al. 2016; Braun et al. 2021), generally related to climate change causing changes in food availability (Atkinson et al. 2004, 2019), reduced access to nest sites (Büßer et al. 2004; Michielsen et al. 2019), or increased human activity in the area (Chwedorzewska and Korczak 2010). Additionally, data of annual observations of WSP on a global scale from the ebird database (ebird.com 2020) suggests that these declines

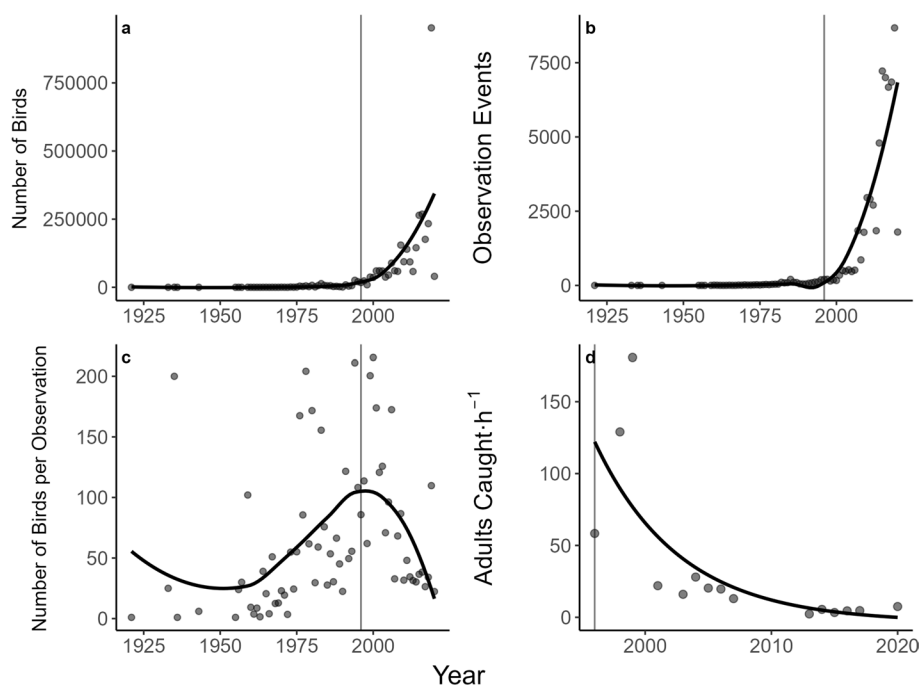


Fig. 4 Wilson's Storm-Petrel observations from the ebird database. Bird-watchers across the world can enter their observations to the ebird database (ebird.com 2020), which is monitored by verified experts and powered by the Cornell Lab of Ornithology. Historical data from checklists, or other sources are included as well. Panel **a** shows the total number of Wilson's Storm Petrels counted across the globe per year, panel **b** shows the total number of observation events (i.e., data entries) per year, and panel **c** shows the mean number of

Wilson's Storm Petrels observed per observation event per year. The solid lines in panel **a–c** show the change over time using local polynomial regression fitting (LOESS) from the *geom_smooth* function with the default LOESS setting (package *ggplot2*; Wickham 2016). Panel **d** shows the number of adults caught per hour at the Argentinian Base Carlini (CA) with the bootstrapped regression line (Fig. 3d). The vertical lines show the start of the study period at CA (1996)

are due to a global decline in WSP numbers, rather than due to relocation (Fig. 4). While the total number of WSP observed has exponentially increased over time (Fig. 4a), so has observation effort (Fig. 4b), but the number of WSP observed per observation event steeply declined in the early 2000s (Fig. 4c).

Changes in WSP adult survival may have had profound effects on the population size, as in long-lived species with low reproductive output, such as storm-petrels, changes in adult survival have a high impact on population size (Sandvik et al. 2012). The decrease in WSP adult activity over time was accompanied by decreases in colony-wide laying success and hatching success calculated as the number of eggs and chicks per maximum number of nests in the area. However, fledging success did increase (Fig. 3k), implying that the few chicks that did hatch were relatively often raised successfully (Reid et al. 2013). Parental quality may thus not have driven the decline in breeding output, but this decline is likely due to a reduction in adult numbers. The age structure of the adult population does not appear to have changed (Fig. 3e) suggesting that the breeding propensity of the different age classes is similar between years and juveniles are still recruited into the breeding population. Combined with

the increased fledging success, this may imply that the cause of the population decline lies at least partially outside of the breeding season (Reiertsen et al. 2014). Indeed, while predation at the breeding grounds and invasive species pose a threat to many Storm Petrel species (Dias et al. 2019; Pollet et al. 2023), the colonies at KGI do not experience excessive predation risks nor have invasive species taken residence in the area.

Non-breeding food availability may affect adult survival rates (Reiertsen et al. 2014), and energy expenditure during the non-breeding period may have carry-over effects on the following breeding period (Clay et al. 2018). There is very little detailed information about the behaviour of WSP during the non-breeding period (Quillfeldt et al. 2005, 2017; Gladbach et al. 2007; Aulsems et al. 2021), but field observations (e.g., bird-watchers) show that they might migrate as far north as the northern Atlantic (ebird.com 2020; Aulsems et al. 2021), an area that has undergone substantial changes in environmental conditions and prey compositions (Hedd et al. 2009; Gaston et al. 2009; Wanless et al. 2018). In addition to changes in food availability, increased human activity in the marine landscape encountered during the non-breeding period may negatively affect WSP survival rates as well.

Light pollution may cause strandings of seabirds (Rodríguez et al. 2017), including Storm Petrels (Lieske et al. 2019), and persistent organic pollutants and trace metals like mercury (Pacyna et al. 2019), picked up in more polluted areas (Wagner et al. 2019) may have negative effects on various breeding parameters, including adult survival (Goutte et al. 2014). While most pollutant concentrations in WSP were lower around 2015 than in the late 1990s or early 2000s (Kuepper et al. 2022), the high concentrations may have played a role in the population crash observed here and supported by the data from ebird (Fig. 4c; ebird.com 2020).

While WSPs breeding on the coast of Adélie Land, continental Antarctica advanced their breeding season (Barbraud and Weimerskirch 2006), we found no significant change in the hatching date of WSP on KGI (Fig. 3). However, we did find significant effects of environmental conditions on hatching dates, particularly SIC anomalies, and ambient weather conditions during the pre-breeding and incubation period (Fig. 2). Hatching dates were mostly affected by changes related to food availability, though generally factors associated with higher spring productivity (e.g., high SAM, SIC) seemed to delay hatching dates (Fig. 2). However, the lack of a significant change in hatching date may be driven by a few relatively late years (2015–2016) later in the study period (Fig. 3), and total laying or hatching failure in the two years prior (2013–2014). Snowstorms were observed during the laying and incubation periods in 2013, 2015 and 2016, potentially explaining the total failures or late hatching as adults may not have been able to access nest burrows (Büßer et al. 2004; Descamps et al. 2023).

Chick growth may be depressed or delayed in response to unfavourable conditions as shown, for example, in the Atlantic Puffin, *Fratercula arctica* (Øyan and Anker-Nilssen 1996). We found that both wing and body mass growth were significantly slower in later years than at the beginning of the study period (Fig. 3). At the same time, the maximum body mass of the chicks did not significantly change (Fig. 3), indicating that eventual chick body size remained the same. Moreover, conversely, tarsus growth rate increased over time (Fig. 3). Variation in chick growth rates was related to a combination of environmental conditions affecting food availability at sea and weather conditions both at the nesting site and at sea (Fig. 3). In an earlier study based on data collected at HA in 2017 and 2018, we also showed significant, but contrasting interannual differences in chick body mass and tarsus growth, but not in wing growth (Ausems et al. 2020). Tarsus growth was higher in 2017, characterised by higher SSTs and an earlier chlorophyll-*a* peak than 2018, while body mass growth was higher in 2018 (Ausems et al. 2020).

The divergence in growth rate change, without affecting the eventual, maximum body mass of the chick, cannot be explained based solely on our results. To fully understand

why interannual environmental variation leads to contrasting effects on WSP chick growth rates, further research is needed. While food loads did not change over the study period (Fig. 3), it is possible that krill quality did change in response to environmental conditions (Clarke 1984; Ikeda 1985; Wasilewski 1986; Polito et al. 2013; Shelton et al. 2013), affecting chick growth (Romano et al. 2006).

Alternatively, within-season variation in hatching date might affect the length of the nestling period, potentially favouring faster chick growth in later chicks to finish breeding before seasonal deterioration of environmental conditions (Wanless and Harris 1988; Murphy 1995; Quillfeldt and Peter 2000). While hatching date in our study was not significantly delayed, contrary to other Antarctic species and locations (Barbraud and Weimerskirch 2006; Chambers et al. 2014), a similar drive for shortened nestling periods may exist due to the increased variability of environmental conditions (Turner et al. 2014) and thus increased unpredictability of food availability. Generally, body mass growth is more variable than tarsus or wing growth (Øyan and Anker-Nilssen 1996; Gębczyński and Jadwiszczak 2000), and body mass growth might respond more quickly to changes in food availability. Therefore, the observed increase in tarsus growth rate may reflect an evolutionary adaptation to environmental change, while the lowered body mass growth may be a short-term response to lower food availability or quality.

We are aware of some limitations of this study. Although our study includes the longest dataset available for WSP, the fact that it consists of several long- and short-term studies limited the consistency of the data. Aside from logistical challenges, records of exact nest locations were often lost for the historical data, thus impeding calculations of the number of unique nests sites. Moreover, colony-wide laying success is a conservative estimate as nests were often hard to find, and unhatched eggs were likely missed. However, the data still provides a unique insight in the population changes over the last decades in light of ongoing climate change. Additionally, we could only include the effects of environmental variation on the breeding grounds. As WSP is a highly migratory species (Gladbach et al. 2007; Ausems et al. 2021; BirdLife International 2021), environmental variation or changes in prey availability at the non-breeding sites may also have led to changes in population dynamics during the breeding period (Desprez et al. 2018). However, further studies into their exact non-breeding distribution are necessary before the effect of environmental variation during the non-breeding period can be assessed.

Conclusion

Our study shows a substantial decline in population size (estimated at approximately 90%) and breeding output for WSP breeding on KGI in maritime Antarctica. WSP surveys from the other site of Antarctica (Pointe Géologie archipelago, East Antarctica) reported a 23% decrease in the number of nests, and a 40% decline in the number of breeding pairs in 2016 compared to 1984 (Barbraud et al. 2017). These alarming results thus potentially contradict the IUCN stable population trend status (BirdLife International 2021) as the decline is mirrored in reductions in global observation numbers (Fig. 4; ebird.com 2020). The population changes were associated with changes in environmental conditions at the breeding site affecting food availability and nest accessibility. Additionally, we showed that other breeding parameters, such as hatching date and chick growth rates, were also affected by environmental variation. The relationships between environmental conditions and breeding output were often complex, and ongoing environmental change may thus impact WSP population dynamics in unexpected ways. However, our study sheds additional light on the potential impacts of environmental change on the breeding output of smaller Antarctic seabird species. Additional research into the effects of environmental change during the non-breeding period on population dynamics is also vital for effective conservation efforts. Monitoring the population dynamics of Antarctic seabirds is vital to increase our understanding of climate change-induced changes in polar food webs. WSP is not only the smallest endotherm breeding in the Antarctic, but also one of the world's most numerous seabird species. As such, changes in their numbers may have far reaching effects on the world's marine ecosystems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-023-03154-4>.

Acknowledgements We would like to thank all field assistants who helped with data collections throughout the years, and Hans-Ulrich Peter (Friedrich-Schiller University Jena, Germany) for the initiation and long-term support at Potter Peninsula. We also thank two anonymous reviewers for their constructive and helpful comments.

Author contributions ANMAA, NDK, PQ and DJ: conceived the research. ANMAA and NDK: assimilated the data and analysed the data. JT: provided meteorological data and analytical tools. ANMAA, NDK, DA, CB, AKG, AG, SH, PJ, PK, MML, SL, BR, AR, TS, ST, KW, DJ, and PQ: carried out the fieldwork to collect data. ANMAA wrote the manuscript. All authors read and approved the manuscript.

Funding This work was supported by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the priority program SPP 1158 "Antarctic Research with comparative investigations in Arctic ice areas" by the following grants: Qu 148/12-1, Qu 148/18-1, Qu 148/32-1, and by personal grants PE 454/1 ff. The work was further funded by a grant from the Polish National Science Center: 2015/19/B/NZ8/01981. AA

additionally received funding from the Erasmus + program for a traineeship and SH received funding from the Deutscher Akademischer Austauschdienst (DAAD).

Data availability The Wilson's storm-petrel datasets generated during and/or analysed during the current study are available in the PAN-GAEA database: <https://issues.pangaea.de/browse/PDI-34626>.

Declarations

Conflict of interest The authors declare no conflict of interest.

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