



# Population trends of penguins in the French Southern Territories

Christophe Barbraud<sup>1</sup> · Karine Delord<sup>1</sup> · Charles A. Bost<sup>1</sup> · Adrien Chaigne<sup>2</sup> · Cédric Marteau<sup>2</sup> · Henri Weimerskirch<sup>1</sup>

Received: 31 July 2019 / Revised: 21 April 2020 / Accepted: 29 May 2020 / Published online: 3 June 2020  
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

## Abstract

Penguins are important top consumers in marine food webs and are one of the most threatened bird families, especially by climate change and food web alterations by marine fisheries. Yet, long-term population trends are lacking or are uncertain for many populations. Seven species of penguins breeding at the French Southern Territories in the southern Indian Ocean on the Crozet, Kerguelen, Saint-Paul–Amsterdam archipelagos and in Terre Adélie/Adelie Land, Antarctica are monitored regularly. This monitoring started in the early 1950s and most populations have been surveyed during the past four years, allowing assessments of population trends. King penguins increased at nearly all breeding sites within the Crozet and Kerguelen archipelagos. Emperor penguins have decreased at Terre Adélie/Adelie Land, with a partial recovery of the colony during the 2010s. Gentoo penguin populations at Crozet and Kerguelen are highly variable but stable. Adélie penguins have been increasing in Terre Adélie/Adelie Land. The trends in eastern rockhopper penguins vary between colonies and archipelagos. Northern rockhopper penguins have continuously decreased in numbers at Amsterdam Island, but appear to have increased at the nearby Saint-Paul Island. Macaroni penguins have first increased and then stabilized since the 2000s at Kerguelen and are stable at the Crozet Islands. Overall, most penguin populations breeding in the French Southern Territories increased or were stable over the past 30–60 years, with the exception of the northern rockhopper penguin, king and gentoo penguins on Crozet and the emperor penguin. The ecological reasons for these trends are poorly understood and require further investigation.

**Keywords** Crozet · Kerguelen · Saint-Paul · Amsterdam · Terre Adélie/Adelie Land · Monitoring · Density dependence

## Introduction

Among bird species, seabirds are extremely threatened with rapid population decline or extinction (Croxall et al. 2012). The penguin family includes 18 species, and in 2019, 10 (55.6%) were listed as threatened (5 endangered and 5 vulnerable), 3 as near threatened, and only 5 as of least concern (IUCN 2019). Breeding habitat degradation, fisheries bycatch, competition with fisheries, climate variability and

change, and marine pollution remain the primary threats for penguin species (Garcia-Borboroglu and Boersma 2015; Trathan et al. 2015; Ropert-Coudert et al. 2019). The Southern Ocean is home to more than 90% of all penguins and penguins are recognized as important top consumers in the Southern Ocean food web (Croxall and Lishman 1987; Guinet et al. 1996). As top consumers, penguins have relatively high body mass, large populations, and high energy demands. Together with Procellariiformes, penguins are the principal marine avian biomass, with an annual consumption of 23.6 Mt of food (Brooke 2004). Being non-flying, swimming and diving predators, penguins are particularly sensitive to oceanographic changes. Their sensitivity is especially acute during the breeding period, because of their low traveling speed and limited foraging ranges (Weimerskirch 2007). Their populations therefore likely reflect variability and trend in oceanographic production within several hundred kilometers of their colonies (Fraser et al. 1992; Crawford 1998; Barbraud and Weimerskirch 2001; Ainley

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00300-020-02691-6>) contains supplementary material, which is available to authorized users.

✉ Christophe Barbraud  
barbraud@cebc.cnrs.fr

<sup>1</sup> Centre d'Etudes Biologiques de Chizé, CNRS UMR 7372, 79360 Villiers en Bois, France

<sup>2</sup> Réserve Naturelle Nationale des Terres Australes Françaises, TAAF Rue Gabriel Dejean, 97458 Saint-Pierre, France

et al. 2004; Forcada et al. 2006; Trivelpiece et al. 2011; Bost et al. 2015). Consequently, penguins have been identified as marine sentinels (Boersma 2008) and have been used as marine ecosystem monitoring species (Agnew 1997). Accordingly, regular and ongoing monitoring of penguin populations is necessary for assessments of population status and trends, for ascribing causes to population change, and in the development of effective conservation measures. Coarse assessments of penguin population trends can be made at a relatively large number of sites but detailed time series of population abundance are known at a limited number of sites where long-term monitoring programs have been conducted over the past 50 years. However, regional differences in climate changes and human activities such as fisheries imply that penguin populations are not responding in a uniform way within their distributional range (Trathan et al. 2007; Constable et al. 2014). Therefore, trend analyses at multiple sites and for multiple species are essential to assess the conservation status of penguins and their global response to environmental changes (Boersma et al. 2019).

The French Southern Territories include the Crozet, Kerguelen and Saint-Paul–Amsterdam archipelagos in the southern Indian Ocean, and Terre Adélie/Adélie Land in East Antarctica. These territories host seven species of penguins (39% of the total number of penguin species). Since 2006, the Crozet, Kerguelen and Saint-Paul–Amsterdam archipelagos are included in the National Reserve of French Southern Territories. Several islands and capes of the Terre Adélie/Adélie Land coasts are designated as Antarctic Specially Protected Areas under the Antarctic Treaty. Several penguin populations have been monitored in these French protectorates since the early 1950s. Over the last 20 years, some populations have exhibited increases, such as the king penguin *Aptenodytes patagonicus* on Ile de la Possession/Possession Island (Delord et al. 2004; Bost et al. 2015), and the Adélie penguin *Pygoscelis adeliae* at Pointe Géologie (Jenouvrier et al. 2006). Other populations have decreased such as the emperor penguin *A. forsteri* at Pointe Géologie (Barbraud and Weimerskirch 2001), the gentoo penguin *P. papua* at Kerguelen (Lescroel and Bost 2006), the northern rockhopper penguin *Eudyptes moseleyi* at Amsterdam Island (Guinard et al. 1998; Jaeger et al. 2018), and the king penguin on Ile aux Cochons/Pig Island (Weimerskirch et al. 2018). However, due to the extent and remoteness of several sites of the archipelagos, many breeding sites are rarely visited and the trends of several important colonies of penguins are unknown. In addition, the importance of density dependence as a regulating factor of penguin populations is poorly known, although some studies suggest it might play a role (Delord et al. 2004; Bost et al. 2015). However, knowledge of density-dependent processes is regarded as important to understand fluctuations in population growth rates and for making decisions on the management of wildlife

populations. Therefore, quantifying density dependence is also important for a better understanding of long-term population trends.

The aims of this study were (1) to provide an update of the penguin breeding population trends in the French Southern Territories, (2) to provide an update of breeding population sizes for species in which all colonies have been surveyed, and (3) to estimate the importance of density dependence in population growth rates.

## Materials and methods

The French Southern Territories include the Crozet Islands (50–52 °E, 46 °S), the Kerguelen Islands (68–70 °E, 48–50 °S), the Saint-Paul and Amsterdam Islands (77 °E, 37–38 °S) and Terre Adélie/Adélie Land (136–142 °E, 67–90 °S) (Fig. 1).

### Crozet

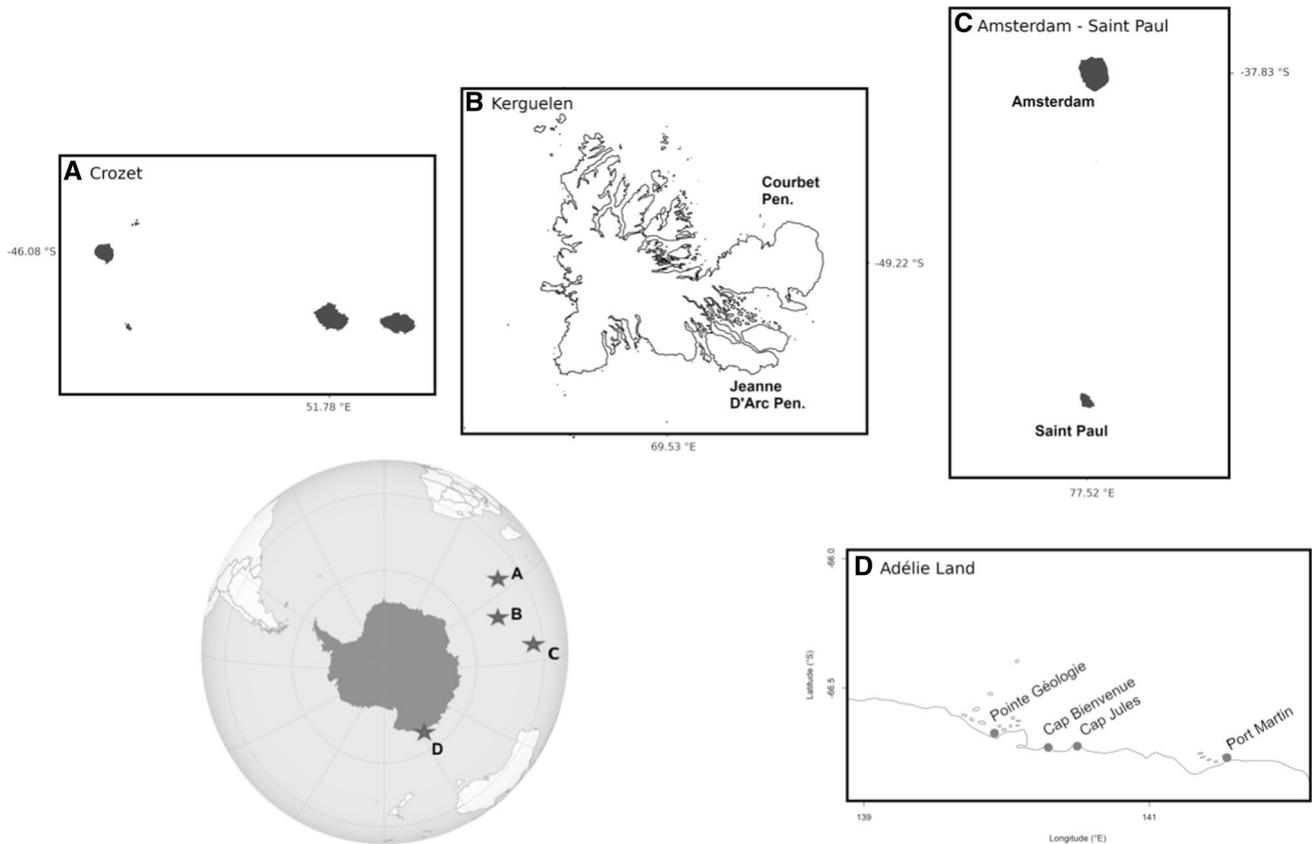
The Crozet Islands consist of five islands: Ilots des Apôtres/Apostle Islets (2 km<sup>2</sup>), Ile des Pingouins/Penguin Island (3 km<sup>2</sup>), Ile aux Cochons/Pig Island (67 km<sup>2</sup>), Ile de l'Est/East Island (130 km<sup>2</sup>), and Ile de la Possession/Possession Island (150 km<sup>2</sup>). Penguins breed on all islands of the archipelago, which hosts four species: king penguins, gentoo penguins, eastern rockhopper penguins *E. filholi* and macaroni penguins *E. chrysolophus*. Long-term monitoring studies have been conducted on Ile de la Possession, the site of the sole permanent research station in the archipelago. All islands except Ile de la Possession/Possession Island have strict protection.

### Kerguelen

The Kerguelen Islands comprise a large main island (6600 km<sup>2</sup>) and ≈ 300 smaller islands and islets giving a total surface of 7200 km<sup>2</sup>. Four species (king penguins, gentoo penguins, eastern rockhopper penguins, and macaroni penguins) breed on the main island and on several of the smaller islands. Monitoring studies are centered on the eastern part of the main island where a research station is located. Other parts of the archipelago are poorly known.

### Saint-Paul and Amsterdam

Saint-Paul and Amsterdam Islands are 8 and 58 km<sup>2</sup>, respectively. Northern rockhopper penguins are the only breeding species of the archipelago, and they breed on the two islands. Long-term monitoring studies have only been conducted at Amsterdam Island which hosts a permanent research station. Saint-Paul Island is a strictly protected area.



**Fig. 1** Map of the southern Indian Ocean showing the location of the French Southern Territories, with detailed maps of the Crozet, Kerguelen, Saint-Paul–Amsterdam and Terre Adélie/Adelie Land archipelagos

## Terre Adélie/Adelie Land

Terre Adélie/Adelie Land is mainly covered by ice but comprises six capes and two archipelagos of small islands and islets along the coast of Antarctica. From West to East these are: Rocher X (0.02 km<sup>2</sup>) Rocher Janet (0.02 km<sup>2</sup>), Pointe Géologie (1.5 km<sup>2</sup>, ≈ 60 islands and islets), Cap Bienvenue (0.21 km<sup>2</sup>), Cap Jules (1.3 km<sup>2</sup>), and Port Martin (3.5 km<sup>2</sup>, ≈ 60 islands and islets). Adélie penguins breed at all these localities except Rocher X, and emperor penguins breed on sea ice at Pointe Géologie only. The emperor penguin colony and approximately 40% of all colonies of Adélie penguins are included in an Antarctic Specially Protected Areas.

## Monitored breeding sites

Long-term studies have been carried out on penguins since the early 1950s on the islands with permanent research stations, and some colonies have been monitored annually for the past 65 years (Barbraud and Weimerskirch 2001; Delord et al. 2004; Jenouvrier et al. 2006; Bost et al.

2015). However, the remoteness and difficulty of access of the other islands of the archipelagos or capes of the Terre Adélie/Adelie Land coast make population estimates to just a few (Table 1). All king penguin colonies and all gentoo penguin colonies from Ile de la Possession/Possession Island have been surveyed regularly, but this is not the case for colonies of eastern rockhopper penguins and macaroni penguins. At other islands of the archipelago, surveys are scarce and have been conducted at least twice only on king penguins. At Kerguelen, nearly all king penguin colonies have been surveyed at least twice, but only a small proportion of the colonies of gentoo penguin, eastern rockhopper penguin and macaroni penguin have been regularly monitored. Eastern rockhopper penguins were only monitored at one colony while breeding colonies of gentoo penguins and macaroni penguins were monitored at several localities. On Amsterdam Island, some breeding colonies of northern rockhopper penguins have been monitored annually, but surveys covering the entire island as well as Saint-Paul Island are relatively few. At Terre Adélie/Adelie Land, all breeding colonies of Adélie

**Table 1** Species-specific proportions of penguin colonies monitored at least twice in the French Southern Territories

Archipelago	Species	Number of breeding sites/ colonies monitored	Number of known breeding sites/colonies	%
Crozet	King penguin	17 <sup>a</sup>	17	100.0
	Gentoo penguin	18 <sup>a</sup>	33	54.5
	Eastern rockhopper penguin	2 <sup>a</sup>	47	4.3
	Macaroni penguin	2 <sup>a</sup>	50	4.0
Kerguelen	King penguin	6 <sup>a</sup>	7	85.7
	Gentoo penguin	44 <sup>a</sup>	79	55.7
	Eastern rockhopper penguin	1 <sup>a</sup>	130	0.8
	Macaroni penguin	7 <sup>a</sup>	42	16.7
Amsterdam–Saint-Paul	Northern rockhopper penguin	14 <sup>a</sup>	15	93.3
Terre Adélie/Adelie Land	Emperor penguin	1 <sup>a</sup>	1	100.0
	Adélie penguin	38 <sup>b</sup>	39	97.4

<sup>a</sup>Colony<sup>b</sup>Island and/or Cape

penguins and emperor penguins at Pointe Géologie have been monitored annually, but surveys covering the other capes and archipelagos of the Antarctic coast are scarce.

### Monitoring methods

The numbers of breeding pairs at each of the monitored colonies were estimated using three main counting techniques. The first technique consisted of visual counts of breeding pairs. Large colonies (> 100 pairs) were divided into sectors using natural geological features, and numbers from all sectors in the colony were summed to derive a total colony estimate. In smaller colonies (< 100 pairs), pairs were individually counted. This technique was used for Adélie penguins (Barbraud et al. 1999), gentoo penguins (Lescroel and Bost 2006), eastern rockhopper penguins, and for some king penguin colonies in the 1960s (Despin et al. 1972). For northern rockhopper penguins we used a variant of this technique (Guinard et al. 1998). Indeed, northern rockhopper penguins often breed in dense vegetation ( $\approx 0.8$  m high) on Amsterdam and Saint-Paul Islands and nests are concealed by vegetation. For this species, breeding colonies were mapped and their surface area was calculated. Within each colony, at least two quadrats of 30m<sup>2</sup> were delimited and the number of nests within each quadrat was counted. The average density (nests/m<sup>2</sup>) on these quadrats was then multiplied by the surface area of the colony to obtain an estimate of the number of breeding pairs. For all colonies where this technique was applied, the number of nests sites occupied by one or two adults was taken as the number of breeding pairs. When using this technique, two to three duplicate fieldworkers counted each colony and their estimates were checked against each other and repeated again

if they varied more than 10% or averaged if they varied less than or equal to 10%.

The second technique consisted of counting individuals using oblique photographs of colonies taken from promontories overlooking colonies. This technique was used for king penguins (Delord et al. 2004), emperor penguins (Barbraud and Weimerskirch 2001), and Adélie penguins (Barbraud et al. 1999). Counts were either directly made on printed photographs or photographs were scanned at the maximum resolution available and counts were made on a computer screen. Count repeatability on photographs was high (Delord et al. 2004). For all colonies counted using this technique, the number of nests sites occupied by one or two adults was taken as the number of breeding pairs.

The last technique consisted of counting individuals using vertical aerial photographs of colonies taken from helicopters, aerial kites, or satellites. This technique was used for king penguins (Bauer 1967; Guinet et al. 1995; Delord et al. 2015; Weimerskirch et al. 2018), Adélie penguins (Barbraud et al. 1999), and macaroni penguins (Bauer 1967; Delord et al. 2015). To minimize disturbance while taking photographs, helicopter flights were made at a minimum of 200 m above colonies. Kites were always launched in areas  $\approx 20$ –30 m from penguins' colonies. Individuals were counted on photographs taken from helicopters or aerial kites and the number of nests sites occupied by one or two adults was taken as the number of breeding pairs. Despite the relatively good resolution of recent satellite images (31 cm from the WorldView-3 VHR satellite), penguins could not be distinguished and counted individually. In this case, which only concerned the king penguin, the surface areas of the colonies were estimated from the satellite images and multiplied by the density of breeders (1.6 nests/m<sup>2</sup>) measured in

reference colonies and assumed to be fairly constant (Guinet et al. 1995). When using the two techniques relying on photographic counts, two duplicate fieldworkers counted each colony and their estimates were checked against each other and repeated again if they varied more than 5% or averaged if they varied less than or equal to 5%.

Since nest failures occur throughout incubation, the best period for counting breeding seabirds is just after laying ends. Thus, all surveys were carried out during the early incubation period for all species: early January for king penguins, mid-June for emperor penguins, early August for gentoo penguins, mid-November for Adélie penguins, early December for eastern rockhopper penguins, mid-September for northern rockhopper penguins, and early November for macaroni penguins. For three colonies of king penguin at Kerguelen, the most recent counts were made in late March 2017. This resulted in underestimating the size of the colonies due to chick mortality that occurred between the end of the laying period and late March. To take into account this underestimation when modeling breeding population trends at these colonies we inflated the 2017 estimates by a coefficient  $c$ . From published estimates of breeding success and hatching success (Williams 1995), we calculated a daily chick mortality rate which was then applied to the period early January—late March to obtain  $c$ . We then modeled the abundance  $N_{2017}$  as a uniform distribution  $U(a,b)$ , where  $a = N_{late\ March} + c_{low}N_{late\ March}$  and  $b = N_{late\ March} + c_{high}N_{late\ March}$  with  $c_{low} = 1.11$  and  $c_{high} = 1.25$ .

### Estimating density dependence and observation error

We used the stochastic Gompertz population model for making inference about density dependence in some of the colonies. By log transforming the number of breeding pairs in year  $t$  ( $N_t$ ) and putting  $x_t = \ln(N_t)$ , this model was defined as follows:

$$x_{t+1} = r + (1 - b)x_t + \varepsilon_t$$

where  $1 - b$  is the lag 1 autocorrelation of the log transformed number of breeding pairs,  $r$  is the growth rate for  $N = 1$  breeding pair,  $b$  is a measure of the strength of density dependence, and  $\varepsilon_t$  is the normally distributed process error with mean zero and standard deviation  $\tau$  (Lebreton and Gimenez 2013). When  $b = 0$  the process is density independent. Uncertainty in numbers of breeding pairs was modeled with a log normal distribution so that the log transformed number of breeding pairs estimate in year  $t$  was given by  $y_t = x_t + \eta_t$ , where  $\eta_t$  is observation error with mean zero and standard deviation  $\sigma$ .

Models were fitted to data using a Bayesian approach implemented in R via JAGS (Plummer 2003). We chose

weakly informative normal priors for parameter  $b$ , and weakly informative uniform priors on the interval 0–3 for parameter  $\tau$ . As recommended by Lebreton and Gimenez (2013), we used an informative prior for  $r$  based on demographic invariant approach (Niel and Lebreton 2005). This prior was a normal distribution with mean species-specific values (king penguin: 0.087, emperor penguin: 0.076, gentoo penguin: 0.129, Adélie penguin: 0.103, eastern rockhopper penguin: 0.124, northern rockhopper penguin: 0.106, macaroni penguin: 0.109) and standard deviation 0.02. We also used an informative prior for  $\sigma$  to separately estimate observation and process variance. This prior was a normal distribution with mean 0.15 and standard deviation 0.04. Inferences were drawn for posterior distributions based on 200,000 Markov Chain Monte Carlo simulations with two chains after a burn-in set of 50 000 updates and a thinning interval of 10 iterations. We assessed the convergence of the model fit by visually checking the trace of the posterior parameter estimates and computed Gelman and Rubin's R-hat convergence statistics.

Although missing values can be accounted for in state-space models for time series analyses (Clark and Bjørnstad 2004), the model was fitted for time series with a minimum of 10 counts. Analyzing time series with fewer data points led to inflated observation and process errors, poor convergence and estimates heavily influenced by priors.

### Estimating trends in breeding population

From the counts of the number of breeding pairs, we estimated annual population growth rates  $\lambda$  using the relationship:

$$\left(\frac{N_t}{N_0}\right)^{\left(\frac{1}{T}\right)},$$

where  $N_0$  is the number of breeding pairs at the time when the first count of the period was made,  $N_t$  the number at the end of the same period, and  $T$  the number of years elapsed between 0 and  $t$  (Caughley 1977). We also estimated the percent change in the numbers of breeding pairs using the relationship:

$$\frac{N_t - N_0}{N_0}$$

To account for the uncertainty in numbers of breeding pairs due to the different monitoring techniques,  $N_t$  and  $N_0$  were modeled as uniform distributions  $U(a,b)$ , where  $a = N_i - 2\sigma N_i$  and  $b = N_i + 2\sigma N_i$  for  $i = (0,t)$  and where  $\sigma$  was the observation error. Estimates of observation errors for each species were obtained from previous studies (Bauer 1967; Guinet et al. 1995; Bost et al. 2015; Southwell et al. 2015) or from state-space models fitted to time series.

## Results

### King penguin

All breeding sites except one were surveyed at least twice. Overall numbers of king penguins breeding on the Crozet and Kerguelen archipelagos have increased at twelve colonies (70.6%), decreased at two (11.8%), remained stable at one (17.6%) of the 18 known colonies (Table 2).

#### Crozet

At Crozet archipelago, all colonies increased at 1.4% to 13.5% per year, except two of the larger colonies of the archipelago. The Baie du Marin colony on Ile de la Possession/Possession Island decreased by nearly 46% since 1961; and the largest colony, Ile aux Cochons/Pig Island, decreased by 75% since 1963. One colony on Ile de l'Est/East Island was stable. Detailed population surveys at Ile de la Possession show that two new colonies appeared during the late 1970s and early 1980s. Detailed surveys also indicated that two large colonies of Ile de la Possession/Possession Island (Jardin Japonais and Petite Manchotière) and the large Ile aux Cochons/Pig Island colony showed a decrease since mid-1990s following a period of increase since the early 1960s (Fig. 2).

#### Kerguelen

At Kerguelen, all colonies increased at 3.5% to 9.8% per year, except two colonies that remained stable. Contrary to colonies from the Crozet archipelago, colonies from Kerguelen did not show a decrease during the 1990s. It is only more recently, since the 2010s, that some colonies such as that at Cape Ratmanoff showed signs of decline (Fig. 2). Only discovered recently, the colony at Pointe Richard on the west coast of Kerguelen hosted at least 28,200 breeding pairs in 2017.

### Emperor penguin

Emperor penguins breed at only one colony at Pointe Géologie. The breeding population of emperor penguins at Pointe Géologie has decreased by nearly 43.5% between 1952 (6075 pairs) and 2018 at a rate of 0.9% per year (Table 2). Annual counts of breeding pairs at the colony show a large decrease between the mid-1970s and the early 1980s, followed by a period of stability until the

mid-2000s (Fig. 3). The breeding population has been increasing since then up to nearly 4500 pairs in 2016.

### Gentoo penguin

Gentoo penguins breed at several localities at Kerguelen and in the Crozet archipelago, but not all colonies are monitored because some are located on remote islands or too far from the permanent station. At Kerguelen, all colonies situated on the Péninsule Courbet/Courbet Peninsula (East of Kerguelen) are regularly monitored as well colonies situated on two islands (Ile Penn/Penn Island and Ile Longue/Longue Island) and four capes within the Golfe du Morbihan/Morbihan Gulf. All colonies remained relatively stable during the period 1988–2018 despite important fluctuations, but seem to be decreasing since 2010 (Table 2, Fig. 4). On the Crozet archipelago, all colonies on Ile de la Possession/Possession Island are regularly monitored. There was strong evidence for a decrease (−32.6%) of the number of breeding pairs at Ile de la Possession/Possession Island between 1992 and 2018, the probability that the mean annual population growth rate was < 1 was 0.953 (Table 2).

### Adélie penguin

Adélie penguins breed at five main localities at Terre Adélie/Adelie Land and have been monitored at four, the fifth colony only hosting a couple score breeding pairs. The number of breeding pairs increased at all localities since 1985 at rates varying between 1.5 and 12.3% per year (Table 2). At Pointe Géologie, the annual monitoring indicated a 64.5% increase of the number of breeding pairs between 1985 and 2018 (Fig. 3).

### Eastern rockhopper penguin

Eastern rockhopper penguins breed at many localities on Kerguelen and Crozet archipelago, but regular monitoring was only conducted at one colony at Kerguelen (Ile Mayes/Mayes Island) and at two colonies at Ile de la Possession/Possession Island (Crozet). At Ile Mayes/Mayes Island, the number of breeding pairs increased since 1994 at 1.9% per year (the probability that the annual population growth rate was positive was 0.932, Table 2). This resulted in a 62.1% increase between 1994 and 2018 (Fig. 4). At Ile de la Possession/Possession Island, one colony was stable whereas the other colony decreased at a rate of 9.9% per year between 2010 and 2017.

### Northern rockhopper penguin

Northern rockhopper penguins breed in several colonies at Amsterdam and Saint-Paul Islands. On Amsterdam Island,

**Table 2** Population trends for penguin species breeding at different localities in the French Southern Territories

Species	Archipelago	Breeding site	<i>N</i>	$\lambda$	Pr( $\lambda < 1$ )	Period	<i>T</i>	% Change		
King penguin	Crozet	Possession—Baie du Marin	23,919 (2018)	0.989 (0.983–0.995)	1	1961–2018	57	–45.9		
		Possession—Jardin Japonais	25,793 (2018)	1.032 (1.025–1.039)	0	1966–2017	52	424.5		
		Possession—Petite Manchotière	11,213 (2018)	1.019 (1.013–1.026)	0	1964–2018	54	184.9		
		Possession—Chaloupe	1311 (2018)	1.103 (1.096–1.110)	0	1966–2018	52	16,561.3		
		Possession—Mare aux Eléphants	6458 (2018)	1.135 (1.123–1.147)	0	1985–2018	33	6465.3		
		Ile aux Cochons/Pig Island	76,640 (2015)	0.973 (0.965–0.983)	1	1963–2015	52	–74.4		
		Est/East—Baie de l'Abondance	67,735 (2019)	1.014 (1.004–1.026)	0	1971–2019	48	104.9		
		Est/East—Plaine des Moraines	113,522 (2019)	1.025 (1.015–1.037)	0	1971–2019	48	243.7		
		Est/East—Vallée des Phoquiers	36,026 (2019)	1.135 (1.124–1.148)	0	1971–2019	48	45,856.2		
		Est/East—Vallée Désolée	4397 (2019)	1.098 (1.087–1.111)	0	1971–2019	48	9217.8		
	Est/East—Vallée du Naufrage	10,057 (2019)	0.999 (0.989–1.010)	0.607	197–2019	48	–3.2			
	Kerguelen	Ratmanoff	87,120 (2017)	1.038 (1.031–1.045)	0	1963–2017	51	591.9		
		Cap Digby	55,868 (2017)	1.039 (1.032–1.046)	0	1963–2017	53	667.4		
		Vallée du Telluromètre	28,656 (2012) <sup>a</sup>	1.012 (1.001–1.025)	0.019	1983–2012	29	45.7		
			18,918 (2017) <sup>b</sup>	1.003 (0.993–1.014)	0.286	1983–2017	34	13.5		
Anse de l'Antarctique		2867 (2012) <sup>a</sup>	1.128 (1.114–1.143)	0	1985–2012	27	2550.3			
Emperor penguin	Kerguelen	Doigt de Sainte-Anne	2184 (2017) <sup>b</sup>	1.104 (1.091–1.116)	0	1985–2017	32	2283.6		
		Doigt de Sainte-Anne	91,644 (2012) <sup>a</sup>	1.092 (1.082–1.101)	0	1973–2012	39	3005.7		
			64,776 (2017) <sup>b</sup>	1.076 (1.068–1.085)	0	1973–2017	44	2490.3		
		Plage du Feu de Joie	46,783 (2017)	1.005 (0.994–1.017)	0.209	1987–2017	30	18.9		
		Pointe Géologie*	Baie des empereurs	3396 (2018)	0.991 (0.987–0.995)	1	1952–2018	66	–43.5	
		Gentoo penguin	Kerguelen	Péninsule Courbet/Courbet Peninsula	8392 (2018)	1.002 (0.986–1.018)	0.406	1988–2018	30	9.5
				Ile Penn/Penn Island	106 (2011)	1.000 (0.979–1.021)	0.500	1988–2011	23	3.2
				Ile Longue/Longue Island	60 (2018)	0.907 (0.854–0.963)	1	2010–2018	8	–52.7
				Anse des Léopards	115 (2018)	0.943 (0.888–1.001)	0.972	2010–2018	8	–35.5
				Anse des Papous	67 (2018)	0.988 (0.930–1.049)	0.651	2010–2018	8	–6.6
				Anse des Pachas	15 (2018)	0.907 (0.853–0.962)	1	2010–2018	8	–53.1
				Pointe Guite	220 (2018)	0.997 (0.939–1.058)	0.544	2010–2018	8	0.4
				Crozet*	Ile de la Possession/Possession Island	577 (2018)	0.984 (0.966–1.002)	0.953	1992–2018	26
		Adélie penguin	Pointe Géologie*	All islands and nunataks	47,058 (2018)	1.015 (1.003–1.026)	<0.001	1985–2018	33	64.5
			Cap Bienvenue*	All islands and nunataks	24,146 (2017)	1.035 (1.023–1.048)	0	1985–2017	32	208.3
Cap Jules*	All islands and nunataks		43,259 (1998)	1.123 (1.074–1.182)	0	1985–1998	13	375.3		
Port Martin*	All islands and nunataks		20,171 (1998)	1.042 (1.006–1.080)	0.003	1985–1998	13	74.8		

**Table 2** (continued)

Species	Archipelago	Breeding site	<i>N</i>	$\lambda$	$\text{Pr}(\lambda < 1)$	Period	<i>T</i>	% Change
Eastern rockhopper penguin	Crozet	Possession—Jardin Japonais	44 (2017)	0.901 (0.832–0.973)	1	2010–2017	7	–50.2
		Possession—Pointe Basse	237 (2017)	0.999 (0.924–1.080)	0.512	2010–2017	7	3.3
	Kerguelen	Ile Mayes/Mayes Island	772 (2018)	1.019 (0.996–1.042)	0.068	1994–2018	24	62.1
Northern rockhopper penguin	Amsterdam*	Entrecasteaux	12,161 (2015)	0.963 (0.952–0.974)	1	1972–2015	43	–79.8
		Subcolony North	15 (2018)	0.895 (0.876–0.913)	1	1995–2018	23	–92.1
		Subcolony South	504 (2018)	0.966 (0.946–0.986)	1	1995–2018	23	–53.6
	Saint-Paul*		7580 (2018)	1.014 (1.003–1.024)	0	1971–2018	47	95.6
Macaroni penguin	Crozet	Possession—Jardin Japonais	938 (2017)	0.996 (0.929–1.066)	0.555	2009–2017	8	0.2
		Possession—Pointe Basse	167 (2017)	1.017 (0.949–1.088)	0.331	2009–2017	8	18.4
	Kerguelen	Courbet 23_26	52,029 (2014)	1.009 (0.999–1.020)	0.051	1963–2014	51	67.8
		Courbet 1_6	21,488 (2015)	1.012 (1.001–1.023)	0.008	1963–2015	52	92.5
		Péninsule Jeanne d'Arc/Jeanne d'Arc Peninsula	18,554 (2017)	0.977 (0.891–1.069)	0.687	2009–2017	6	–9.8

\*Indicates that the entire breeding population of the archipelago was monitored. *N* indicates the most recent count of the number of breeding pairs,  $\lambda$  the population growth rate,  $\text{Pr}(\lambda < 1)$  the posterior probability that  $\lambda$  was lower than 1, *T* the time span over which  $\lambda$  was calculated

<sup>a</sup>Estimates obtained from the most recent counts made in early January

<sup>b</sup>Estimates obtained from the most recent counts made in late March (see Materials and Methods for a description of the approach used to take into account underestimation of population size in March)

all colonies are situated in the cliffs of Entrecasteaux and the breeding population decreased by 79.8% between 1972 and 2015 at a rate of 3.7% per year (Table 2). Regular monitoring at two subcolonies at Entrecasteaux also indicates important decreases (53.6% and 92.1%) between 1995 and 2018 (Fig. 5). At Saint-Paul Island, northern rockhopper penguins breed at two colonies but only one was monitored. The number of breeding pairs increased at 1.4% per year between 1971 and 2018, resulting in a 95.6% increase (Fig. 5).

## Macaroni penguin

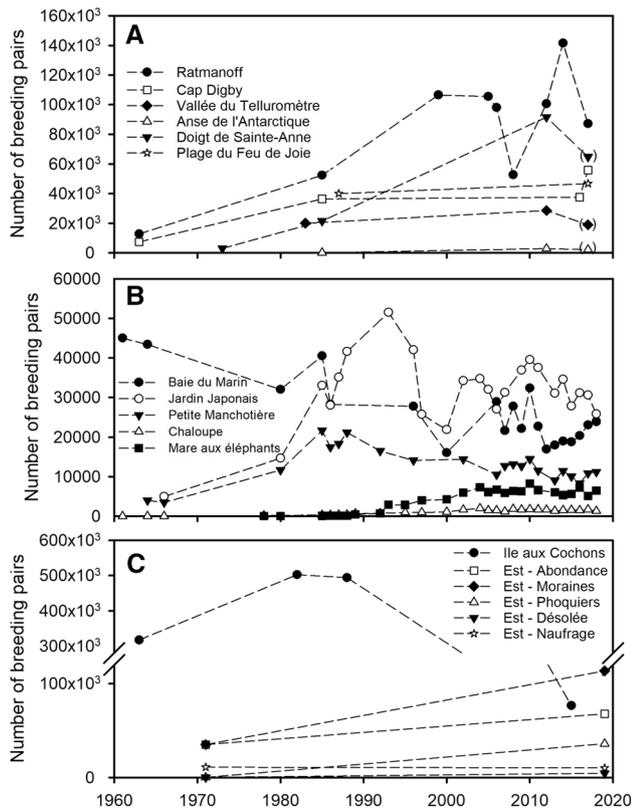
Macaroni penguins breed at numerous sites at Kerguelen and Crozet archipelagos.

Monitoring was conducted at three colonies situated at Kerguelen (Péninsule Courbet/Courbet Peninsula and Péninsule Jeanne d'Arc/Jeanne d'Arc Peninsula) and at two colonies at Ile de la Possession/Possession Island. During the period 1963 to the mid-2010s, the number of breeding pairs was stable or even slightly increasing at rate of 0.9 to 1.2% per year at the Péninsule Courbet/Courbet Peninsula (Table 2, Fig. 4). Surveys at the Péninsule Jeanne d'Arc/Jeanne d'Arc Peninsula indicate stable breeding numbers between 2009 and 2017, although the probability of a

decrease was 0.69. At Ile de la Possession/Possession Island the two monitored colonies seemed relatively stable between 2009 and 2017, although there was a probability of increase of 0.669 for one colony (Ile de la Possession/Possession Island—Pointe Basse, Table 2).

## Density dependence

There was evidence for density dependence for all colonies and species analyzed, except for two colonies of king penguins (Table 3). The two most recent colonies of king penguin at Ile de la Possession/Possession Island (Chaloupe which appeared in 1966, and Mare aux Elephants which appeared between 1981 and 1985) did not show evidence of density dependence. Observation error ( $\sigma$ ) estimates varied between 0.100 and 0.167 depending on species and colonies (Table 3). At the species level, the lowest observation error was for emperor penguins (0.100) and the highest was for eastern rockhopper penguins (0.162). For most time series analyzed (67%) process error dominated or was similar to observation error.

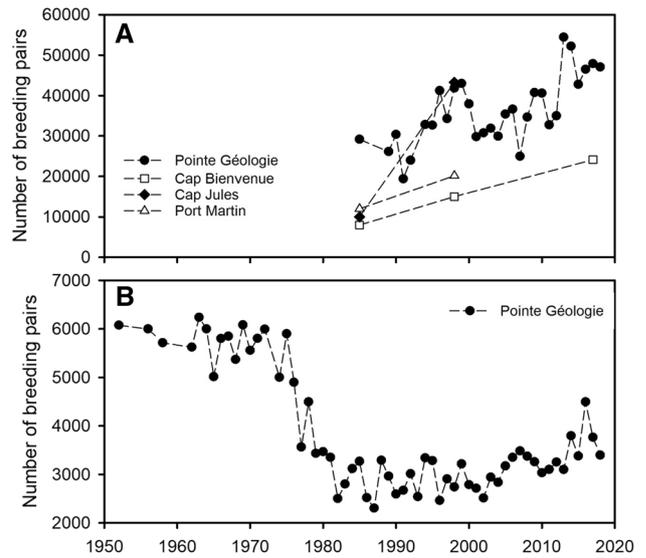


**Fig. 2** Observed changes in the number of breeding pairs of king penguins at **a** Kerguelen (six colonies), **b** Ile de la Possession/Possession Island at Crozet (five colonies), **c** Ile aux Cochons/Pig Island (one colony) and Ile de l'Est/East Island (five colonies) at Crozet over the past 58 years (1961–2019). Parentheses indicate counts made in late March, probably underestimating breeding numbers. Raw data can be found as Online Resources ESM\_1

**Discussion**

This is the first estimation of breeding population trends for all penguin species of the French Southern Territories. Compared to previous studies, we updated population trend estimates, obtained trend estimates at remote breeding sites, and estimated population trends for eastern rockhopper penguins and macaroni penguins. Overall, all species increased or remained stable since the 1960–1970s, except the emperor penguin, the gentoo penguin at Crozet and the northern rockhopper penguin, despite the protected status afforded the breeding islands and offshore areas for all these species (Figs. 6, 7 and 8). For closely monitored colonies, Gompertz models detected density dependence for all species. Trend estimates explicitly took into account uncertainty in counts of breeding pairs.

Model-based estimates of observation error varied between 10 and 17% (Table 3) suggested that the precision of counts was reasonable. Observation errors were lower or similar to process errors, suggesting that breeding

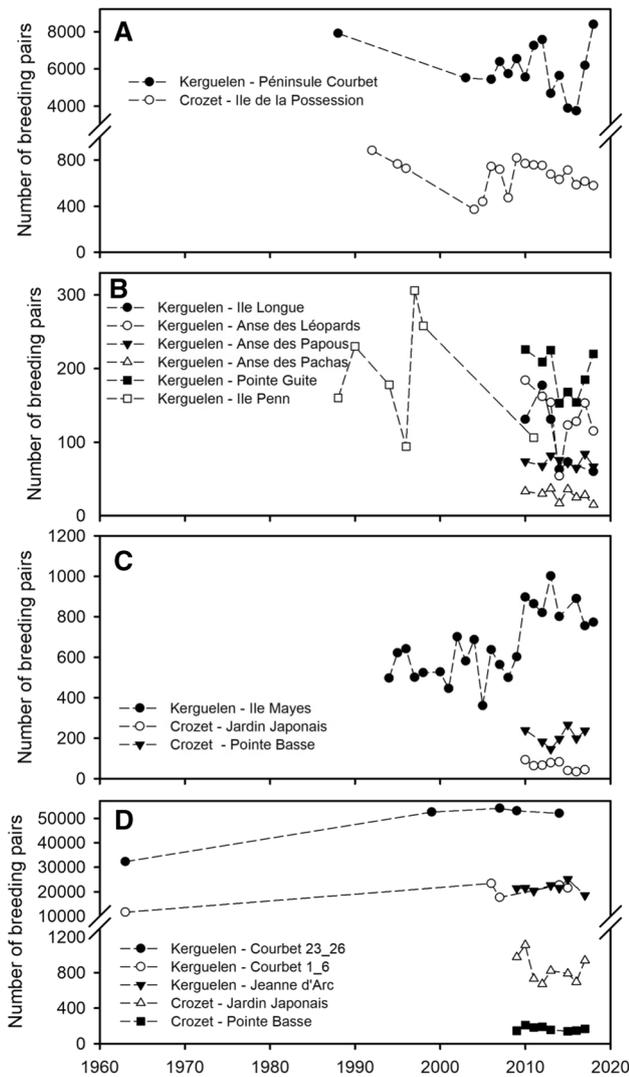


**Fig. 3** Observed changes in the number of breeding pairs of **a** emperor penguins and **b** Adélie penguins at Terre Adélie/Adelie Land over the past 66 years (1952–2018). Raw data can be found as Online Resources ESM\_1

populations were fairly carefully censused (Clark and Bjørnstad 2004). Best precision was generally obtained for large and conspicuous species (king and emperor penguins), whereas counts of smaller species nesting in complex habitats such as boulders or dense vegetation (rockhopper penguins) were less precise. Count uncertainties obtained from Gompertz models were similar to those estimated in other studies [king penguin: Bost et al. (2015); Adélie penguin: Lynch et al. (2012); Southwell et al. (2015); western rockhopper penguin *E. chrysocome*: Baylis et al. (2013)].

**King penguin**

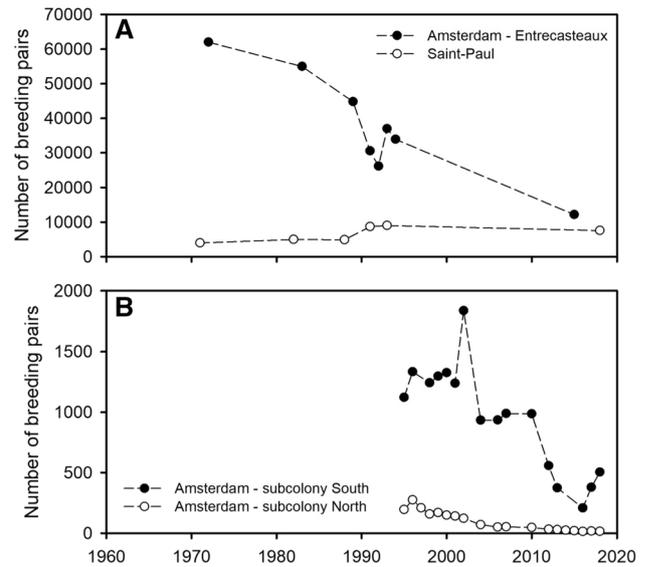
The French Southern Territories are home to 36% of the global population of king penguins (Table 4); after South Georgia, Crozet and Kerguelen are respectively the second and third largest breeding sites for the species. At Crozet and Kerguelen the species increased at most of its colonies. Increases in king penguin populations during the second part of the twentieth century at all breeding sites (Woehler and Croxall 1997; Foley et al. 2018) have been attributed to recovery from past exploitation during the ninetieth century (Rounsevell and Copson 1982). At Ile de la Possession/Possession Island (Crozet), breeding populations have stabilized since the 2000s following a period of decline in the mid-1990s (Delord et al. 2004). Density dependence and climate anomalies seemed to have contributed to this decline (Olsson and Van der Jeugd 2002; Delord et al. 2004; Le Bohec et al. 2008; Bost et al. 2015). Most colonies from Ile de la Possession/Possession Island have been stable since the



**Fig. 4** Observed changes in the number of breeding pairs of **a** gentoo penguins at Crozet (Ile de la Possession/Possession Island) and Kerguelen (Péninsule Courbet/Courbet Peninsula), **b** gentoo penguins at six localities in the Golfe du Morbihan/Morbihan Gulf (Kerguelen), **c** eastern rockhopper penguin at Crozet (two colonies) and Kerguelen (one colony), and **d** macaroni penguins at Crozet (two colonies) and Kerguelen (three breeding localities) over the past 55 years (1963–2018). Raw data can be found as Online Resources ESM\_1

early 2000s, and our results suggest that the breeding population have probably reached a plateau and fluctuate around carrying capacity due to density-dependent feed backs and oceanographic variability.

Although few counts were available for Ile aux Cochons/Pig Island, they suggest an increase until the 1990s and a sharp decrease since then (Weimerskirch et al. 2018). However, the decrease at Ile aux Cochons/Pig Island was proportionally more important than the decreases observed at Ile de la Possession/Possession Island. Although there is no clear plausible explanation for the massive decline at



**Fig. 5** Observed changes in the number of breeding pairs of northern rockhopper penguins at **a** Amsterdam and Saint-Paul Islands, **b** two colonies from Amsterdam Island over the past 47 years (1971–2018). Raw data can be found as Online Resources ESM\_1

Ile aux Cochons/Pig Island (Weimerskirch et al. 2018), it is interesting to note that the strength of density dependence (the  $b$  parameter in the Gompertz equation, Table 3) seems to be positively related (although not significantly) to the maximum size of king penguin colonies at Ile de la Possession/Possession Island (Spearman correlation coefficient between  $b$  estimated for each colony and the maximum size of each colony:  $\rho = 0.60$ ,  $p = 0.28$ ). We therefore suspect stronger over-compensatory density dependence in larger colonies of king penguins, allowing the breeding population to overshoot carrying capacity. The colony can thus grow well above some critical density, and is then reduced much below carrying capacity for several time steps after. This may produce large oscillations (Royama 2012), such as the ones seen for the Jardin Japonais or Petite Manchotière at Ile de la Possession/Possession Island. In addition, strong climate anomalies, such as the exceptional warming of the southwest Indian Ocean in 1997 for king penguins (Bost et al. 2015), may affect population growth more strongly at high density than at low density (Barbraud and Weimerskirch 2003; Stenseth et al. 2004). Interestingly, the population trends at Kerguelen differed from those observed at Crozet. At Kerguelen, breeding colonies are still increasing, suggesting differences in mechanisms regulating population sizes, weak or no density dependence, or populations still in the build-up phase. At Kerguelen, king penguins forage at closer distances from their colony [263 km during brooding, Scheffer et al. 2016] than at Crozet [ $452 \pm 91$  km, Bost et al. (2015)], and they may fare better during warm climate

**Table 3** Stochastic Gompertz population models testing for the effects of density dependence on the breeding population size of penguins at different localities in the French Southern Territories

Species	Archipelago	Breeding site	b	Pr(b > 0)	$\sigma$	$\tau$
King penguin	Crozet	Possession—Baie du Marin	0.010 (0.002)	1	0.167 (0.029)	0.072 (0.055)
		Possession—Jardin Japonais	0.006 (0.003)	0.967	0.120 (0.034)	0.174 (0.039)
		Possession—Petite Manchotière	0.008 (0.003)	0.991	0.117 (0.031)	0.147 (0.034)
		Possession—Chaloupe	0.004 (0.006)	0.757	0.121 (0.033)	0.217 (0.042)
		Possession—Mare aux Eléphants	−0.001 (0.008)	0.442	0.144 (0.037)	0.346 (0.068)
Emperor penguin	Pointe Géologie	Baie des empereurs	0.010 (0.003)	1	0.100 (0.014)	0.070 (0.015)
Gentoo penguin	Kerguelen	Péninsule Courbet/Courbet Peninsula	0.014 (0.008)	0.949	0.149 (0.038)	0.221 (0.095)
		Crozet	Ile de la Possession/Possession Island	0.023 (0.007)	0.999	0.147 (0.034)
Adélie penguin	Pointe Géologie	All islands and nunataks	0.008 (0.003)	0.998	0.139 (0.027)	0.100 (0.043)
Eastern rockhopper penguin	Kerguelen	Ile Mayes/Mayes Island	0.017 (0.005)	0.997	0.162 (0.028)	0.112 (0.058)
Northern rockhopper penguin	Amsterdam	Subcolony North	0.026 (0.010)	0.989	0.146 (0.039)	0.284 (0.082)
		Subcolony South	0.050 (0.010)	1	0.127 (0.033)	0.152 (0.049)

Values in parentheses indicate standard deviations for  $b$  (density dependence parameter),  $\sigma$  (observation error), and  $\tau$  (process error). Pr( $b > 0$ ) indicates the posterior probability that the density-dependent parameter  $b$  was positive. Only time series with at least 10 counts were analyzed

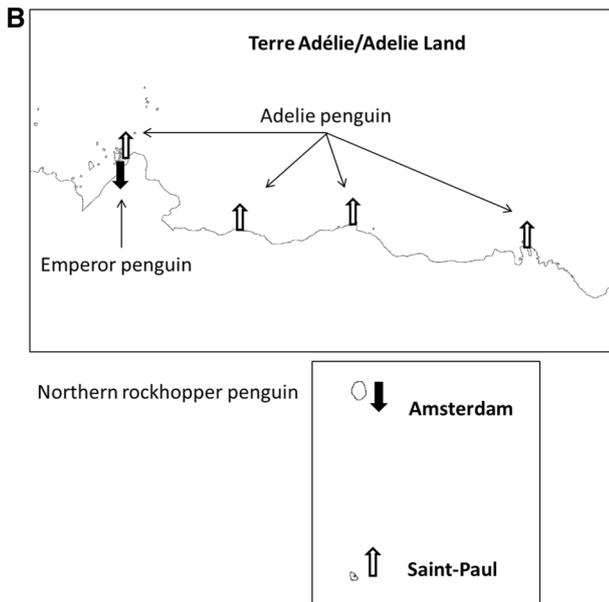
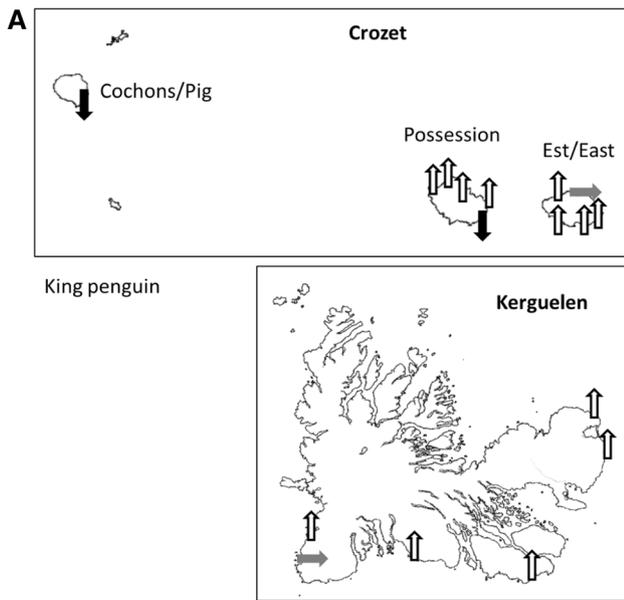
anomalies, causing a southward movement of their main feeding ground, the Polar Front (Bost et al. 2015).

### Emperor penguin

Emperor penguins have declined at Pointe Géologie over the past 66 years, as observed at Haswell Island (Barbraud et al. 2011), Dion Island (Trathan et al. 2011), and Taylor Glacier (Robertson et al. 2014), where the winter breeding colonies have been monitored over the long term. Stable or positive trends were reported at other monitored colonies in the Ross Sea (Kooyman and Ponganis 2016), although these trends are more difficult to interpret since they were based on chick counts that were performed late in the breeding season. Such counts were likely biased by egg and chick mortality. Changes in seasonal formation and decay of sea ice and polynyas during the mid-1970s and mid-1980s are consistent with the decline of our three closely monitored colonies that were observed during the same time period, and have been proposed as major causes of decline (Barbraud and Weimerskirch 2001; Ainley et al. 2005; Jenouvrier et al. 2009a; Barbraud et al. 2011). At Pointe Géologie, emperor penguin breeding numbers have increased since the mid-2000s. This was likely due to an improvement of breeding success between 1998 and 2012 (i.e., an average 0.665 chicks per breeding pair), allowing recovery of the population as a result of better recruitment (Jenouvrier et al. 2009b).

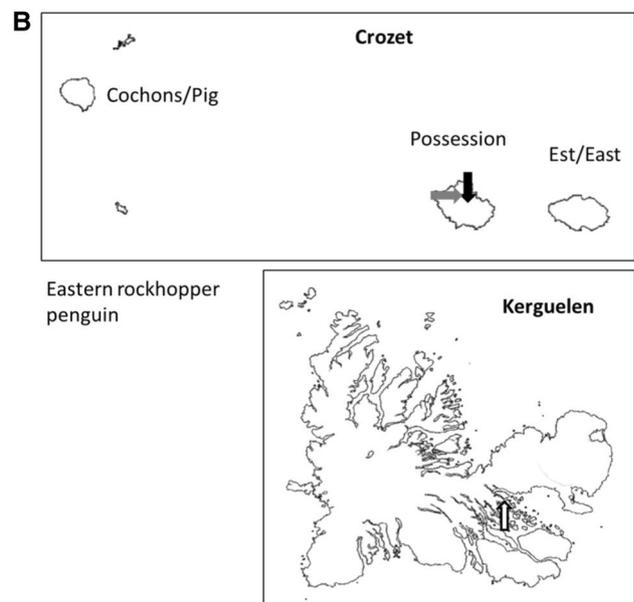
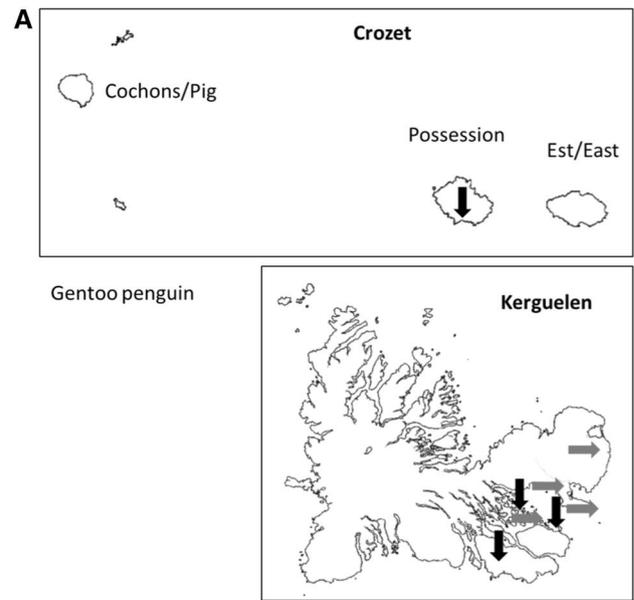
### Gentoo penguin

Gentoo penguins appear stable at Kerguelen and are likely to be decreasing at Ile de la Possession/Possession Island. However, at both sites, breeding numbers declined between the late 1980s/early 1990s and the mid-2000s, as reported by Lescroel and Bost (2006) at Kerguelen, before increasing thereafter. These population trajectories are very similar to those observed at other northern localities such as at Marion and Prince Edward Islands (Crawford et al. 2009) and at South Georgia (Forcada and Trathan 2009). However, these patterns differ from those observed on Falkland Islands (Clausen and Huin 2003; Baylis et al. 2012) and on the Antarctic Peninsula, where populations are steadily increasing (Forcada and Trathan 2009; Lynch et al. 2012). Forcada and Trathan (2009) found a negative relationship between the number of breeding pairs of gentoo penguins at Bird Island (South Georgia) and the Southern Annular Mode (SAM), which is linked to variations in temperature over Antarctica, sea-surface temperature throughout the Southern Ocean. Given the positive trend in SAM observed during the last few decades, the declining population trends observed at the northernmost breeding sites for this species (Marion and Crozet archipelagos, and during the past 30 years), may constitute the early warning signs of a northern range contraction. Such a contraction would parallel the southward range expansion observed during the last 50 years associated with warming (Forcada and Trathan 2009; Lynch et al. 2012). From a demographic point of view, the large inter-annual fluctuations observed for gentoo penguins could be caused by the important variability in reproductive success reported in this species with complete failures in some years



**Fig. 6** Map summarizing the population trends of **a** king penguins and **b** emperor penguins, Adélie penguins and northern rockhopper penguins. Black arrow up indicates increases, white arrow down indicates decreases and horizontal gray arrow indicates stability

(Garcia-Borboroglu and Boersma 2015). Recent decreases observed since 2010 at Kerguelen and Crozet remain unexplained, but massive chick mortalities (CEBC unpublished data) have been observed and potential explanatory factors (disease, predation) require further study. Large inter-annual fluctuations may also be due to the mobility of individuals between nesting sites, a renowned characteristic of gentoo penguins (Bost and Jouventin 1990), although this may be unlikely at the scale of entire islands (Ile de la Possession/

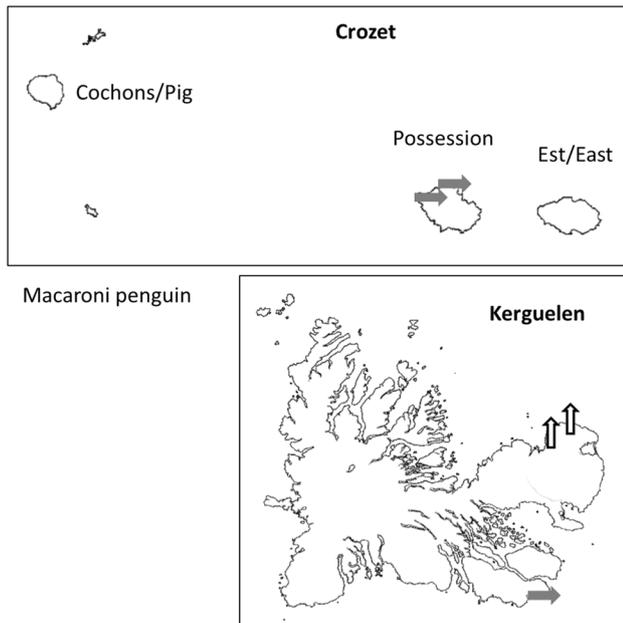


**Fig. 7** Map summarizing the population trends of **a** gentoo penguins and **b** eastern rockhopper penguins. Black arrow up indicates increases, white arrow down indicates decreases and horizontal gray arrow indicates stability

Possession Island) or peninsulas (Péninsule Courbet/Courbet Peninsula at Kerguelen).

### Adélie penguin

Adélie penguins have increased at all breeding sites in Terre Adélie/Adelie Land over the past 30 years as observed for other East Antarctic breeding populations (Southwell et al. 2015). Highly variable breeding success generates high variability in breeding population size in this species (Barbraud



**Fig. 8** Map summarizing the population trends of macaroni penguins. Black arrow up indicates increases, white arrow down indicates decreases and horizontal gray arrow indicates stability

et al. 2015; Ropert-Coudert et al. 2015), but overall sea ice conditions and climate change at Terre Adélie/Adelie Land and adjacent seas seem to have been favorable to the long-term population growth of Adélie penguins during the second half of the twentieth century (Iles et al. 2020).

**Eudyptes penguins**

The populations of eastern rockhopper penguins show contrasting trends at Kerguelen and Crozet, with an increase at Kerguelen, and stability or a decrease at Crozet. By comparison, on the nearby Marion Island and on Antipodes Islands, populations of eastern rockhopper penguins have been decreasing (Crawford et al. 2009; Hiscock and Chilvers

2014), whereas at Falkland Islands in the southwest Atlantic Ocean, the population of western rockhopper penguins has increased (Baylis et al. 2013). However, population trends at Kerguelen and Crozet are only based on three colonies, which represent a very small proportion of the total numbers of breeding pairs at both archipelagos, and may not be representative of trends across the entire population.

Northern rockhopper penguins have declined substantially (~80%) at Amsterdam Island over the past 40 years. Major declines (> 90%) were also observed at Tristan da Cunha and Gough Islands, but occurred during a longer time period starting before our study period at Amsterdam Island (Cuthbert et al. 2009). Over a similar period (1970–2000s), the decrease at Tristan da Cunha and Gough Islands was lower (~20%, from Table 1 in Cuthbert et al. 2009) than the one observed at Amsterdam. From a demographic point of view, the decrease at Amsterdam Island was partly due to very low breeding success (and therefore recruitment), with complete breeding failure in some colonies since 2012 (Jaeger et al. 2018). Curiously, the breeding population of northern rockhopper penguins on the nearby Saint-Paul Island (100 km south) has been increasing during the same time period. We hypothesize that this contrasting situation between Amsterdam and Saint-Paul Island may be due to several factors that differ between the two islands. First, introduced mammals (black rat *Rattus rattus*, European rabbit *Oryctolagus cuniculus*, feral cats *Felis catus*) have been eradicated or went extinct on Saint-Paul Island, contrary to Amsterdam Island where feral cats and Norway rats (*R. norvegicus*) still persist and may predate penguins eggs and chicks (Micol and Jouventin 2002). Second, the infectious agent *Erysipelothrix rhusiopathiae* (a causal agent of erysipelas) was detected in live northern rockhopper penguins from Amsterdam Island, and may induce extensive chick mortality (Jaeger et al. 2018). In addition, the bacteria *Pasteurella multocida* (the causal agent of avian cholera) was a likely cause of chick mortality for several albatross species on Amsterdam Island (Bourret et al. 2018; Gamble et al.

**Table 4** Updated numbers of penguin species for which all breeding colonies were surveyed (number of breeding pairs) breeding in the French Territories of the Southern Ocean in 2017–2018

	Crozet	Kerguelen	Saint-Paul–Amsterdam	Terre Adélie/Adelie Land	% World population
King penguin	377,071 (39,667)	341,938 <sup>a</sup> (35,971)	–	–	48.2
Emperor penguin	–	–	–	3396 (305)	1.3
Adélie penguin	–	–	–	175,141 (21,892)	4.6
Northern rockhopper penguin	–	–	18,440 (2729)	–	8.8

This estimate includes the 28 200 breeding pairs counted at the Pointe Richard colony in 2017. Values in parentheses represents uncertainty calculated using the mean species-specific observation errors estimated in Table 3

2019). *Pastorella multocida* was detected in live northern rockhopper penguins (Jaeger and Lagadec, unpublished data), although it is currently unknown how it affects the species (Jaeger et al. 2018). Third, Amsterdam Island hosts a brown skua *Catharacta lonnbergi* population of  $\approx 50$ –60 breeding pairs which predates northern rockhopper penguin eggs and chicks (CEBC unpublished data). Until recently brown skuas were not breeding on Saint-Paul Island and only five breeding pairs were found there in December 2018 (CEBC unpublished data).

The populations of macaroni penguins have been increasing on Kerguelen over the past 50 years, and appear stable on Crozet and Kerguelen over the past decade, although the proportion of the colonies monitored at Crozet remained small and may not be representative. This contrasts with population trends estimated at other breeding sites: at South Georgia a decline of  $\approx 70\%$  was estimated between the 1980s and the early 2000s and populations were relatively stable during the 2000s and 2010s (Horswill et al. 2016); the overall population at Marion Island decreased by more than 30% between the mid-1990s and the late 2000s (Crawford et al. 2009), and at Macquarie Island the population size of the former royal penguin (*E. schlegeli*, Frugone et al. 2018) was stable or slightly decreasing between 1984 and 2016 (Salton et al. 2019). At South Georgia, the decline in macaroni penguins was attributed to a combination of top down (predation) and bottom up (climate) factors (Horswill et al. 2016), while disease outbreaks may have contributed to the decline of the Marion Island population (Cooper et al. 2009). Ecological and demographic factors contributing to the increase of macaroni penguins at Kerguelen are unknown, and more research on demography and feeding ecology of this species is needed.

## Conclusion

For most species, results from our study suggest that penguin populations of the same species nesting at various sites in the same biogeographic regions show relatively similar long-term trends, indicating that common factors may affect their populations, despite heterogeneity in population trends between colonies at finer spatial scales. With the exception of northern rockhopper penguins and emperor penguins, most populations were stable or increased over the past 40–60 years. Less attention has been paid to the understanding of these increases compared to decreases. Increases are probably caused by a combination of factors, including changes in trophic webs following the human exploitation of large species (whales) competing for the same prey, climate change (which may favor some species such as king penguins expanding down the Antarctic peninsula with

decreasing ice presence around some of the islands) and recovery from past exploitation (Aubert de la Rue 1932; Laws 1977; Heupink et al. 2012; Southwell et al. 2015). This does not mean that identified threats must be overlooked as some of these factors and others have been identified as the major cause of declines at specific sites, e.g., climate change in Antarctica for emperor penguins (Jenouvrier et al. 2009b). Rather, further studies are needed to understand the demographic and ecological drivers of penguins population trends. Finally, density dependence was detected in nearly all species, suggesting that this may be a widespread phenomenon in penguin populations, although more research is required to decipher the underlying demographic and ecological mechanisms.

**Acknowledgements** This study was funded by the French Polar Institute (project IPEV 109), Réserve Naturelle Nationale des Terres Australes Françaises, and the Zone Atelier Antarctique (LTSER France, CNRS-INEE). We thank all the fieldworkers involved in the long-term monitoring programs at Terre Adélie, Crozet, Kerguelen, Amsterdam and Saint-Paul archipelagos. We thank F. Stephen Dobson and two anonymous reviewers for helpful comments on the manuscript.

## Compliance with ethical standards

**Conflict of interest** All authors declare that they have no conflict of interest.

**Ethical approval** The study took place in the National Reserve of “Terres Australes Françaises” and was approved by the Préfet des TAAF, the ethics committee of IPEV and the “Comité de l’Environnement Polaire”.

## References

- Agnew DJ (1997) The CCAMLR ecosystem monitoring programme. *Antarct Sci* 9:235–242
- Ainley DG, Clarke ED, Arrigo K et al (1990s) Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarct Sci* 17:171–182
- Ainley DG, Ribic CA, Ballard G et al (2004) Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. *Ecol Monogr* 74:159–178
- Aubert De La Rue E (1932) La pêche aux Iles Saint-Paul et Amsterdam. *Revue des Travaux de l’Institut des Pêches Maritimes* 5:53–109
- Barbraud C, Delord K, Micol T, Jouventin P (1999) First census of breeding seabirds between Cap Bienvenue (Terre-Adélie) and Moyes Islands (King George V Land), Antarctica: new records for Antarctic seabird populations. *Polar Biol* 21:146–150
- Barbraud C, Delord K, Weimerskirch H (2015) Extreme ecological response of a seabird community to unprecedented sea ice cover. *Royal Soc Open Sci* 2:140456
- Barbraud C, Gavrilo M, Mizin Y, Weimerskirch H (2011) Comparison of emperor penguin declines between Pointe Géologie and Haswell Island over the past 50 years. *Antarct Sci* 23:461–468
- Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. *Proc Royal Soc Lond B* 270:2111–2116

- Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. *Nature* 411:183–186
- Bauer A (1967) Dénombrement des manchotières de l'archipel des Crozet et des îles Kerguelen à l'aide de photographies aériennes verticales. *Terres Australes et Antarctiques Françaises* 41:3–21
- Baylis A, Wolfaardt A, Crofts S et al (2013) Increasing trend in the number of southern rockhopper penguins (*Eudyptes c. chryso- come*) breeding at the Falkland Islands. *Polar Biol* 36:1007–1018
- Baylis AM, Zuur AF, Brickle P, Pistorius PA (2012) Climate as a driver of population variability in breeding gentoo penguins *Pygoscelis papua* at the Falkland Islands. *Ibis* 154:30–41
- Boersma PD (2008) Penguins as marine sentinels. *Bioscience* 58:597–607
- Boersma PD, Borboroglu PG, Gownaris NJ, Bost CA, Chiarada A, Ellis S, Schneider T, Seddon P, Simeone A, Trathan AN, Waller LJ, Wienecke B (2019) Applying science to pressing conservation needs for penguins. *Conserv Biol*. <https://doi.org/10.1111/cobi.13378>
- Bost CA, Jouventin P (1990) Evolutionary ecology of the gentoo penguin *Pygoscelis papua*. In: Davis L, Darby J (eds) *Penguin biology*. Academic Press, New York, pp 85–112
- Bost CA, Cotté C, Terray P et al (2015) Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat Commun* 6:8220
- Bourret V, Gamble A, Tornos J, Jaeger A, Delord K, Barbraud C, Tortosa P, Kada S, Thiebot JB, Thibault E, Gantelet H, Weimerskirch H, Garnier R, Boulinier T (2018) Vaccination protects endangered albatross chicks against avian cholera. *Conserv Lett* 11:e12443
- Brooke M (2004) *Albatrosses and petrels across the world*. Oxford University Press, Oxford
- Caughley G (1977) *Analysis of vertebrate populations*. Wiley, London
- Clark JS, Bjørnstad ON (2004) Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85:3140–3150
- Clausen AP, Huin N (2003) Status and numerical trends of king, gentoo, and rockhopper penguins breeding in the Falkland Islands. *Waterbirds* 26:389–403
- Constable AJ, Melbourne-Thomas J, Corney SP et al (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob Change Biol* 20:3004–3025
- Cooper J, Crawford RJM, De Villiers MS, Dyer BM, Hofmeyr GJG, Jonker A (2009) Disease outbreaks among penguins at sub-Antarctic Marion Island. *Mar Ornithol* 37:193–196
- Crawford R (1998) Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. *Afr J Mar Sci* 19:355–364
- Crawford RJ, Whittington P, Upfold L et al (2009) Recent trends in numbers of four species of penguins at the Prince Edward Islands. *Afr J Mar Sci* 31:419–426
- Croxall J, Lishman G (1987) The food and feeding ecology of penguins. In: Croxall JP (ed) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, pp 101–133
- Croxall JP, Butchart SHM, Lascelles B et al (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv Int* 22:1–34
- Cuthbert R, Cooper J, Burle MH, Glass CJ (2009) Population trends and conservation status of the Northern Rockhopper Penguin *Eudyptes moseleyi* at Tristan da Cunha and Gough Island. *Bird Conserv Int* 19:109–120
- Delord K, Barbraud C, Weimerskirch H (2004) Long-term trends in the population size of king penguins at Crozet archipelago: environmental variability and density dependence? *Polar Biol* 27:793–800
- Delord K, Roudaut G, Guinet C et al (2015) Kite aerial photography: a low-cost method for monitoring seabird colonies. *J Field Ornithol* 86:173–179
- Despin B, Mougin J, Segonzac M (1972) Oiseaux et mammifères de l'île de l'Est. *CNFRA* 31:1–106
- Foley CM, Hart T, Lynch HJ (2018) King penguin populations increase on South Georgia but explanations remain elusive. *Polar Biol* 41:1111–1122
- Forcada J, Trathan P, Reid K et al (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Glob Change Biol* 12:411–423
- Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Change Biol* 15:1618–1630
- Frugone MJ, Lowther A, Noll D, Ramos B, Pistorius P, Dantas GPM, Petry MV, Bonadonna F, Steinfurth A, Polanowski A, Raya Rey A, Lois NA, Pütz K, Trathan P, Wienecke B, Poulin E, Vianna JA (2018) Contrasting phylogeographic pattern among *Eudyptes* penguins around the Southern Ocean. *Sci Rep* 8:17481. <https://doi.org/10.1038/s41598-018-35975-3>
- Fraser W, Trivelpiece W, Ainley D, Trivelpiece S (1992) Increase in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol* 11:525–531
- Gamble A, Garnier R, Jaeger A, Gantelet H, Thibault E, Tortosa P, Bourret V, Thiebot JB, Delord K, Weimerskirch H, Tornos J, Barbraud C, Boulinier T (2019) Exposure of breeding albatrosses to the agent of avian cholera: dynamics of antibody levels and ecological implications. *Oecologia* 189:939–949
- Garcia-Borboroglu PG, Boersma PD (2015) *Penguins: natural history and conservation*. University of Washington Press, Seattle
- Guinard E, Weimerskirch H, Jouventin P (1998) Population changes and demography of the Northern Rockhopper Penguin on Amsterdam and Saint Paul islands. *Colon Waterbirds* 21:222–228
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–65. *Antarct Sci* 8:23–30
- Guinet C, Jouventin P, Malacamp J (1995) Satellite remote sensing in monitoring change of seabirds: use of spot image in king penguin population increase at Ile aus Cochons, Crozet Archipelago. *Polar Biol* 15:511–515
- Heupink TH, van den Hoff J, Lambert DM (2012) King penguin population on Macquarie Island recovers ancient DNA diversity after heavy exploitation in historic times. *Biol Lett* 8:586–589
- Hiscock JA, Chilvers BL (2014) Declining eastern rockhopper (*Eudyptes filholi*) and erect-crested (*E. sclateri*) penguins on the Antipodes Islands New Zealand. *N Z J Ecol* 38:124–134
- Horswill C, Ratcliffe N, Green JA, Phillips RA, Trathan PN, Matthiopoulos J (2016) Unravelling the relative roles of top-down and bottom-up forces driving population change in an oceanic predator. *Ecology* 97:1919–1928
- Iles D, Lynch H, Ji R, Barbraud C, Delord K, Jenouvrier S (2020) Sea ice predicts long-term trends in Adélie penguin population growth, but not annual fluctuations: results from a range-wide multi-scale analysis. *Glob Change Biol*. <https://doi.org/10.1111/gcb.15085>
- IUCN (2019) The IUCN Red List of Threatened Species. Version 2019–1. <https://www.iucnredlist.org>
- Jaeger A, Lebarbenchon C, Bourret V et al (2018) Avian cholera outbreaks threaten seabird species on Amsterdam Island. *PLoS ONE* 13:e0197291. <https://doi.org/10.1371/journal.pone.0197291>
- Jenouvrier S, Barbraud C, Weimerskirch H (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. *Polar Biol* 29:413–423

- Jenouvrier S, Barbraud C, Weimerskirch H, Caswell H (2009a) Limitation of population recovery: a stochastic approach to the case of the emperor penguin. *Oikos* 118:1292–1298
- Jenouvrier S, Caswell H, Barbraud C et al (2009b) Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proc Natl Acad Sci USA* 106:1844–1847
- Kooyman GL, Ponganis PJ (2016) Rise and fall of Ross Sea emperor penguin colony populations: 2000 to 2012. *Antarct Sci* 29:201–208
- Laws RM (1977) Seals and whales of the Southern Ocean. *Phil Trans R Soc Lond B* 279:81–96
- Le Bohec C, Durant JM, Gauthier-Clerc M et al (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci USA* 105:2493–2497
- Lebreton J, Gimenez O (2013) Detecting and estimating density dependence in wildlife populations. *J Wildl Manage* 77:12–23
- Lescroel A, Bost C-A (2006) Recent decrease in gentoo penguin population at Iles Kerguelen. *Antarct Sci* 18:171–174
- Lynch HJ, Naveen R, Trathan PN, Fagan WF (2012) Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93:1367–1377
- Micol T, Jouventin P (2002) Eradication of rats and rabbits from Saint-Paul Island, French Southern territories. In: Veitch CR, Clout MN (eds) *Turning the tide: the eradication of invasive species*. IUCN SSC Invasive Species Specialist Group, IUCN, Gland, pp 199–205
- Niel C, Lebreton JD (2005) Using demographic invariants to detect overharvested bird populations from incomplete data. *Conserv Biol* 19:826–835
- Olsson O, Van der Jeugd HP (2002) Survival in king penguins *Aptenodytes patagonicus*: temporal and sex-specific effects of environmental variability. *Oecologia* 132:509–516
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Austria, Vienna
- Robertson G, Wienecke B, Emmerson L, Fraser AD (2014) Long-term trends in the population size and breeding success of Emperor Penguins at the Taylor Glacier colony, Antarctica. *Polar Biol* 37:251–259
- Ropert-Coudert Y, Chiaradia A, Ainley D et al (2019) Happy feet in a hostile world? The future of penguins depends on proactive management of current and expected threats. *Front Mar Sci* 6:248
- Ropert-Coudert Y, Kato A, Meyer X et al (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* 38:111–113
- Rounsevell DE, Copson GR (1982) Growth rate and recovery of a king penguin, *Aptenodytes patagonicus*, population after exploitation. *Aust Wildl Res* 9:519–525
- Royama T (2012) *Analytical population dynamics*. Springer Science & Business Media, Berlin
- Salton M, Kliska K, Carmichael N, Alderman R (2019) Population status of the endemic royal penguin (*Eudyptes schlegeli*) at Macquarie Island. *Polar Biol* 42:771–781
- Scheffer A, Trathan PN, Edmonston JG, Bost CA (2016) Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Progress Oceanogr* 141:1–16
- Southwell C, Emmerson L, McKinlay J et al (2015) Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adélie penguin populations. *PLoS ONE* 10:e0139877
- Stenseth NC, Chan K-S, Tavecchia G et al (2004) Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proc R Soc Lond B* 271:1985–1993
- Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Phil Trans R Soc B* 362:2351–2365
- Trathan PN, Fretwell PT, Stonehouse B (2011) First recorded loss of an emperor penguin colony in the recent period of Antarctic regional warming: implications for other colonies. *PLoS ONE* 6:e14738
- Trathan PN, García-Borboroglu P, Boersma D et al (2015) Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conserv Biol* 29:31–41
- Trivelpiece WZ, Hinke JT, Miller AK et al (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci USA* 108:7625–7628
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Le Bouard F, Ryan PG, Bost C (2018) Massive decline of the world's largest king penguin colony at Ile aux Cochons, Crozet. *Antarct Sci* 30:236–242
- Williams TD (ed) (1995) *The penguins*. Oxford University Press, Oxford
- Woehler EJ, Croxall JP (1997) The status and trends of Antarctic and sub-Antarctic seabirds. *Mar Ornithol* 25:43–66

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.