



Factors affecting adult body condition in the endangered northern rockhopper penguin

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Abstract

Understanding the factors that drive the dynamics of populations of long-lived species presents a unique challenge for conservation management. Here, we investigated long-term change in the body condition of adult northern rockhopper penguins *Eudyptes moseleyi* at Amsterdam Island, southern Indian Ocean, which hosts 5–10% of the global population of this endangered species. Analysis of a long-term dataset (1994–2016), concurrent to the population's rapid decline, revealed no trend in adult northern rockhopper penguin body condition over time at the stages considered in this study, i.e. *breeding* and *moulting*. However, body condition varied between years and sexes and part of this variation was explained by environmental factors. Males were on average in better condition than females whatever the stage and individuals on average were in better condition during the *moulting* compared to the *breeding* period. The environmental conditions [sea surface temperature anomaly (SSTa), Subtropical Indian Ocean Dipole (SIOD) and Southern Annular Mode (SAM)] appeared to impact non-linearly the body condition. Overall, females were in better condition for negative values of SAM, SIOD and SSTa. The body condition of males exhibited similar but less complex and more significant patterns, with decreasing body condition for increasing SAM, SIOD and SSTa. The absence of long-term trends in male and female body condition suggests that the very low reproductive output and declining population since 1997 is probably not the result of environmental conditions during pre-breeding and pre-moult and necessitates further research into possible drivers during the breeding season.

Introduction

Understanding the factors that drive changes in wildlife populations is central to population ecology and conservation biology, being the first step permitting robust prediction of population trends. In a context of global warming, the marine environment has changed during recent decades and climate scenarios predict changes to continue (Parmesan and Yohe 2003; Cabré et al. 2015). As a consequence, processes

controlling primary productivity are affected resulting in modification of food availability in some marine ecosystems (Moline et al. 2004). Food resources are known to affect body mass of individuals with potential effect on reproductive investment and/or survival (Boutin and Larsen 1993; Kitaysky et al. 1999; Oro and Furness 2002; Altmann and Alberts 2005). In response, morphological traits of animals (i.e., body mass of consumers / higher trophic level predators) were found to be partly sensitive to global warming (Weimerskirch et al. 2012) as well as phenological traits, i.e. timing of biological events, such as reproduction or migration (Radchuk et al. 2019).

As diving and flightless seabirds, penguins are particularly sensitive to oceanographic changes and have been identified as marine sentinels of ecosystems (Boersma 2008; Bost et al. 2015; Iles et al. 2020). Penguins are important top consumers in the Southern Ocean food web and the Southern Ocean hosts more than 90% of all penguins (Croxall and Lishman 1987; Guinet et al. 1996). Penguins (Spheniscidae) are also amongst the three most threatened groups of seabirds, with 10 of 18 species classified as Endangered or

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Vulnerable (Dias et al. 2019). *Eudyptes* are the largest genus by number of species, and are amongst the most threatened with six of seven species being globally threatened (Borboroglu and Boersma 2013; BirdLife International 2018). Most *Eudyptes* penguin species are endangered exhibiting recent dramatic population decline mainly due to climate-induced reduction in prey availability or quality, causing nutritional stress and low demographic rates (BirdLife International 2018; Crawford et al. 2009; Hiscock and Chilvers 2014; Trathan et al. 2015; Morrison et al. 2015; Barbraud et al. 2020). Among the major current threats identified for *Eudyptes* penguins are climate change (increasing sea surface temperature, wind regime changes or extreme weather conditions) and environmental variability often resulting in shifts in marine food webs (Guinard et al. 1998; Barlow et al. 2002; Hilton et al. 2006; Dehnhard et al. 2013a, b; Horswill et al. 2014; Demongin et al. 2010; Wolfaardt et al. 2012), although the availability of resources exploited by fisheries and the increase in predation pressure (i.e., by giant petrels *Macronectes* spp. and fur seals *Arctocephalus* spp.) may play a role in some sites (Cuthbert et al. 2009; Morrison et al. 2015). Other factors, such as diseases, could also be implicated in population declines (De Lisle et al. 1990; Cooper et al. 2009; Horswill et al. 2014; Jaeger et al. 2018).

The global population of northern rockhopper penguins (*Eudyptes moseleyi*, Mathews and Iredale, 1921), an endangered species breeding on seven remote islands in the temperate South Atlantic and southern Indian oceans, experienced severe declines during recent decades (57% over the past 37 years; Cuthbert et al. 2009; Birdlife International 2018; Barbraud et al. 2020). The population of northern rockhopper penguins breeding at Amsterdam Island (37°50' S; 77°33' E), southern Indian Ocean, has been declining at an average rate of 3–4% per year since the early 1970s (Guinard et al. 1998; Barbraud et al. 2020) in line with a significant decline of the breeding success since 1997 (Fig. 1, Jaeger et al. 2018). In this study, we focus on the Amsterdam Island population only. Northern rockhopper penguins are exposed to epizooties, namely to the erysipelas diseases (*Erysipelothrix rhusiopathiae*) and potentially to avian cholera (*Pasteurella multocida*), and although it has been hypothesized that this may be one of the causes believed to be responsible for the population decline, their impact remains unknown (Jaeger et al. 2018).

Eudyptes penguins body mass and phenology are sensitive to climate conditions, i.e. increasing or changing ocean temperatures may reduce nutrients/productivity and ultimately alter food availability, which in turn has been shown to be a known driver of body mass and reproductive success (Dehnhard et al. 2015a, b). Low body mass or body condition in penguins generally negatively affects reproductive success (Robinson et al. 2005; Crawford et al. 2006, 2008). Indeed, *Eudyptes* penguins

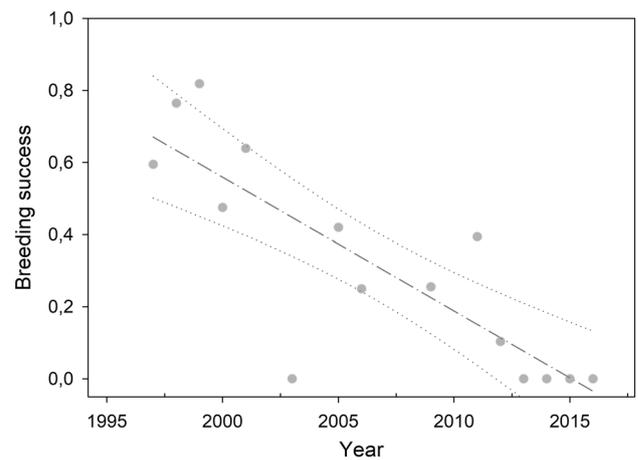


Fig. 1 Breeding success of adult northern rockhopper penguin on Amsterdam Island from 1997 to 2016. Linear regression (dash-dotted line; $r_2=0.70$) with 95% confidence intervals (dotted lines) are shown

exhibit an extremely long courtship-incubation fast (35–49 days) with males assuming an incubation/guard fast of 31–40 days (Williams 1995). Both sexes were found to alter their provisioning and foraging efforts in relation to poor food conditions, with males provisioning less food to their chicks during the crèche stage than females (Morrison et al. 2016).

One ecological hypothesis (food resources hypothesis) to explain the dramatic decline of the northern rockhopper penguin could be modification of food resources at sea (through reduction or displacement of prey) encountered by the birds throughout their annual cycle, as a result of environmental changes. Since northern rockhopper penguins mainly feed on low trophic level prey (euphausiid *Thysanoessa gregaria*, small fish and juvenile squid (Tremblay and Cherel 2003)), this makes them potentially sensitive to changes in oceanographic conditions that affect primary productivity within their foraging range. Furthermore, penguins are capital breeders, i.e. organisms that accumulate energy reserves for breeding before reproductive events (Cherel et al. 1988a; Meijer and Drent 1999). Consequently the birds need to acquire the necessary body reserves for reproduction before the breeding period, but also before the moulting period, which is particularly energy-demanding in penguins due to a prolonged fasting period during a catastrophic moult (Cherel et al. 1988b; Adams and Brown 1990). For southern rockhopper penguins *E. chrysocome*, it has been suggested that the pre–post-moult period could be critical for adult survival, the environmental conditions during this period being correlated with adult survival (Dehnhard et al. 2013a, b).

Based on this knowledge and under the hypothesis that declines in breeding success and abundance of northern rockhopper penguins at Amsterdam Island are caused by a changing of food resources at sea, we used data from a

23-year (1994–2016) study of northern rockhopper penguins at Amsterdam Island to estimate male and female adult body condition at two key stages of their annual cycle (the onset of breeding and moulting) to test this hypothesis. Using this dataset, we addressed the following questions: (1) does male and female body condition show a temporal trend? (2) are male and female body condition and breeding success affected by climatic factors? We predicted a relationship between body condition, breeding success and climate factors known to affect primary productivity in the species' foraging areas.

Materials and methods

Study area and species

Northern rockhopper penguins were studied at Amsterdam Island (37°50' S; 77°33' E) in the southern Indian Ocean, located just north of the SubTropical Front (STF; Graham and De Boer 2013). The entire population of Amsterdam Island (12,000 breeding pairs representing 5–10% of global population and 62% of the Indian Ocean population; Bird-Life International 2018; Barbraud et al. 2020) breeds in several and separate sub-colonies in the area of the Entrecasteaux cliffs (Jaeger et al. 2018). Males arrive at the breeding colonies during the second half of July and females during the first half of August (Duroselle and Tollu 1977; Tollu 1978; Thiebot et al. 2014b). After laying in early September, both parents incubate the two eggs alternately until hatching. Incubation is generally divided in three shifts, the first shared between males and females, the second by female and the third by male. Incubation lasts 33–39 days. Hatching takes place in October. Only males are guarding the chick, which leads to a prolonged fasting period after incubation (17–26 days; Williams 1995). At best, only one chick per pair reaches the crèche stage, when both parents forage simultaneously and leave their chick unguarded in October–November. The chicks fledge in late December, about 60–70 days after hatching. Then both adults depart on their pre-moult trip for 3 to 4 weeks (up to 8 weeks) and return to the breeding colony in March for a prolonged fasting period to moult.

Northern rockhopper penguins are opportunistic foragers, hunting in different areas during the breeding and non-breeding seasons. The foraging range of northern rockhopper penguins has been investigated during the breeding period on Amsterdam Island (Heerah et al. 2019; C. A. Bost, unpublished data) and during the non-breeding period (Thiebot et al. 2012). Incubating penguins perform looping trips, with a mean foraging range of 230 km south of Amsterdam, although some breeders may forage as far as 410 km off their colony. Brooding birds usually forage much closer to the

colony, staying within the region of the shelf (8–80 km; C. A. Bost, unpublished data). Tracking data further revealed that birds disperse after moult over an area stretching to the East of Amsterdam (approx. 47° S and 110° E), performing long-range movements of up to 2200 km away from the colony, without any return to land (Thiebot et al. 2012). The majority of birds head South-east, along the Indian Ridge and forage south of the southern boundary of the SubTropical Front using deep waters (3000–3500 m) with very heterogeneous sea surface temperature anomalies and chlorophyll concentrations (Thiebot et al. 2012).

Northern rockhopper penguins are relying mainly on pelagic crustaceans, in particular euphausiids (Cherel et al. 1999) and juvenile squid at Amsterdam Island (Tremblay and Cherel 2003). Dietary studies from Amsterdam Island show seasonal changes in diet with crustaceans and cephalopods, respectively, dominating the diet during the early crèche stage, while fish being the main prey item in the later stages of chick-rearing (Tremblay et al. 1997; Tremblay and Cherel 2003). Isotopic values of blood collected at the arrival in the colony in spring indicate that adult birds also forage in subtropical waters in late winter (Thiebot et al. 2012).

Biometry and breeding success

Body size measurements (culmen length (± 0.1 mm) using calipers, and body mass (± 50 g) using a Pesola® spring balance) were obtained annually since 1994 on a sample of adults (263 ± 37 individuals each year) captured on arrival at their colony at two key phases of their annual cycle. First, on arrival at the colony at the onset of the breeding season (July–August; hereafter named *breeding*), when individuals return from their non-breeding grounds. Second, after their pre-moult trip (hereafter named *moulting*) between 8 and 20 February, when they return to the colony to moult following the breeding period. Individuals were sexed according to their arrival date at the colony after winter migration (males 20 July–3 August; females 10–26 August). The frequency distribution of the culmen length of sexed birds was then used to determine a culmen length threshold used to sex individuals captured during the moulting period when both sexes arrive together (Warham 1970; Steinfurth et al. 2019). Since there is a slight overlap between male and female culmen length, we removed individuals belonging to the 90th percentile of the culmen length frequency distribution for females and the 15th percentile for males to remove potential sexing errors. This resulted in removing 15.4% and 14.5% of females and males, respectively. A threshold value of 46 mm was used to sex individuals captured during the moulting period (males ≥ 46 mm, females < 46 mm). Since our sexing method excluded the smaller males and the larger females, it may have biased our results. We thus conducted a sensitivity

analysis by creating another dataset where the 15% largest males and the 15% smallest females were removed and re-ran the analyses.

Breeding success was calculated since 1997 on a sample of 14–170 nests depending on the year, as the ratio between the number of chicks counted in December just before their departure at sea and the number of incubating adults (i.e. number of breeding pairs) counted in the first half of September to coincide with the peak egg laying.

Environmental variables

Three environmental covariates were considered to explain inter-annual variations in body condition. The local sea surface temperature anomaly (SSTa) and two climate indices: the Subtropical Indian Ocean Dipole (SIOD) and the Southern Annular Mode (SAM), which are major modes of climate variability in the southern Indian Ocean (Behera and Yamagata 2001; Hall and Visbeck 2002; Hermes and Reason 2005; Terray 2011). As detailed below, these three environmental covariates were chosen as they likely characterize the marine environment used by the penguins at the times of interest from the local, regional and global scales, respectively (Thiebot et al. 2012).

We considered two periods for the climate indices: (i) between the end of the breeding period and the beginning of the moulting period (pre-moult; December of year $t-1$ to January of year t) to test for an effect of climate conditions on body condition prior to moulting, (ii) between the end of the moulting period and the beginning of the following breeding period (pre-breeding; March to July of year t) to test for effects of climate conditions on body condition prior to the breeding period and on breeding success.

Sea surface temperature (SST) plays a fundamental role in net primary production (Behrenfeld et al. 2006), which may have an effect on the distribution and abundance of northern rockhopper preys. SST is known to affect body condition and demographic parameters in several seabird and penguins species (Le Bohec et al. 2008; Barbraud et al. 2012; Dehnhard et al. 2013b; Horswill et al. 2014; Bost et al. 2015). SSTa is regulated by different climate processes/modes operating at different spatial scales (e.g. local, regional and global scales).

Monthly in situ SSTa data were obtained from https://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCEP/EMC/CMB/GLOBAL/Reyn_SmithOIv2/monthly/ssta/. To take into account the variation in the spatio-temporal distribution of adult northern rockhopper penguins, SSTa was extracted during the pre-moult (from December of year $t-1$ to January of year t) for the sector 37°–44° S, 75°–82° E, and during the pre-breeding (wintering from March to July of year t) for the sector 37°–40° S, 75°–90° E when birds use a larger foraging area (Thiebot et al. 2012; Heerah et al. 2019). Finally, SSTa

during the incubating period (September) was extracted for a restricted area 35°–40° S, 75°–80° E (Heerah et al. 2019) to test for effects of climate conditions on breeding success.

The SIOD is defined as the leading mode of the SST variability (i.e., a time series) in the domain 30° E–150° E and 10° S–50° S (Behera and Yamagata 2001; Terray 2011). This index is standardized (e.g. mean and standard deviation equals to 0 and 1, respectively) and positive values of the index (e.g. positive SIOD events) correspond to positive and negative SSTa, respectively, in the southwest and northeast of the southern Indian Ocean basin. This SSTa pattern is linked to a strengthening of the Mascarene high (e.g., a zone of high Sea Level Pressure near Mascarene Island), which corresponds to a blocking atmospheric situation and an undulation of the westerly mean flow with more southeasterly (northwesterly) wind anomalies eastward (westward) of Amsterdam Island. This implies increased (decreased) wind speed eastward (westward) of Amsterdam Island. Note that Amsterdam Island is located exactly at the zero point of the SSTa gradient between the two poles of the SIOD on average. In other words, the in situ SSTa and SIOD bring complementary information on the climate conditions, which may impact northern rockhopper penguins. Consequently, SIOD was used in the analyses during both pre-moult and pre-breeding periods as it may affect northern rockhopper penguins indirectly through its effect on SST and thermocline regional anomalous patterns in addition to in situ SST and thermocline anomalies. It has been shown to affect the foraging behaviour and population dynamics of king penguins *Aptenodytes patagonicus* breeding at Crozet islands (Bost et al. 2015).

Finally, SAM is a global large-scale climatic index defined as the difference in the normalized monthly zonal mean sea level pressure between 40° S and 65° S (Gong and Wang 1999). Monthly SAM values were obtained from the online database of the Koninklijk Nederlands Meteorologisch Instituut <https://climexp.knmi.nl/selectindex.cgi>.

SAM index measures the surface pressure gradient (e.g. the "see-saw" of atmospheric mass) between the middle (around 30° S–50° S) and high (around 50° S–70° S) latitudes of the southern hemisphere (Marshall 2003). It is the dominant mode of atmospheric variability in the southern hemisphere (Hall and Visbeck 2002). Positive values of the SAM index correspond in most cases to stronger westerlies over the high latitudes (50°S–70°S) and weaker westerlies at mid-latitudes. The reverse is true for negative values. As the SAM is a large-scale and low-frequency (e.g., month to month or inter-annual variations) index, it does not correspond necessarily to the in situ wind conditions (direction and speed) in the southern Indian Ocean. As such, its link with the local SST or SIOD is complex. In other words, it is not a redundant climate variable of in situ SSTa/wind conditions or the SIOD. However, SAM may affect northern

rockhopper penguins indirectly through its effect on westerly winds and Ekman transport (i.e., the 90° net transport of the surface layer of a fluid by wind forcing) affecting upwelling intensity and mixed layer depth, and consequently biological productivity and prey availability in the STF zone (Thompson et al. 2011).

In a nutshell, local SSTa, SIOD and SAM provide different details of the background climate conditions from the local, regional and global scales, respectively, and the relations between local SST and wind with both SAM and SIOD are not direct.

We tested for a temporal trend in environmental variables using a generalised linear model (GLM) with a Gaussian family distribution and identity link function. Year was fitted as a continuous variable. The GLM model was fitted using the R package *lme4*.

To assess the robustness of association between the body condition of penguins and the physical environment, we also computed correlation maps between body condition of males and females during the *breeding* and *moulting* periods and the SST time series over the Indian Ocean for the two seasons preceding: the pre-breeding and pre-moult periods. Such correlation maps are standard statistical tools of climate analysis (see Von Storch and Zwiers 1999 for illustration) and they have been very useful in this science to discover new phenomena or modes of climate variability. In our context, although we extracted some environmental variables from the distribution areas of penguins during different periods of their life cycle, which we then used as explanatory variables for body condition, correlation maps are complementary to this analysis by focusing on larger spatial scales and shed light on the spatial structure of climate anomalies, which may be associated with changes in body condition.

Modelling body condition

To estimate body condition, we used the scale mass index (SMI) as recommended by Peig and Green (2009). The SMI (hereafter referred to as body condition) was calculated for each individual i according to the formula:

$$SMI_i = M_i * (x/L_i)^b$$

where M_i and L_i are, respectively, the body mass and the bill length of the individual i , x is mean of bill length (47.22 mm for females and males pooled) and b is the value of the slope estimate of a standard major axis regression (SMA) of bill length and body mass (0.532 for females and males pooled). The SMA between bill length and body mass was fitted using the R package *lmodel2*.

First, we tested for the effects of sex, day of the year, year, stage (*breeding*, *moulting*) and the interaction

between sex and stage on body condition using a GLM with a Gaussian family distribution and identity link function. Year was fitted as a categorical effect to test for inter-annual variations in body condition, and day of the year as a continuous variable. To test for a trend in body condition, year was fitted as a continuous variable. The GLM model was fitted using the R package *lme4*.

As we suspected strong non-linear effects of climate covariates on body condition, their effects were tested using generalised additive models (GAM) with a Gaussian family and identity link function. The advantage of GAMs is the smoothing function which enables to model non-linear relationships between the response variable and the predictors (Wood 2004, 2017). Because sex and stage effects were found on body condition using GLM (see “Results”) and due to potentially complex non-linear interactions between sex, stage and environmental covariates, separate GAM were developed for males and females and for each stage. Models included day of the year, SSTa, SIOD and SAM as fixed factors modelled with non-parametric smoothing functions (Wood et al. 2017). We a priori expected non-linear effects of the date at which birds arrived at the colony and were weighed because body condition is known to be influenced by several intrinsic factors (such as age, experience, individual quality...) which may affect arrival at the colony in a complex way. We proceeded with a forward-stepwise modelling approach, by fitting one variable at a time to estimate the variance explained by each (Carneiro et al. 2016). We limited the amount of smoothing (k) to 3 degrees of freedom for each spline to avoid excessive flexibility and model overfitting that would have no ecological meaning (Wood 2004). As there was a single very early date of arrival (day of the year = 23 for 2004) during *moulting*, we tested the same forward-stepwise modelling approach on a dataset excluding this year (see results on Online Resource 1, Table S2 and Fig S1). The models selected were similar whatever the dataset used (see “Results“ and Online Resource 1, Table S1, S2). We thus considered the original dataset.

Finally, we investigated (at the population level) whether body condition between i) the *breeding* and subsequent *moulting* period and ii) the *moulting* period and subsequent *breeding* period were correlated. We first checked for normality of the body condition using Shapiro–Wilk tests and then performed correlation tests (accordingly Spearman rank correlation test (Shapiro–Wilk test; $P < 0.05$) for i), and Pearson’s test (Shapiro–Wilk test; $P > 0.05$) for ii).

Modelling breeding success

The effects of climate covariates and body condition on breeding success were tested using GAM with a Gaussian

family and identify link function. Models included body condition of females and males during breeding, SSTa and SAM during the winter preceding the breeding event, and SSTa during the incubating period as fixed factors modelled with non-parametric smoothing functions (Wood et al. 2017).

Prior to GAM analysis (body condition and breeding), we used the variance inflation factor to assess collinearity between climate variables and removed covariates for which $GVIF > 2$ (Zuur et al. 2009). Residual normality was visually verified. The starting models included all the main effects. The best candidate model (i.e. the model containing the most informative set of covariates) was selected based on the Akaike's information criterion (AIC). A difference of more than 2 AIC units was taken to indicate strong support for the model with the lower AIC (Burnham and Anderson 2002). The GAM models were fitted using the R package *mgcv* and *MASS*. Data were analysed using R 3.4.1 (Team RC 2019).

Results

Adult body condition

There was a high inter-annual variability in body condition of male and female northern rockhopper penguins for both sexes and stages over the study period 1994–2016 (Fig. 2). A similarly high variability was observed for body mass whatever the sexes and the stages considered (Fig. S2). However, no long-term temporal trend was detected for the body condition whatever the period (*breeding* vs. *moulting*) or the sex considered (Fig. 2). At the population level, no correlation was found for body condition i) between the breeding and subsequent moult period (Spearman rank correlation, $r_s = -0.12$, $N = 19$, $P = 0.63$), and ii) between the moult and subsequent breeding period (Pearson's correlation, $r = 0.29$, $N = 20$, $P = 0.22$). Individuals were in better condition during the *moulting* period compared to the *breeding* period, and males were on average in better condition than females (Table 1, Figs. S2, 2). Body condition also varied between sexes, stages and date of the year (see Online Resource 1, Table S1). Body condition was negatively related to day of the year, indicating that individuals arriving earlier at the colony whatever the period (*breeding* vs. *moulting*) were in better condition.

All three climate covariates (SSTa, SIOD, SAM) exhibited significant temporal trends over the study period ($P < 0.001$) except SAM during the pre-moult (for female $P = 0.011$ and for male, non-significant; see Online Resource 1, Table S4–S7). SSTa and SAM tended to increase (pre-breeding) while SIOD tended to decrease (pre-breeding and pre-moult). All three climate covariates and day of the year

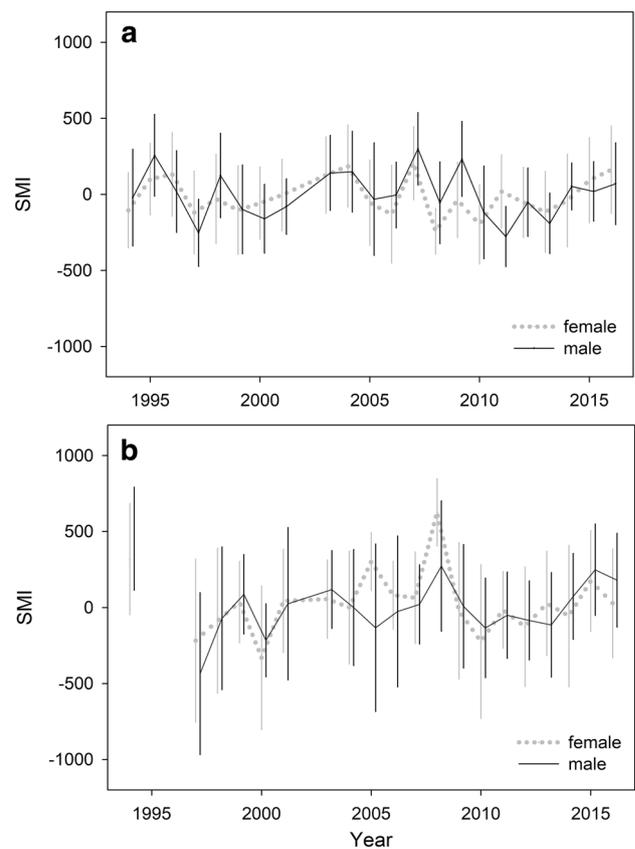


Fig. 2 Body condition (scale mass index: mean \pm standard deviation) in adult northern rockhopper penguins on Amsterdam Island from 1994 to 2016 corrected for the effect of day of the year during **a** *breeding* stage and **b** *moulting* stage in females (dotted grey) and males (black). To correct for the effect of day of the year we used the residuals from a GAM modelling body condition as a function of day of the year

affected male and female condition during pre-breeding and pre-moult (see Online Resource 1, Table S2). The GAM models explained $\sim 48\%$ and $\sim 32\%$ of the deviance during the *breeding* and the *moulting* periods, respectively. The day of the year explained a large part of the variation of body condition ($\sim 41\%$ and $\sim 25\%$ of the deviance during *breeding* and *moulting*, respectively), the climate covariates explaining the remaining part ($\sim 7\%$, 2.7–11.3; see Online Resource 1, Table S2). Among covariates, SSTa (4%) for females and SAM (12.4%) for males better explained body condition variations during pre-breeding, while SIOD (7% and 3.5%, respectively, for females and males) better explained body condition variations during pre-moult.

During *breeding*, body condition decreased with increasing arrival date at the colony for males and females (see Online Resource 1, Tables S4–S7, Fig. 3a). These relationships were similar during the *moulting* period, with a clear pattern for late arriving individuals that were in lower body condition whatever the sex (Fig. 4a).

Table 1 Average body measurements and body condition (scale mass index, body condition) for male and female northern rockhopper penguins from Amsterdam Island, southern Indian Ocean, for the 1994–2016 period

Period	Sex	N	Bill length (mm)	Bill length range (mm)	Body mass (g)	Body mass range (g)	Body condition	Body condition range
Breeding	Male	2110	49.89 (1.91)	46.0–57.6	3499.3 (381.9)	1850–4750	3399.9 (365.9)	1810–4575
	Female	1529	43.69 (1.42)	37.0–45.9	3205.2 (377.1)	1925–4500	3341.2 (389.4)	2012–4579
Moulting	Male	804	49.68 (1.80)	46.1–56.0	3970.9 (488.4)	1700–5200	3865.8 (471.0)	1646–5077
	Female	572	43.33 (1.57)	37.9–45.9	3631.5 (463.9)	1675–4800	3802.4 (484.1)	1778–5059

Values are mean (SD)
N number of individuals

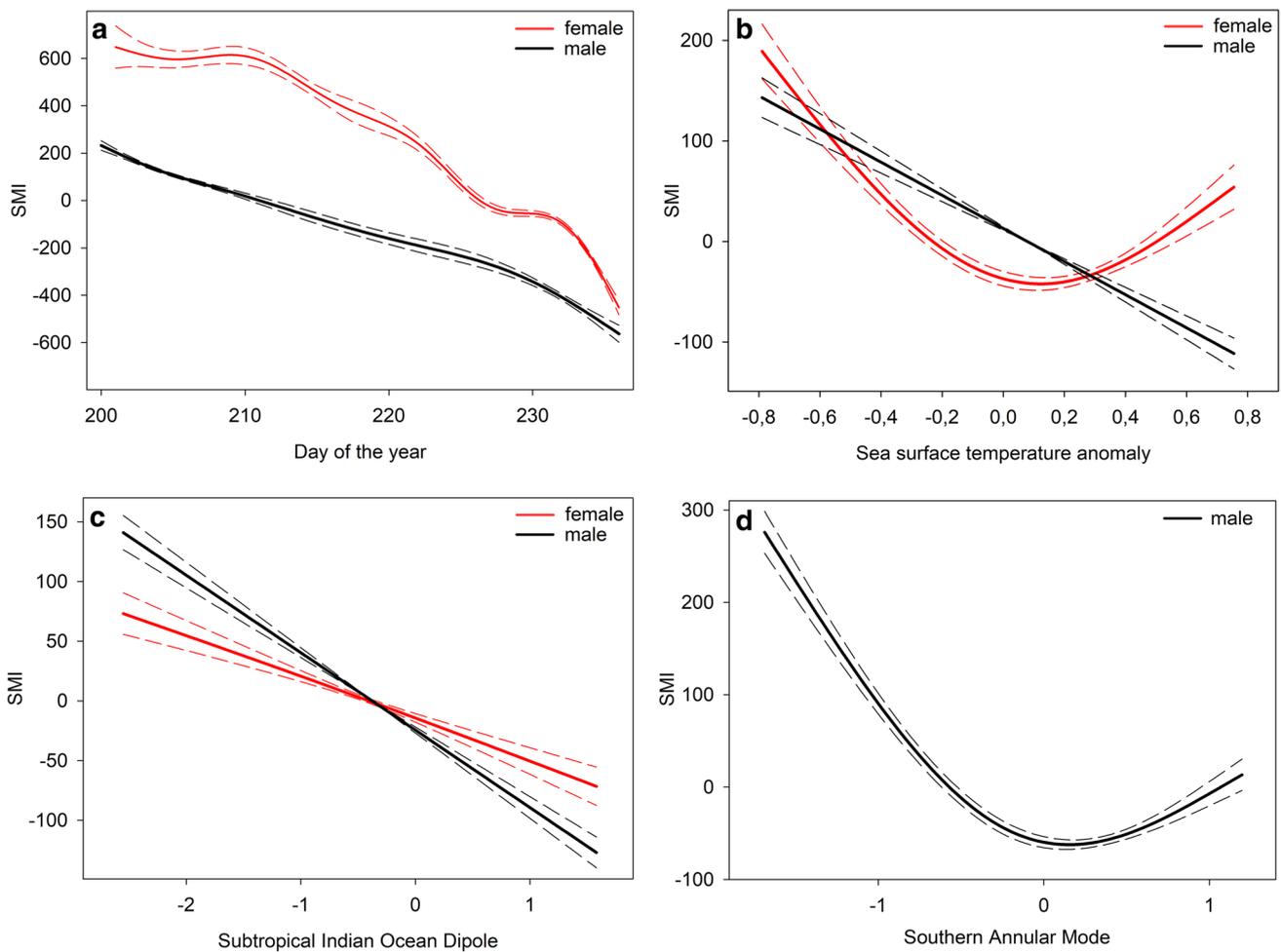


Fig. 3 Estimated smoothing curves (with s.e.) for environmental covariates during pre-breeding period in relation to the body condition of northern rockhopper penguins during the *breeding* stage in

females and males. Covariates considered in the model were **a** day of the year, **b** sea surface temperature anomaly, **c** Subtropical Indian Ocean Dipole and **d** Southern Annular Mode

Nonetheless, very early arriving individuals during the *moulting* period (days 23; Fig. 4a) had lower body condition compared to birds arriving later in late January and early February (days 27–35). These results remained

robust when excluding the most extreme years (see Online Resource 1, Tables S2–S3, Figs. 4, S1).

SSTa had an effect on body condition only during the pre-breeding period (see Online Resource 1, Tables S4–S5, Fig. 3b). Male body condition decreased almost linearly

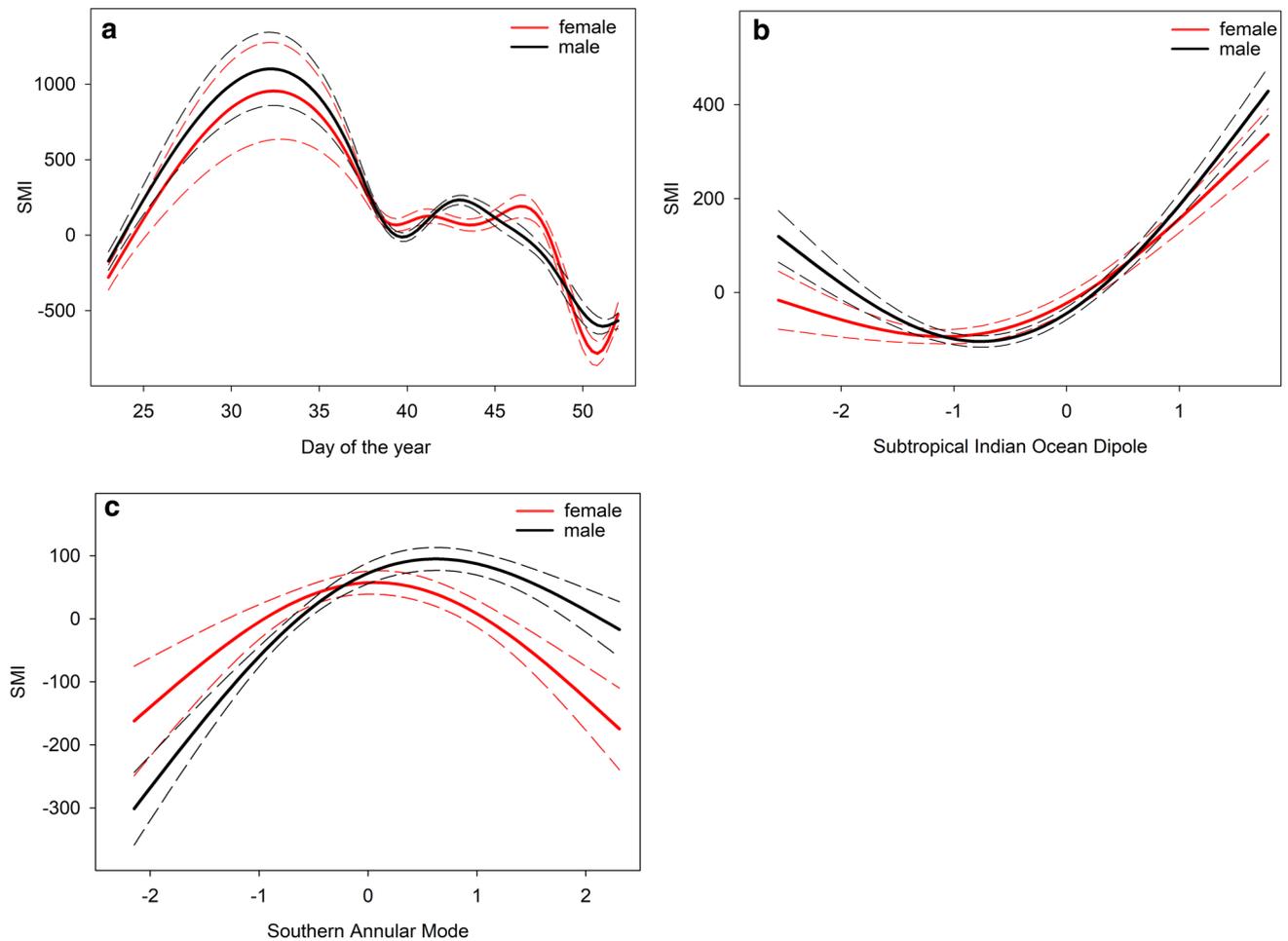


Fig. 4 Estimated smoothing curves (with s.e.) for environmental covariates during pre-moult period in relation to the body condition of northern rockhopper penguins during the *moulting* stage in females

and males. Covariates considered were **a** day of the year, **b** Subtropical Indian Ocean Dipole and **c** Southern Annular Mode

with increasing SSTa. Female body condition decreased with increasing values of SSTa up to null anomalies (~ 0) and then increased for warmer SSTa. Maps of correlation with Indian Ocean SST support the results obtained using the above models (Fig. 5). There were negative correlations significant at the 95% confidence level in the foraging area around Amsterdam Island during *breeding*, while no particular link occurred in the southeast area during pre-moult. Spatial patterns of correlation were similar for males and females, but more significant for males during the two periods (Fig. 5).

The body condition of males and females decreased with increasing SIOD during the pre-breeding period, almost linearly for both sexes (Fig. 3c). During pre-moult, body condition of males and females increased with increasing SIOD in a non-linear way (Fig. 4b).

SAM was non-linearly related to body condition in males and females whatever the period considered (see Online Resource 1, Tables S2, S5–S7, Figs. 3d, 4c) except

for females during pre-breeding (the full model was not selected despite a slightly lower AIC value $\Delta = -0.71$ for the model including SAM). During the pre-breeding period, the body condition of males decreased with increasing SAM but increased for high values of SAM (Fig. 3d). Reversed relationships were observed during the pre-moult period, with values of body condition maximized for slightly positive values of SAM (Fig. 4c). Our sensitivity analysis testing for an effect of the sexing method indicated that all results remained very similar when the 15% largest males and 15% smallest females were removed from the dataset (results not shown).

Breeding success

There was a long-term temporal trend in breeding success with a continuous decline during the period 1997–2016 (Fig. 1) and extremely low values for recent years ($\sim 0\%$). Neither the body condition of females or males during the

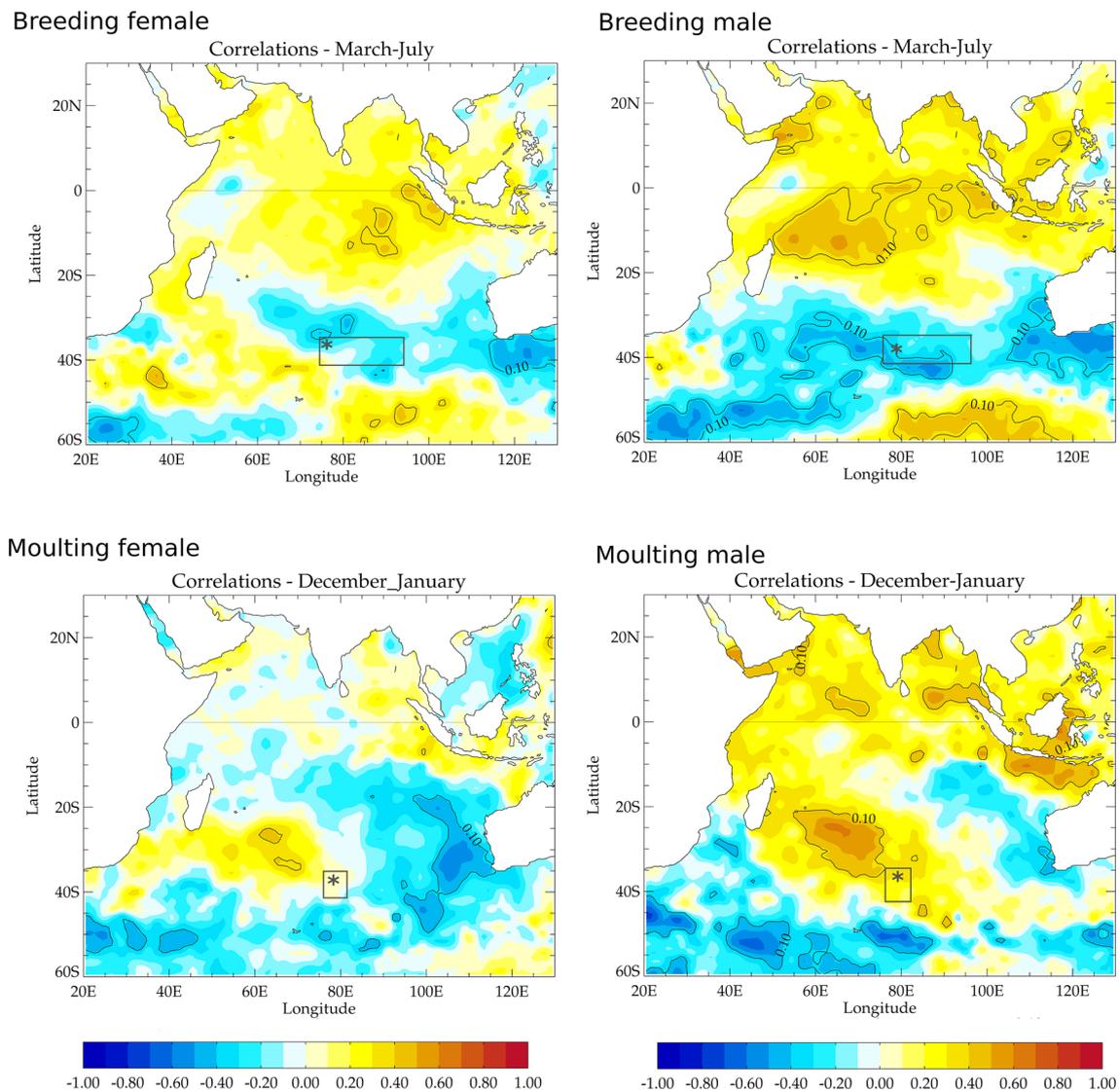


Fig. 5 Map of correlations between penguin body condition and time series of sea surface temperature according to the period (*breeding* stage correspond to pre-breeding austral winter period and *moulting* stage to pre-moult austral summer period) and sex. Amsterdam

Island (grey star) and foraging areas considered to extract sea surface temperature anomaly (grey rectangle) are shown. Contours indicate where the correlation exceeds the 95% confidence level, based on a Student's *t* test

breeding period, nor the environmental variables (SAM, SIOD and SSTa) did influence breeding success (see Online Resource 1, Table S8).

Discussion

This study examined body condition variation over a 23-year period (1994–2016) of a threatened migratory seabird, the northern rockhopper penguin at Amsterdam Island. Contrary

to the prediction of the food resources hypothesis, the body condition of males and females exhibited no long-term temporal trend, whatever the stage considered (i.e. *breeding* or *moulting*), whereas breeding success declined during the same period. Parental body condition at the start of the breeding season, and therefore food availability during the pre-breeding period, can therefore be ruled out as an explanation for the observed low breeding success in recent years. It remains open whether low breeding success in this population is explained by environmental conditions and

food availability near Amsterdam Island during the breeding season (i.e. during the chick-rearing period, chicks starving during poor conditions not necessarily imply lower body condition of adults (Morrison et al. 2016)), disease or other factors, such as predation (Authors's unpublished data). As predicted by life-history theory, this could reflect a trade-off between current and future reproduction (Stearns 1976). This may lead, when resources are scarce, to abandonment by adults of the current breeding episode if risks to their survival are too great (Goodman 1974; Drent and Daan 1980). Alternatively, the decline in breeding success can be due to disease (Jaeger et al. 2018) or other factors, such as predation.

Sex-specific body condition

Body condition varied between years and sexes and part of this variation was explained by the environmental factors investigated in the study. Sex-specific sensitivity to environmental variability is rather common (Badyaev 2002). Ecological theory predicts that larger animals have higher energetic demands than smaller animals, and that in times of food shortage small size confers an advantage (e.g. Wikelski and Wrege (2000)). As northern rockhopper penguins are sexually size dimorphic, with females being generally smaller than males (Warham 1970; Steinfurth et al. 2019; Cuthbert 2013), low resource availability would disproportionately affect males, which is suggested by the higher sensitivity to variability in SSTa (Figs. 4, 5). Nevertheless, males were on average in better condition than females whatever the stage. This could be linked to different parental roles. Females require additional energy reserves to produce the eggs, while males are fasting during a longer period at the colony between arrival and incubation period (~47 days; Williams 1995) compared to females (~39 days), and also during moult (20–30 days, up to ~60 days of fasting). Other non-exclusive hypotheses are that these patterns in body condition could be driven by males and females using different areas prior to arriving in their colonies, or feeding on different prey, or by the time lag in arrival between males and females.

Body condition and timing of arrival at colony

The body condition of both sexes was negatively related to the day of the year, indicating that individuals arriving earlier at the colony for each of the two stages were in better condition. Timing of egg laying (which correlates with timing of arrival) and body mass were also linked with clutch mass in the closely related southern rockhopper penguin (Dehnhard et al. 2015a, b, 2016). Similarly, considering body mass at arrival (after their incubation trip), possible relationships between body mass and timing of reproduction

were suggested in macaroni penguins *E. chrysolophus* (Horswill et al. 2016). Larger body sized females may be more likely to initiate breeding slightly earlier.

Reduced reproductive success for adults in poor body condition has been documented in *Eudyptes* penguins (southern rockhopper penguin; Crawford et al. 2006, 2008; macaroni penguin; Horswill et al. 2016). A carry-over effect, i.e. influence of pre-breeding stages on subsequent stages of the breeding cycle, was also evidenced from winter body mass with timing of breeding and reproductive success in penguins (macaroni penguin: Crossin et al. 2010; little penguin *Eudyptula minor*: Salton et al. 2015). Individuals in good body condition (i.e. *breeding* body mass) were more likely to breed early (little penguin: Salton et al. 2015; southern rockhopper penguin: Dehnhard et al. 2015b; Morrison et al. 2016). Nonetheless, at the population level, no correlation was evidenced here for body condition between the breeding and subsequent moult period and between the moult and subsequent breeding period. Clutch initiation date was found to be highly consistent in individual southern rockhopper penguins, but not affected by individual pre-breeding foraging ranges revealing a likely individual trait (Dehnhard et al. 2015b, 2016; Morrison et al. 2016). Other parameters, such as sex, age or individual quality, could influence the date of return to the colony to breed (Thiebot et al. 2014b). Unfortunately, the information on breeding success at the individual level was missing in our study and did not permit to explore the relationships between body condition, timing of arrival and breeding success.

Body condition and climate factors

The body condition of males and females was impacted by all the climate factors considered, while there was no effect on breeding success. This could indicate that body condition has been kept above a certain threshold where it did not impact breeding success or that the extreme impact of diverse causes (i.e. weather, predation and/or pathogens) was overlying any trends. In the closely related southern rockhopper penguin, the body mass was evidenced to be affected by climate variables (Dehnhard et al. 2015a). We evidenced complex relationships between the body condition of individuals and the climatic conditions preceding the breeding season. The body condition of females during the *breeding* period was non-linearly related to the remote environmental variables (except for SIOD). Overall, females were in better body condition for negative values of SIOD and SSTa, although their body condition seemed to increase for positive SSTa. The body condition of males exhibited similar but less complex and more significant patterns, with decreasing body condition for increasing SAM, SIOD and SSTa but with slight increases in body condition for positive values of SAM. Positive values of SAM in South Atlantic Ocean

(i.e. lower SST and stronger westerly winds) were found to increase body mass in the southern rockhopper penguin (Dehnhard et al. 2015a). Nevertheless, inter-annual variation in body mass should vary among studied populations (Dehnhard et al. 2013a; Crawford et al. 2006, 2008) reflecting possible regional differences in the environmental conditions. Similarly, the SAM-associated climatic conditions have already previously been associated with better foraging conditions and higher survival rates (southern rockhopper penguin; Dehnhard et al. 2011, 2013a, b). The SAM was also best explanatory factor for clutch initiation date in rockhopper penguins (i.e. earlier under positive SAM; Dehnhard et al. 2015b). Furthermore, Dehnhard et al. (2015b) demonstrated that heavier females producing heavier clutches and laid heavier eggs under lower SST. Finally, larger chicks at fledging positively correlated to higher provisioning rate by parents have greater likelihood of surviving to recruit into the population (Morrison et al. 2016; Horswill et al. 2014, 2017).

The area around Amsterdam Island presents characteristics of a subtropical gyre, i.e. quiescent conditions with little mixing from winds and occasional occurrence of mesoscale eddies leading to generally oligotrophic conditions. However, medium levels of production at the surface indicate a transition area between the Southern ocean and subtropical gyre (Visser et al. 2015). The subtropical gyre is characterized by globally low productivity due to weak mixing and mesoscale eddy activity as reported by satellite data (Antoine et al. 1996), oceanographic models (Machu et al. 2005), and in situ sampling (Visser et al. 2015).

In the Amsterdam Island area, positive SAM and SIOD correspond, respectively, to less wind at mid-latitude and warmer surface water (Lovenduski and Gruber 2005). Favourable oceanographic conditions would be generated by negative phases of both SIOD and SAM during pre-breeding while positive phases of these climate indices would correspond to beneficial conditions during pre-moult. These statements are supported by the relationships obtained between SSTa and body condition. Colder surface waters and strong wind during the austral winter period resulted in weak stratification and enhanced mixing of the water column (Fig. 6a, favourable conditions on the left panel vs unfavourable conditions on the right panel). These environmental conditions potentially injected deeper waters enriched in nutrients to refuel the biological production in the surface layer. The new biological production may sustain high prey abundance, which is an important process in the oligotrophic subtropical context. Nonetheless, it will take a considerable amount of time from increased nutrients over primary productivity to generate prey for penguins. Colder surface waters and increased wind could also directly affect the distribution of prey swarms and therefore foraging success (Dehnhard et al. 2013a). During the succeeding austral summer period and

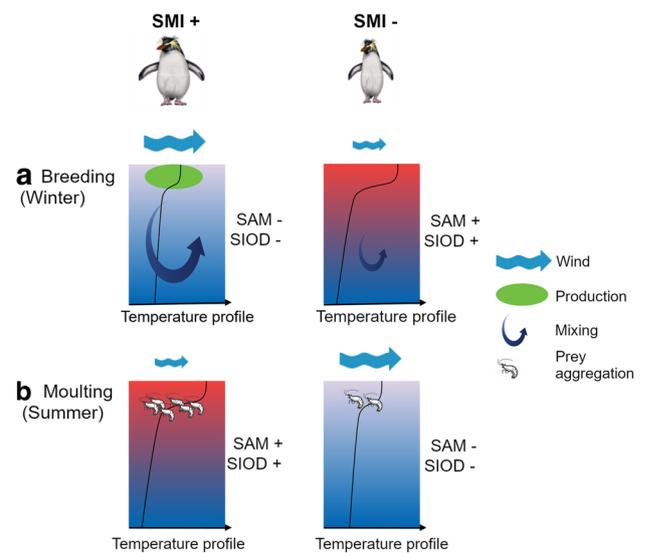


Fig. 6 Schematic effects of climatic factors [Southern Annular Mode (SAM) and Subtropical Indian Ocean Dipole (SIOD)] and the derived physical (wind and mixing) and trophic (primary production and prey densities) conditions during pre-breeding and pre-moult periods on body condition in adult northern rockhopper penguin on Amsterdam Island from 1994 to 2016 during **a** breeding and **b** moulting stages. Favourable conditions for body condition on the left panels versus unfavourable conditions on the right panels. The black line illustrates a typical temperature profile in the subtropical domain depicting either a weak or a strong stratification. Symbols (\pm) represent, respectively, positive and negative SAM and SIOD

its associated bloom, warm surface waters induced stratified water column. The seasonal biological production accumulates at the thermocline and, as a result, mid-trophic levels are attracted by this vertical aggregation of biological production. Such oceanographic features may create favourable conditions for prey concentrations available at the depth of the thermocline for diving predators, such as penguins (Pelletier et al. 2012; Van Eeden et al. 2016). During the austral summer, a high stratification of the water column required for the bloom was maintained by weak winds conditions and, as a result, for the accumulation of biological production at the bottom of the surface layer (Fig. 6b). These climatic and oceanographic processes operating during the austral summer may explain the different (and nearly opposite) patterns which were observed during the pre-moult period compared to the pre-breeding period. During *moulting*, females and males had maximum body condition for intermediate values of SAM, and their body condition increased with increasing values of SIOD during the austral summer. The pre-moulting months are a key period for individuals that need to replenish their energetics reserves through a period of hyperphagia at sea (Thiebot et al. 2014a) before initiating their moult. We do not know where the individuals forage in the months during this particular period but we can hypothesize that females and males behaved similarly or at least

they forage in areas similarly influenced by climatic factors. Nevertheless, the correlation maps allowed investigating spatial associations between body condition and SSTa patterns without a selection of a priori climate indices. Spatial patterns of correlation are similar for males and females, but more significant for males during the two periods (see Fig. 5). Here, this approach supports the robustness of the GAM analysis which provides congruent results. Despite the exploratory nature of this correlation analysis, such methods have also been proven to be useful in discovering new climate teleconnections (Von Storch and Zwiers 2001) and can be useful here to generate hypotheses on the potential foraging areas and to suggest other important remote climate forcing phenomena on penguins' body conditions (e.g. El Niño-Southern oscillation (ENSO)).

For northern rockhopper penguins, we found that individuals on average were in better condition during the *moulting* period compared to the *breeding* period, suggesting that body condition was probably fully restored during the pre-moulting months but not during the pre-breeding months (i.e., austral winter period previous to the onset of breeding). Birds used considerable reserves of energy during moulting explaining why they need to be in better condition before this stage. This dissimilarity in condition can also mirror the different seasonal availability of trophic resources or might indicate different foraging areas. Indeed *Eudyptes* penguins tended to exhibit large-scale dispersal during the pre-moult period (Lowther et al. 2014; Thiebot et al. 2014a; Horswill 2015; Whitehead et al. 2016).

Our results, showing no long-term trend in northern rockhopper penguin adult body condition at two critical periods of the life cycle, concurrent with changes in climate variables, combined with the synchronous dramatic long-term decline in breeding success and its lack of association with climatic factors, suggest that the causes of the long-term decline of the Amsterdam Island population does not originate solely from bottom-up effects linked to changing marine environment, at least during the pre-breeding and pre-moulting periods. Population declines should be due to low breeding success as observed here, but also to low adult survival, and low survival of immatures between fledging and recruitment at the colony, but no information is available for these two last parameters. Pathogen outbreaks (avian cholera and erysipelas causative agents) were identified to threaten seabird species on Amsterdam Island (Jaeger et al. 2018). Nonetheless, the effects of these pathogens on northern rockhopper penguins remain to be quantified and the responsible mechanisms to be identified. Other potential land-based factors are top-down effects due to predation pressure and/or harassment level. Native brown skuas *Catharacta antarctica lonnbergi*, introduced invasive brown rats *Rattus norvegicus* or feral cats *Felis catus* are known to predate on similar sized penguins and on northern

rockhopper penguins at Amsterdam Island (Berruti 1981; Hunter 1990; Simeone and Luna-Jorquera 2012; Authors, personal observation). Fur seals *Arctocephalus spp.* occasionally hunt and prey upon northern rockhopper penguins (Roux and Hes 1984) and may be an additional cause of the population decline (Guinard et al. 1998). However, although the number of sub-Antarctic fur seals *A. tropicalis* at Amsterdam Island increased dramatically between the 1970s and late 1990s, it has stabilized since the mid-2000s (Pacoureaux et al. 2017).

Conclusion

In conclusion, we suspect that northern rockhopper penguin population decline at Amsterdam Island might result from effects of top-down pressure (i.e. on land threats: predation or harassment), disease, and bottom-up environmental forces (i.e. food resources) (Regehr and Montevecchi 1997; Horswill et al. 2016), which may act individually or more likely in combination. Further information on the drivers of the population decline and particularly the low breeding success is needed. Additional field and modelling studies are needed to understand and estimate the effects of potential disease outbreaks and predators on the demography and population dynamics of northern rockhopper penguins, which will help designing management plans aiming at conserving this endangered species.

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Availability of data and material The data used in the present article will be provided for open access as supplementary.

Code availability The custom code used in the present article will be provided for open access as supplementary.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflicts of interest.

Ethics approval The Ethics Committee of IPEV and the Comité Environnement Polaire approved the field procedures for the French Southern Territories.

Consent to participate All authors have agreed to participate in the study and its writing in the form of an article.

Consent for publication All authors have given their consent for the article to be submitted to Marine Biology.

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